THE UNIVERSITY OF MANITOBA

The role of small mammals in the population dynamics of the *Semiothisa* complex, Lepidoptera:Geometridae:Ennominae.

by

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A thesis
submitted to the Faculty of Graduate Studies in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Winnipeg, Manitoba

October 1972

Abstract

Population models involving larch loopers of the Semiothisa Hübner complex and small mammal numbers suggested possible interspecific relationships to exist between these two groups. Masked shrews (Sorex cinereus Kerr) and redback voles (Clethrionomys gapperi loringi Bailey) showed particularly well their effect on the numbers of larch looper pupae by registering strong positive numerical and functional responses to densities of larch looper pupae. The importance of the larch looper pupal stage in the population dynamics of larch loopers was stressed when a key-factor analysis using the logarithm of survival of pupae (log S) instead of the logarithm of the previous generation (log h_n) improved the predictability of future larch looper populations. However, the use of the logarithm of survival of pupae from small mammals (log S_n) did not improve the predictability; this suggested the non-importance of the small mammal populations as a determining factor (key-factor) in the population dynamics of this insect group.

Field experiments that consisted of 'food preference tests', 'stomach analyses' and 'pupae planting' confirmed the existence of interspecific relationships between the two groups, as suggested by the statistical analysis. Small mammal populations, especially masked shrews and redback voles, expressed strong positive numerical and functional responses to the densities of larch looper pupae. The role of larch looper populations acting as a buffer food supply for small mammals of Manitoba bogs is discussed.

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Introduction

Field studies on the population dynamics of major harmful insect species have been in progress for many years. The recent outbreak of larch sawfly, *Pristiphora erichsonii* Hartig permitted students of ecology to find its main regulating factors (Lejeune and Hildahl 1954, Lejeune 1955, Ives and Turnock 1959, Ives 1962,1963 and 1964). Thus, the importance of small forest vertebrates as predators of this defoliator species has been given considerable attention (Buckner 1955, 1958, 1959 and 1966). Birds have been shown to prey heavily upon the adult and larval stages (Buckner and Turnock 1965), whereas small mammals are particularly important as predators of the cocoon stage (Buckner 1959, 1966a and 1966b). Because the sawfly remains within the cocoon for at least 10 months and sometimes for a year or more (Ives 1964), it is particularly vulnerable to small fossorial mammals.

Populations of sawfly vary considerably both in time and in space, and in periods of sawfly scarcity alternative prey must be consumed. Holling (1959 and 1965) has shown the importance of alternate food supplies in the predation complex involving the European Pine Sawfly, *Neodiprion sertifer* Geoff. He found that the total food consumption of white-footed mice (*Peromyscus leu-*

copus Rafinesque) remained constant, with an increase in sawfly consumption when the alternate food had a low palatability, and vice-versa.

Secondary defoliators of tamarack trees in the Manitoba bogs are known to exist because of their regular occurrence in various larch sawfly sampling traps. One of the most consistent groups to be collected on the larch trees is the Semiothisa Hübner complex represented by the species sexmaculata Pack., signaria Gn., oweni Swett and bicolorata Fabr. The Semiothisa group forms a part of the order Lepidoptera, family Geometridae and subfamily Ennominae. These larch looper populations are characterized by a ground-inhabiting stage which is probably preyed upon by small mammal species sharing the same habitat.

As the final component of this system, the small mammal species, of which the masked shrew (Sorex cinereus cinereus Kerr), the American pygmy shrew (Microsorex hoyi (Baird)), the short-tail shrew (Blarina brevicauda manitobensis Anderson) and the redback vole (Clethrionomys gapperi loringi Bailey) appear to be the main mortality-causing factors.

The purpose of the study was to determine the impact of small mammal populations on the numbers of Semiothisa spp. and to determine the role of this available food supply for small mammals in tamarack bogs of

Manitoba. The small mammal and larch looper interactions were evaluated in the light of current theories of predation. The possible role of this insect group as a buffer food supply for small mammals is also investigated.

The effects of small mammals on larch loopers cannot be explained until we know the impact of loopers on each other and the effects of sawflies on the larch looper populations. These interactions are included in the statistical analysis of the first section along with the relationships between the mammalian populations and larch looper numbers.

The second and third sections of the thesis correlate the actual field data analyses with that of the statistical approach. The food preference tests were designed to give an answer as to whether or not the small mammals knew the existence of the larch looper material. Buckner (1952 to 1970) showed that the shrew and vole species were extensively using various insect material as food. The determination of the optimum potential predation of small mammals on larch looper pupae was used to set up the upper limits of the mortality caused by individual mammals or populations, and used as a mean to compare it to that of the actual field mortality; this optimum predation is usually calculated by dividing the metabolic requirements of individual mammals by the caloric value of a given food item. The stomach analyses and the 'pupae planting technique' represent the two fundamental and final field experiments whose aims were to confirm the qualitative and quantitative aspects of the study. The field confirmation that small mammals do indeed eat this larch looper material and the quantitative determination of the extent of this mortality might suggest the very important role of such a food supply for both the small mammals and the larch sawflies of the Manitoba bogs.

Literature review

A. Semiothisa spp. populations

a. Taxonomy

The Semiothisa group forms a part of the order Lepidoptera, family Geometridae and subfamily Ennominae. According to Forbes (1948), the classification of the subfamily is still unsatisfactory; he divided the genus Semiothisa into tribes by consideration of the male antennae and genitalia. The pupae, so far as known today, can be classified only by making microscopic mounts. Keys to subfamilies of Geometridae larvae, pupae and adults can be found in papers by McGuffin (1946 and 1967) and a description of the more common species is revised by Forbes (1948). Descriptions of larvae and adult stages can be found in McGuffin (1947).

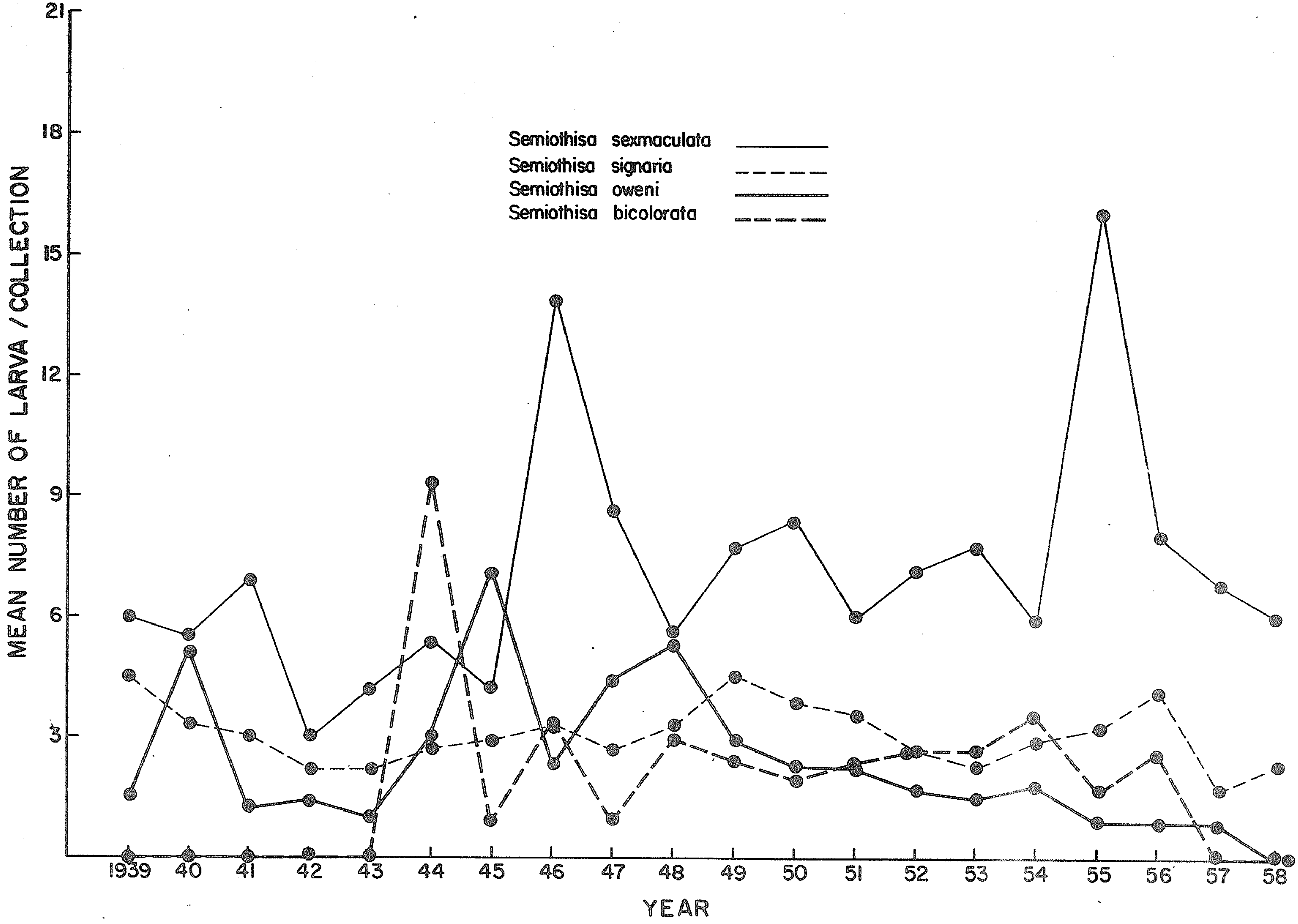
b. Factors affecting populations

Very little is known about the population dynamics of the subfamily Ennominae. Recently, Luk'jancikov (1967) discovered and described a new virus of the larch moth forming no inclusion bodies. Herrebout (1967) described the habitat selection of Eucarcelia rutilla Vill. (Diptera, Tachinidae) which parasitize larch looper populations. Two years earlier, Melvin and Turnock (1965) had found that Bessa harveyi (Tnsd.), a well known parasite of sawfly larvae, attacked lepidopterous larvae including Semiothisa. The number of emerging adults of Bessa from parasitized larvae indicated the species S. granitata to be the most favorable host and S.bicolorata and S.oweni as secondary ones. One can, however, gain some insight as to the important mortality factors of Semiothisa spp. by examining those of P.erichsonii Htg. Mortality factors such as the parasitism of sawfly larvae have been particularly well studied and related to population changes. Parasites such as Mesoleius tenthredinis Morley and Olesicampe nr. nematorum have received special attention (Criddle 1928, Hopping et al 1943, Muldrew 1967). Among vertebrates, frogs (Buckner 1952), birds (Buckner and Turnock 1965) and small mammals (Graham 1928) were assessed to be very important predators of sawflies, destroying at times up to 90 percent of local populations. Egg and larval stages were also found to be prone to invertebrate predation; four species of mirids and one species of anthorocids were found to eat as much as 4 eggs per day (Ives 1967); 23 species of insects and spiders were observed to feed on larch sawfly larvae (Ives 1967, Muldrew 1955). Floods can destroy from 50 to 100 percent of the larch sawfly cocoon populations (Ives and Nairn 1966, Lejeune et al 1955). Further effects of weather on the survival of eggs, larvae and cocoons were evaluated by Graham and Sutterland (1959), Heron (1960) and Ives (1961). Eight genera of parasitic fungi and bacteria were also found to play a role in the natural control of sawfly numbers (Mac Leod and Heimpel 1955) by acting on larvae and cocooned larvae. Defoliation (Ives 1963) and premature larval drop (Ives 1967) were postulated, as well, to explain the larch sawfly population fluctuations. Similar mortality factors are undoubtedly responsible for the population changes of larch loopers, although their mode of action might somewhat differ from those acting on the larch sawfly.

c. Life history and ecology

In Manitoba, adults begin to appear in May with the peak of emergence in July and August (Prentice(ed.) 1963); the larvae begin to feed on their hosts from July until very late in October (Atwood 1944, Forbes 1948). The pupae, which are formed after 20 to 50 days of development from the egg stage, are probably present in the bogs from July to early May of the following year. The larval populations of the four species mentioned above are given in Table 1 of the Appendices. All four species tend to exibit population peaks (Figure 1). The species S. sexmaculata is particularly noticable for its 9-year interval peaks while the other three species offer more regular and stable popu-

Figure 1. Numbers of *Semiothisa* larvae collected across Canada for a period of 20 years (after Prentice (ed.) 1963).


Semiothisa sexmaculata
Semiothisa signaria
Semiothisa oweni
Semiothisa bicolorata
MEAN NUMBER OF LARVA / COLLECTION
21
18
15
12
9
6
3
1939
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
YEAR

lations.

Broadly speaking, these solitary defoliators seem to prefer swamps where tamarack (*Larix laricina* (Du Roi) K. Koch) and Western larch (*Larix occidentalis* Nutt.) can grow easily (Prentice (ed.) 1963). The species *S.sexmaculata* and *S.oweni* feed mainly upon tamarack while *S.signaria* and *S.bicolorata* are recorded most frequently on Balsam Fir (*Abies balsamea* (L.) Mill.) and Jack Pine (*Pinus banksiana* Lamb.).

No complete description of the distribution of *Semiothisa* spp. is available in the literature. Forbes (1948) and Prentice (ed. 1963) indicate that their larvae are collected regularly from Newfoundland to eastern British Columbia, from Labrador and Ungava (55°49' north) to Great Slave Lake, south to central Massachusett and New York. The distribution of *S.sexmaculata*, the most numerous of the four species in Ontario, Manitoba and Saskatchewan regions (Figure 2) suggests a heavier population in the southern part of these three provinces. They are however found in every tamarack stand throughout these regions (Prentice (ed.) 1963).

B. Small mammals

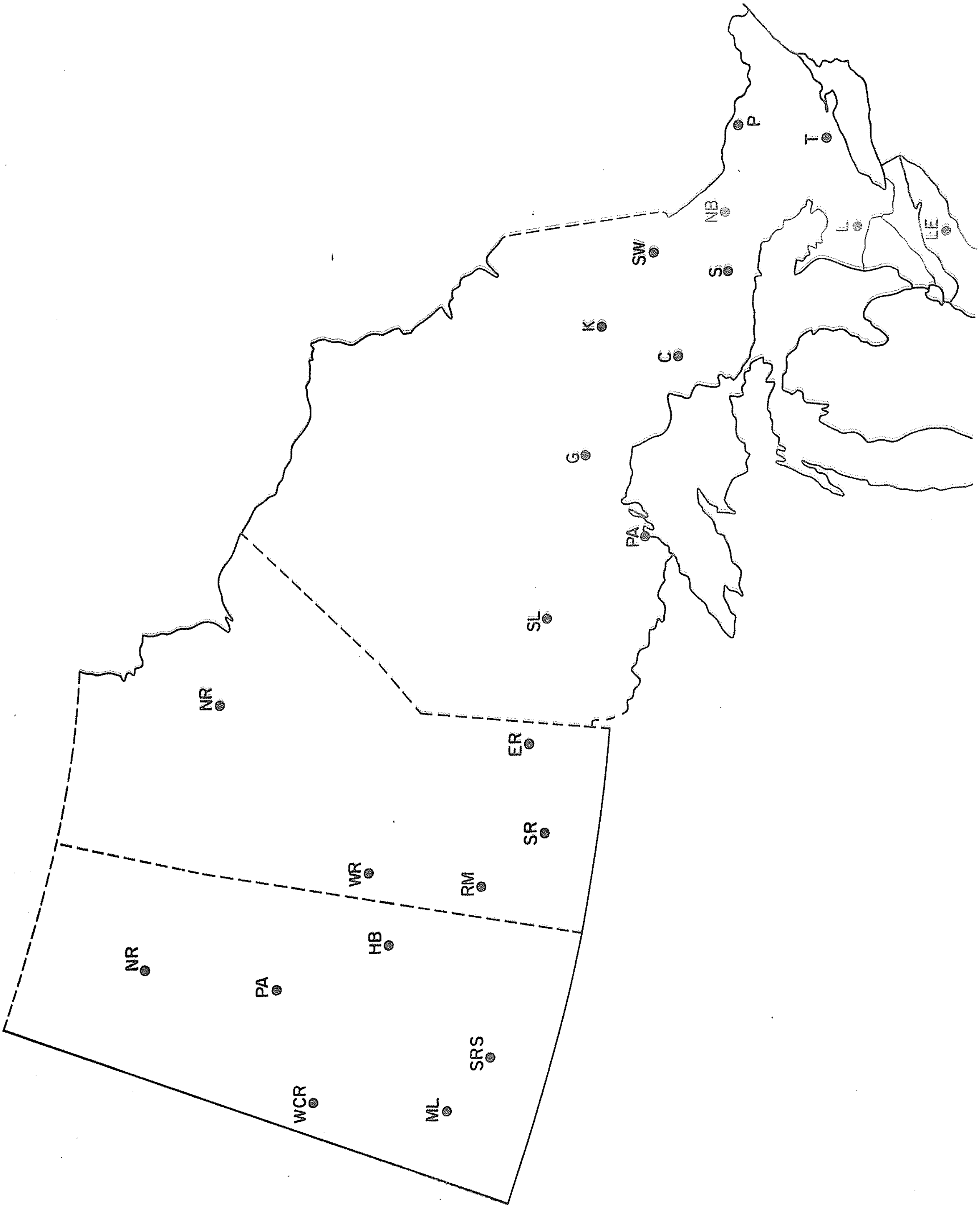
a. Trapping techniques

Population density means the number of animals

Figure 2. The distribution of *S.sexmaculata* Pack. in the forest districts of Ontario, Manitoba and Saskatchewan (from samples collected by the Rangers of the Insect and Disease Survey Team of Manitoba).

L, Lindsay 1952
T, Tweed 1955-1967
P, Pembrooke 1955
LE, Lake Erie 1962
NB, North Bay 1959
S, Sudbury 1959
C, Chapleau 1959
K, Kapuskasing 1964-1967
SW, Swastika 1955-1967
PA, Port Arthur 1962
G, Geraldton 1955-1962-1967
SL, Sioux Lookout 1943-1959

SR, Southern Region 1957-1958-1959-1963-1964-1965
ER, Eastern Region 1959-1964-1965-1967
NR, Northern Region 1958-1963-1964-1965-1967
WR, Western Region 1958-1963-1964
RM, Riding Mountains National Park 1957-1966-1967
HB, Hudson Bay 1959-1963-1964-1965
PA, Prince Albert 1963-1964-1965
ML, Meadow Lake 1959-1963-1964-1965
NR, Northern Region 1963-1964-1966
SRS, Southern Region of Saskatchewan 1964-1965
WCR, West Central Region 1966


P
T
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G
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ER
SR
WR
RM
HB
NR
PA
SRS
WCR
ML

per unit area or the ratio between the animal numbers and the spatial area they occupy (Andrzejewski 1962). The capture-recapture techniques are often used in small mammal censuses. A basic assumption of the method is that all the animals in the trappable population must have equal risk of capture; there must be no differential trap response between the marked and unmarked animals (Leslie et al 1953). When large numbers of individuals are present, the calculation of the population density is usually made by means of the Lincoln Index. Some basic assumptions are: the equivalence of mortality between the marked and the unmarked animals; the durability of the marks; the random mixture of the marked individuals with the unmarked and the constancy of the population under study (Southwood 1966). The reliability of the technique was tested by Buckner (1957) and he showed that shrew and rodent population estimations were valid at the 95 percent level. However, the heterogeneity of trap-response showed by trap-shy and trap-addicted mice (Young et al 1952, Tanaka 1956), the preference of certain voles and mice to a given trap (Morris 1968) and the mis-evaluation of small mammal populations because of the edge effect (Pelikan 1968) contradict some of the basic assumptions of the method.

Population studies can also be made with snap-back trap methods. The impossibility of distinguishing between resident and non-resident animals and the removal of local individuals which allows the composition of the population to be altered by the invasion of others, are partly responsible for the inaccuracy of the method (Smyth 1968). Furthermore, the better performances showed by pitfalls (Mac Leod and Lethiecq 1963), live traps (Sealander and James 1958) and Schuyler traps (Pruitt and Lucier 1958) when compared to the common snap-back traps, make them inappropriate. Another comparison between live traps and snap-back traps effectiveness can be found in Duran (1968). Buckner (1957) observed that estimates of small mammal populations were similar regardless of the trapping method used; live traps on grid, snap-back traps on grid and snap-back traps on standard lines yielded approximately the same results. Where a rapid census is required, snap-back traps gave usually reliable results in late summer; the use of snap-back traps should usually be avoided when trapping is to be made over long periods, because of the possible severe and prolonged effects on the populations (Buckner 1957).

Methods such as live trapping on a checkerboard line (Manville 1950) and short term but intensive removal of animals from a given area and the estimation of their number by means of the regression method (Hayne 1949) proved to be accurate methods for estimating vole populations. The observation of the marked animals by means of recaptures and the calculation of the number known to be alive by means of the calendar of catches (Evans 1942) served to determine Apodemus and Clethrionomys numbers. Prebaiting followed by intensive removal (Grodzinski et al 1966) was used as a good estimator of rodent numbers. Population estimations based on the change of composition caused by a selective removal (Chapman 1955), the study area surrounded with sheets of corrugated iron (Dieterlen 1967), and the digging out of the burrows (Smith 1968) served as accurate means of measuring mice and vole numbers. The reproduction, breeding season and intensity of breeding were indirectly measured by Krebs (1966) using live trapping techniques on voles. The same method permitted Andrzejewski (1962) and Andrzejewski and Wierzbowska (1961) to determine movements and dispersal of small rodents.

According to Chitty (1937), the proposed grid of 15 X 15 meters for small mammal trap positions is satisfactory; a larger grid would cause an excessive dilution of the trapping positions while a smaller one would reduce the activity of animals. Pelikan (1968) thinks that short-term estimates of density lasting at most for the first 3 to 5 days of trapping, are best, although more reliable data are obtained with longer trapping periods when determining the average home range.

Indirect methods of population assessments such as the automatic photographic recorders (Spitz 1963, Sanderson 1966), radiotransmitters (Godfrey 1954, Beal 1967) and radioactive tracers (Impens et al 1965) showed to be good aids in determining movement patterns of mice and voles. Dropping boards (Emlen et al 1957, Tester and Emlen 1960) revealed a greater sensivity for certain species, notably shrews; the types of board used were also subject to preferences for certain species of mammals, especially shrews (Tester and Emlen 1960). It should be noted that nesting boxes, smoked paper and dyes are now widely used in population density studies.

b. Feeding habits

There are several techniques for determining the natural food of small mammals. The most commonly used are: the analysis of stomach contents (Krefting and Roe 1949, Golley 1967, Drozdz 1967, Holisova 1967), the analysis of feces (Krefting and Roe 1949), food preference experiments (Hatfield 1940, Buckner 1964), and determination of the natural feeding grounds and supplies (Myrcha 1965).

The food intake of small mammals is often determined by stomach content analysis. It is usually necessary to know the relationship existing between the weight of the stomach contents after a single feeding, and its weight after a daily intake (Golley 1967). Storr (1963) and Schmid (1965) used this technique to study the feeding habits of wild mourning doves and wallabies. Buckner (1964) used it to determine the importance of larch sawfly eonymphs in the diet of four shrew species of Manitoba. Drozdz (1966) determined the percentage of greens (40%) and seeds (40%) in the diet of bank voles (Clethrionomys glareolus Schreber) and the percentage of seeds (74%) and invertebrates (15%) of field mice (Apodemus flavicollis Melch) in a beech forest. Similar experiments revealed the economic values of mice (Holisova 1960) by showing their role in the destruction of harmful insects.

The analysis of feces is not often used because of the inaccuracy in determining the previous food intake. Krefting and Roe (1949) used it to find the role of birds and mammals in seed germination. Adams (1957) determined the food intake of large mammals. Food preference experiments are useful because they give a more reliable numerical response when different food items are tested, and because they offer a good way to estimate the frequency and duration of the activity periods of animals (Buckner 1964).

In preference experiments, Holling (1955) found that masked shrews could open more healthy pine sawfly cocoons than parasitized ones; it is also of some importance to know that the selection occurred in the digging, removing, opening and eating phases of the search for cocoons. Similar trends were observed by Buckner (1958) for the larch sawfly. It was found later that shrews and mice used only olfactory stimuli in the digging, removing and opening phases of the sawfly cocoon predation (Holling 1958).

While studying mammalian predation on larch sawfly in Manitoba, Buckner (1958) found that 12 species of small mammals fed upon cocoons; the stomach remains contained from 37 to 98 percent of sawfly material. Shrews destroyed more cocoons than any other group of animals, although they were outnumbered by them. The five techniques used to determine the predation by small mammals are described in Buckner (1959). When available, larch sawfly material made up to 70 percent of the diet of shrew species (Buckner 1964). Beside the mammalian predation upon sawfly cocoons, it was later found that 44 species of birds preyed upon larch sawfly life stages (Buckner and Turnock 1965); birds preferred adults when they were available but large and small larvae were also readily ingested.

Feeding habits of shrews were studied in comparison to their body weight and from season to season; Wolk (1969) showed that young common shrews (Sorex araneus L.) ingested from 50.7 to 62.1 percent of their body weight late in the season, while old ones ate from 44.6 to 76.9 percent. He showed also that the daily food intake of overwintering shrews was 9.7 percent higher than the summer one.

Invertebrate contents found in shrew stomachs are usually of the following orders: Coleoptera, Lepidoptera, Diptera, Hymenoptera, Hemiptera and Aranae (Hamilton 1930, Rudge 1968, Williams 1955, Whitaker and Ferraro 1963); snails and slugs can also form part of their diet (Ingram 1942).

Wagg (1963) observed that redback voles and deer mice (*Peromyscus maniculatus*) could eat as much as 1000 seeds of lodgepole pine and 2000 seeds of white spruce in a season; he also found that the seeds of lodgepole pines were preferred over those of white spruce. Voles and mice were shown to exibit a distaste for balsam fir seeds (Abbott 1962), while they had a preference for red pine and white pine seeds over white spruce. These results contrast with those found by Abbott and Hart (1960) where voles and mice preferred spruce seeds and evidently ate balsam fir seeds when the former food item was not available. Wood mice (*Apodemus sylvaticus*) were found to be mainly seed eaters (Watts 1968) although they did ingest arthropods; bank voles also showed the same pattern. At mid-summer, when greens were available, bank voles mainly utilized 6 species of plant found later to be the most palatable ones (Fleharty and Olson 1969). When grassy plant material was not available, voles were found to eat insect remains (Hamilton and Hamilton 1954) and mushrooms (Williams and Finney 1964). Since voles and mice are mainly grass-eaters, Chitty (Chitty et al 1968) determined that a 2 foot square area per day for forage was the minimum space requirement of overwintering voles.

c. Metabolism and metabolic requirements

The metabolism of terrestrial vertebrates can be measured directly or extrapolated from laboratory experiments (Golley 1967). Direct methods such as the D_2O_{18} technique (Lifson et al 1955), the used of radioactive isotopes (Odum and Golley 1963), and telemetry already showed their usefulness. The indirect methods used by Brody (1945) and Swift and French (1954) are now well known and particularly useful in long term studies. The metabolism of small mammals is often determined by measuring the oxygen consumption (Morrison 1947), carbon dioxide production (Brody 1945) and urinary-nitrogen excretion (Hawk et al 1949).

It is known that the oxygen consumption can be based on body weight (kg), metabolic size ($kg^{2/3}$ and $kg^{3/4}$), and surface area (m^2) (Chiu and Hsieh 1960). But it appears that the most useful equation was established by Brody (1945), where the relationship existing between metabolism and body weight is expressed by the formula $Y = a W^b$;

where Y = BMR
W = body weight in kg
a = specific metabolism = 70.5
and b = a power of transformation = 0.73

On the basis of such information, Buckner (1964) calculated the daily metabolic requirements of four species of shrews (S. cinereus, S. arcticus, M. hoyi and B. brevicauda) to be 6.1, 6.9, 6.7 and 9.7 Kcal respectively. To satisfy such requirements, it was found that they would have to ingest 87, 99, 95 and 138 sawfly eonymphs respectively, but might actually kill many more. There were no differences between the sexes (Buckner 1964, Nelson and Asling 1962). Similar results had been calculated by Pearson (1947) by assuming a RQ (respiratory quotient) of 0.80. The energy requirements of short-tail shrews were found to be a little lower than previously reported (Martinsen 1969), probably as a result of keeping them on a restricted diet. The metabolism of shrews can also change from season to season as shown by Gebczynski (1965); he found that ADMR (average daily metabolic requirement) was 8.8 Kcal in summer, 8.5 in autumn and 7.5 in winter.

It is easy to understand that most studies were conducted on rodents and mice since they are easier to keep in the laboratory. However, laboratory strains of wild populations showed metabolic differences from wild strains at temperatures of 10 to 20°C (Gorecki 1966). Measures of metabolic rates should be put on a RMR (resting metabolic rate) or a ADMR basis, although the latter form is more convenient for computing daily energy budgets (Grodzinski 1969). Oxygen uptake was found to be independent of the oxygen supply down to about 80 mm Hg during rest at 27°C, to about 115 mm Hg at 5°C (Segrem and Hart 1967). The RMR of European common voles (Microtus arvalis (Pall.)) was found to vary in a straight-line fashion between 5 and 30°C (Trojan and Wojciechowska 1967); at temperatures between 5 and 10°C, the RMR of females was higher than that of males. The oxygen consumption is known to increase with a decrease of ambient temperature, as shown by Dawson (1955), McNab and Morrison (1963), and Murie (1961). Fat deposits do not influence the metabolism of animals provided they stay within standard limits of 20 percent of the total body weight (McNab 1968).

The DEB (daily energy budget) of bank voles was estimated at 10.2 Kcal during winter and 10.6 Kcal during summer; 13.5 and 12.6 Kcal for European common voles; 11.2 and 12.3 Kcal for field mice (Grodzinski 1966). Metabolism and hemoglobin contents of voles were positively correlated except in winter, when high oxygen consumption was observed with the lowest blood hemoglobin content (Shevchenko 1968). Harvest mice (Reithrodontomys fulvescens) showed a reverse energy expenditure pattern; in summer they consumed 5.6 Kcal per day and in winter 8.8 Kcal per day (Gaertner 1968), an 80 percent increase in energy requirement.

Pregnancy and lactation are periods of intense energetic requirements for European common voles; pregnant females reached a consumption of 18.8 Kcal per day and lactating ones 21.0 Kcal per day (Trojan and Wojcieschowska 1967); this represented increases of 23 and 37 percent energy expenditure compared to non-reproducing females. Kaczmarski (1966) estimated these two functions to require 32 and 122 percent more energy; he also showed that a litter of 4 would require a total of 364 Kcal from the mother. Migula (1969) found that the production and nursing of one young vole required 75.9 Kcal.

Besides reproduction, the DEB model is composed of nest life and search for food (Trojan and Wojciechowska 1969). It was found that mice could spend 2.3 Kcal per day in voluntary activity under different temperatures (10-20-30°C), which made up 12, 16 and 27 percent of their total daily expenditure. The working oxygen consumption of European common voles was 6.5 times the resting value while that of the bank voles was 7 times the resting value (Jansky 1959). The act of swimming in white rats was found to consume 2 or 3 times the basic values (Lustinec 1958). Similar results were obtained for bank voles (2.0-2.1) and field mice (1.6) (Grodzinski and Gorecki 1967).

The influence of nest life on the metabolism of animals was indirectly estimated. Darkness was found to decrease by 27 percent the oxygen consumption of European common voles (Trojan and Wojciechowska 1968). The effect of huddling with 6 animals or more was also found to decrease the basic requirements of voles by 36 percent (Trojan and Wojciechowska 1968). Using 4 animals at a time, Grodzinski and Gorecki (1967) lowered the requirements of bank voles by 13 percent.

C. Interactions between small mammals and insects

We usually understand by population dynamics studies those which determine changes in qualities and quantities of populations of living things (Waters 1967). Several methods can be used to study the dynamics of populations among which the life table approach is probably the most widely known. In developing life tables of natural populations of insects, special considerations are usually given to sampling techniques (Harcourt 1969). The sampling methods used must consider the following basic conditions: selection of sampling unit, timing of samples, multiple habitats, border effects and the simultaneous sampling of two or more species. Other considerations, such as the destruction of a population by sampling and the identification of mortality factors, contribute to the difficulty of sampling scarce insects (Knight 1967). Since discrepancies are bound to occur between sampling techniques, it has been suggested that several methods should be used to estimate a given population parameter (Hanson and Hovanitz 1968). Furthermore, in building up population models, students of populations should, as suggested by Levins (1966), sacrifice precision to realism and generality (Mac Arthur's approach) instead of sacrificing generality to realism and precision (Holling's and Watt's approaches). Because of its realism and generality, it is not surprising to see the population dynamics data often analysed in a life table fashion.

The life table studies of gypsy moth populations suggested the larval and pupal stages to be the most important factors in their population fluctuations (Campbell 1967). This constituted the greatest source of variation in density among dense populations and this is where vertebrate predators do show their main impact. Small mammals and birds are usually important predators when populations are low because of their impact on residual populations (Embree 1965). It has been determined that small mammals can locally destroy between 14 and 90 percent of a given insect population (Buckner 1964, Embree 1965, McLeod 1966), where predation followed the accessibility of the food. Buckner (1964) showed, for example, that a masked shrew could destroy 833 sawfly cocoons per day while the basic requirements of such animals would not pass 87; this was also the case for three other shrew species of Manitoba bogs.

Small mammals can have a very important influence on the dynamics of populations by feeding mainly on a given sex. Holling (1958) showed that wild shrews and mice opened more female than male sawfly cocoons; he found that masked shrews, short-tail shrews and deer mice opened respectively 4, 11, and 7 percent more female cocoons. McLeod (1966) suggested that small mammals might consume the smaller male cocoons where found while they would transport the larger female ones for greater distances.

Some authors reported a numerical response of predators to populations of forest insects but such responses are still rarely mentioned in the literature. Holling (1965) showed that certain shrew and rodent species changed numerically following changes in European pine sawfly populations in plantations. These numerical responses of predators to prey populations are usually of four types (Varley and Gradwell 1970): directly density-dependent, inversely density-dependent, delayed density-dependent and density-independent.

It was shown that numbers of singing male birds increased from 49.4 per 100 acres in 1965 to 94.3 per 100 acres in 1967 following a twofold increase in budworm predation (from 1.8 to 3.5 percent, Gage et al 1970). Buckner and Turnock (1965) found that predators (resident birds) of adult sawflies responded to changes in adult populations, predators of larvae to changes in larval populations and predators of both larvae and adults either to larval populations or to populations of both the larvae and adults. Some birds (wood warblers and bay-breasted warblers) showed a very rapid increase to high population levels of spruce budworms (Morris et al 1958); masked and short-tail shrews showed also a direct numerical change while deer mice and redback voles registered inverse responses. However, Morris (1963) reported that small mammals did not influence epidemic populations of spruce budworms (Choristoneura fumiferana (Clem.)) although they might have a certain role when such populations reached their low. According to Buckner (1967), the predatory populations responded numerically in two ways: through breeding, which formed a breeding numerical response, and through behavior, where population movements accounted for the increase in the numbers of predators. It was found in some instances that numerical responses of shrews were behavioral (Buckner 1969).

Density-dependent relationships of predators to prey densities were shown to form what is called a functional response. Holling (1965) determined three general types of curves that predators usually registered when feeding on prey species. The first (I) and second (II) types of curve showed by invertebrates followed respectively a linear and a curvilinear increase to a plateau. The third (III) type, thought to be only a vertebrate fashion, represented a sigmoid or S-shaped curve which apparently held true only for species possessing a certain learning capacity.

The functional response of some invertebrate predators was found to be correlated to hunger and a whole array of other physiological conditions (Holling 1966) which of course determined the shape of the curve. Phytoseiid predators showed a curvilinear rise to a plateau (Sandness and McMurtry 1970) while parasitic wasps registered a sigmoid one (Takahashi 1968). Buckner and Turnock (1965) found that responses of resident birds were of the three types mentioned earlier, although several species responded to prey population by a sigmoid curve. Some small mammal species showed a type III curve in their predation upon sawfly cocoons (Holling 1965). He also proved that the outline of the curve stayed the same even with the effects of alternate foods which decreased sawfly consumption in proportion to the increased consumption of the buffer food item.

One of the purposes of studying a predator-prey system is to be able to predict future population levels. Morris (1959) used the single-factor analysis (key-factor) to improve the predictability of future generations of budworms. He found that parasitism, as a key-factor, improved the predictability of future populations of budworms from 45 to 86 percent and from 38 to 46 percent for sawflies. Parasitism was also found to be a key factor acting on sawflies in the Maratime provinces (Neilson and Morris 1964). These workers showed that parasitism, as a key-factor increased the predictability of sawfly populations by 13 percent (from 59 to 72 percent). They also attributed a key role to the vertebrate predators in the population dynamics of sawflies. Although Morris (in Morris (ed.) 1963) showed that small mammals played an insignifiant role in the dynamics of budworms, small birds were found to be one of the major controlling factors of low budworm populations. Embree (1965) noted the importance played by small mammal predators, but they were usually overshadowed by parasitism effects. The impact of shrews acting as a key-factor in the dynamics of Jack Pine sawflies (Neodiprion swainei Middleton) was stressed by McLeod (1966). On the whole, the studies show that the small mammal predation upon epidemic forest insects does not play a key role in their population regulation.

Study areas and plot description

Small mammal and larch looper populations were studied in the 7 permanent investigation plots of the Larch Sawfly Team of Manitoba. The plots were situated as follows:

Rennie, 10 miles north of Rennie town
Telford, 7 miles east of Rennie town
Seddon's Corner, 3 miles east of Seddon's Corner
Pine Falls, 9 miles north of the power dam
Riverton, 23 miles north of Riverton
Darwin, 5 miles north of the fireguard road
Hodgson, 15 miles east of Hodgson

In addition to this, 11 new locations of tamarack stands were chosen wherein trapping and 'pupae planting' experiments could be undertaken. They were situated as follows:

A, Canadian National bog, 5 miles north of Rennie town
B, 2 miles north of Rennie town
C, 2 1/2 miles north of Rennie town
D, 2 3/4 miles north of Rennie town
E, 1 mile east of the Forestry Field Station
F, 1 mile east of the Forestry Field Station, opposite to E
G, 7 1/2 miles east of Rennie town
H, 3 1/2 miles east of Seddon's Corner
I, 1/2 mile north of Rennie town
J, tamarack bog beside the Forestry Field Station
K, 19 miles north of Rennie town

Their exact location is shown in Figure 3. A more complete description of these plots in terms of tamarack trees and moisture conditions of the forest floor is given in Table 1.

Buckner (1957 and 1959) described in more detail the vegetation cover of two typical tamarack bogs (Rennie and Telford plots). Tamarack stands are often mixed with Black Spruce (*Picea mariana* (Mill.) BSP) or Swamp Birch (*Be-*

Figure 3. The location of sampling plots.

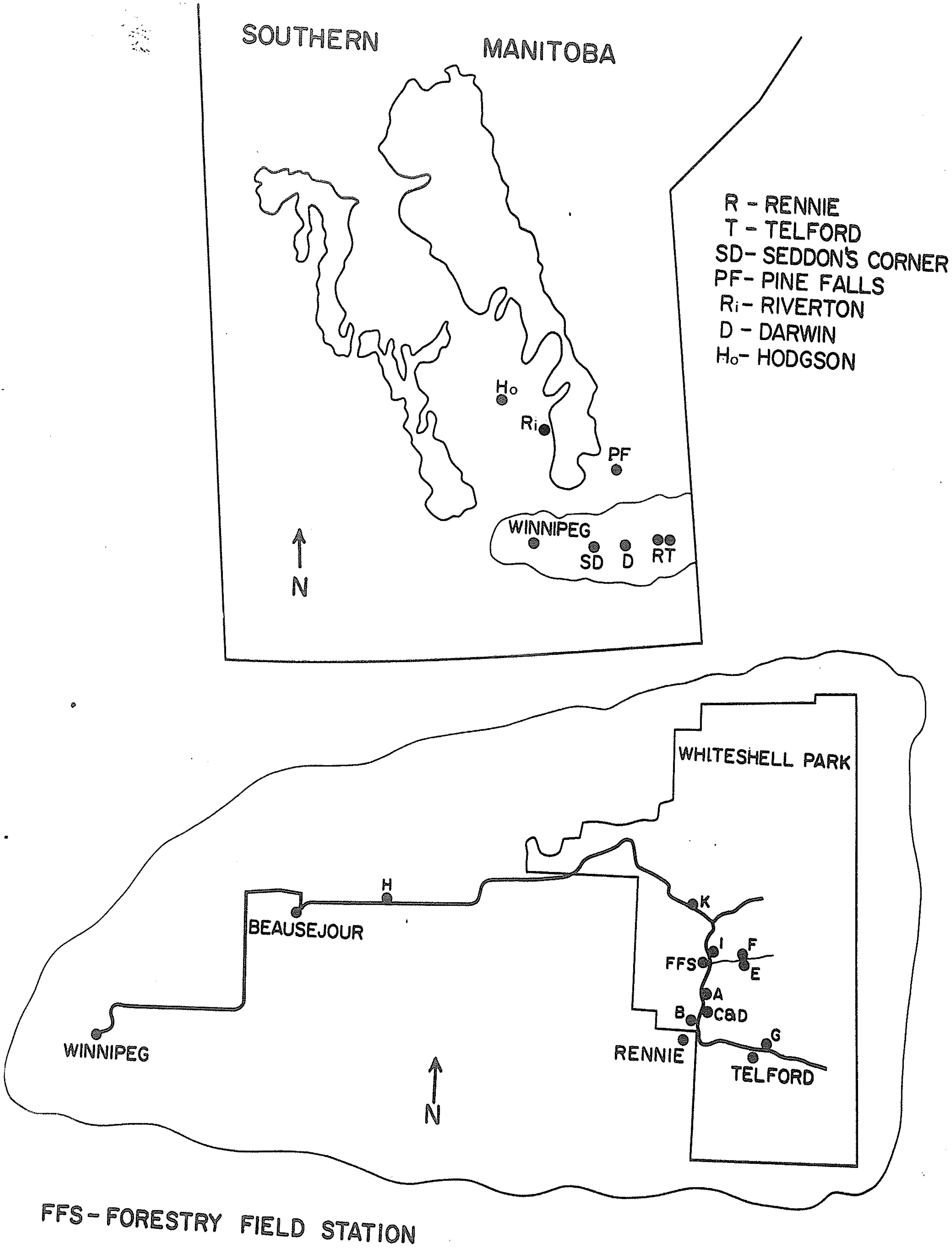

SOUTHERN MANITOBA
R - RENNIE
T - TELFORD
SD- SEDDON'S CORNER
PF- PINE FALLS
Ri- RIVERTON
D - DARWIN
Ho- HODGSON
Ho
Ri
PF
WINNIPEG
SD
D
RT
N
WHITESHELL PARK
H
K
BEAUSEJOUR
I
F
FFS
E
A
B
C&D
G
WINNIPEG
RENNIE
TELFORD
N
FFS - FORESTRY FIELD STATION

Table 1. A summary description of the sampling plots.

Plot	No. of living **larch** trees/acre (1970)	Moisture conditions	Remarks
Rennie	267	dry	understory: sphagnum moss and Labrador tea.
Telford	236	very wet	few Balsam firs; understory: sphagnum moss, Labrador tea, pitcher plants, grasses and sedges.
Seddon's Corner	491	wet	understory: sphagnum moss.
Pine Falls	551	dry	understory: sphagnum moss and Labrador tea.
Riverton	268	very wet	understory: sphagnum moss, pitcher plants, grasses and sedges.
Darwin	178	wet	understory: sphagnum moss, grasses and sedges.
Hodgson	338	very dry	sand.
A	64^{+}	dry	mixed with alder; understory: sphagnum moss and Labrador tea.
B	36^{+}	dry	few Balsam firs, birches and Jack pines; understory: sphagnum moss and Labrador tea.
C	25^{+}	wet	few birches; understory: sphagnum moss, pitcher plants, herbs and grasses.

Table 1. Continued.

Plot	No. of living larch trees/acre (1970)	Moisture conditions	Remarks
D	57[+]	wet	few birches; understory: sphagnum moss, pitcher plants, herbs and grasses.
E	76[+]	very wet	understory: sphagnum moss, herbs and grasses.
F	31[+]	wet	understory: sphagnum moss.
G	--	dry	understory: sphagnum moss.
H	--	wet	few poplars and alders; understory: sparce sphagnum moss and peat moss.
I	--	dry	few alders; understory: sphagnum moss and Labrador tea.
J	--	wet	few Jack pines; understory: sphagnum moss.
K	--	wet	few Jack pines and alders; understory: sphagnum moss and Labrador tea.

[+] Number of trees on a 0.1 acre grid.

tula pumila L.) or Trembling Aspen (Populus tremuloides Michx) depending on the site of the plot. The understory comprises different combinations of the following herbacious plants and mosses: sphagnum and peat mosses, Labrador tea (Ledum groenlandicum Oeder), pitcher plants (Sarracenia purpura L.), grasses and sedges. Surface water occupies also some of the substratum, especially in wet plots such as Telford and Darwin.

Material and methods

A. Sampling techniques for insects

a. Population dynamics

Techniques for the study of the larch sawfly populations have also proved to be useful for measuring Semiothisa populations. In the case of the larch sawfly investigations, population 'fixes' were made at three points in their life cycle: egg, larvae and adult stages (Ives et al 1968). Ives (1967) used oil drop funnels to measure populations and population parameters of the larch sawfly, a technique which has proved useful in the current study on Semiothisa. This technique consisted of a funnel with a two square foot collecting area directed downwards towards a trap filled with a mixture of oil, alcohol and water which preserved the fallen larvae. The role of the water in the trap is to keep a constant amount of oil-alcohol mixture in it. There were 30 of these traps in each investigation plot.

The 1968 populations of emerging adults were estimated by emerging cages (Turnock 1957). One hundred units were set out randomly in each plot. The cage consists of an inverted funnel whose opening is directed to a terminal plastic container possessing a small styrene funnel. The emerging adults, attracted by the light coming through the hole in the lid, are trapped and killed instantly by a killing substance ('Vapona' cube).

The estimated populations of larch loopers used for the life table analyses were calculated by the following formula: $N1/N2 = X1/X2$, where

$N1$ = the number of larch sawfly larvae found in oil drop funnels,
$N2$ = the number of larch looper larvae found in oil drop funnels,
$X1$ = the estimated population per acre of a given larch sawfly stage,
$X2$ = the unknown parameter.

The formula was applied assuming similar mortality rates for both insects.

Field data concerning larch looper and larch sawfly populations are shown in Tables 9, 10, 11 and 12 of the Appendices.

b. The caloric values of larch looper life stages

The caloric values of larch looper life stages were determined the same way as those of other bog Lepidoptera (Bergeron and Buckner 1970). The adult, larval and pupal stages were collected in or near the permanent sampling plots of the Larch Sawfly Team of Manitoba. Adult populations were collected from emergence cages (see 'Sampling techniques of insects', for more details). The larval collections came from the larvae sampling traps commonly named oil drop funnels (Ives 1967). The larvae were identified by J.C.E. Melvin, a senior technician of the Forest Insect and Disease Survey, Winnipeg; they were later classified by instars following McGuffin's description (McGuffin 1947). Pupae were obtained by beating the trees to collect the falling larvae on a canvas sheet spread underneath, and rearing these larvae to the pupal stage on tamarack foliage.

The specimens were dried for a week at 100°C and weighed. They were burnt afterwards in an Automatic Adiabatic Bomb Calorimeter, and their caloric values determined. The caloric measurements were applied in terms of 'potential biomass' and potential intake for small mammals of the Manitoba bogs (Bergeron and Buckner 1970).

B. Sampling techniques of small mammals

a. Trapping techniques

The small mammal populations were estimated from the 'capture-recapture' and snap-back trapping methods. The former technique consisted of setting out, on a 8 X 8 grid, 64 trapping stations having 2 traps each. Each set of traps was put at a chain interval (66 feet). The Sherman live traps were baited with peanut butter which had proven previously to be very effective (Buckner 1957); some nesting material was also included. The pitfall traps, as described by Buckner (1955) were baited with mealworms and visited several times during the day. The animals were handled by releasing them into a plastic bag through which species and age were readily determined. They were then marked by toe-clipping and released.

At low population levels, complete recapture was usually possible, but at higher densities the population was estimated using the Lincoln Index. The formula consists of the following equation: $P = a\ n/r$, where

P = the total estimate
a = the number previously marked
n = the newest sample caught
r = the marked animals caught in this sample

The conditions for the validity of the equation were discussed earlier in the text. Buckner (1957) suggested the use of the final determination (sample) for more accuracy since the confidence interval decreased on successive determinations.

In addition, 11 plots were trapped using standard trap lines of 50 snap-back traps; each plot was trapped for 3 to 5 consecutive nights. The method involved setting 5 traps per horizontal section of 15 feet, each being 40 feet apart. The area thus trapped amounted approximately to 1/10 of an acre. The results were put in an Index format and used in correlation to stomach contents and for determinations of the small mammalian predation upon larch looper pupae.

b. Food preference tests

Because of the scarcity of larch looper material at the time of study, indirect methods were used to assess the preference for larch looper and larch sawfly overwintering stages.

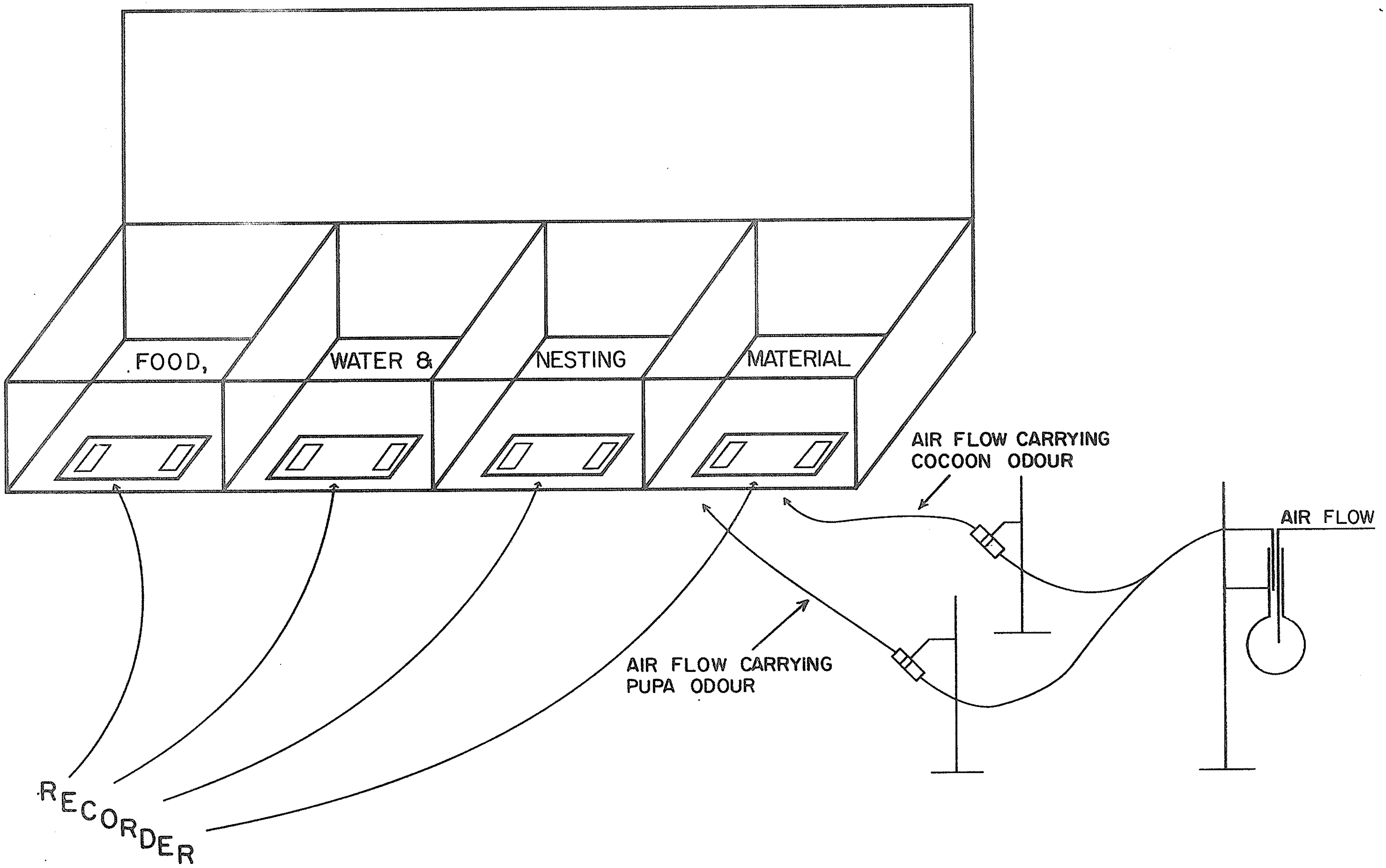
Eight olfactometers based on Holling's apparatus (Holling 1955) and modified by Buckner (1964) were placed in wooden cages. Air streams passed over pupae and cocoons; the number of visits to each air stream was recorded by means of microswitch treadles (Ray D.G.H. 1969, unpublished manuscript) connected to a 20 pen Esterline Angus Recorder. The general outline of the apparatus is given in Figure 4.

Experiments were conducted with shrews and voles. The former group was tested as soon as they were caught because of the difficulty of keeping them alive under artificial conditions. Voles, at times, were kept away from pupae and cocoon odors as much as two weeks before the experiment. A three-day acclimatization period was allowed before weighing and sexing the voles; the experiments lasted for another three-day period. Shrews were analysed under near natural conditions of the summer months (1970 and 1971) and were given food and water supplies *ad libidum*. The redback voles were analysed under constant temperature of a cold room adjusted to 40°F.

The choices given to the voles were composed as follows:

1. One healthy larch looper pupae vs one healthy larch sawfly cocoon
2. One healthy larch looper pupae vs one parasitized larch sawfly cocoon

Figure 4. Outline of the food preference test apparatus.


FOOD,
WATER &
NESTING
MATERIAL
AIR FLOW CARRYING COCOON ODOUR
AIR FLOW
AIR FLOW CARRYING PUPA ODOUR
RECORDER

3. One healthy larch looper pupae vs 10 healthy larch sawfly cocoons
4. Ten healthy larch looper pupae vs one healthy larch sawfly cocoon.

Shrews were analysed using the first series of experiments.

c. Metabolic requirements of small mammals

The metabolism of redback voles was determined by their oxygen consumption. The apparatus was a modification of the closed-system automatic respirometer used by Buckner (1964). The metabolic cages consisted of battery jars containing a screen mesh floor partly covered underneath by a sheet of polyethelene plastic in order to protect the urinary excretions and soda lime pellets from fecal contamination and permit the latter ones to absorb water and carbon dioxide. The apparatus had also feeding trays and water bottles kept to the side of the jars by suction cups (Figure 5). Food* and water were given ad libidum at all times. Some nesting materials were also included in the system.

The oxygen consumption was recorded automatically by a manometer-type-respirometer (Ray D.G.H., 1969, unpublished manuscript) connected to an Esterline Angus Recorder; readings were corrected for each 24-hour period by the introduction of a thermobarometer in the water bath. The manometers were calibrated after each experiment to mi-

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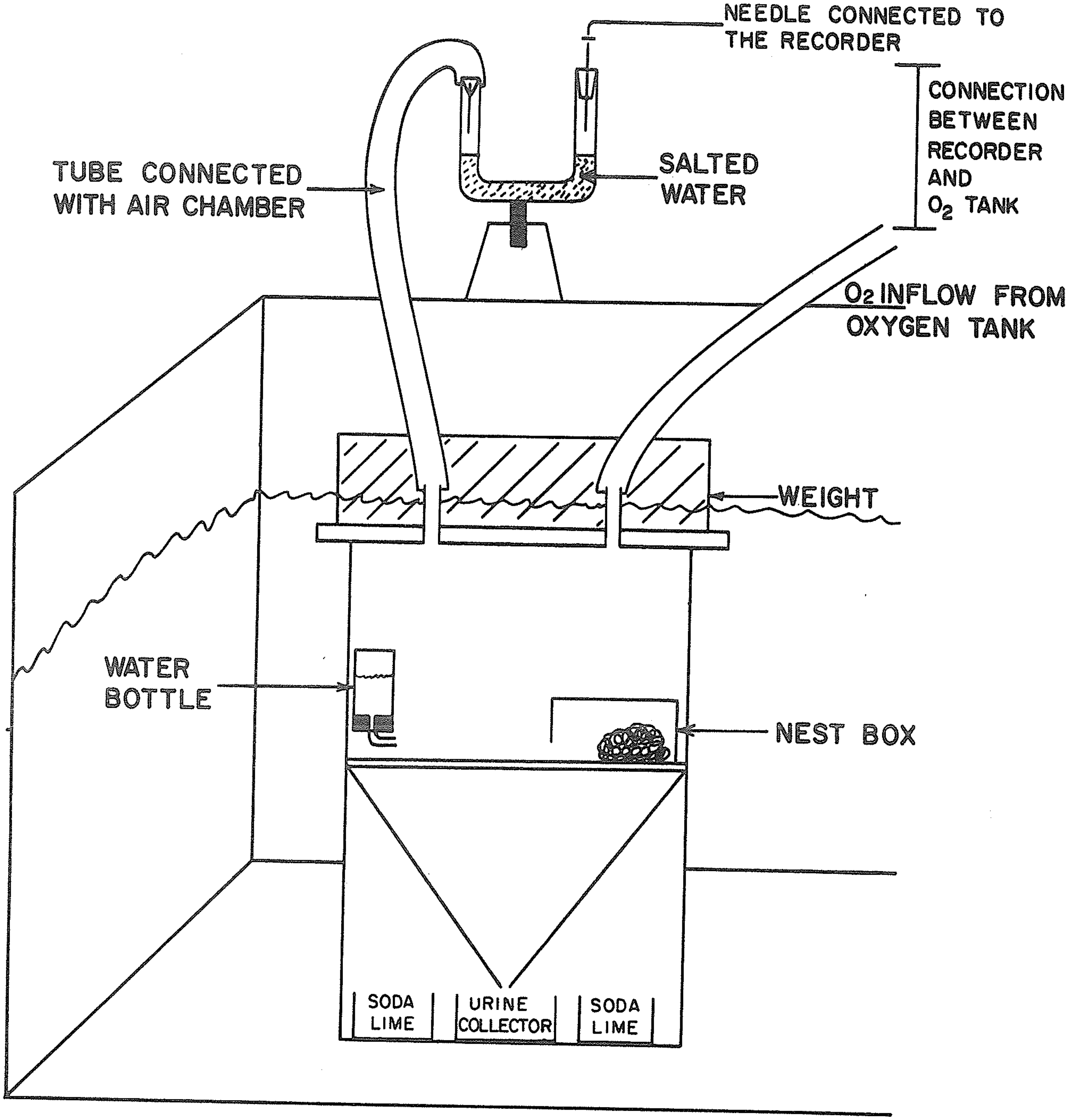
* The pig starter pellets used were composed of: 12.7% free water, 18.1% crude protein, 40.0% crude fat, 3.0% salt,

Figure 5. Typical metabolism cage used to determine the metabolic requirements of redback voles.


NEEDLE CONNECTED TO THE RECORDER
CONNECTION BETWEEN RECORDER AND O2 TANK
TUBE CONNECTED WITH AIR CHAMBER
SALTED WATER
O2 INFLOW FROM OXYGEN TANK
WEIGHT
WATER BOTTLE
NEST BOX
SODA LIME
URINE COLLECTOR
SODA LIME

nimize the possible effect of the room temperature on the water.

The redback voles were captured partly in auxillary trap-lines of a permanent sampling plot of the Vertebrate Ecology Team, and partly from another plot near the Nuclear Research Center of Pinawa, Manitoba. The newly captured voles were brought to the laboratory and acclimatized to their new environment for a minimum of a month. They were then placed under experimental conditions for a one-day period and finally tested for another 24 hours. The metabolic cages were immersed in a water bath kept at a constant temperature for the period of the experiment. The temperatures ranged from 53 to 73° F (11.6 to 22.8 ° C). The caloric utilization in the metabolic process was calculated after Brody's technique (Brody 1945).

C. Sampling techniques to find small mammal and insect relationships

a. Stomach analyses

Mice, voles and shrews were trapped in 12 tamarack plots of the Whiteshell region (A to K and Seddon's Corner plot). The trapping period lasted from 3 to 5 consecutive days using standard lines as described earlier. The

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0.85% calcium, 0.65% phosphorus, 0.008% zinc, traces of nitrate, 4000 IU/lb of Vitamin A, 600 IU/lb of Vitamin D; the caloric value of the food was estimated by the author at 4.47 kcal/g of dry weight.

plots were snap-back trapped in July, August, September and October of 1970 and February, March, April, May, September and October of 1971.

The newly caught specimens were frozen. They were later cut along a mid-ventral line to remove the stomach. The volume of contents was then measured with the use of a graduated test tube. Stomach contents were washed afterwards in moderately hot water to remove fat and gastric juice (Williams 1959). The contents were then placed in a petri dish, the bottom of which had been scribed into 500 equal portions using a needle and a ruler. The contents were examined under a binocular microscope (400X) and compared with control slides which had been prepared before. These control slides were prepared after allowing the small mammals to feed freely on larch looper and larch sawfly cocooned stages. These animals were killed after the period of free-feeding, and their stomach contents examined and mounted for reference purposes.

b. Pupae planting technique

Among the 5 techniques used by Buckner (1959) to determine the sawfly cocoon predation by small mammals, the cocoon planting technique proved to be very useful. The technique consisted of tying a single pupa with nylon thread to three-inch tree tags followed by burying in tamarack bogs to a depth of approximately 2 inches. Pupae were planted in 12 plots using the following density pattern: 6 plots planted with 25 pupae, 5 with 50, 2 with 75, 1 with 100, 1 with 125, 1 with 150, and 1 with 175 pupae. The pupae were left in the plots for the predation period and then brought back to the laboratory for further analysis. The pupae were left in the bogs for a 9-month period in 1970 (from August to May) and for a 3-month period in 1971 (from August to November). To determine the fate of a given pupae, different categories were used:

- preyed at the tag location
- hoarded (not found at the planting site)
- not preyed because of parasitism
- not preyed because of disease
- already emerged at the time of recovery.

This pupae planting gave a picture of the total mortality experienced by the larch looper pupal stage.

To determine the mortality caused by other predacious species on larch looper populations, one 'small-mammal-free-cage' was set out in each plot. The cage was triangular in shape and contained 20 larch looper pupae buried in the moss. Quarter-inch mesh screen was used to isolate these pupae from mammalian predation although beetles and other predatory insects could act freely. These cages were left in the bogs the same length of time as that of the pupae exposed to predation, and were analysed the same. By subtracting this partial mortality caused by other predatory species, from the total mortality, a direct estimate of the mammalian predation was assessed.

The small mammal populations were determined using standard trap-lines of 50 traps as described earlier. They were usually trapped in early fall.

Results and discussion

A. The population ecology of the Semiothisa complex

a. Population dynamics

1. Life table analysis

The life table data were analysed only for the most numerous species, the green larch loopers, S. sexmaculata. However, further data on hand suggest that the 2 other species follow the same pattern. Table 2 of the Appendices shows the 2 methods used to convert the data as suggested by Harcourt (1969). The first one, the fractional survivals (survival rates = S_x) of the age intervals is given by the following formula:

generation survival = $S_g = S_1 \times S_2 \times S_3 \ldots$ or

$\log S_g = \log S_1 + \log S_2 + \log S_3 \ldots$

The second conversion proposed by Varley and Gradwell (1960) makes use of the k-values which are measured by the difference existing between the successive values of $\log l_x$ within a generation. The method gives a measure of the killing power of a mortality factor or mortality factors affecting the stage. The total mortality K is usually calculated by adding the individual values k_1, k_2, k_3 etc... resulting from the partial mortality of different stages.

The k-values for the pupal stage are very high and tend to be larger than those affecting the other stages. As suggested by Varley and Gradwell (1970), the density-dependent mortality could be established by the formula

$$k = a + b \log(N)$$

where k is the interval mortality, b the slope of the regression, a the intercept and N the number per unit area. Such relationships were compiled and tabulated in Table 2. The table indicates strong density-dependent mortality in 3 of the 6 investigation plots. It is thought also that similar relationships do indeed exist in the other plots, although not shown. This is suggested by the fact that most published data on density-dependent mortalities have values for the slope greater than 0.2 but less than 1.0 (Varley and Gradwell 1970). On the basis of this criterion, it appears that Rennie plot would be the only one not to show the density-dependent mortality. Some authors believe, however, that in such cases the density-dependent effects of each stage interval could be additive and could combine to give a very important total effect.

2. Intrageneric relationships

The last section suggested that the green larch looper populations could be regulated by density-dependent factors. The intrageneric competition which could be reflected by the numbers of larvae collected from the inves-

Table 2. Density-dependent mortality in *S. sexmaculata* as shown by the formula $k = a + b\ (\log N)$.

Plot	Type of analysis			
	r	t	d.f.	k
Rennie	0.116	----	5	$1.002 + 0.185 \log N$
Telford	0.905^{**}	4.76	5	$-0.932 + 0.834 \log N$
Seddon's Corner	0.375	----	5	$-1.232 + 0.607 \log N$
Pine Falls	0.301	----	5	$-1.456 + 0.607 \log N$
Riverton	0.834^{*}	2.92	4	$-0.769 + 0.724 \log N$
Darwin	0.907^{+}	3.05	2	$-1.048 + 0.722 \log N$

** Probability > 99 % level.
* Probability > 95 % level.
\+ Probability > 90 % level.

tigation plots offers a first attempt to explain the larch looper mortality.

The numbers of fallen larvae from tamarack trees probably offer the best population analysis since they show only the true recoveries of a given population and not the estimation of the population level from statistical analysis. The collected larvae from 7 permanent sampling plots are plotted for 8 consecutive years in Figure 1 of the Appendices. Peaks and dips of the three studied species tend to coincide. This is especially true in Rennie plot where the species followed the same pattern of fluctuation. Pine Falls and Darwin plots illustrate the same trends. Table 3 of the Appendices shows some of the relationships existing between the species when their numbers are analysed into a density-dependent pattern. In Darwin plot, a positive correlation exists between S.signaria numbers of the present generation and those of the following one (n+1 year basis). Similar positive correlations exist between S.signaria and S.oweni numbers and between S.sexmaculata and S.oweni larvae of some plots. The less numerous species tend to be highly correlated with the numbers of the 2 most numerous ones. In certain plots, these relationships could act as reflections of what is happening in the later stages of the insects. This might be shown by the analysis of the pupae populations. Such relationships are listed in Table 4 of the Appendices and appear to show better the existing interrelations among the 3 species. When analysed on a (n+1) year basis, the relationships, although not statistically significant, tend to be related into negative patterns. The trends are particularly strong among S.oweni numbers, where 5 of the 6 plots showed such relationships; the sixth plot indicated a positive correlation to exist between S.sexmaculata and S.oweni pupae populations.

S.sexmaculata and S.signaria pupae populations are positively related in 3 plots. The S.sexmaculata pupae show also a positive correlation with those of S.oweni of Pine Falls plot, while the opposite holds true in Riverton. This negative relationship is interesting because it shows clearly the impact of one species' numbers on the other. In this particular case, we see that the negative correlation existing between the two species, when analysed on a yearly basis, turns out to a positive one when analysed on a (n+1) year basis. This relationship tends to indicate that low numbers of S.sexmaculata pupae would permit the other species to reach higher populations, and vice-versa. This observation would explain why the 2 species show positive and negative correlations depending on the type of analysis. The same table shows also a significant density-dependent relationship within S.signaria numbers. Such a relationship already existed in the density-dependent analysis of larvae populations.

On the whole, the relationships apparently tend to show up better among the pupae populations and tend to be related into density-dependent patterns. This was already confirmed in the previous section using k-values (mortality) for one of the species of larch loopers. The latter analysis showed that such relationships do exist within the other two species and also among the three species taken together.

3. Interspecific relationships

Previous sections showed that larch looper populations tended to fluctuate with those of the previous generations. These density-dependent relationships could be due to a whole array of factors that could influence the numbers of pupae of every species. Since sawflies and small mammal populations represent 2 of the most numerous groups of animals that inhabit bogs with the larch loopers, these populations should be analysed in regard to larch looper fluctuations. Field and laboratory analyses will show the potential and actual predation done by small mammal numbers, without showing, however, the long term influences caused by these species. Such relationships will be examined with the key-factor analysis and Holling's numerical and functional responses.

i. Sawfly populations

Relationships between the larch looper and larch sawfly populations are shown in Figure 1 and Table 5 of the Appendices. As before, the larvae collections were chosen as the first step of analysis. Five plots indicate positive relationships to exist between larch looper and larch sawfly numbers. However, Darwin plot shows the numbers of *S.signaria* to be inversely related to larch sawfly numbers. The less numerous species of larch loopers (*S.oweni*) seems to be particularly related to sawfly numbers, while the most abundant one (*S.sexmaculata*) shows less. The influence of sawfly numbers is further stressed when populations of larch loopers are analysed at one-year intervals. According to such an analysis, the 3 species of larch loopers show positive correlations with sawfly numbers of 3 plots, while *S.signaria* populations are inversely related to them in Seddon's Corner plot. This indicates that sawfly numbers do indeed influence the yearly populations of larch loopers, though not always in a positive way.

A second way to analyse these relationships is to plot the populations of larch looper pupae and sawfly cocoons. The resulting coefficients of correlation are listed in Table 6 of the Appendices. Generally speaking, they do not indicate stronger relationships than those showed by the previous analysis of larvae populations. Only Rennie plot indicates inverse relationships. The presence of sawfly cocoons seems to influence negatively the numbers of future generations of larch looper pupae, indicating then a kind of interspecific strife between the 2 populations that the previous analysis did not reveal (significantly). These inverse relationships might be due to specific mortality factors affecting one species more than the other, once a certain population threshold is attained.

To obtain a clearer picture of the interrelations among these populations, it might be useful to plot the mortality of pupae and cocoon stages for successive generations. We note in Figure 2 of the Appendices that larch looper populations tend to be less stable than sawfly ones, fluctuating widely in all the investigation plots. This is especially true for S.signaria and S.oweni populations, whose numbers are very low in the bogs. The green larch looper and sawfly populations tend to fluctuate less than the last two species, probably because of their higher numbers. In some plots, particularly in Rennie and Telford, the number of dead individuals of the pupae and cocoon stages seems to be inversely related. Such models fit well in the theory of 'compensation factors' which are mainly used where parasites and predators form a complex system. The same figure shows that when the sawfly mortality drops, the mortality of green larch loopers rises, and vice-versa; sometimes, as in the Pine Falls plot, a species of third importance, S.signaria, acts also like a compensating factor.

This might be an indication that the larch looper populations do indeed act as an auxillary source of food in the Manitoba bogs and serve as buffer species in the population dynamics of the larch sawfly.

Relationships existing between larch looper and larch sawfly ground-inhabiting stages were also analysed by comparing the numbers of dead individuals of each. Although not statistically significant, the curves show interresting trends (Figure 3 of the Appendices). Since the green larch loopers are by far the most numerous species among the larch loopers, only their numbers were compared with larch sawfly populations. The total number of Semiothisa pupae were also plotted against numbers of sawfly cocoons. In Rennie plot, the number of dead green larch looper pupae is related to the number of dead sawfly cocoons by the formula

$$Y = a\ X^b$$

where Y represents the number of dead larch looper pupae per acre, X the number of dead larch sawfly cocoons per acre, a the intercept and b the slope. The green larch looper numbers fitted the curve better than those of all Semiothisa, as the probability of the first fit proved to be significant at the 98 percent level compared to 90 percent for the second. At Telford plot, the Semiothisa numbers were related in the same pattern as shown above ($P > 95\%$ level), while the numbers of dead green larch looper pupae were linked by a straight-line relationship to those of sawfly cocoons. Although not significant, the curves of the remaining plots approximate the best fit which could explain the larch looper population fluctuations. From what is shown, it is thought that larch looper and larch sawfly populations are related by exponential curves. This indicates then, that larch looper numbers can have a certain impact in determining future larch sawfly population levels. The first relationship mentioned above is particularly interesting to study since it approaches what would be expected in a simple predator (small-mammal)-prey (sawfly cocoon) system, having larch looper pupae as an alternate food supply. Since such relationships exist in at least 3 of the plots, it can be argued that these populations, the larch looper pupae and the larch sawfly cocoons, are interacting as expected for a predator-prey-alternate prey system, where small mammals would be responsible for the biggest part of the predation.

ii. Small mammal populations

The importance of small mammal populations in regard to the fluctuations of the larch sawfly is shown by comparing Table 7 with Figure 4 of the Appendices. In years of high small mammal density, the resultant mortality of sawfly cocoons increases to the 80 percent level. The table particularly shows 2 generations of sawfly cocoons that suffered such a heavy mortality. When such losses are compared to small mammal population levels, we note that redback voles and masked shrews represent the 2 main species of mammals that were particularly high in those years. The assumption can be made that the same mammalian species also affect the larch looper pupae numbers.

We have already shown, in the preceeding section, that the total mortality of the ground-inhabiting stages of the two main defoliators were not straight lines but exponential in shape. These curves are very useful in determining the percentage of larch looper pupae dying from mammalian interactions. Such percentages are termed 'actual mortality' as compared to the 'total mortality' used as such in the previous section.

Table 3 illustrates the relationships existing between small mammal and larch looper populations. The table shows some of the larch looper populations to be inversely related to redback vole numbers in 3 plots, while the numbers of <u>S.oweni</u> pupae per acre indicate a direct relationship with masked shrew populations. Table 8 of the Appendices shows another way to analyse such relationships, where small mammal populations are plotted against adult populations of the following year(adults of the following year = number of pupae left after the overwintering predation = pupae mortality). The redback vole populations and the overwintering losses of the larch looper pupae tend to be negatively related in all plots but one. We note also that the other shrew and rodent spe-

Table 3. Relationships between the small mammal populations per acre and the estimated numbers of larch looper pupae per acre as analysed by the correlation method.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
C.gapperi/acre(n) vs						
S.sexmaculata pupae/acre(n+1)	-0.362	-0.388	0.323	0.273	-0.336	-0.688^{+}
S.signaria pupae/acre(n+1)	-0.578^{+}	0.335	-0.230	0.388	0.763	-0.647
S.oweni pupae/acre(n+1)	0	-0.651^{+}	0.509	0.094	0.480	0
S.cinereus/acre(n) vs						
S.sexmaculata pupae/acre(n+1)	-0.309	0	-0.258	0.363	-0.041	0.120
S.signaria pupae/acre(n+1)	-0.082	0.431	0.110	0.173	-0.456	-0.040
S.oweni pupae/acre(n+1)	0.580	0.375	0.173	0	0.309	0.937*

* Probability ≥ 95 % level.
+ Probability ≥ 80 % level.

cies show direct relationships with larch looper adult numbers. The trend is particularly strong for the masked shrews where such relationships are found to be significant in 4 of the 6 plots. Some of the small mammals might compete with redback voles in such a way that both shrew and insect populations increase in numbers when redback voles are absent, and vice-versa. This concept would explain the positive correlations existing between shrews, rodents and larch looper adults and would explain also the negative relationships existing between redback voles and larch looper numbers.

A third way to analyse such relationships is to correlate small mammal populations against the number of dead pupae or the percentage of dead pupae of the larch looper species. As shown by Table 4, redback voles and masked shrews tend to be directly related with the total mortality of larch looper pupae. This is true for the relationships existing between redback voles and 2 looper species of Rennie plot, 1 of Seddon's Corner, 1 of Riverton and 1 of Darwin. The masked shrew populations on their part are related with 2 looper species of Telford, 1 of Pine Falls and 2 of Darwin. On the whole, the larch looper populations tend to be highly correlated with those of small mammals. The combined action of the 2 main species of small mammals (redback voles and masked shrews) influences 2 larch looper species at Rennie plot, 2 at Telford, 1 at Seddon's Corner, 1 at Riverton and 3 at Darwin.

Table 4. Relationships between the small mammal populations per acre and the total mortality of larch looper pupae per acre as analysed by the correlation method.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
C.gapperi/acre vs						
# dead pupae/acre S.sex.	0.595^{++}	-0.080	-0.318	0.159	0.955^{++}	0.558
# dead pupae/acre S.sign.	0.916^{*}	-0.644	0.754^{+}	0.224	0.244	0.385
# dead pupae/acre S.oweni	0.312	-0.165	-0.355	0	-0.398	0.822^{++}
% dead pupae/acre S.sex.	0.397	0.438	0.266	0.273	0.573	0.936^{1}
% dead pupae/acre S.sign.	0.393	0.106	0.385	0.265	0.490	0.546
% dead pupae/acre S.oweni	0.795^{2}	-0.144	-0.547	-0.486	-0.411	0.275
S.cinereus/acre vs						
# dead pupae/acre S.sex.	-0.434	-0.778^{+}	-0.023	-0.246	-0.841	0.866^{+}
# dead pupae/acre S.sign.	-0.012	0.810^{3}	-0.245	0.745^{3}	-0.015	0.793^{++}
# dead pupae/acre S.oweni	-0.370	-0.016	-0.330	-0.531	-0.365	-0.493
% dead pupae/acre S.sex.	-0.094	-0.455	-0.432	0.170	-0.996^{*}	0.412
% dead pupae/acre S.sign.	0.333	0.835^{3}	-0.428	0.225	0.350	0.237
% dead pupae/acre S.oweni	-0.465	-0.212	0.172	0.043	-0.431	-0.662

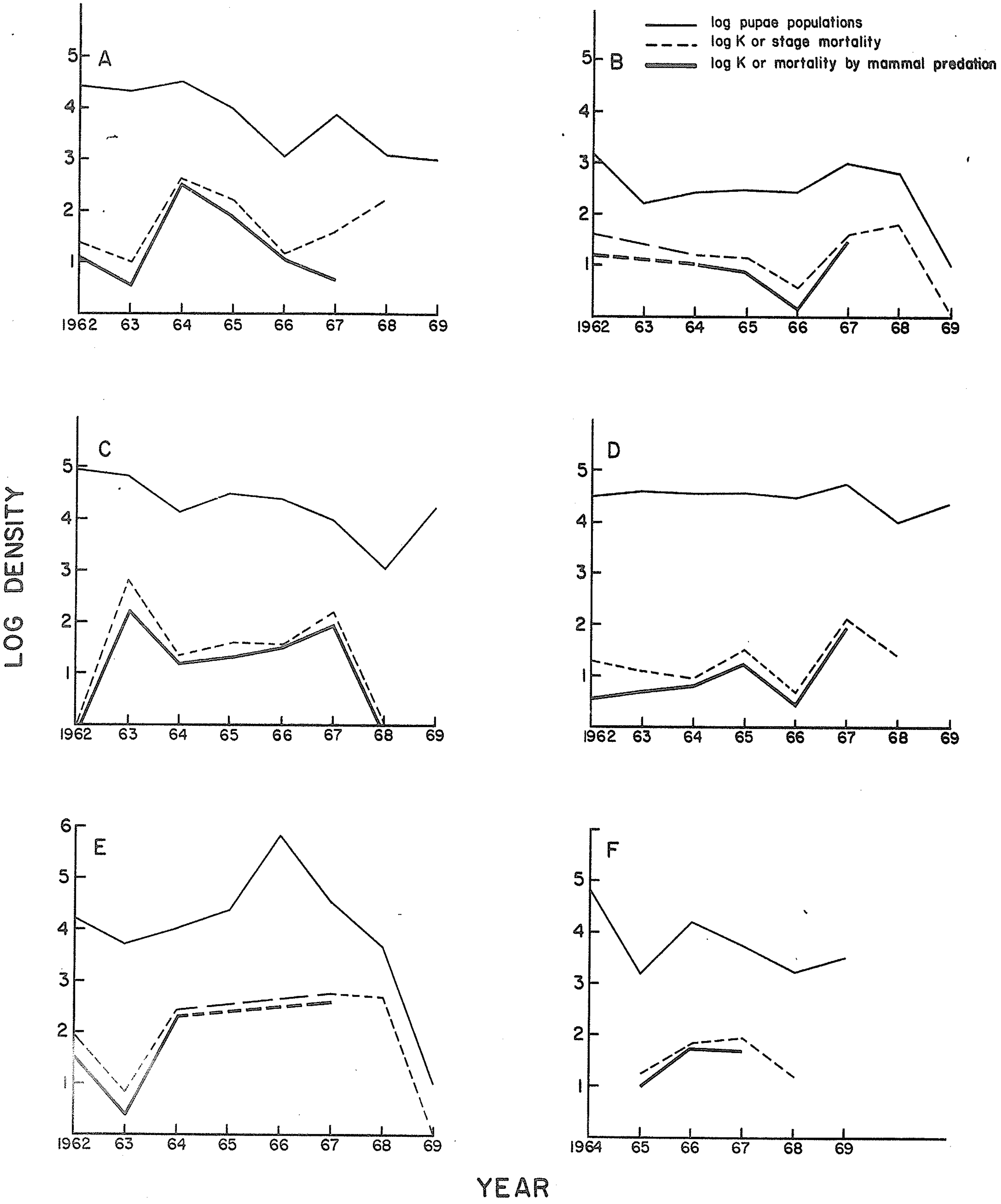
* Probability > 95 % level.
\+ Probability > 85 % level.
++ Probability > 80 % level.

1 Probability > 93 % level.
2 Probability > 94 % level.
3 Probability > 90 % level.

The positive relationships existing between the small mammal populations and the total mortality of larch looper adults, as shown by Table 8 of the Appendices, suggest a numerical response between the 2 groups. However, the total mortality of Semiothisa as a group, is probably composed of a series of mortality factors among which would be included the mortality caused by small mammal populations on the pupal stage. Such a mortality was estimated for the green larch looper species and is viewed in comparison to the total mortality affecting the pupal stage (Figure 6). This partial mortality estimation was based on cocoon mortality of larch sawflies by small mammal populations (Table 7 of the Appendices; the K and k values are given in Table 2 of the Appendices). As shown by the figure, this partial mortality of larch looper pupae seems to be a very important factor in the pupal survival and in the population dynamics of the species. We note that the k-value (mortality) caused by small mammals seems to follow closely the K value of the pupal stage. Similar trends were observed to occur also in the 2 other species of larch looper pupae.

As suggested by Morris (1959), such population patterns can be seen better when successive generations are plotted. The usual way to do so is to plot the relationship between log h_{n+1} over log h_n of a given population and treat the points as a scatter diagram. The re-

Figure 6. The importance of the mammalian predators of the pupal stage (log k) of _S_._sexmaculata_ Pack.

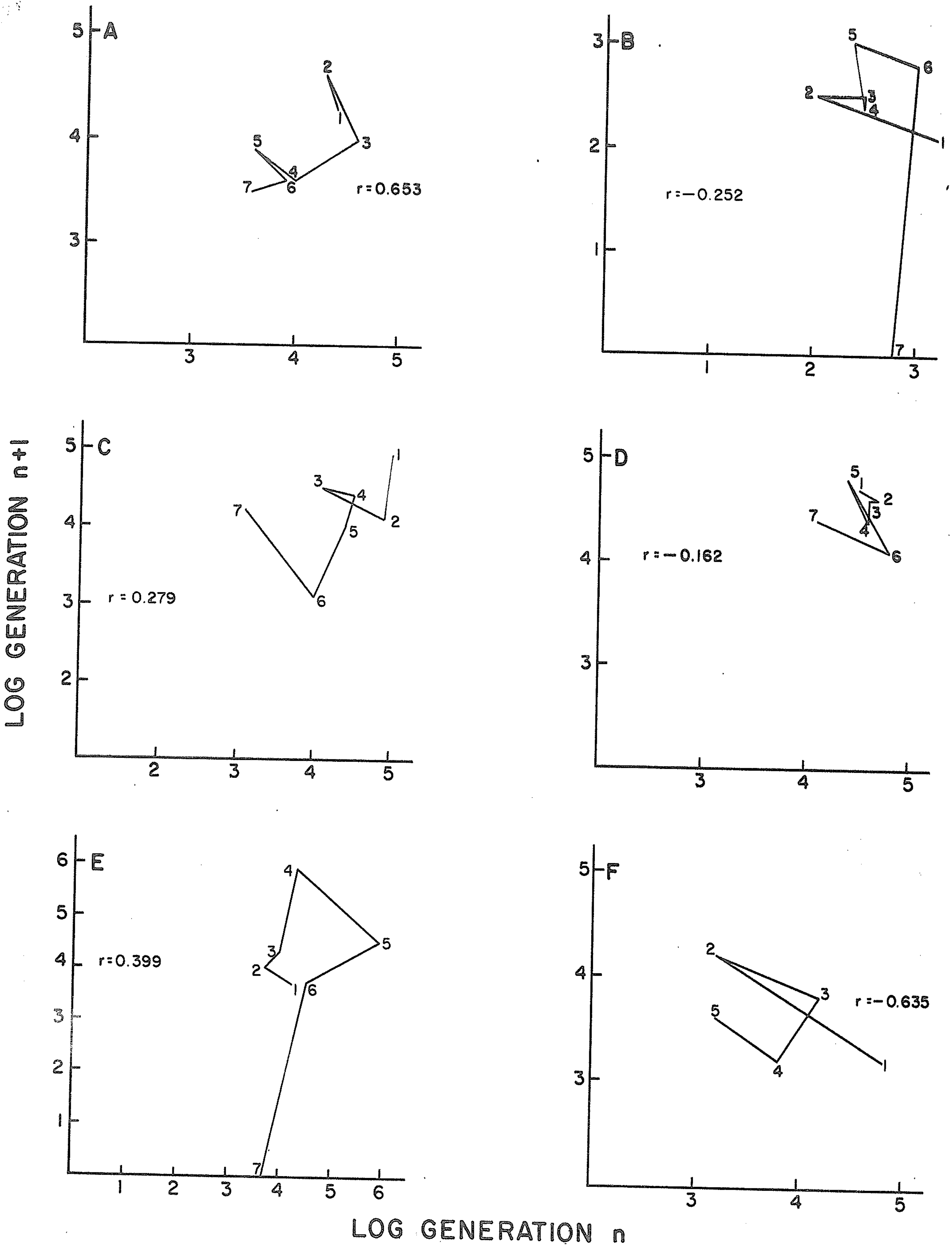

log pupae populations
log K or stage mortality
log K or mortality by mammal predation
LOG DENSITY
YEAR
A
B
C
D
E
F
1
2
3
4
5
6
1962
1964
63
64
65
66
67
68
69

sulting r^2 value from the regression gives the percentage of the variance in the logarithm of the individuals in generation n+1 which is explained by the logarithm of the numbers in generation n.

The populations of the green larch loopers (S.sexmaculata) were treated this way in 6 plots of the Larch Sawfly Team. We note that in Figure 7 the population fluctuations tend to form irregular polygones opened at one end. This is usually the characteristic of very unstable populations and is also the indication of incomplete population cycles. There are, however, indications that certain populations can indeed be predicted in the prescribed manner. The green larch loopers of Rennie and Darwin plots show a predictability of 43 and 40 percent respectively. The two other secondary species (Figure 5 of the Appendices) show weaker indications of such a tendency in Rennie and Riverton plots, where the logarithmic numbers in generation n explains only 28 percent of the variance of the logarithmic numbers in generation n+1.

Since a certain degree of predictability was shown to exist among larch looper populations and since the pupal stage had already been shown to be of a certain value in the dynamics of larch loopers (Figure 6), a key-factor analysis using the whole generation survival was designed to improve the predictability of future larch

Figure 7. *S. sexmaculata* populations in generation n+1 in relation to populations in generation n, with both expressed as common logarithms.


A
r=0.653
B
r=-0.252
C
r = 0.279
D
r=-0.162
E
r=0.399
F
r=-0.635
LOG GENERATION n+1
LOG GENERATION n

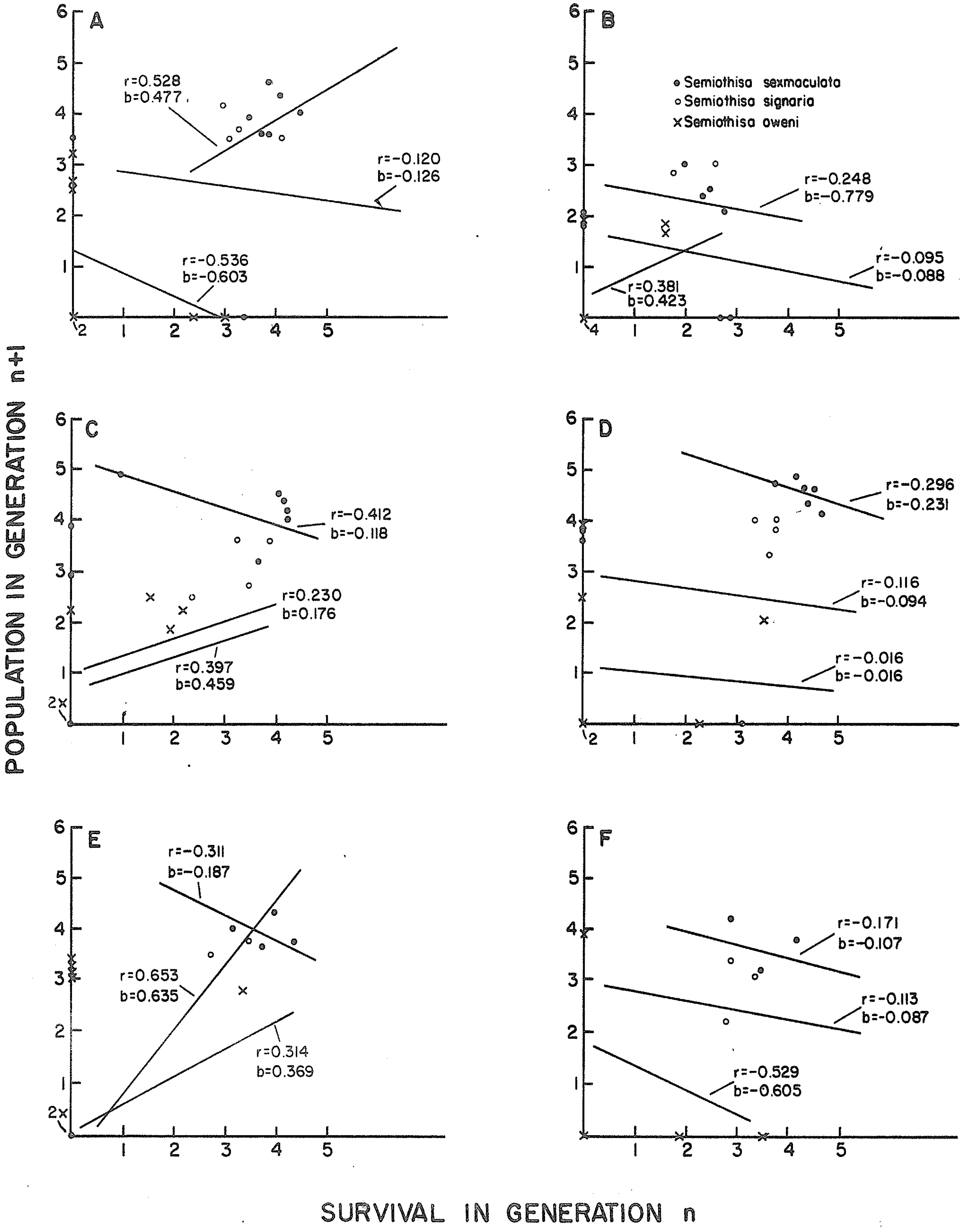
looper populations. This predictability was improved in all plots but one when using the log of survival of the generation of pupae (Table 2 of the Appendices). We note that in 3 plots, the predictability increased by at least twice the amount that could be given by using the log of the present generation (log h_n). This improvement shows also the importance of the pupal stage in the dynamics of larch loopers.

The pupal stage, being a key stage in the determination of future larch looper populations is probably attacked or controlled by a whole array of factors among which small mammals are thought to be one. To show this, a key-factor analysis using the logarithm of pupae survival from small mammal predation (log S_n) over the logarithm of pupae in generation n+1 was calculated. Table 5 and Figure 8 show the results of such an analysis. The overall pattern of the analysis indicates the non-predictability of the pupal survival from small mammal predation (log S_n) to explain future populations of larch loopers (log h_{n+1}). The small mammal predation does not appear to be one of the controlling factors at such levels of larch looper populations. As shown by Table 5, the predictability of future populations (log h_{n+1}) is better when using the logarithm of survival of pupae (log S, where S = total survival). There are only 3 instances where the survival of pupae from mammalian predation pro-

Table 5. The Morris key-factor analysis applied to larch looper populations.

Plot	Species	r^2 values		
		$\log h_{n+1}$ / $\log h_n$	$\log h_{n+1}$ / $\log S$	$\log h_{n+1}$ / $\log S_n$
Rennie	S. sexmaculata	0.426	0.471	0.279
	S. signaria	0.013	0.003	0.014
	S. oweni	0.285	0.280	0.287
Telford	S. sexmaculata	0.064	0.017	0.062
	S. signaria	0.011	0.131	0.010
	S. oweni	0.140	0.326	0.145
Seddon's Corner	S. sexmaculata	0.078	0.082	0.170
	S. signaria	0.120	0.630	0.053
	S. oweni	0.119	0.162	0.158
Pine Falls	S. sexmaculata	0.026	0.013	0.087
	S. signaria	0.011	0.006	0.013
	S. oweni	0.000	0.002	0.000
Riverton	S. sexmaculata	0.159	0.010	0.097
	S. signaria	0.279	0.874	0.426
	S. oweni	0.005	0.112	0.098
Darwin	S. sexmaculata	0.403	0.728	0.027
	S. signaria	0.003	0.072	0.013
	S. oweni	0.171	0.093	0.281

Figure 8. Populations of larch loopers in generation n+1 in relation to survival in generation n, with both expressed as common logarithms.


A
r=0.528
b=0.477
r=-0.120
b=-0.126
r=-0.536
b=-0.603
B
● Semiothisa sexmaculata
○ Semiothisa signaria
× Semiothisa oweni
r=-0.248
b=-0.779
r=-0.095
b=-0.088
r=0.381
b=0.423
C
r=-0.412
b=-0.118
r=0.230
b=0.176
r=0.397
b=0.459
D
r=-0.296
b=-0.231
r=-0.116
b=-0.094
r=-0.016
b=-0.016
E
r=-0.311
b=-0.187
r=0.653
b=0.635
r=0.314
b=0.369
F
r=-0.171
b=-0.107
r=-0.113
b=-0.087
r=-0.529
b=-0.605
2
4
2x
1
2
3
4
5
6
POPULATION IN GENERATION n+1
SURVIVAL IN GENERATION n

ved to be better than that of log h_n (h_n = pupae of the previous generation). The cases occurred in Seddon's Corner, Riverton and Darwin plots, where the predictability increased from 7.8 to 17.0 percent, 27.9 to 42.6 and 17.1 to 28.1 percent for some of the larch looper populations. In all cases, the logarithm of survival (log S) proved to be the best predicting factor.

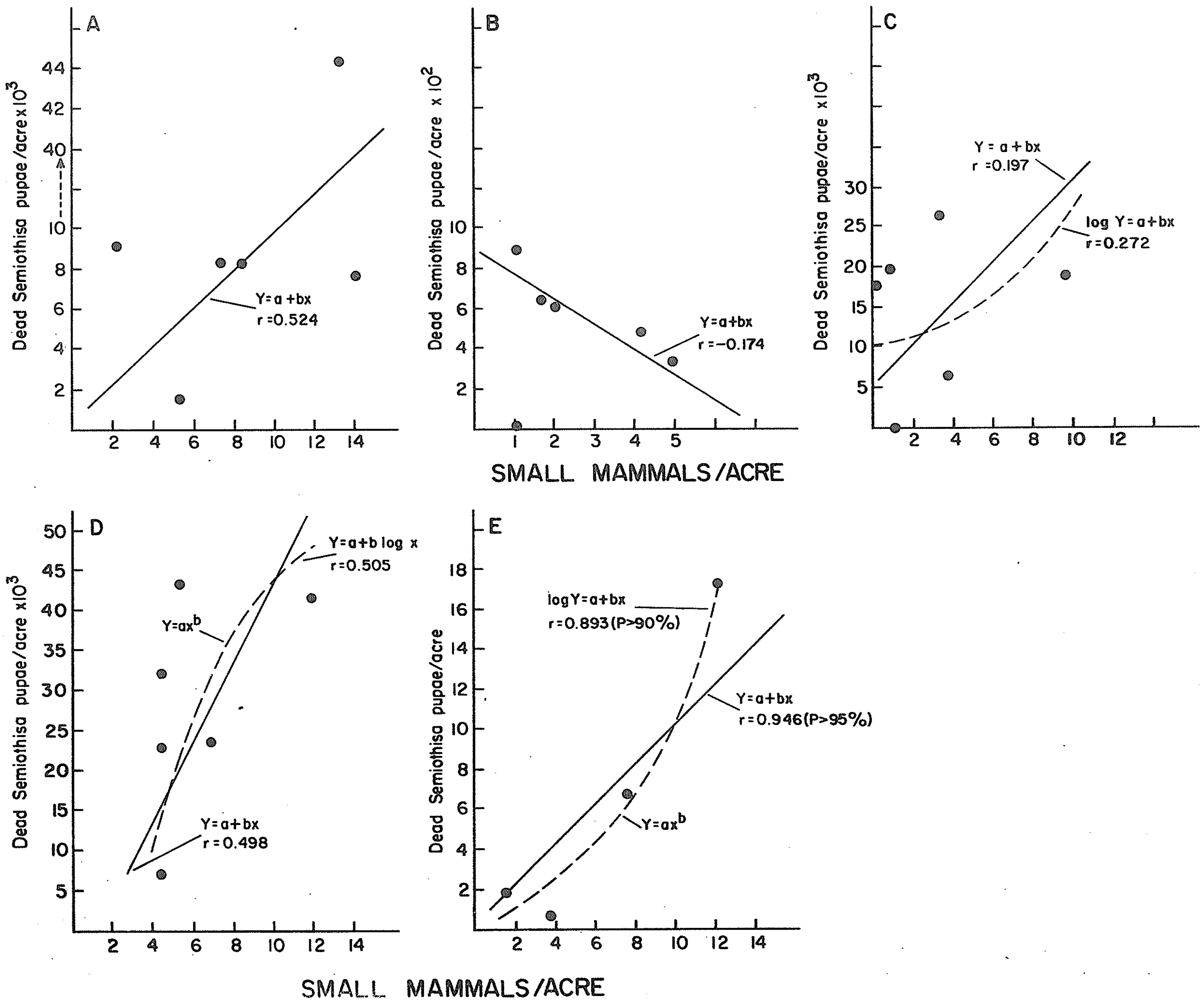
The importance of small mammals to larch looper fluctuations can be shown by the existence of a numerical response between small mammal numbers and the partial mortality of larch looper pupae. Earlier in this section, it was shown that small mammal numbers did not follow larch looper pupae populations although redback voles and masked shrews indicated direct responses to the total mortality of larch looper pupae of some plots. Table 6 illustrates the numerical response of small mammals to the actual numbers of dead larch looper pupae (actual mortality). It appears that small mammal numbers are directly related to numbers of dead larch looper pupae. Telford plot is the only location where small mammals do show a constant inverse response to pupae. Small mammals show statistically significant direct responses only to brown larch loopers of Rennie and Seddon's Corner and to green larch loopers of Darwin. Figure 9 shows the fit of the straight-line and logarithmic curves which explain the response of small mammals. Although not all statisti-

Table 6. Relationships between small mammals per acre and the actual number of dead larch looper pupae per acre as analysed by the correlation method.

Type of analysis	r values				
	Rennie	Telford	Seddon's Corner	Pine Falls	Darwin
Small mammals/acre					
vs					
S.sexmaculata pupae/acre(n+1)	0.420	-0.281	-0.055	0.476	0.902[1]
S.signaria pupae/acre(n+1)	0.746*	-0.415	0.851***	0.550	0.771
S.oweni pupae/acre(n+1)	0.118	-0.131	-0.236	-0.170	0.194
Semiothisa pupae/acre(n+1)	0.524	-0.174	0.197	0.498	0.946*

** Probability > 99 % level.
* Probability > 95 % level.
*** Probability > 98 % level.
1 Probability > 90 % level.

Figure 9. The numerical response of small mammals to the actual numbers of dead larch looper pupae.


A
Dead Semiothisa pupae/acre x10^3
44
42
40
10
8
6
4
2
2 4 6 8 10 12 14
Y=a+bx
r=0.524
B
Dead Semiothisa pupae/acre x 10^2
10
8
6
4
2
1 2 3 4 5
Y=a+bx
r=-0.174
C
Dead Semiothisa pupae/acre x10^3
30
25
20
15
10
5
2 4 6 8 10 12
Y = a + bx
r =0.197
log Y=a+bx
r=0.272
SMALL MAMMALS/ACRE
D
Dead Semiothisa pupae/acre x10^3
50 45 40 35 30 25 20 15 10 5
2 4 6 8 10 12 14
Y=a+b log x
r=0.505
Y=ax^b
Y=a+bx
r=0.498
E
Dead Semiothisa pupae/acre
18 16 14 12 10 8 6 4 2
2 4 6 8 10 12 14
log Y=a+bx
r=0.893(P>90%)
Y=a+bx
r=0.946(P>95%)
Y=ax^b
SMALL MAMMALS/ACRE

cally significant, these relationships indicate a direct response of small mammal numbers to those of dead larch looper pupae.

We have analysed so far the numerical response of small mammals to dead larch looper pupae. It would be interesting to analyse individual mammalian species in regard to the numbers of dead larch looper pupae. Table 7 and 8 give the results of such analyses. The general trend is toward a direct numerical response of small mammal species to dead pupae. It is particularly true for Rennie and Darwin plots where rodent and shrew species showed direct responses for the 2 important groups of larch loopers. Short-tail shrews, arctic shrews and deer mice show a direct response to dead pupae at Telford, while masked shrews respond negatively. Numbers of redback voles and meadow voles change directly with numbers of dead pupae at Seddon's Corner, while the opposite is true for short-tail shrews of Pine Falls. It might be worthy to note also that the green and brown larch looper groups are those which had shown in the previous sections the effects of small mammals on their population fluctuations.

It appears that each mammalian species has its own effects on a given larch looper population. On the basis of Table 8, we showed the patterns of the responses of small mammals to changes in prey density (dead prey density), treating the 2 variables as scatter diagrams. But it could be of some importance to know other patterns of res-

Table 7. Relationships between the numbers of small mammals per acre and the actual number of dead larch looper pupae per acre as analysed by the correlation method.

Type of analysis	r values				
	Rennie	Telford	Seddon's Corner	Pine Falls	Darwin
C.gapperi/acre vs					
S.sexmaculata pupae/acre	0.750*	-0.024	-0.065	0.566	0.362
S.signaria pupae/acre	0.908**	-0.623	0.871**	0.492	0.251
S.oweni pupae/acre	0.392	-0.160	-0.266	-0.028	0.844¹
Semiothisa pupae/acre	0.817***	-0.237	0.193	0.578	0.529
S.cinereus/acre vs					
S.sexmaculata pupae/acre	-0.306	-0.886***	0.177	-0.306	0.954*
S.signaria pupae/acre	0.003	0.152	-0.150	0.587	0.927*
S.oweni pupae/acre	-0.396	-0.216	-0.380	-0.566	-0.473
Semiothisa pupae/acre	-0.230	0.015	0.110	-0.195	0.878
S.arcticus/acre vs					
S.sexmaculata pupae/acre	-0.131	-0.611	0.559	0	0.928*
S.signaria pupae/acre	0.252	0.785¹	0.208	0	0.973***
S.oweni pupae/acre	-0.071	0.471	-0.152	0	-0.488
Semiothisa pupae/acre	-0.023	0.299	0.556	0	0.861¹
B.brevicauda/acre vs					
S.sexmaculata pupae/acre	-0.698	0.819*	-0.653	-0.690	0.660
S.signaria pupae/acre	-0.551	-0.719¹	-0.273	-0.819*	0.500
S.oweni pupae/acre	-0.155	0.707¹	-0.091	-0.050	-0.582
Semiothisa pupae/acre	-0.670	0.491	-0.664	-0.761*	0.535

Table 7. Continued.

	r values				
Type of analysis	Rennie	Telford	Seddon's Corner	Pine Falls	Darwin
P.maniculatus/acre vs					
S.sexmaculata pupae/acre	0.976^{**}	0.923^{***}	0	0.345	0.988^{**}
S.signaria pupae/acre	0.938^{**}	-0.488	0	0.483	0.960^{*}
S.oweni pupae/acre	0.064	0.477	0	-0.372	-0.343
Semiothisa pupae/acre	0.980^{**}	0.637	0	0.350	0.938^{*}
M.pennsylvanicus/acre vs					
S.sexmaculata pupae/acre	0.784^{*}	0.026	-0.424	0.463	-0.523
S.signaria pupae/acre	0.780^{*}	-0.674	-0.259	0.507	-0.742
S.oweni pupae/acre	0.609	-0.105	0.778^{*}	-0.214	0.487
Semiothisa pupae/acre	0.811^{***}	-0.224	-0.448	0.472	-0.473

** Probability ≫ 99 % level.
* Probability ≫ 95 % level.
*** Probability ≫ 98 % level.
1 Probability ≫ 90 % level.

Table 8. The numerical response of small mammals to numbers of dead larch looper pupae.

Semiothisa species	investigation plot				
	Rennie	Telford	Seddon's Corner	Pine Falls	Darwin
sexmaculata	+Cg +Pm +Mp	+Bb -Sc +Pm			+Sc +Sa +Pm
signaria	+Cg +Pm +Mp	+Sa -Bb	+Cg	-Bb	+Sc +Sa +Pm
oweni		+Bb	+Mp		+Cg

Legend:

Cg, Clethrionomys gapperi
Pm, Peromyscus maniculatus
Mp, Microtus pennsylvanicus
Sc, Sorex cinereus
Sa, Sorex arcticus
Bb, Blarina brevicauda

+, positive and direct response
-, inverse response

ponse for the mammalian species which would clarify the cases where small mammals showed no response to dead pupae. Such an analysis was done on shrew species and red-back voles in relation to the most numerous looper species, i.e. the green and brown larch loopers (S.sexmaculata and S.signaria).

Masked shrews had already shown direct responses to green and brown larch looper pupae of Darwin plot following a straight-line relationship (Table 7). A more rigorous mathematical analysis suggests, however, that their numbers are inversely related to green larch loopers and directly related to brown loopers. As indicated by Table 9, numbers of dead larch loopers tend to follow exponential curves rather than linear ones. Green larch loopers are statistically related by logarithmic and linear relationships to masked shrews of Telford and by a linear one in Darwin; brown larch loopers showed a positive logarithmic (log-log) relationship to shrews of Telford, a negative one for Seddon's Corner, and a positive linear curve for Darwin plot.

The numerical response of arctic shrews to larch looper pupae is illustrated in Table 10. The shrews show a negative logarithmic-type of response in Telford and a positive linear relationship to dead green larch looper pupae of Darwin, both being statistically significant. The numerical response of shrews to brown larch loopers is positive in both Telford and Darwin plots and tend

Table 9. The numerical response of masked shrews to the numbers of dead larch looper pupae (r values represent the fitness of a given curve).

a. S.*sexmaculata* pupae (Y)

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	-0.306	-0.266	-0.260	-0.248
Telford	-0.886***	-0.957**	-0.846*	-0.854*
Seddon's Corner	0.177	0.018	-0.360	-0.215
Pine Falls	-0.306	-0.506	-0.112	-0.307
Darwin	0.954*	0.754	0.814	0.514

b. S.*signaria* pupae (Y)

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	0.003	0.027	0.280	0.226
Telford	0.152	0.707	0.950**	0.973**
Seddon's Corner	-0.150	-0.760*	-0.266	-0.301
Pine Falls	0.587	0.540	0.330	0.202
Darwin	0.927*	0.760	0.509	0.348

** Probability ≫ 99 % level.
* Probability ≫ 95 % level.
*** Probability ≫ 98 % level.

Table 10. The numerical response of arctic shrews to the numbers of dead larch looper pupae (r values represent the fitness of a given curve).

a. *S. sexmaculata* pupae (Y)

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	-0.131	0.080	-0.171	-0.039
Telford	-0.611	-0.666	-0.793[2]	-0.754
Seddon's Corner	0.559	0.561	0.256	0.256
Pine Falls	0	0	0	0
Darwin	0.928*	0.606	0.793	0.362

b. *S. signaria* pupae (Y)

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	0.252	0.457	0.372	0.367
Telford	0.785[1]	0.788[3]	0.631	0.737
Seddon's Corner	0.208	0.209	0.375	0.375
Pine Falls	0	0	0	0
Darwin	0.973***	0.735	0.737	0.508

* Probability > 95 % level.
*** Probability > 98 % level.
1 Probability > 90 % level.
2 Probability > 94 % level.
3 Probability > 93 % level.

to follow a linear relationship. There is no response of shrews in Pine Falls because of their repeated absence in this plot ever since 1963. There are indications of a direct response of shrews to the 2 groups of larch loopers of Seddon's Corner plot, although their response was not statistically significant; shrews of the Rennie plot showed no response at all.

Short-tail shrews show statistically significant responses to dead larch looper pupae in almost all the plots. The best curvilinear relationships between shrews and loopers are listed in Table 11. All plots except Darwin indicate an exponential-type of response for short-tail shrews to numbers of dead green larch looper pupae; this response is found to be negatively density-dependent for three plots and positively dependent in Telford plot. The brown larch loopers show a somewhat similar pattern where shrews of Telford and Pine Falls plots show an inverse response to larch loopers. The shape of the curve is once more a logarithmic one, although the straight line fit was also statistically significant. Shrews of Rennie and Seddon's Corner plots tend to indicate an inverse logarithmic-type of response, while shrews of Darwin plot are positively related to brown larch loopers.

Unlike shrews, the numerical response of red-back voles is positively related to green and brown larch

Table 11. The numerical response of short-tail shrews to the numbers of dead larch looper pupae (r values represent the fitness of a given curve).

a. <u>S.sexmaculata</u> pupae (Y).

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	-0.698	-0.736*	-0.821***	-0.803*
Telford	0.819*	0.822*	0.830*	0.834*
Seddon's Corner	-0.653	-0.550	-0.955**	-0.713^{2}
Pine Falls	-0.690	-0.407	-0.846***	-0.533
Darwin	0.660	0.550	0.465	0.348

b. <u>S.signaria</u> pupae (Y).

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	-0.551	-0.523	-0.588	-0.409
Telford	-0.719^{1}	-0.736^{1}	-0.793^{2}	-0.797^{2}
Seddon's Corner	-0.273	0.046	-0.487	-0.098
Pine Falls	-0.819*	-0.842***	-0.991**	-0.690
Darwin	0.500	0.397	-0.010	-0.150

** Probability ≥ 99 % level.
* Probability ≥ 95 % level.
*** Probability ≥ 98 % level.
1 Probability ≥ 90 % level.
2 Probability ≥ 94 % level.

loopers (Table 12). Voles show a linear relationship to dead loopers of Rennie plot, although the logarithmic one seems to fit better for brown larch looper pupae. They show also a statistically significant negative logarithmic-type of response to brown larch loopers of Telford, while a statistically significant and linear one holds true in Seddon's Corner plot.

The overall numerical response of small mammals to numbers of dead larch looper pupae can give a good indication of the mammalian effects on looper populations (Table 13). In Darwin plot, both the masked and arctic shrews show a significant direct response to dead larch looper pupae. In Pine Falls, short-tail shrews are negatively related to looper numbers. In the remaining plots, the patterns of fluctuations change so much from species to species that no possible pattern can be drawn from these relationships. In Telford plot, for example, among the 4 species of small mammals, both positive and negative relationships occur; in Rennie and Seddon's Corner plots, short-tail shrews and redback voles show also opposite responses, so that no clear picture can be drawn.

The last few tables suggest that something other than small mammal predation influences larch looper numbers. This is shown particularly well in Tables 8 and 13 where some of the shrew species express inverse numerical responses to dead larch looper pupae. Masked and short-tail shrews (Table 8) of Telford and Pine Falls plots indicate respecti-

Table 12. The numerical response of redback voles to the numbers of dead larch looper pupae (r values represent the fitness of a given curve).

a. *S.sexmaculata* pupae (Y).

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	0.750*	0.534	0.565	0.323
Telford	-0.024	0.407	0.213	0.608
Seddon's Corner	-0.065	0.317	0.260	0.684
Pine Falls	0.566	0.594	0.512	0.544
Darwin	0.362	0.592	0.630	0.810

b. *S.signaria* pupae (Y).

Investigation plot	r value of fit			
	Y=a+bX	Y=a+b logX	logY=a+bX	logY=a+b logX
Rennie	0.908**	0.772*	0.461	0.354
Telford	-0.623**	-0.904***	-0.110	-0.518
Seddon's Corner	0.871	0.682	0.557	0.702[1]
Pine Falls	0.492	0.442	0.386	0.414
Darwin	0.251	0.485	0.418	0.560

** Probability ≥ 99 % level.
* Probability ≥ 95 % level.
*** Probability ≥ 98 % level.
1 Probability ≥ 93 % level.

Table 13. The pattern of the numerical response of small mammals to the numbers of dead larch looper pupae using the best curvilinear fit (statistically significant).

Investigation plot	Semiothisa species	Small mammal species			
		S. cinereus	S. arcticus	B. brevicauda	C. gapperi
Rennie	sexmaculata			$\log Y=a+bX$ (-)[1]	$Y=a+bX$ (+)
	signaria				$Y=a+bX$ (+)
Telford	sexmaculata	$Y=a+b\log X$ (-)	$\log Y=a+bX$ (-)	$\log Y=a+b\log X$ (+)	
	signaria	$\log Y=a+b\log X$ (+)	$Y=a+b\log X$ (+)	$\log Y=a+b\log X$ (-)	$Y=a+b\log X$ (-)
Seddon's Corner	sexmaculata			$\log Y=a+bX$ (-)	
	signaria	$Y=a+b\log X$ (-)			$Y=a+bX$ (+)
Pine Falls	sexmaculata			$\log Y=a+bX$ (-)	
	signaria			$Y=a+b\log X$ (-)	
Darwin	sexmaculata	$Y=a+bX$ (+)	$Y=a+bX$ (+)		
	signaria	$Y=a+bX$ (+)	$Y=a+bX$ (+)		

1. The sign in parentheses refer to the sign of the best (statistically significant) curvilinear relationship of a given response.

vely inverse response to numbers of dead green and brown larch looper pupae. As Table 8 shows, however, this seems to be the exception rather than a general rule, since only 3 cases of inverse response appeared on a total of 25 cases.

Since shrews and voles showed as a rule positive numerical responses to dead larch looper pupae, it might be of some importance here to discuss the existence of functional responses. This response is usually thought to be the number of prey eaten by a predator which changes proportionately with the density of prey (availability of prey) until the curve reaches a certain plateau.

A functional response of small mammals was calculated following an index of complexity as shown by Table 14. The complexity increases from left to right by the addition of new species of larch loopers, thus changing the ratio of the number of prey eaten per predator and per density of prey; the complexity increases also from top to bottom, where new species of mammals are entered in the system.

Masked shrews of Rennie plot (Table 14a) show a statistically significant functional response to larch looper pupae; the response follows a straight line which could represent the first part of Holling's exponential curve for small mammals (Holling 1965). The table shows also that the fitness (shown by the r value) decreases as the complexity increases, that is from left to right. The relationship ex-

Table 14. The functional response of small mammals to densities of larch looper pupae.

a. Rennie

No. pupae eaten per predator	No. pupae per acre		
	S.sexmaculata	S.sexmaculata S.signaria	S.sexmaculata S.signaria S.oweni
C.gapperi	0.406	0.320	0.308
S.cinereus	0.944**	0.940**	0.939**
C.gapperi S.cinereus	0.531	0.486	0.481
C.gapperi S.cinereus S.arcticus	0.524	0.478	0.472
C.gapperi S.cinereus S.arcticus B.brevicauda	0.528	0.483	0.477
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus	0.522	0.475	0.468
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus M.pennsylvanicus	0.500	0.446	0.438

** Probability ≥ 99 % level.

b. Telford

No. pupae eaten per predator	No. pupae per acre		
	S.sexmaculata	S.sexmaculata S.signaria	S.sexmaculata S.signaria S.oweni
C.gapperi	0.915	0.901	0.875
S.cinereus	0.913*	0.221	0.239
C.gapperi S.cinereus	0.910*	0.429	0.440
C.gapperi S.cinereus S.arcticus	0.911*	0.384	0.395
C.gapperi S.cinereus S.arcticus B.brevicauda	0.917*	0.441	0.455
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus	0.930*	0.553	0.564
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus M.pennsylvanicus	0.910*	0.446	0.804

* Probability ≫ 95 % level.

c. Seddon's Corner

No. pupae eaten per predator	No. pupae per acre		
	S.sexmaculata	S.sexmaculata S.signaria	S.sexmaculata S.signaria S.oweni
C.gapperi	0.862*	0.830*	0.652
S.cinereus	0.432	0.317	0.313
C.gapperi S.cinereus	0.363	0.604	0.607
C.gapperi S.cinereus S.arcticus	0.363	0.603	0.605
C.gapperi S.cinereus S.arcticus B.brevicauda	0.363	0.602	0.608
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus	0.363	0.602	0.608
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus M.pennsylvanicus	0.329	0.603	0.609

* Probability $>$ 95 % level.

d. Pine Falls

No. pupae eaten per predator	No. pupae per acre		
	S.sexmaculata	S.sexmaculata S.signaria	S.sexmaculata S.signaria S.oweni
C.gapperi	0.649	0.630	0.646
S.cinereus	0.714	0.580	0.656
C.gapperi S.cinereus	0.773[3]	0.729[1]	0.761[2]
C.gapperi **S.cinereus** S.arcticus	0.773[3]	0.729[1]	0.761[2]
C.gapperi S.cinereus S.arcticus B.brevicauda	0.800[5]	0.756[2]	0.784[4]
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus	0.794[4]	0.755[2]	0.785[4]
C.gapperi S.cinereus S.arcticus B.brevicauda P.maniculatus M.pennsylvanicus	0.794[4]	0.755[2]	0.785[4]

1 Probability > 90 % level.
2 Probability > 91 % level.
3 Probability > 92 % level.
4 Probability > 93 % level.
5 Probability > 94 % level.

isting in Telford plot is somewhat similar (Table 14b), where shrews indicate also a direct response of a straight line type. Only green larch looper populations are so related to small mammal numbers. In Seddon's Corner plot (Table 14c), only redback vole populations showed a significant functional response to green and brown larch looper pupae; the relationship was once more of a straight line type. Pine Falls plot (Table 14d) shows that the combined numbers of masked shrews and redback voles are needed to register a significant response to larch looper pupae, whereas the single population of either species does not show any response.

b. Ecology and life history of larch looper populations from field data

According to the number of larvae collected in larval sampling traps (oil drop funnels), the bulk of falling larvae of _S.sexmaculata_, the green larch looper, occurs in August and September (Table 15). The table shows a spread of recoveries of these larvae beginning in June and extending until October, and possibly November. This tends to indicate a year-round presence of their pupae in the Manitoba bogs.

The second most numerous species of the larch looper group, _S.signaria_, the brown larch looper, shows a somewhat similar pattern; the collection of larvae occurred

Table 15. The occurrence of *S. sexmaculata* (green larch looper) larvae (the larvae were collected with funnel traps placed beneath tamarack trees).

Year Month	1962	1963	1964	1965	1966	1967	1968	1969	Total
June	0	0	0	1	0	0	1	0	2
July	28	0	77	16	41	22	13	4	201
August	212	169	456	329	315	219	46	249	1995
September	103	92	90	117	42	445	30	40	959
October	0	0	0	0	0	24	13	0	37
Total	343	261	623	463	398	710	103	293	3194

mainly in July and August, with the bulk of recoveries in August (Table 16). All plots supported the idea of an earlier appearance in the bogs. These pupae then would be present in the plots in early August and September, following the emergence of adults.

The third and least numerous species of the group, S. oweni, follows very closely the pattern showed previously by the green larch loopers (Table 17). Three of the plots, however, showed a late occurrence of larvae: Rennie, Telford and Darwin plots. The remaining plots registered also late August and September occurrences while Seddon's Corner plot recorded mainly July and August recoveries. This indicates that this species occurs a little later in the season, compared to the former two.

A fourth species of larch looper, S. bicolorata Fabr. , appeared only once in the plots. In 1963, a total of 19 larvae were collected in Rennie (12) and Seddon's Corner (6) plots in early and late August, and in Riverton (1) plot in late July.

c. Caloric values of larch looper life stages

Special emphasis has been placed upon the energy values of Semiothisa spp., as it is one of the most numerous group of insects in the bogs and is likely to play an important role as a buffer for small vertebrate predators (Bergeron and Buckner 1970).

Table 16. The occurrence of *S.signaria dispuncta* (brown larch looper) larvae (the larvae were collected with funnel traps placed beneath tamarack trees).

Year Month	1962	1963	1964	1965	1966	1967	1968	1969	Total
June	0	0	0	0	2	3	0	0	5
July	0	15	25	17	57	20	3	0	137
August	11	29	144	78	54	8	2	65	391
September	0	0	0	28	0	12	0	5	45
October	0	0	0	0	0	0	0	0	0
Total	11	44	169	123	113	43	5	70	578

Table 17. The occurrence of *S.oweni* larvae (the larvae were collected with funnel traps placed beneath tamarack trees).

Year Month	1962	1963	1964	1965	1966	1967	1968	1969	Total
June	0	0	0	0	0	0	0	0	0
July	0	0	0	4	2	3	0	0	9
August	0	0	1	7	8	26	1	3	46
September	0	0	0	0	0	38	3	0	41
October	0	0	0	0	0	1	3	0	4
Total	0	0	1	11	10	68	7	3	100

The caloric values of the larch looper life stages are recorded in Table 18. Larch looper pupae offer a surprisingly high caloric value, if compared to larch sawfly eonymphs. Buckner (1964) determined the caloric value of one sawfly eonymph to be 0.074 kcal; the caloric value of one gram of eonymph (or 15 individuals) amounted to 1.2 kcal. In comparison, the looper pupae yielded a caloric value of 0.056 kcal per pupae and 5.40 kcal per gram of pupal material (or 27 individuals). It is unlikely that any stage below the third instar would provide a major food source for small forest vertebrates, but the energy values of the later stages compare favorably with those of the other groups. The highest value per individual is achieved in the pupal stage and the highest per gram of dry weight in the third instar larvae.

The metabolic requirements of redback voles and several shrew species in terms of larch looper pupae are recorded in Table 19. Such parameters are usually determined by dividing the DEB value of small mammals by the caloric value of a given food item. This energy budget of redback voles was determined using their oxygen consumption, carbon dioxide production and urinary-nitrogen content as shown in the next section. The potential daily intake by small mammals is often referred to as the 'optimum potential predation'. These results represent of course approxi-

Table 18. Caloric values of larch looper life stages of the *Semiothisa* complex, prob. *S.sexmaculata* Pack., Lepidoptera:Geometridae:Ennominae (after Bergeron and Buckner 1970).

Stage	Number of specimens	Individual weight (mg)		water	Caloric value of item	
		alive	dry		kcal/ind.	kcal/g
Adult	37	5.09	4.37	14	0.023	5.26
Larvae 1	0	----	----	--	-----	----
2	3	----	0.40	--	0.0025	6.37
3	11	----	0.75	--	0.0139	8.63
4	61	----	1.81	--	0.0107	2.55
5	94	----	5.14	--	0.0326	6.58
Whole pupae	12	38.50	11.50	29	0.069	5.98
Pupae(-shell)	--	----	----	--	0.0565	5.40

Table 19. The number of larch looper pupae (*Semiothisa* sp.) required to satisfy the metabolism of small mammals.

Species	Daily metabolic requirements (kcal)	No. of pupae to satisfy metabolism		
		pupae/day	cocoon/day	pupae/90-day period
S.cinereus	6.09[1]	108	87	9720
S.arcticus	6.94[1]	123	99	11070
M.hoyi	6.67[1]	118	95	10620
B.brevicauda	9.69[1]	172	138	15480
C.gapperi	9.91 (22.7 C)[2]	175	142	15750
	12.53 (17.1 C)[2]	222	179	19980
	13.25 (11.7 C)[2]	235	189	20250

[1] After Buckner 1964.

[2] See section on metabolism.

mations of what is really happening in the Manitoba bogs. The table shows also the potential intake of small mammals for a fixed 90-day predation period that could very well occur in the Manitoba bogs (the newly available pupae material is present in the bogs from August to November). By comparing these results to the population estimations of larch looper pupae (Tables 9, 10 and 12 of the Appendices), one could attribute such low numbers to the intensive predation of small mammals on their pupae.

An indication of the total calories available from <u>Semiothisa</u> spp. was derived from data collected in 1968 by the author, and although that year represented a low point in the population of this insect, nevertheless substantial energy values were afforded by it (Table 20). This component, even if utilized exclusively, could sustain populations of many of the insectivorous vertebrates for periods up to about one month.

B. Studies of small mammal populations

a. Relationships within small mammal populations

The role of mammalian predation upon larch looper pupae was determined hypothetically in the first section using population estimations of both groups. It was shown, particularly in the last part of the latter section that small mammal predators were related to larch looper

Table 20. Biomass of the 1968 *Semiothisa* sp. populations (after Bergeron and Buckner 1970).

Plot	Population/acre			Caloric values (Cal)		
	adult	larvae V	pupae	adult	larvae V	pupae
Rennie	0	5383	3968	0	175.5	252.2
Telford	529	9975	737	12.2	325.2	41.6
Seddon's Corner	0	4277	1623	0	139.4	91.7
Pine Falls	27420	3169	11488	630.7	103.3	649.1
Riverton	0	21902	5578	0	714.0	315.2
Darwin	909	6501	1939	20.9	211.9	109.5
Hodgson	2723	1260	221	62.6	41.1	12.5

numbers by exponential curves. It was also found that pupal mortality from small mammals allowed to predict, to a certain degree, future larch looper populations and that certain species of small mammals showed numerical and functional responses. The present study will show the patterns of small mammal population fluctuations and give simple relationships existing among them.

The small mammal population fluctuations involving the 5 most numerous species of the Maniotba bogs are shown in Figure 4 and Table 13 of the Appendices. Generally speaking, we see that only one vole and one shrew species form the bulk of small mammals in the bogs. We note also that redback vole population peaks do not coincide with those of masked shrews; high vole populations are usually registered following low levels of masked shrews and vice-versa. This is particularly true for the Riverton plot where both populations seem to be inversely related. The population estimations of these 2 most numerous species of small mammals were compared and statistically analysed against populations of other small mammal species. The results shown in Table 21 suggest certain relationships to exist among them in all plots. In Rennie, masked and arctic shrews on one hand, and meadow and redback voles on the other, appear to be directly related at the 99 percent level. It is interesting to note that the former relationship holds true in all but Pine Falls plot,

Table 21. Relationships within small mammal populations as revealed by the correlation method.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
S.cinereus/acre (n) vs						
B.brevicauda/acre (n)	-0.018	-0.379	0.489	0.091	0.804*	0.407
S.arcticus/acre (n)	0.805**	0.630[1]	0.741*	0	0.940**	0.968**
M.pennsylvanicus/acre(n)	-0.405	-0.057	-0.408	-0.323	0.810*	-0.355
P.maniculatus/acre (n)	-0.289	-0.622[1]	0	-0.304	0	0.191
C.gapperi/acre (n) vs						
S.cinereus/acre (n)	0.012	-0.145	-0.343	-0.340	-0.454	-0.034
B.brevicauda/acre (n)	-0.464	-0.150	-0.322	-0.189	-0.079	0.053
S.arcticus/acre (n)	0.406	-0.306	-0.025	0	-0.530	0.003
M.pennsylvanicus/acre(n)	0.887**	0.955**	0.174	0.903**	-0.081	0.269
P.maniculatus/acre (n)	0.424	-0.176	0	0.491	0	0.625

** Probability > 99 % level.

* Probability > 95 % level.

1 90 % ≤ Probability ≤ 95 %.

while the latter one holds true in only 3 plots. Furthermore, masked shrew numbers are related statistically to those of short-tail shrews and meadow voles of Riverton, and to deer mice of Telford.

However, recent field data on hand do not fit in the mentioned population patterns. Table 14 of the Appendices shows an index of abundance of small mammals caught in the 1970 and 1971 period. Although masked shrews and redback voles formed the biggest part of the trapped animals in 23 sampling locations, there are no indications of population relationships in the form as mentioned above.

b. Food preference tests

The food preference trials were given special emphasis for masked shrews and redback voles since these species represent up to 77 percent of the small mammal numbers in the Manitobs bogs (Table 14 of the Appendices). Complementary data were taken from secondary species of shrews, voles and mice, although the number tested was not high enough to lead to any valid conclusions.

1. Shrews

Food preference tests involving healthy larch looper pupae and healthy larch sawfly cocoons were conducted on 37 adult shrews of 4 species: 25 S.cinereus, 2 S. arcticus, 5 M.hoyi and 5 B.brevicauda. On the whole, 15 animals showed a preference for larch looper pupae compared to 21 for the sawfly cocoons (Table 22). The shrews seemed to react towards the food items as individuals rather than as a group. This is stressed by the χ^2 analysis of the number of visits made to the two food items; the calculated 'P' values were 438.8, 167.4 and 63.7 for the masked, pigmy and arctic shrews' responses to the given choice.

The tendency to prefer one of the given food item becomes negligible when the total number of visits are considered. As a group, masked shrews registered 1596 visits to the looper pupae compared to 1587 to the sawfly cocoons (Table 15 of the Appendices); the non-preference to one of the food items is shown by the t value of 0.04. The non-preference is also shown by arctic shrews, as they averaged 33 visits to the pupae and 89 to the cocoons (t = -7.00 with 1 d.f.); pigmy shrews, 223 to the pupae and 300 to the cocoons (t = -0.57 with 4 d.f.); and short-tail shrews, 302 to the pupae and 337 to the cocoons (t = -0.39 with 4 d.f., Table 16 of the Appendices).

The daily number of visits of individual shrew species is tabulated in Table 23. Masked shrews show a similar number of visits to both food items, as they registered 34 visits per day to the pupae compared to 33 to the sawfly cocoons. The reverse is true for the other 3 species

Table 22. Food preferences of 4 shrew species in their choice between healthy larch looper pupae and healthy larch sawfly cocoons.

Animal characteristics			Food preference	
Species	Sex	No. tested	larch looper pupae	larch sawfly cocoon
S.cinereus	male	13	5	8
	female	10[1]	4	5
	---	2	1	1
S.arcticus	male	1	0	1
	female	1	0	1
M.hoyi	male	4	2	2
	female	1	0	1
B.brevicauda	male	2	2	0
	female	2	0	2
	---	1	1	0
Total		37	15	21

[1] One masked shrew showed no preference.

Table 23. The daily number of visits of 4 shrew species to the tested food items.

Species	No. tested	Daily number of visits per shrew					
		larch looper pupae			larch sawfly cocoon		
		male	female	whole	male	female	whole
S.cinereus	25	38	32	34	40	29	33
S.arcticus	2	9	3	6	25	9	17
M.hoyi	5	39	10	34	33	51	37
B.brevicauda	5	12	10	13	15	20	15

of shrews as the sawfly cocoons were visited more often.

There seems to be no definite pattern of preference between the sexes; male masked shrews, for example, averaged 38 visits per day to the pupae and 40 per day to the cocoons ($t = -0.25$ with 12 d.f.). Females showed a higher number of daily visits to the pupae as they averaged 35 visits to that food item compared to 32 to the cocoons ($t = 0.45$ with 8 d.f.). Although not statistically significant, the daily visits suggest that sawfly cocoons are preferred by male masked shrews while females tend to prefer larch looper pupae. The table shows also that the former food item seems to be preferred by males and females of the 3 other shrew species, except male pigmy shrews.

2. Voles

Food preference trials were conducted on 35 C. gapperi: 6 subadult males, 12 subadult females, 12 adult males, and 5 adult females. The weight of subadult males ranged from 15.2 to 19.2 g, and the females, from 14.4 to 19.8 g. Both groups had the same average weight of 17.7 g. The adult females averaged 23.6 g (20.2-25.0) and the males, 22.4 (20.3-30.0).

When given the choice between a healthy larch looper pupae and a healthy larch sawfly cocoon, C.gapperi reacted as individuals rather than as a group. They visited the larch looper pupae 1453 times compared to 1912 visits to the sawfly cocoon (Table 17 of the Appendices). Although not significant (t of choice = $-1.34 \leqslant$ t of tables), the animals made an average of 19.2 daily visits more to the sawfly cocoon for the whole period of investigation. Eleven voles preferred the pupae, whereas 12 chose the sawfly cocoon. The tendency to prefer sawfly cocoons is stronger when analysed by specific age and sex groups (Table 24). Among the voles that preferred the larch looper pupae, seven females averaged 79.1 daily visits compared to 19.0 by four males. Among those that selected the sawfly cocoon, five females registered 130.2 daily visits and the eight males, 118.7. It is interesting to note that the pattern of selection came from adult animals, whereas subadults did not show a preference for either choice. We see that although the preference for sawflies over larch looper pupae is very weak, those animals that preferred sawfly cocoons registered the highest number of visits and seemed thus to be more active. As a whole, the 96 day-experiment pattern did not show a marked variance over what was demonstrated before; the preference for sawfly cocoons was registered in 41 days compared to 40 days of selection for the pupae. The remaining 15 days showed no preference at all.

The second test involved a choice between a healthy larch looper pupae and a parasitized sawfly cocoon.

Table 24. The selection by redback voles between healthy larch looper pupae and healthy larch sawfly cocoons (analysed by age and sex).

Age	Sex	No. tested	Preference	
			larch looper pupae	larch sawfly cocoon
Subadult	male	4	2 (26.0)[1]	2 (208.5)
Subadult	female	8	4 (68.2)	4 (138.0)
Adult	male	8	2 (12.0)	6 (88.8)
Adult	female	4	3 (93.3)	1 (99.0)

[1] The numbers in parentheses represent the average number of visits per vole.

Although not statistically significant (t of choice = $0.94 \leqslant t$ of tables), the single pupae was preferred, probably indicating an ability by redback voles to differentiate between parasitized and healthy insects. This ability has been demonstrated for other situations (Holling 1955). Sixteen animals showed a marked preference for the looper pupae, and seven voles chose the parasitized cocoon (Table 18 of the Appendices). By comparing the two latter tables, one can see three ways that the voles reversed their selection. The first one is shown by the majority of voles that simply changed their preference in favor of the larch looper pupae. The second one came from those animals that preferred the pupae in both tests. The gain was further increased by the voles that showed no preference in the first experiment but shifted their choice to the pupae in the second one. The change occurred mainly in the adult group although some subadults indicated a similar pattern.

The number of visits registered to the larch looper pupae amounted to 1403 compared to 1189 for the cocoon. This shows that the animals decreased their daily number of visits only in regard to the cocoon selection. The voles averaged 58.0 daily visits to the pupae compared to 49.5 to the parasitized cocoon. As a whole, males made more visits (77.1 per vole) than females (69.3 per vole, Table 25). Among the animals that showed a preferen-

Table 25. The selection by redback voles between healthy larch looper pupae and parasitized sawfly cocoons (analysed by age and sex).

			Preference	
Age	Sex	No. tested	larch looper pupae	larch sawfly cocoon
Subadult	male	4	3 (59.7)[1]	1 (66.0)
Subadult	female	8	5 (26.6)	3 (49.0)
Adult	male	8[2]	6 (65.8)	1 (84.0)
Adult	female	4	2 (135.0)	2 (62.5)

[1] The numbers in parentheses represent the average number of visits per vole.

[2] One redback vole showed no preference.

ce for the pupae, seven females registered 80.0 daily visits on the average, compared to 76.6 for nine males. A reverse pattern occurred among those that selected the sawfly cocoon, where two males averaged 75.0 daily visits compared to 54.4 for five females. As shown by the latter table, only adult males did not show the preference for the larch looper pupae. In a total of 91 day-experiment, voles indicated a selection towards pupae for 44 days compared to 35 for the alternate choice; in the remaining days, the voles did not show a preference for either choice.

It was shown in the first part of the study that larch loopers were outnumbered by sawfly cocoons. Examination of Tables 9, 10, 11 and 12 of the Appendices indicates that sawfly cocoons occur between 10 and 1000 times as frequently as do larch looper pupae. On this basis, an experiment was designed to see the voles' preferences between larch looper pupae and a concentration of sawfly cocoons. For the convenience of the experiment, a concentration of 10 sawfly cocoons was tested against a single healthy larch looper pupae.

Among the 23 redback voles, 12 preferred the concentration of cocoons compared to 8 that selected the looper pupae; some voles did not show any preference for either choice. The tendency of choosing the sawfly cocoons is accentuated when comparing these individual selections

(Table 19 of the Appendices) to those registered in the previous experiments (Table 17 and 18 of the Appendices). Among the voles that selected the pupae, only 2 animals showed a clear tendency in choosing the pupae, the remaining 6 ones offering erratic responses such as selecting the pupae, in this case, after having shown a preference for the parasitized cocoon of the previous experiment. Among the voles that chose the concentration of cocoons, five animals came from the group which had shown already a preference for the looper pupae, while 5 others showed a clear gradient of responses, selecting in a row the cocoon of the first test, the pupae of the second experiment, and the concentration of cocoons of the third trial. One vole constantly selected sawfly cocoons whatever the choice offered, and another one showed an erratic response similar to the one cited above.

The number of visits to the treadles averaged 689 for the pupae compared to 954 for the cocoons (t of choice = $-1.38 <$ t of tables). Among the voles that selected the former food item, three males registered 31.2 daily visits compared to 24.7 for 5 females (Table 26). Seven males recorded 43.0 daily visits to the concentration of cocoons compared to 83.0 for 5 females. It is interesting to note that subadults showed the highest number of visits for the cocoon-prone animals while adults did the same for the pupae selection. Over an 88 day experimental period, 41 days indicated a trend for the cocoons selec-

Table 26. The selection by redback voles between healthy larch looper pupae and a concentration of healthy larch sawfly cocoons (analysed by age and sex).

Age	Sex	No. tested	Preference	
			larch looper pupae	larch sawfly cocoons
Subadult	male	3[1]	0	2 (60.5)[2]
Subadult	female	8	3 (7.8)	5 (83.0)
Adult	male	9	4 (59.0)	5 (36.0)
Adult	female	3	2 (66.5)	1 (16.0)

[1] One redback vole showed no preference.
[2] The numbers in parentheses represent the average number of visits per vole.

tion compared to 31 for the alternate choice, the remaining 16 days showing no selection for either choice.

Concentrations of loopers were also tested against a single sawfly cocoon to simulate those instances where loopers may be more abundant than sawflies. Eleven voles selected the concentration of looper pupae against 10 for the alternate choice (Table 20 of the Appendices). The overall number of visits made to the concentration of pupae totalled 1023 (46.5 per vole) compared to 815 (37.0 per vole) for the single cocoon (t of choice = 0.65 < t of tables). Among the animals that preferred the first item, five males recorded 43.6 daily visits compared to 95.0 for 6 females. Among those that selected the sawfly cocoon, 5 males registered 76.0 daily visits as opposed to 38.6 for a same number of females (Table 27). The concentration of larch looper pupae reversed the previous pattern of selection as shown in the first and third experiments, where the voles preferred slightly sawfly cocoons over the larch looper pupae.

The complementary tests of 10 meadow voles (*M. pennsylvanicus*) and 2 deer mice (*P. maniculatus*) showed the same preference patterns as shrews and voles did. As a whole, half of them preferred the larch looper pupae and the other half, the sawfly cocoon. Meadow voles made 452 visits to the pupae compared to 549 to the cocoon; the deer mice totalled 268 visits to the pupae and 160 to the cocoon (Table 21 of the Appendices). The daily visits of meadow voles to the larch looper pupae averaged 12 per day

Table 27. The selection by redback voles between a concentration of larch looper pupae and one healthy sawfly cocoon (analysed by age and sex).

Age	Sex	No. tested	Preference	
			larch looper pupae	larch sawfly cocoon
Subadult	male	2	2 (82.0)[1]	0
Subadult	female	8	6 (92.0)	2 (5.5)
Adult	male	9[2]	3 (18.0)	5 (76.0)
Adult	female	3	0	3 (60.7)

[1] The numbers in parentheses represent the average number of visits per vole.
[2] One redback vole showed no preference.

compared to 13 to the larch sawfly cocoon; the deer mice registered 38 visits per day to the pupae and 19 per day to the cocoon.

c. Metabolism and metabolic requirements of shrews and voles

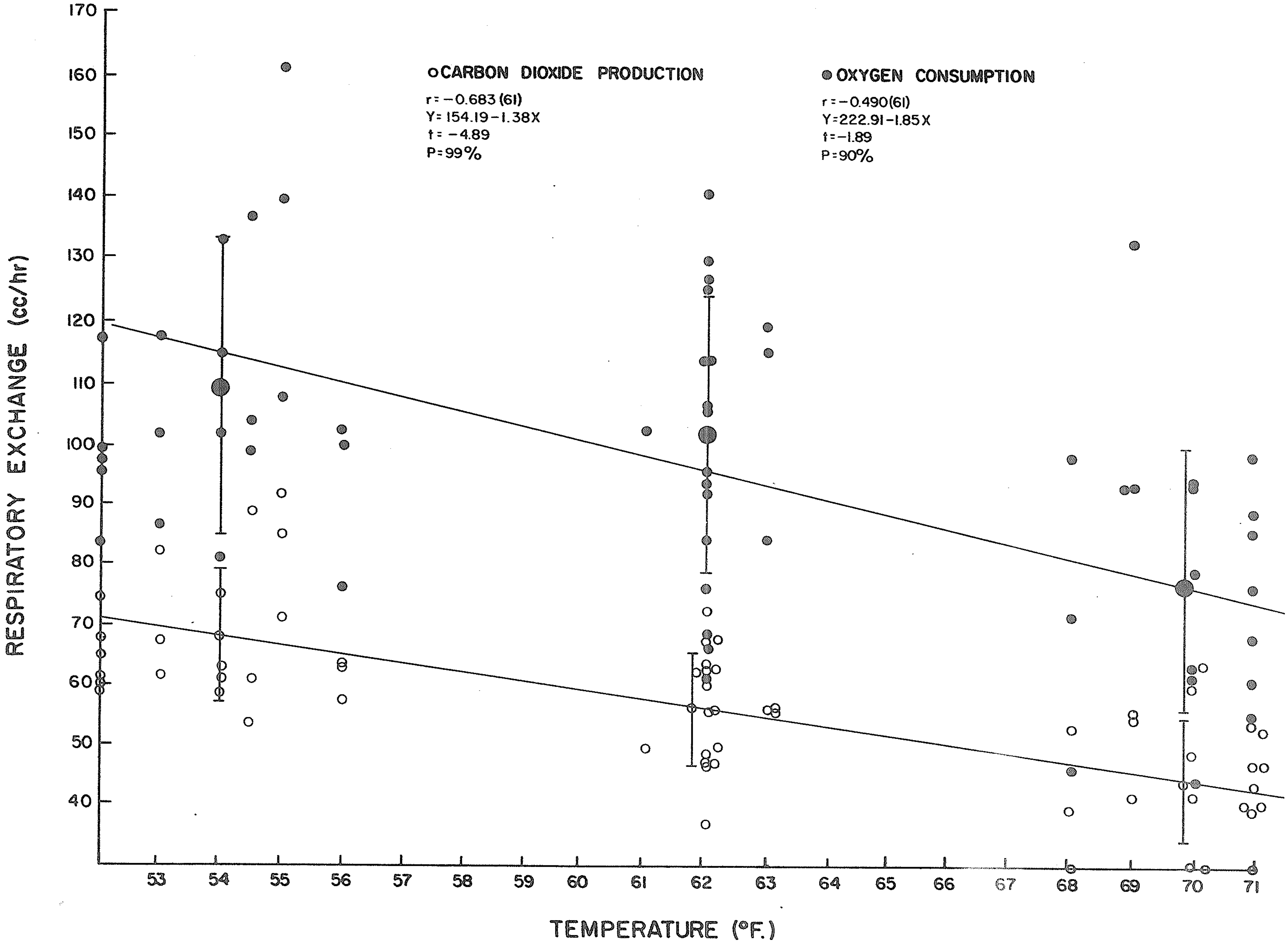
The mean values of daily oxygen consumption and carbon dioxide production of redback voles are listed in Table 28. The table shows that oxygen consumption and carbon dioxide production increased as temperature decreased. The oxygen consumption increased however, at a greater rate than did carbon dioxide production (Figure 10), so that the RQ values were lower than expected. The redback voles consumed daily 4.59 cc of oxygen per g-hr at 69-72°F, 5.92 cc at 62-64°F and 6.33 cc at 53-57°F. The carbon dioxide production averaged 2.90, 3.60 and 4.20 cc per g-hr for the same gradient of temperatures. The latter figures are surprisingly low when compared to those of Pearson (1962) and Morrison (1948). Assuming RQ values of 0.70 and oxygen intakes such as shown above, the CO_2 production should average 3.21, 4.14 and 4.43 cc per g-hr at similar temperatures.

When oxygen consumption and carbon dioxide production were plotted against their respective temperatures, a linear relationship held true at the 90 percent level for the oxygen and 99 percent for the CO_2 production (Fi-

Table 28. Mean values of oxygen consumption and carbon dioxide production of 20 redback voles tested under 3 different temperatures.

Temperature (°F)	Mean weight of animals (g)	O^2 consumption		CO^2 production	
		cc per hr	cc per g-hr	cc per hr	cc per g-hr
69-72	19.7	88.6±21.8	4.59±1.02	55.6±10.2	2.88±0.51
62-64	19.0	111.9±22.7	5.92±0.95	67.1±8.8	3.61±0.64
53-57	19.1	119.4±24.2	6.33±1.26	78.8±10.9	4.17±0.65

Figure 10. Oxygen consumption, carbon dioxide production and temperature relationships of 20 redback voles.


○CARBON DIOXIDE PRODUCTION
r = −0.683 (61)
Y = 154.19 − 1.38X
t = −4.89
P = 99%
● OXYGEN CONSUMPTION
r = −0.490 (61)
Y = 222.91 − 1.85X
t = −1.89
P = 90%
RESPIRATORY EXCHANGE (cc/hr)
170
160
150
140
130
120
110
100
90
80
70
60
50
40
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
TEMPERATURE (°F.)

gure 10); as stipulated earlier, oxygen consumption tended to increase at a higher rate than CO_2 production did. Table 29 shows the relationship existing between the respiratory quotients of voles and their corresponding O_2 and CO_2 values. The oxygen consumption appeared to be related directly to the RQ values while CO_2 production did not show such relationship.

When analysed by age and sex groups, the oxygen consumption and carbon dioxide production gave interesting trends. Generally speaking, the average consumption of oxygen was higher in males than in females (Table 22 of the Appendices). This contradicts the general tendency to give higher O_2 consumption to females; such results have already been compiled for Peromyscus (Cook and Hannon 1954), tree-shrews (Nelson and Asling 1962), and common voles (Trojan and Wojciechowska 1967). On the contrary, my results support the belief that males are particularly sensitive to mild stress when compared to females (Chitty 1960, Schell 1967). The oxygen consumption of males was found to be 1.06, 1.08 and 1.08 times those of females for the decreasing order of temperatures. Subadult males consumed more oxygen than did females, although the trend was less obvious among adults, where females consumed more at 62-64°F and much less at the two extremes. The carbon dioxide production was a little higher in males at both maximum and minimum temperatures. The production of males amounted to 1.02, 0.96 and 1.04

Table 29. Relationships between oxygen consumption, carbon dioxide production and the respiratory quotients (RQ) of 20 redback voles.

Temperature	O^2 and RQ		CO^2 and RQ	
(°F)	r	Y	r	Y
69-72	-0.632**	169.20 - 125.32 X	0.028	---
62-64	-0.788**	193.32 - 131.08 X	0.223	---
53-57	-0.663**	257.86 - 207.28 X	-0.186	---

** Probability > 99 % level.

times those of females for the decreasing order of temperatures.

The carbon dioxide production of redback voles was found to be statistically related to the oxygen consumption at the two extreme temperatures ($P \geqslant 99$ percent), while at the middle temperature range tested these two values were related only at the 93 percent level (Table 23 of the Appendices). The relationship held true at all temperatures only when voles with RQ of 0.73 and over were analysed ($P \geqslant 99$ percent). The relationship appeared to be weaker when oxygen and carbon dioxide values were converted to a volume per g-hr basis. This suggests that the weight of animals could have had an influence on either the O_2 consumption or the CO_2 values or on both of them. This contradicts the studies by Pearson (1962) when he mentioned that one need not correct the CO_2 output for weight at various temperatures.

The daily urinary-nitrogen measurements were performed on 5 voles using a gradient of temperatures similar to that which was used for their metabolism studies (Table 24 of the Appendices). The daily overall production averaged 46.9 mg for animals weighing 20.9 g. The fluctuations of the nitrogen measurements at different temperatures suggested no correlation between the latter values. However, a decrease in nitrogen excretion seemed to have occurred as temperature increased; the average nitrogen excretion at 54, 66 and 72°F indicated a slow decrease from 59.4 to 44.1 mg, to finally reach 43.7 at the highest temperature.

Based on oxygen consumption, carbon dioxide production and urinary-nitrogen excretion, the metabolic requirements of redback voles are listed in Table 30. In order to sustain their needs at a fairly low temperature, the voles need to increase their energy intake by 34 percent. At a temperature of 53-57°F, which is thought to be about the yearly average temperature of the Manitoba bogs (Buckner 1964), the voles had to burn up to 12 percent of their daily energy budget (DEB) to sustain their protein metabolism. The DEB of redback voles fell within the limits set by several workers (Kaczmarski 1966, Trojan and Wojcieschowska 1967). However, the increase of their daily budget from 69-72°F to 53-57°F contradicted the results of Gorecki (1968).

The requirements were also calculated using the calorific conversion of oxygen and maximum values of RQ. Although such estimations are of maximum values, they fall very close to those produced earlier (Table 25 of the Appendices), that is within 2 percent of the former values.

According to Brody (1945), the relationship existing between metabolism and body weight in mammals may be expressed by the equation

$M = a\ W^b$, where

M = BMR
a = specific metabolism = 70.5

Table 30. The metabolic requirements of redback voles.

Type of analysis	Temperature (°F)		
	53-57	62-64	69-72
Mean daily urinary-nitrogen excretion (mg/vole)	59.35	44.14	43.70
Daily energy for protein catabolism (kcal)	1.57	1.17	1.16
Daily metabolic requirements (kcal)	13.25 13.50[1]	12.53 12.77[1]	9.91 10.15[1]
SDA for proteins; 40% of calories derived from protein catabolism (kcal)	0.629	0.468	0.463

[1] Derived from data of Table 18 of the Appendices.

W = weight of animals expressed in kg
and b = a power transforming weight into metabolic active weight = 0.73.

By substituing these values in the equation, one can calculate the expected BMR. For redback voles weighing 19.1g, the basal requirements should amount to 3.97 kcal per day. Their calculated ADMR at 70-72°F amounted to 6.45±2.48 kcal per day and the ADMR corrected for SDA (Specific Dynamic Action) of proteins averaged 5.98±2.48 kcal per day. The wide discrepancy between the observed and calculated values suggests that the measurements were not made in the thermoneutral zone, which is known to be above 72°F for voles. A simple χ^2 analysis between the observed and calculated values supports this idea ($\chi^2 = 52.1 > \chi^2$ of tables at 36.2). It is believed however, that a good proportion of the population was in or near the thermoneutral zone. This is supported by the fact that if we do not consider the 3 voles which showed the highest individual χ^2, the newly formed value amounted to 29.2 and proved to be statistically significant at the 99 percent level. This suggested then that 85 percent of the laboratory vole population could have reached a near BMR level. The discrepancy between the two values surely would have been reduced had the measurements been taken at a still higher temperature.

The metabolic requirements of masked shrews have already been calculated by Buckner (1964). He determined their daily requirements to average 6.02±0.26 kcal. Their minimal daily energy intake averaged 3.10 kcal. The BMR values of shrews ranged from 1.9 to 2.3 kcal per day, the former value being determined by Brody's formula and the latter one estimated with the minimum intake of oxygen and corrected for SDA of proteins. The metabolic requirements of individual shrew species have been estimated at 6.94, 6.67 and 9.69 kcal per day for S.arcticus, M.hoyi and B.brevicauda respectively. These values represent of course the sum of the active and passive metabolisms of animals.

C. Studies of small mammal and insect relationships

The population dynamics studies and the food preference tests suggested that the larch looper material could play a role in the diet of small mammals. This section of the study was designed to show the actual field occurrence of these interactions and to determine the importance of larch looper pupae in the diet of animals. The stomach analyses should give a direct and qualitative value of the first supposition while the planting technique will give a quantitative one in terms of predation by small mammals.

a. Stomach analyses

The analyses were performed on animals trapped in the summer and fall of 1970 and spring, summer and fall of 1971. The trapping index thus derived for a 10 month period is shown in Table 26 of the Appendices. The 1970 trapping period yielded 139 animals among which shrews totalled 60 percent. The shrews were of 3 species with a preponderance of short-tail shrews (48) over masked (35) and arctic (1) shrews. Voles were only of 2 species, with redback voles (34) more common than meadow voles (20); jumping mice (Z.hudsonius) were caught only once in the trapping period. The 1971 trapping session extended from February to September. Among the 179 trapped animals, 93 were masked shrews, 76 redback voles, 7 meadow voles and 3 bog lemmings (Synaptomys cooperi). We note the absence of short-tail shrews in the winter, spring and summer months of that year.

The stomach contents of 318 shrews and voles were determined volumetrically and the percentages of larch looper and larch sawfly materials assessed. An additional 173 samples came from gut analyses of the various shrew species. The volume of stomach contents by plot, species, age and sex are listed in Table 27 of the Appendices. As a whole, the volume of the contents varied so widely between individuals that no clear-cut picture can be drawn. Generally speaking, the monthly volume of stomach contents of masked shrews averaged

0.05 cc in the summer and winter months with the exception of April 1971, when 16 individuals tripled this volume (Table 31). The May figure of 0.75 cc is misleading since it is derived from only one individual. But it can be said that masked shrews act fortuitously in the sense that they increase their food consumption in the spring months by gorging themselves on newly available material. Short-tail shrews were captured only in the summer months of 1970, and their average stomach volume approached 0.04 cc with no apparent difference between the sexes. Redback vole stomach contents varied from 0.6 to 1.1 cc. The contents of males fluctuated between 0.5 to 0.9 cc; one individual trapped in May 1971 held a record of 2.20 cc. Stomach contents of females varied from 0.4 to 1.5 cc with an extreme value of 3.4 cc from a female of the same location and month.

Meadow voles also showed an average of about 0.8 cc in content through the trapping period. There were no indications of differences between the sexes if we base the figures on months of equal capture of both males and females. The month of August 1970 was such a month and it can be seen that the males averaged 0.8 cc compared to 0.7 cc for the females.

Although not mentioned in the last few tables, the stomach contents of an arctic shrew was estimated at 0.05 cc, which is very close to that for the masked shrews. The two male bog lemmings caught in February and March

Table 31. The mean volume of stomach contents (cc) of the 4 main mammalian species to be caught monthly in snap-back traps.

Time	Volume of contents (cc) by species and sex											
	S.cinereus			B.brevicauda			C.gapperi			M.pennsylvanicus		
	male	female	whole	male	female	whole	male	female	whole	male	female	whole
1970												
July	0.09	0.03	0.07	0.30	0.33	0.31	0.85	1.51	1.07	0.81	1.00	0.84
August	0.03	0.05	0.04	0.35	0.52	0.44	0.87	0.82	0.86	0.82	0.81	0.78
Sept.	0.10	0.00	0.05	0.34	0.50	0.37	----	----	----	----	----	----
Oct.	0.05	0.05	0.05	----	----	----	0.68	0.45	0.58	----	----	----
1971												
Febr.	0.06	0.06	0.06	----	----	----	0.85	0.77	0.80	----	----	----
March	0.10	0.05	0.07	----	----	----	0.72	1.00	0.79	1.10	----	1.10
April	0.17	0.11	0.15	----	----	----	0.92	0.62	0.81	----	----	----
May	----	0.75	0.75	----	----	----	1.52	3.40	1.99	1.67	0.15	0.80
June	0.07	0.00	0.04	----	----	----	0.52	0.90	0.65	0.70	----	0.70
Sept.	0.07	0.05	0.06	----	----	----	1.04	0.82	0.93	----	----	----

1971 had stomach volumes of 0.05 and 0.3 cc respectively, which was much below the values for the other rodent species. The jumping mouse trapped in August 1970 had a stomach content of 0.3 cc of plant material.

The volume of the small and large intestine contents were determined volumetrically the same way as the stomachs were. The volumes, classified by plot, species, age and sex can be found in Table 28 of the Appendices. As a whole, the monthly volume of the gut contents averaged 0.1 cc for masked shrews and 1.1 cc for the short-tail shrews (Table 32). As far as masked shrews are concerned, there seemed to be no difference between the volume of summer and winter gut contents, although the May figure (1971) of 0.4 cc by one female is misleading. Table 28 of the Appendices does not show any existing differences between the volume of contents of the different age groups; the very low numbers of subadults caught in snap-back traps did not permit such a comparison between the two groups. We note also that the gut contents of masked shrews averaged about twice those of the stomachs, while short-tail shrews contained about one-third more. The volume of contents of the arctic shrew was estimated at 0.3 cc, which represented about 6 times the volume of the stomach materials. This common feature will be discussed later in the text as the

Table 32. The mean volume of intestinal contents (cc) of the 2 main shrew species to be caught monthly in snap-back traps.

Time	Volume of contents (cc) by species and sex					
	S.cinereus			B.brevicauda		
	male	female	whole	male	female	whole
1970						
July	0.15	0.23	0.18	1.21	1.34	1.17
August	0.15	0.17	0.17	1.21	1.04	1.12
Oct.	0.03	0.05	0.04	----	----	----
1971						
Febr.	0.13	0.12	0.13	----	----	----
March	0.08	0.14	0.12	----	----	----
April	0.19	0.16	0.18	----	----	----
May	----	0.40	0.40	----	----	----
June	0.07	0.05	0.06	----	----	----
Sept.	0.17	0.15	0.16	----	----	----

gut contents tend to show better the food history of the shrews than the stomach contents do.

The overall picture of the stomach and intestinal contents is shown in Table 33. We note that larch looper material is found in very low percentages in the stomach and intestinal contents of the two main species of shrews, i.e. the masked and short-tail shrews. We see also that this percentage tends to be constant in both analyses while the same is true for the sawfly and 'other insects' materials.

Larch looper remains were found in 1 redback vole and 15 shrews, among which 9 masked and 6 short-tail shrews yielded fairly high percentages of remains (Table 34). We see that they ranged from 0.2 percent in the redback vole to 69 percent in masked shrews.

As a whole, 19 analyses (3.9 percent) showed larch looper remains of which 7 occurrences appeared in the stomach contents. It is noteworthy that the gut contents registered more occurrences of larch looper remains than the stomachs did. As suggested earlier, this might be caused by the fact that more material was available for analysis in the last portion of the digestive system. These occurrences of larch looper remains from the digestive system of small mammals were not local features of certain populations since they came from 7 of the investigation plots.

A more detailed analysis of larch looper re-

Table 33. The overall picture of the stomach and intestinal contents of small mammals.

Species	No. trapped	% of food item in stomach				
		looper	sawfly	other-insect	plant	miscel.
S. cinereus	129	1.7(2)[1]	16(34)	79(110)	1.7(12)	1.6(3)
S. arcticus	1	------	------	100	-------	------
B. brevicauda	48	2(4)	40(24)	54(37)	1(12)	3(4)
C. gapperi	110	+(1)	1(8)	+(33)	99(88)	+(1)
M. pennsylvanicus	26	------	+(2)	+(8)	100(25)	------
Z. hudsonius	1	------	------	1(1)	99(1)	------
Sy.cooperi	3	------	------	-------	100(3)	------

Species	No. trapped	% food item in intestine				
		looper	sawfly	other-insect	plant	miscel.
S. cinereus	129	1.7(7)	18(45)	77(108)	3.3(11)	------
S. arcticus	1	------	------	100(1)	-------	------
B. brevicauda	48	3(5)	34(37)	55(42)	5(19)	3(4)

[1] The numbers in parentheses refer to the number of analyses in which a given food item was found.

Table 34. The mean percentage of larch looper material recovered from small mammal stomach and intestinal contents.

Species	% of larch looper mat.	
	stomach	intestine
S. cinereus	69(2)[1]	20(7)
B. brevicauda	22(4)	23(5)
C. gapperi	0.2(1)	-----

[1] The numbers in parentheses refer to the number of analyses in which the larch looper remains were found.

mains is given in Tables 29 and 30 of the Appendices. The contents were analysed by species and as they occurred on individual plots. A summary of these analyses is shown in Tables 35 and 36, where the percentages of the remains were analysed on a monthly basis. We note that the stomach contents of short-tail shrews contained larch looper remains in July, August and September of 1970, coinciding with the peak of larval occurrences in the plots. The intestinal remains shown by the last table suggested also that masked shrews did eat larch looper material when it was available in August, September and October of the same year, and in April of the following spring.

The larch sawfly material was found in 89 shrews, 9 redback voles and 2 meadow voles for an overall occurrence of 33 percent. Among the 149 cases registered by the 100 animals, 69 were found in stomachs and 80 in the intestinal contents. Masked and short-tail shrews appeared to be the main predators of sawflies as they were the only two species of shrews to be trapped regularly on the plots. The percentage of sawfly remains ranged from traces in voles to 100 percent in some shrews. The mean percentage of the sawfly material recovered from small mammals is shown in Table 37. We note that these values tend to remain the same in both stomach and intestinal analyses of

Table 35. The monthly feeding history of small mammals as shown by the stomach analysis.

Time	Species	% of food item				
		looper	sawfly	other ins.	plant	misc.
1970 July	S.cinereus(18)[1]	--	50	47	3	----
	B.brevicauda(24)	3	62	32	1.5	1.5
	C.gapperi(12)	--	12	3	85	----
	M.pennsylvanicus(6)	--	--	+	100	----
August	S.cinereus(11)	--	25	75	--	----
	S.arcticus(1)	--	--	100	--	----
	B.brevicauda(20)	6	19	70.5	1.5	3
	C.gapperi(13)	+	--	1.5	98.5	----
	M.pennsylvanicus(13)	--	+	1.5	98.5	----
	Z.hudsonius (1)	--	--	1.5	98.5	----
Sept.	S.cinereus(2)	--	22	78	--	----
	B.brevicauda(5)	3	3	72	1.5	20.5
Oct.	S.cinereus(2)	+	--	100	--	----
	C.gapperi(9)	--	--	1	98	1
1971 Febr.	S.cinereus(24)	--	15	72	10	3
	C.gapperi(20)	--	--	3	94	3
	Sy.cooperi(1)	--	--	--	100	----
March	S.cinereus(8)	--	30	68.5	1.5	----
	C.gapperi(4)	--	--	1.5	98.5	----
	M.pennsylvanicus(1)	--	--	--	100	----
	Sy.cooperi(1)	--	--	--	100	----
April	S.cinereus(16)	6	1	93	--	----
	C.gapperi(8)	--	--	1	98	1
May	S.cinereus(1)	--	--	100	--	----
	C.gapperi(4)	--	--	1.5	98.5	----
	M.pennsylvanicus(4)	--	--	--	100	----
June	S.cinereus(1)	--	--	100	--	----
	C.gapperi(3)	--	--	1.5	98.5	----
	M.pennsylvanicus(1)	--	--	--	100	----

Table 35. Continued.

Time	Species	% food item				
		looper	sawfly	other ins.	plant	misc.
1971						
Sept.	S.cinereus(41)	--	10	90	--	----
	C.gapperi(22)	--	--	+	100	----
	M.pennsylvanicus(2)	--	--	--	100	----
Oct.	C.gapperi(14)	--	--	--	100	----

---

[1] The figures in parentheses represent the number of individuals examined.

Table 36. The monthly feeding history of small mammals as shown by the intestinal contents.

Time	Species	% of food item				
		looper	sawfly	other ins.	plant	misc.
1970						
July	S.cinereus(18)[1]	--	55	45	--	--
	B.brevicauda(24)	1	63	33	1.5	1.5
August	S.cinereus(12)	1	8	91	--	--
	S.arcticus(1)	--	--	100	--	--
	B.brevicauda(20)	1.5	20.5	72	3	3
Sept.	S.cinereus(2)	2	20	78	--	--
	B.brevicauda(5)	10	11	75	2	2
Oct.	S.cinereus(2)	6	3	91	--	--
1971						
Febr.	S.cinereus(24)	--	15	72	10	3
March	S.cinereus(8)	--	28	57	15	--
April	S.cinereus(16)	8	3	88	1	--
May	S.cinereus(1)	--	--	100	--	--
June	S.cinereus(2)	--	--	100	--	--
Sept.	S.cinereus(41)	--	12	88	--	--

[1] The figures in parentheses represent the number of individuals examined.

Table 37. The mean percentage of larch sawfly material recovered from the small mammal stomach and intestinal contents.

Species	% of larch sawfly mat.	
	stomach	intestine
S. cinereus	62(34)[1]	49(45)
B. brevicauda	68(24)	51(37)
C. gapperi	10(8)	------
M. pennsylvanicus	0.1(2)	------

[1] The numbers in parentheses refer to the number of analyses in which larch sawfly remains were found.

shrews. We see also that 9 percent of the voles were found to have eaten some sawfly material in July, August and September of 1970, and April of 1971 (Table 27 of the Appendices). Shrews extended their predation on sawfly material from July 1970 to April 1971 with the bulk of occurrences taking place when the larval drop was the most abundant. The overall picture of the sawfly remains can be found in Table 33. It is shown that short-tail shrew stomach contents average twice those of masked shrews. The trend is less obvious in the intestinal contents, although short-tail shrews also show higher values than those of masked shrews.

It might be well to draw here a comparison between the ratios of larch looper and larch sawfly remains as found in the population dynamics data and stomach analyses. We notice in Table 33 that the stomach and intestine analyses showed respectively a 2:16 and a 2:18 ratio. A look at Tables 9, 10, 11 and 12 of the Appendices reveals a ratio of 336:3655 between the larch looper and larch sawfly larvae collected in the larval traps of 1970. This suggests and tends to confirm the fact previously put foward that there is no marked preference existing for either the larch looper or the larch sawfly, as the ratio of the insects found in stomach and intestinal analyses is approximately the same as the one existing at the population level. The larch looper populations could then, play a very important role in the diet of small mammals, if those populations were larger. This conclusion nicely fits Murdoch's thesis on switching behavior of predator populations, where predators tend to change (switch) their preference when prey populations pass a certain threshold (Murdoch 1969). There are indications that such a phenomenon could occur in the larch looper-larch sawfly system once the larch looper numbers reach a certain level. It is believed that such levels were not attained on the investigation plots since larch looper populations were at their lowest ever since 1968.

We included in the 'other-insect' material category those which were not larch loopers and larch sawflies. No attempts were made in the present study to classify these insect remains. Generally speaking, this material was ingested by 169 shrews, 33 redback voles, 8 meadow voles and 1 meadow jumping mouse. It is clear that insects serve other purposes than sustaining shrew populations since more than 50 percent of the voles were found to have ingested a certain quantity. Besides shrews which are the main regular mammalian predators of this material, voles ingested insect remains in all of the 1970 summer and fall months (July, August, September, October) and in all of the spring and summer months of 1971 (February, March, April, May, June; Table 35). Among the 341 examples of predation on insects, 190 came from stomach analyses and 151 from gut contents, for a total occurrence of 72 percent. Masked shrews appeared to be the main users of this 'other insect' material, with insect remains in 220 cases; short-tail shrews followed with 79 cases; redback voles with 33; meadow voles with 8 and the meadow jumping mouse with 1. The other-insect remains occurred in 88 percent of the shrews and it is obvious that they sustain their metabolism only with this category of food item; the other 12 percent seemed to consist mainly of larch sawfly and larch looper material. The percentage of other-insect remains ranged from traces in rodents to 100 percent in many shrews. The mean percentages of the material recovered from small mammals are listed in Table 38. We see that masked shrews show, in both kinds of analyses (stomach and intestinal), higher percentages of remains than short-tail shrews. We note also that the other-insect material in redback vole stomachs average more than twice the amount found in meadow voles.

Plant material was found in 148 mammalian stomachs among which 12 masked and 12 short-tail shrews ingested respectively 17 and 4 percent. All rodents had eaten mostly plant material in the proportion shown in Table 35. In 30 samples, masked shrews averaged 31 percent compared to 5 percent showed in 19 cases from short-tail shrews. This plant material was classified into 4 broad types as they occurred in stomach and gut contents of shrews. The monthly picture of plant remains is shown in Table 39. The

Table 38. The mean percentage of 'other insect' material recovered from the small mammal stomach and intestinal contents.

Species	% of 'other insect' mat.	
	stomach	intestine
S.cinereus	93(110)[1]	90(108)
S.arcticus	100(1)	100(1)
B.brevicauda	70(37)	63(42)
C.gapperi	0.7(33)	------
M.pennsylvanicus	0.3(8)	------
Z.hudsonius	1(1)	------

[1] The numbers in parentheses refer to the number of analyses in which 'other insect' remains were found.

Table 39. The mean percentage of plant material found in stomach and intestinal contents of shrews.

Species	Time	% 'plant' material in stomach			
		soil	bark	stones	green matter
S.cinereus	July 1970	----	2(2)[1]	------	18(1)
B.brevicauda	July 1970	25(1)	7(1)	------	-----
B.brevicauda	August 1970	1(1)	2(5)	------	0.5(3)
B.brevicauda	Sept.1970	5(1)	----	------	0.5(2)
S.cinereus	Febr. 1971	60(2)	12(4)	------	-----
S.cinereus	March 1971	----	4(3)	------	-----

Species	Time	% 'plant' material in intestine			
		soil	bark	stones	green matter
B.brevicauda	July 1970	33(1)	2(3)	1(1)	-----
B.brevicauda	August 1970	4(4)	3(5)	1(1)	1(4)
B.brevicauda	Sept. 1970	2(1)	2(2)	------	-----
S.cinereus	Febr. 1971	47(6)	1(2)	------	-----
S.cinereus	March 1971	50(2)	----	------	1(1)
S.cinereus	April 1971	----	4(1)	------	-----

[1] The numbers in parentheses refer to the number of analyses in which some 'plant' material was found.

analyses showed the plant material to consist mainly of 'soil' and bark remnants. Greens were found only in 1 masked and 5 short-tail shrew stomachs while the gut analyses revealed such remains in only 2 shrews. As a whole, 19 masked shrew stomachs contained some plant material compared to 25 from short-tail shrews. Although fairly common (31 percent), these occurrence are thought to be accidental as they probably resulted from the shrews digging while searching for food. The table shows also that masked shrews had ingested higher percentages of 'soil' materials in the winter time. This also could be attributed to digging since the analyses did not show higher percentages of bark and green plant materials as compared to the summer period.

The analyses showed also the presence of miscellenous material that consisted mainly of hair and pieces of a reddish tissue thought to be muscle. This material never occurred alone and was usually accompanied by certain amounts of hairy remains. The presence of guard hair as such was found in 3 shrews, 1 masked and 2 short-tail shrews. This might be attributable to the fact that the animals were killed recently after a preening period. In such cases, the quantity of hairy material was insignificant and could not be considered as coming from other animals. There were other instances where a quantity of hair occurred and occupied up to 80 percent of the stomach contents. Such cases occurred in winter time with 3 masked shrews when their stomach remains were found to contain 80, 50 and 2 percent respectively. Small quantities of hair were also found in 1 redback vole (2 percent) and 2 short-tail shrew stomach contents (1 percent and 5 percent); these could be as accidental as those seen earlier in masked shrews.

The presence of guard hair attached to pieces of muscular tissues was found in 2 short-tail shrews trapped in August 1970. The fact that these 2 animals showed such remains at 79 percent in their stomachs and 57 in their intestine suggested successive uses of this material for several meals. Whether such material could have been killed by the shrews or simply found dead and readily eaten can be argued. An adult male was found to have some redback vole hair in the stomach (59 percent) and intestine (40 percent) while a second one, a subadult female, was caught with some deer mouse hair (100 percent in stomach and 74 percent in intestine). It is not believed that short-tail shrews are important predators of other animals (small mammals) since such material occurred in only 2 out of 48 trapped animals.

b. Pupae planting technique

The stomach analyses showed that only 15 shrews and 1 redback vole ate larch looper material; this represented 4 percent of the total analysis. They indicated also that the larch looper remains were eaten mainly when the food item was newly available in the bogs, that is, in July, August, September and October. Masked shrews were found to be the main users (9) followed by short-tail shrews (6) and 1 redback vole. The fact that both the stomach and intestinal contents of some shrews consisted of larch looper remains suggested a greater impact of the shrew populations on larch looper numbers. The pupae planting technique was then designed to estimate this actual predation of small mammals and determine their impact on larch looper pupae.

The larch looper larvae and pupae populations were determined using the method described earlier. The population estimations of both groups are listed in Table 31 of the Appendices. Generally speaking, the larvae populations fluctuated from nil to 90,000 per acre and fell within the limits established by the data of the first section; the pupae populations ranged from 500 to 50,000 per acre. The mammalian populations found in the same investigation plots are enumerated in Table 32 of the Appendices and standardized for the purpose of statistical analysis.

Larch looper pupae were planted in August 1970 and 1971 and recovered after the predation period. A total of 1,100 pupae were planted in 12 plots using a gradient of densities as shown by Table 33 of the Appendices. The table includes also the recovery rates of pupae at different densities. The recovery of pupae permitted an estimation of the total mortality experienced by this underground stage; such figures are shown in Table 34 of the Appendices. As a whole, the total mortality ranged from 56 to 97 percent of the 'planted' pupae. Based on such estimations, a total number of pupae destroyed per acre can be established; the number of pupae thus destroyed ranged from 440 to 44,000 per acre (Table 40). Figure 11 offers another view of the number of pupae destroyed at different densities. We note the strong correlation existing between two variables, as the relationship holds true for populations ranging from 500 to 50,000 per acre.

The partial mortality caused by small mammals was determined by subtracting the predation caused by other predatory species from the total predation. As described in another section (see Methods), this mortality caused by other killing agents was estimated by using 'small mammal-free cages' in which 20 pupae had been planted artificially. The partial mortality from small mammals and the number of pupae thus destroyed are shown in Table 40. We note that the mammalian species destroyed from 1 to 89 percent of the available pupae populations, while the total mortality accounted for as much as 97 percent of their numbers. We see also that there exists a strong relationship between the pupae destroyed by small mammals and the populations of larch looper pupae (Figure 12); the

Table 40. The total and partial mortalities of larch looper pupae populations based on the predation of the 'planted' pupae.

Plot	Pupae/acre	Total predation (%)	No. of pupae destroyed per acre	Small mammal predation (%)	Pupae/acre destroyed by small mammals
1970					
A	48293	92	44430	57	27527
B	3979	80	3181	30	1194
C	6116	56	3425	1	61
D	4101	92	3773	37	1517
E	5469	80	4375	60	3281
F	2231	56	1249	36	803
G	500	90	450	57	285
H	17513	97.3	17040	92	16112
Rennie	17828	82	14619	49	8736
Telford	500	88	440	55	275
Seddon's Corner	17513	94	16462	89	15587
Darwin	16333	94	15353	61	9963
1971					
A	8631	96	8286	61	5265
B	11513	75	8635	25	2878
C	8381	70	5867	15	1257
F	800	97	796	77	616
Seddon's Corner	6708	82	5501	77	5165

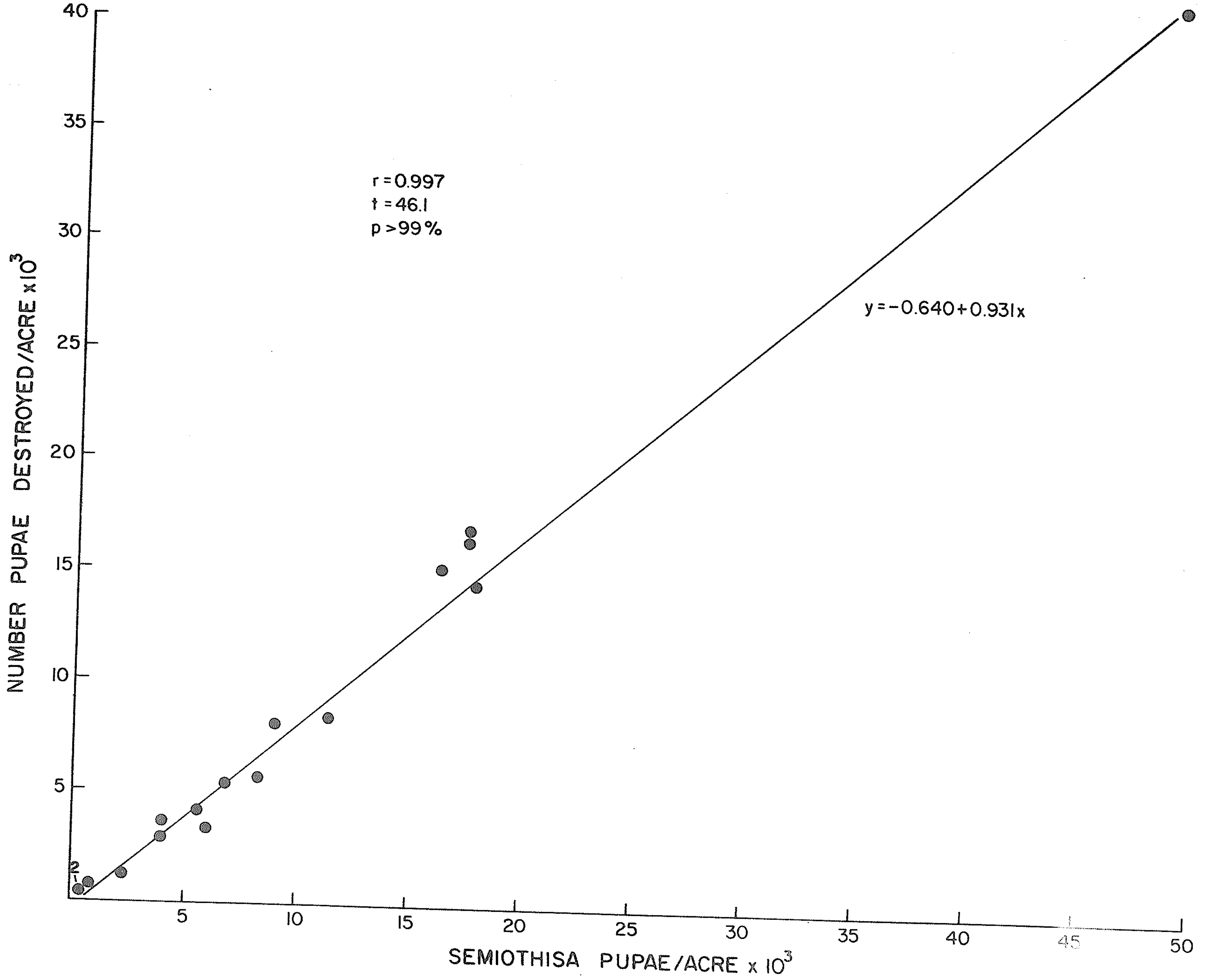
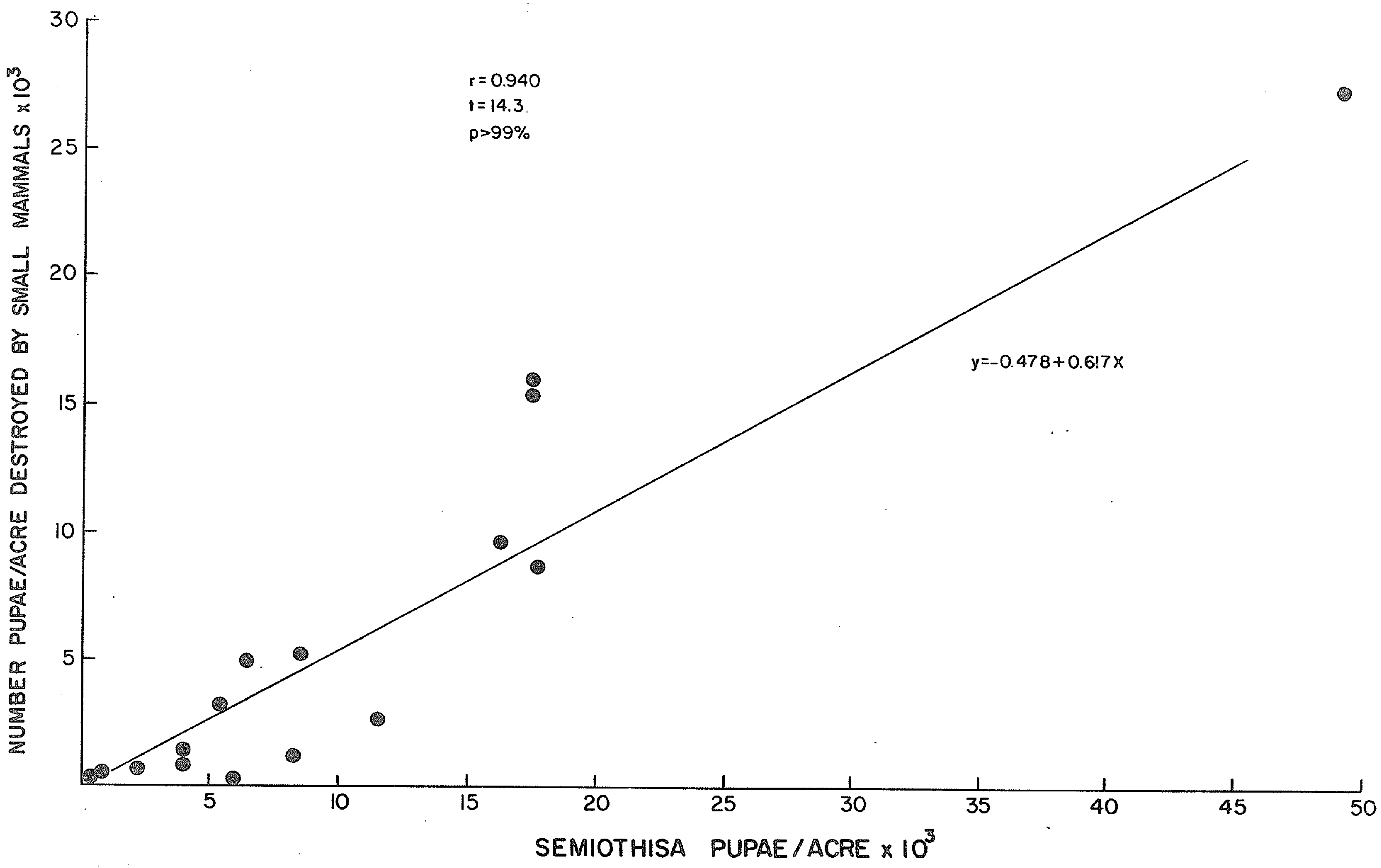

NUMBER PUPAE DESTROYED/ACRE x10^3
40
35
30
25
20
15
10
5
2
1
5
10
15
20
25
30
35
40
45
50
SEMIOTHISA PUPAE/ACRE x 10^3
r = 0.997
t = 46.1
p > 99%
y = -0.640+0.931x

Figure 12. Relationship between the number of pupae destroyed by small mammals and the populations of larch looper pupae.


r = 0.940
t = 14.3
p>99%
y=-0.478+0.617X
NUMBER PUPAE/ACRE DESTROYED BY SMALL MAMMALS x 10³
30
25
20
15
10
5
5
10
15
20
25
30
35
40
45
50
SEMIOTHISA PUPAE / ACRE x 10³

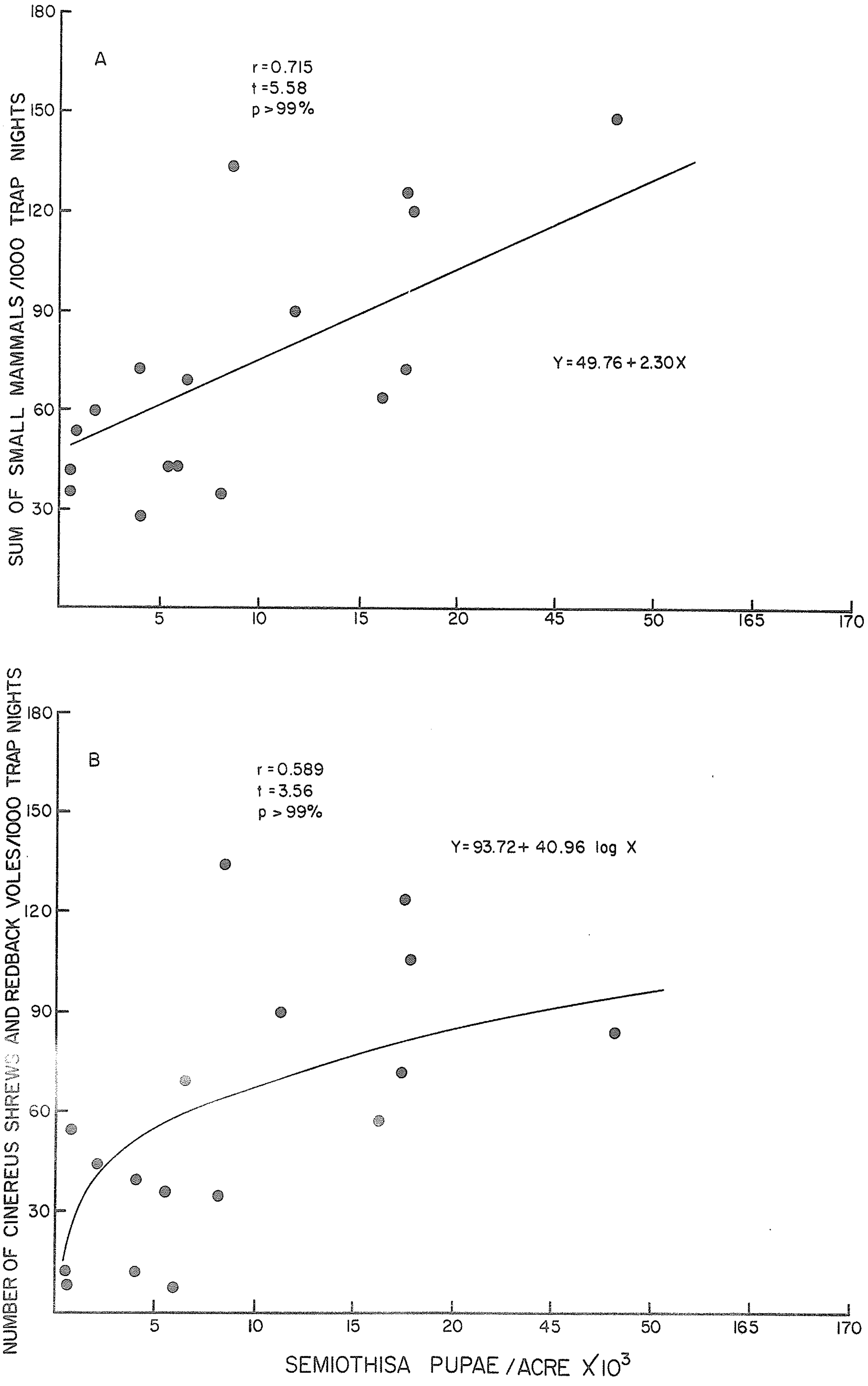
relationship holds true for populations ranging from 500 to 50,000 pupae per acre.

The latter relationships suggest a numerical response between small mammals and pupal populations. In fact, the small mammal populations of 12 plots show a positive and direct numerical response to densities of larch looper pupae, as the relationship holds true at the 99 percent level (Figure 13a). Analysed individually, none of the small mammal species showed such a response but when numbers of masked shrews and redback voles were lumped together, they showed a positive response to larch looper pupae (Figure 13b); the figure suggests however these two parameters to fluctuate in a logarithmic pattern.

Numerical responses of small mammals to densities of destroyed pupae per acre were also calculated. Small mammal populations as a whole showed a positive direct response to numbers of destroyed larch looper pupae per acre (Figure 14a); the relationship held true for densities of dead pupae that fluctuated between 440 and 28,000 per acre. Masked and short-tail shrews did not show any statistically significant responses, while redback voles registered one (Figure 14b). The relationship can be interpreted either as a positive and direct one or as a positive logarithmic one; however, the latter relationship was found to fit the data better, as it showed to be statistically significant at the 99 percent level compared

Figure 13 a. The numerical response of small mammal populations to densities of larch looper pupae.

b. The numerical response of masked shrew and redback vole populations to densities of larch looper pupae.

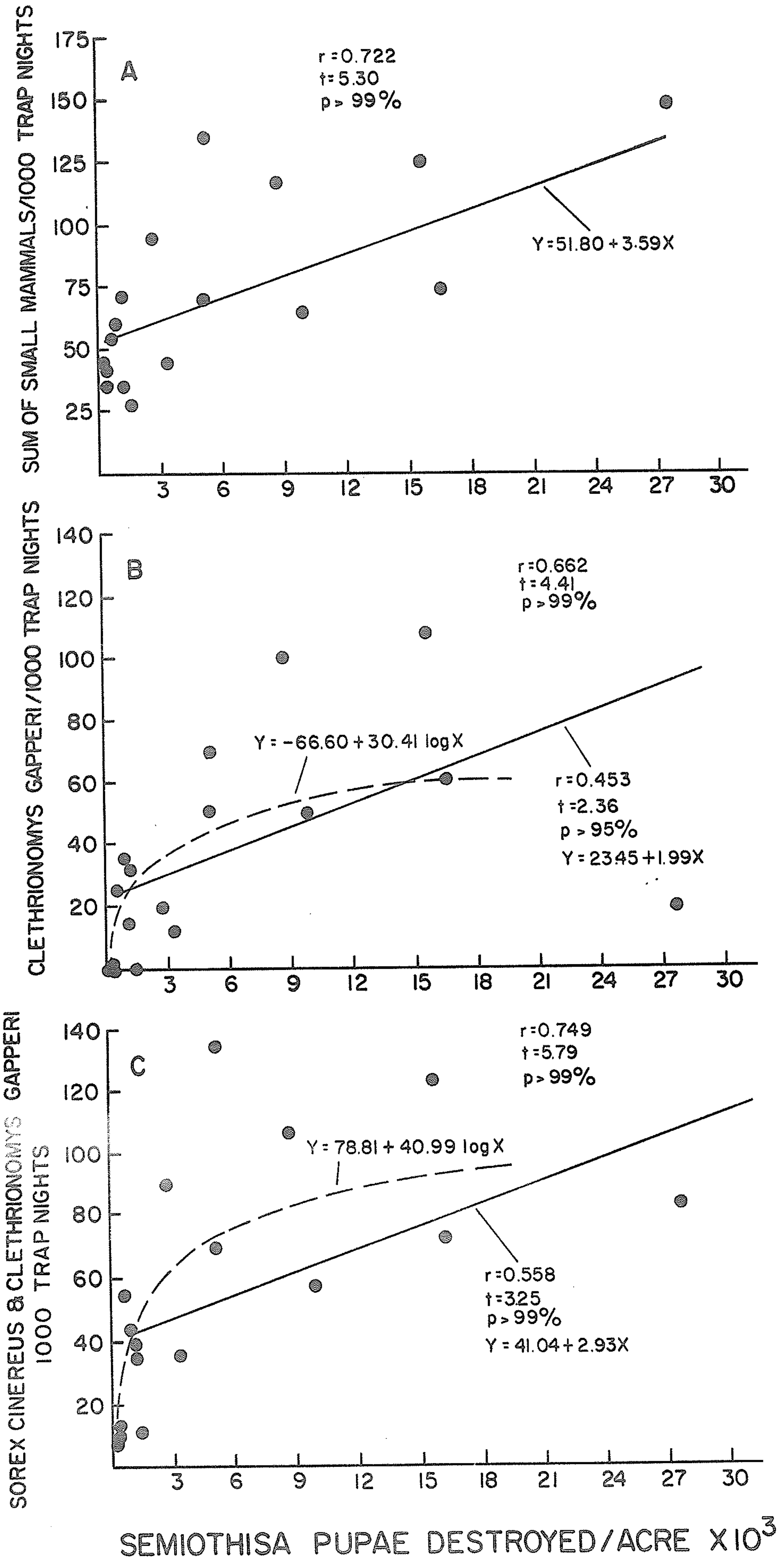


A
r = 0.715
t = 5.58
p > 99%
Y = 49.76 + 2.30X
SUM OF SMALL MAMMALS/1000 TRAP NIGHTS
180
150
120
90
60
30
5
10
15
20
45
50
165
170
B
r = 0.589
t = 3.56
p > 99%
Y = 93.72 + 40.96 log X
NUMBER OF CINEREUS SHREWS AND REDBACK VOLES/1000 TRAP NIGHTS
180
150
120
90
60
30
5
10
15
20
45
50
165
170
SEMIOTHISA PUPAE / ACRE X10³

Figure 14 a. The numerical response of small mammal populations to densities of larch looper pupae destroyed per acre.

b. The numerical response of redback voles to densities of larch looper pupae destroyed per acre.

c. The numerical response of masked shrew and redback vole populations to densities of larch looper pupae destroyed per acre.


A
SUM OF SMALL MAMMALS/1000 TRAP NIGHTS
175
150
125
100
75
50
25
r = 0.722
t = 5.30
p > 99%
Y = 51.80 + 3.59X
3
6
9
12
15
18
21
24
27
30
B
CLETHRIONOMYS GAPPERI/1000 TRAP NIGHTS
140
120
100
80
60
40
20
r = 0.662
t = 4.41
p > 99%
Y = -66.60 + 30.41 log X
r = 0.453
t = 2.36
p > 95%
Y = 23.45 + 1.99X
3
6
9
12
15
18
21
24
27
30
C
SOREX CINEREUS & CLETHRIONOMYS GAPPERI
1000 TRAP NIGHTS
140
120
100
80
60
40
20
r = 0.749
t = 5.79
p > 99%
Y = 78.81 + 40.99 log X
r = 0.558
t = 3.25
p > 99%
Y = 41.04 + 2.93X
3
6
9
12
15
18
21
24
27
30
SEMIOTHISA PUPAE DESTROYED/ACRE X10³

to 95 percent for the former one. The combined populations of both the masked shrews and redback voles were found to fluctuate directly with the numbers of dead larch looper pupae (Figure 14c); this relationship also exists in two forms as the data fitted both a linear and a logarithmic curve.

The impact of small mammals on larch looper pupae can be shown also by the existence of a functional response. The number of dead pupae destroyed per animal is shown to vary proportionately with the density of pupae per acre (Figure 15a); the relationship held true at the 99 percent level. Since the numbers of the mammalian populations of the Manitoba bogs consist of two large groups, the shrews and voles, a functional response for each group was tested. The results of such relationships are plotted in Figure 15b and 15c. The functional response of shrews can be interpreted in two ways as the linear fit revealed to be significant at the 94 percent level compared to 99 percent level for the logarithmic one. The functional response of vole populations varied proportionally to larch looper pupae; the correlation held true at the 99 percent level.

As shown by Table 32 of the Appendices, the shrew populations consist of two species, the masked and short-tail shrews, while that of rodents is formed mainly by redback voles. Specific functional responses were

Figure 15 a. The functional response of small mammal populations to densities of larch looper pupae.

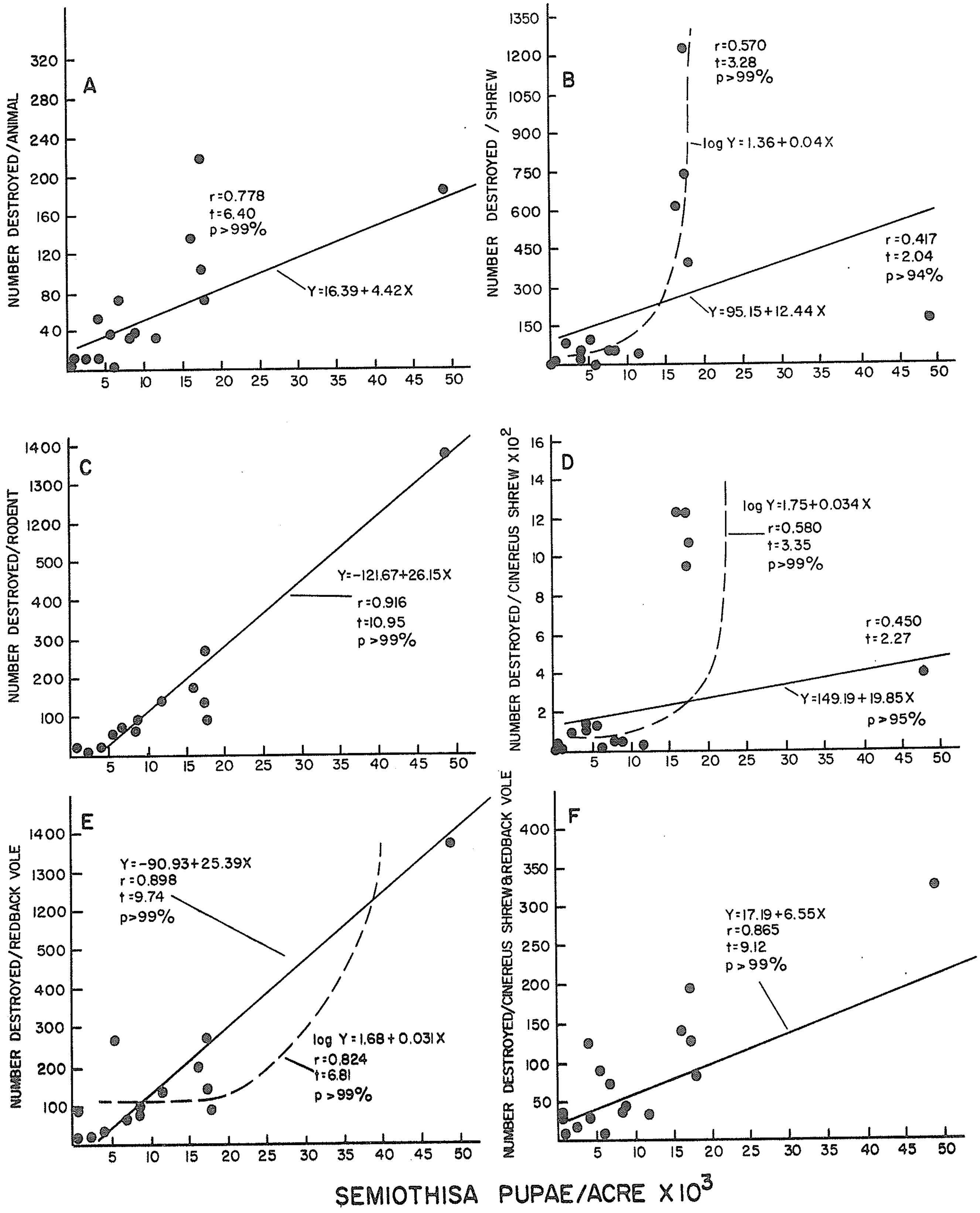
b. The functional response of shrews to densities of larch looper pupae.

c. The functional response of rodents to densities of larch looper pupae.

d. The functional response of masked shrews to densities of larch looper pupae.

e. The functional response of redback voles to densities of larch looper pupae.

f. The functional response of masked shrew and redback vole populations to densities of larch looper pupae.

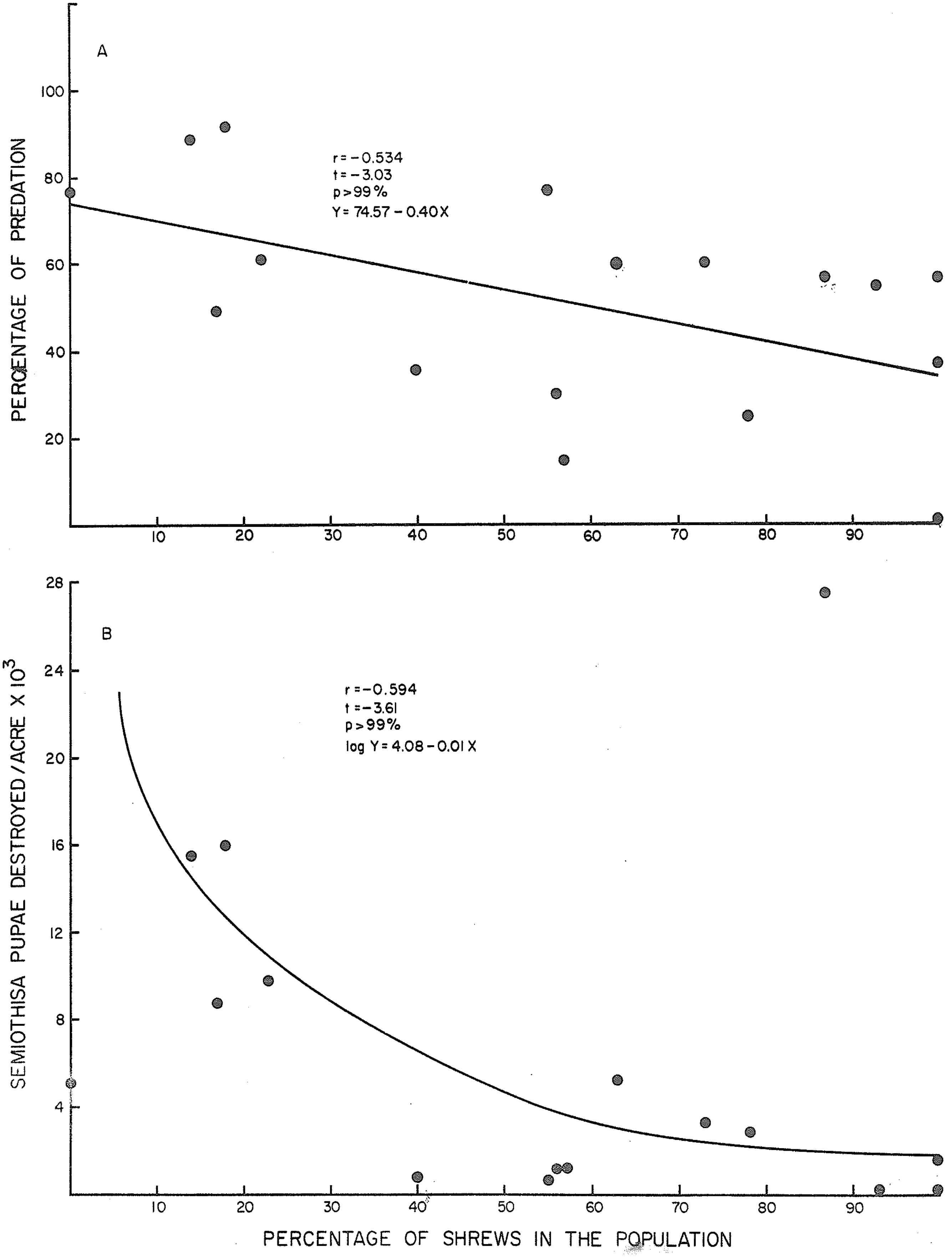

A
NUMBER DESTROYED/ANIMAL
320
280
240
200
160
120
80
40
r=0.778
t=6.40
p>99%
Y=16.39+4.42X
5
10
15
20
25
30
35
40
45
50
B
NUMBER DESTROYED / SHREW
1350
1200
1050
900
750
600
450
300
150
r=0.570
t=3.28
p>99%
log Y=1.36+0.04X
r=0.417
t=2.04
p>94%
Y=95.15+12.44X
C
NUMBER DESTROYED/RODENT
1400
1300
1200
500
400
300
200
100
Y=-121.67+26.15X
r=0.916
t=10.95
p>99%
D
NUMBER DESTROYED/CINEREUS SHREW X10^2
16
14
12
10
8
6
4
2
log Y=1.75+0.034X
r=0.580
t=3.35
p>99%
r=0.450
t=2.27
Y=149.19+19.85X
p>95%
E
NUMBER DESTROYED/REDBACK VOLE
1400
1300
1200
500
400
300
200
100
Y=-90.93+25.39X
r=0.898
t=9.74
p>99%
log Y=1.68+0.031X
r=0.824
t=6.81
p>99%
F
NUMBER DESTROYED/CINEREUS SHREW&REDBACK VOLE
400
350
300
250
200
150
100
50
Y=17.19+6.55X
r=0.865
t=9.12
p>99%
SEMIOTHISA PUPAE/ACRE X10^3

then calculated for the above mentioned small mammal populations. Masked shrews showed a functional response to numbers of larch looper pupae (Figure 15d); the relationship fitted better a logarithmic curve where it proved to be statistically significant at the 99 percent level. The response of short-tail shrews varied logarithmically with the numbers of larch looper pupae, as the relationship was found to be statistically significant at the 95 percent level. Redback voles also showed a response to larch looper numbers (Figure 15e); the data fitted both a straight line and a logarithmic curve, both being statistically significant at the 99 percent level. The combined populations of masked shrews and redback voles showed their response to larch looper pupae to be statistically significant at the 99 percent level (Figure 15f); we note that the combined effect of both proved to vary like a density-dependent pattern.

Although shrew and rodent populations showed numerical and functional responses to larch looper pupae, their impact on the insect populations is believed to be a constant mortality factor having no real effect (no key-factor type of role) on the larch looper fluctuations. This is suggested by the fact that the percentage of predation of the most insectivorous species, the masked and short-tail shrews, is inversely proportional to their presence in the small mammal fauna (Figure 16a). The same is true concerning the number of pupae destroyed per acre (Fi-

Figure 16 a. Relationship between the percentage of predation of larch looper pupae and the percentage of shrews in the small mammalian fauna.

b. Relationship between the number of larch looper pupae destroyed per acre and the percentage of shrews in the small mammalian fauna.


A
PERCENTAGE OF PREDATION
100
80
60
40
20
r = −0.534
t = −3.03
p > 99 %
Y = 74.57 − 0.40X
10
20
30
40
50
60
70
80
90
B
SEMIOTHISA PUPAE DESTROYED / ACRE X 10³
28
24
20
16
12
8
4
r = −0.594
t = −3.61
p > 99%
log Y = 4.08 − 0.01 X
10
20
30
40
50
60
70
80
90
PERCENTAGE OF SHREWS IN THE POPULATION

gure 16b) as the relationship holds true at the 99 percent level. Both figures suggest a higher mortality of larch looper pupae when shrews are low in numbers.

Conclusions

Small mammal populations are undoubtedly very important in the dynamics of larch loopers. This is shown by both the statistical and actual field data analyses. Another important conclusion from the study is that small mammal populations strongly indicated density-dependent relationships to numbers of larch looper pupae available and to numbers of destroyed pupae per acre. This is especially true in the comparison of numerical and functional responses of small mammals to densities of larch looper pupae of the statistical and field data analyses.

Generally speaking, the statistical approach using data gathered by the Larch Sawfly Team since 1962 on one hand, and population estimations based on such data on the other, gave the following trends. Redback vole and masked shrew populations showed strong statistically significant relationships to numbers and percentages of dead larch looper pupae per acre. This is true for such relationships using redback vole numbers of Rennie, Seddon's Corner, Pine Falls and Darwin plots. The density dependence was specially strong when numbers of dead larch looper pupae were used. The same is true for masked shrew populations as they showed a strong correlation with the numbers of dead larch looper pupae per acre of Telford, Pine Falls and Darwin plots. Furthermore, masked shrews indicated inverse density-dependent relationships to numbers of dead green larch looper pupae of Telford plot and to the percentage of dead green larch looper populations of Riverton.

The Morris key-factor analysis suggested the importance of the pupal stage in the dynamics of larch loopers. The fact that the analysis using the logarithm of survival of pupae (log S) instead of the logarithm of the previous generation (log h_n) improved significantly the predictability of future looper populations in all but one plot, stressed the importance of this underground stage. The analysis doubled the predictability of S.sexmaculata populations of Rennie and Darwin plots, and that of S.oweni numbers of Telford plot; it more than tripled also that of S.signaria populations of Seddon's Corner and Riverton plots.

The importance of the pupal stage was emphasized further when small mammal populations showed positive density-dependent relationships to the actual numbers of dead pupae per acre. Individual mammalian species confirmed the general tendency as they each showed such relationships in all but Telford and Pine Falls plots, where numbers of short-tail and masked shrews were related negatively to the green and brown dead larch looper pupae. The masked shrew populations registered a negative and logarithmic numerical response (log transformation of pupae: log X) to dead larch looper pupae of Telford and Seddon's Corner, while they showed also a positive and direct response to the pupae of Darwin plot. Short-tail shrews offerred also a negative pattern of response to dead looper pupae, as shrew numbers are found to vary logarithmically (log transformation of shrew numbers: log Y) with those of the pupae of Rennie, Seddon's Corner and Pine Falls plots. Furthermore, short-tail shrews showed a positive and logarithmic response (log-log transformation) to numbers of dead green larch looper of Telford. The numerical response of arctic shrews was found to be negative and logarithmic (log transformation of pupae: log X) with the numbers of dead pupae of Telford; they registered also a positive and direct one with those of Darwin plot. Redback vole populations responded positively and directly to the numbers of dead green and brown larch looper pupae of Rennie and Seddon's Corner, while they showed a negative and logarithmic one (log transformation of pupae: log X) with the numbers of dead brown larch looper pupae of Telford.

The life table analysis revealed also a functional response to exist between small mammals and larch looper pupae populations. This response was found to vary in a density-dependent manner with the densities of larch looper pupae. Masked shrews showed a positive relationship to the larch looper densities of Rennie and Telford plots, while redback voles registered a similar one in Seddon's Corner. The combined populations of the two mammalian species cited above expressed a direct functional response in Pine Falls plot, whereas each individual species was not indicating any response to densities of the larch loopers.

The field data analysis using the 'pupae planting technique' confirmed almost all the population patterns as shown above. It was found that the number of pupae destroyed per acre was a direct function of the population of pupae per acre. Similarly, the number of pupae destroyed by small mammals proved to be also positively density-dependent on the numbers of available pupae per acre. Consequently, numerical and functional responses were expected. As a whole, the small mammal populations registered positive and direct numerical responses to both the available larch looper pupae per acre and to the number of pupae destroyed per acre. Redback voles recorded a positive and logarithmic response (log transformation of pupae: log X) to the numbers of larch looper pupae destroyed per acre. The combined populations of masked shrews and redback voles indicated also a positive and logarithmic response (log transformation of pupae: log X) to exist with both the densities of larch looper pupae and those of destroyed larch looper pupae per acre. We note that such responses fitted as well to a straight-line model, although the logarithmic fit tended to be statistically significant to a higher degree.

The functional response of small mammals to densities of larch looper pupae were found to be of the same positive patterns as those of the statistical analyses. The functional responses of individual mammalian species fitted statistically to the same straight-line models as those ly in one redback vole stomach. Since the same mammalian populations are also important predators of larch sawflies and possibly for other harmful insect species, the amount of ingested larch looper material becomes very important in the integrated control of such species. This is specially true when the predation of those harmful species is at its maximum, that is to say in the late summer and fall months. This fact was stressed in Figure 3 of the Appendices for three sampling plots of the Larch Sawfly Team, where the numbers of dead larch looper pupae were inversely related to those of sawfly cocoons; the figure expressed this relarionship to be linked by the formula

$Y = a X^b$ (Y = larch looper pupae; X = larch sawfly cocoons).

Furthermore, the calorimetric experiments performed on larch looper pupae showed that one gram of pupae yielded about 4.5 times the calorific value of one gram of sawfly eonymph. Expressed differently, for each 27 larch looper pupae ingested, there are 68 'spared' sawfly cocoons. The 'planting' technique indicated particularly many mammalian numerical responses to dead larch looper pupae for densities (composed of dead numbers of pupae per acre) fluctuating from 400 to 28,000 pupae per acre. Based on this, the number of 'spared' sawfly cocoons fluctuate between 160 and 11,100 cocoons per acre. Giving to each sawfly female a reproductive capacity of 60 eggs, those spared cocoons alone could rebuild a population at an epidemic level by spreading in tamarack bogs from 9,600 to 666,000 eggs per acre. On the other hand, these 400 to 28,000 pupae destroyed by small mammals offer a tremendous supply of calories spread in small amounts in the tamarack bogs. Because larch loopers are usually referred to as 'solitary defoliators' and because each individual pupae represents a high source of energy, one can speculate about their importance as natural caches which are always present and available in the bogs at times of food scarcity.

The importance of larch looper pupae in the diet of small mammals is emphasized by considering their period of appearance in the bogs. The stomach analyses showed that both the larch looper and larch sawfly materials were ingested readily as soon as they formed a newly available food item in tamarack bogs. Considering that the sawfly material is present in tamarack stands (as a new food item) from June to late August, and knowing that the larch looper material appears in July to last until late October and probably mid November, the impact of the latter food item on small mammal populations is certainly important. Despite the impossibility of knowing the real effect of larch looper pupae on individual small mammals, it is possible to speculate on the importance of this late occurring food item on the determination of future small mammal populations. To what extent this food item is important for the small mammalian fall and winter survival is probably impossible to determine. But it remains that this destruction of 400 to 28,000 pupae per acre is accomplished within 3 months of the fall season. As Table 19 shows, this destruction could serve uniquely to sustain the metabolic requirements for any one individual small mammal for this entire 90-day period. Alternatively, this destruction could as well feed one individual of each small mammal species up to a period of 20 days, and very likely for a longer period since not all mammalian species were found with larch looper remains in their digestive system. Furthermore, this larch looper material cannot be qualified as a regular food item such as sawflies (even when this material is available) because of the very low percentage and occurrence of loopers in small mammal stomach and intestinal analyses. This stresses the fact that small mammals would act as individuals rather than populations, where some small mammals of some species would prey on this food item for a certain period.

The importance of loopers as a dietary source is also shown by the fact that female shrews and redback voles expressed a tendency in their preferences to choose larch looper pupae over sawfly cocoons. Whether or not this is related to the energetic requirements of females when giving birth and nursing young late in the summer or early in the spring is merely speculative. The stomach analyses indicated that larch looper remains occurred indiscriminately in both sexes.

Acknowledgments

The completion of this thesis was the result of the assistance and co-operation of a number of people. Dr. C. H. Buckner made many helpful comments and supervised the work. Drs. R. H. Green, C. C. Lindsey. M. Aleksiuk, R. D. Whitney and W. O. Pruitt Jr. read and criticised the thesis. Thanks are due also to Dr. H. E. Welch who permitted the work to be done at the Zoology Department, University of Manitoba. Dr. W. J. Turnock provided useful assistance in coordinating the research. The technical help given by J. A. Drouin and R. H. Smith of the Larch Sawfly Team of Manitoba was greatly appreciated. Mr. I. Reesor was responsible for the clarity and presentation of the figures. My wife Suzanne assisted with all aspects of the study.

The research was supported by grants from the National Research Council of Canada (311-1749-11 and 311-1749-05), and by one NRC Scholarship, one NRC Bursary and two University of Manitoba Fellowships.

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Appendices

Figure 1. Field data concerning the collections of larvae of the main insect species of tamarack bogs.

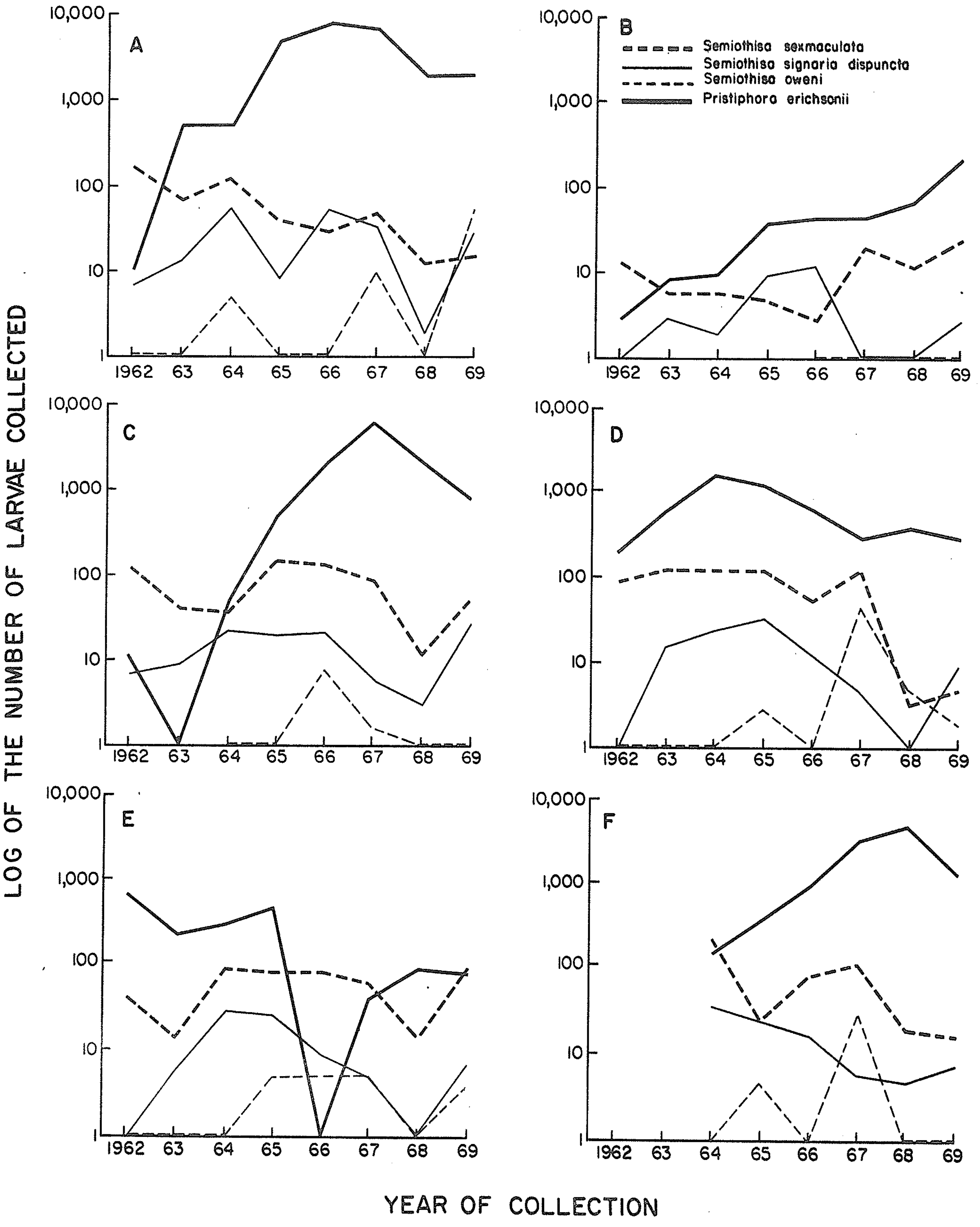
LOG OF THE NUMBER OF LARVAE COLLECTED
YEAR OF COLLECTION
A
B
C
D
E
F
Semiothisa sexmaculata
Semiothisa signaria dispuncta
Semiothisa oweni
Pristiphora erichsonii
10,000
1,000
100
10
1
1962
63
64
65
66
67
68
69

Figure 2. The analysis of the total mortality of the ground-inhabiting stages of the main tamarack defoliators of Manitoba bogs.

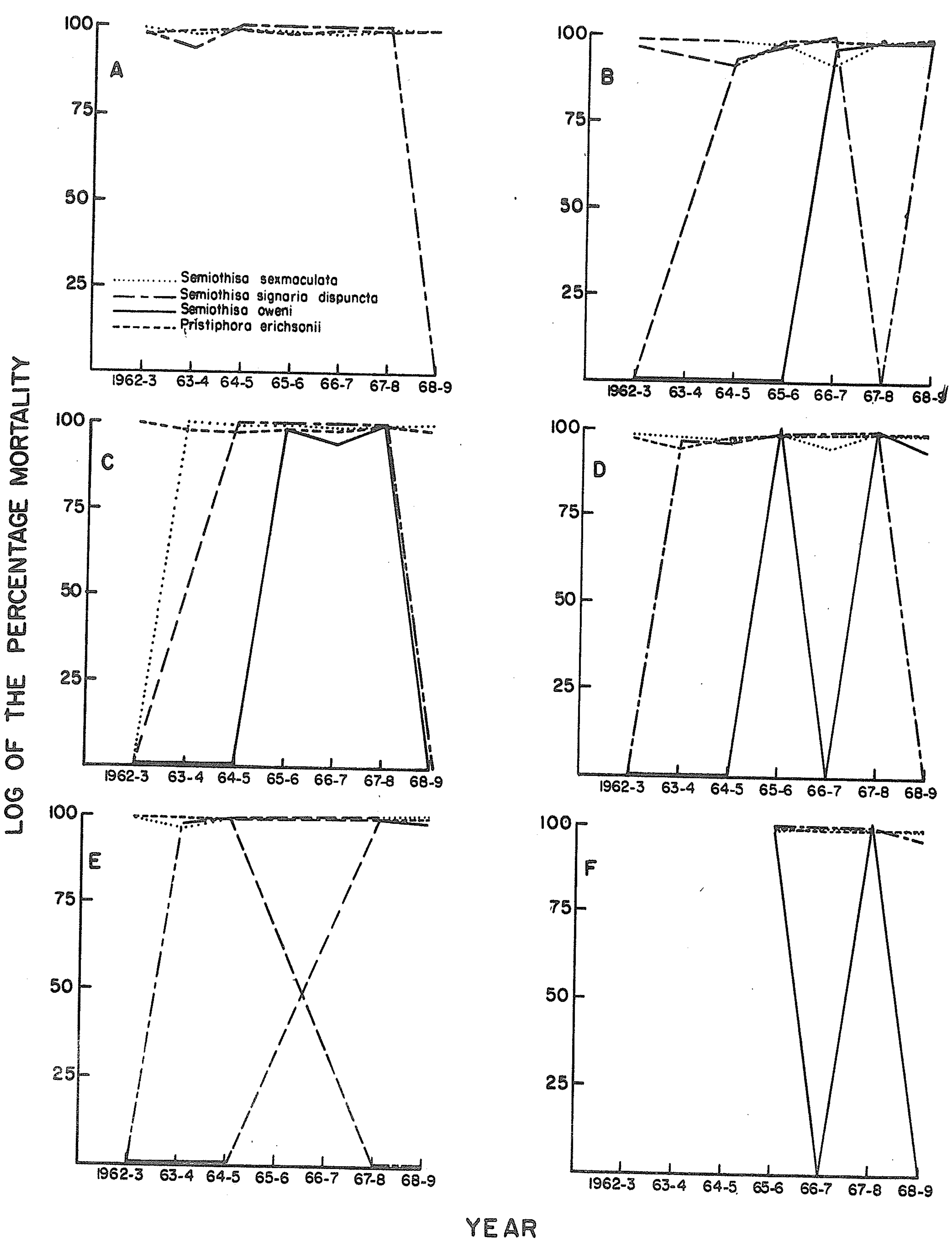
A
B
C
D
E
F
100
75
50
25
1962-3
63-4
64-5
65-6
66-7
67-8
68-9
Semiothisa sexmaculata
Semiothisa signaria dispuncta
Semiothisa oweni
Pristiphora erichsonii
LOG OF THE PERCENTAGE MORTALITY
YEAR

Figure 3. Relationships between the larch looper and the larch sawfly ground-inhabiting stages as shown by the number of dead individuals.

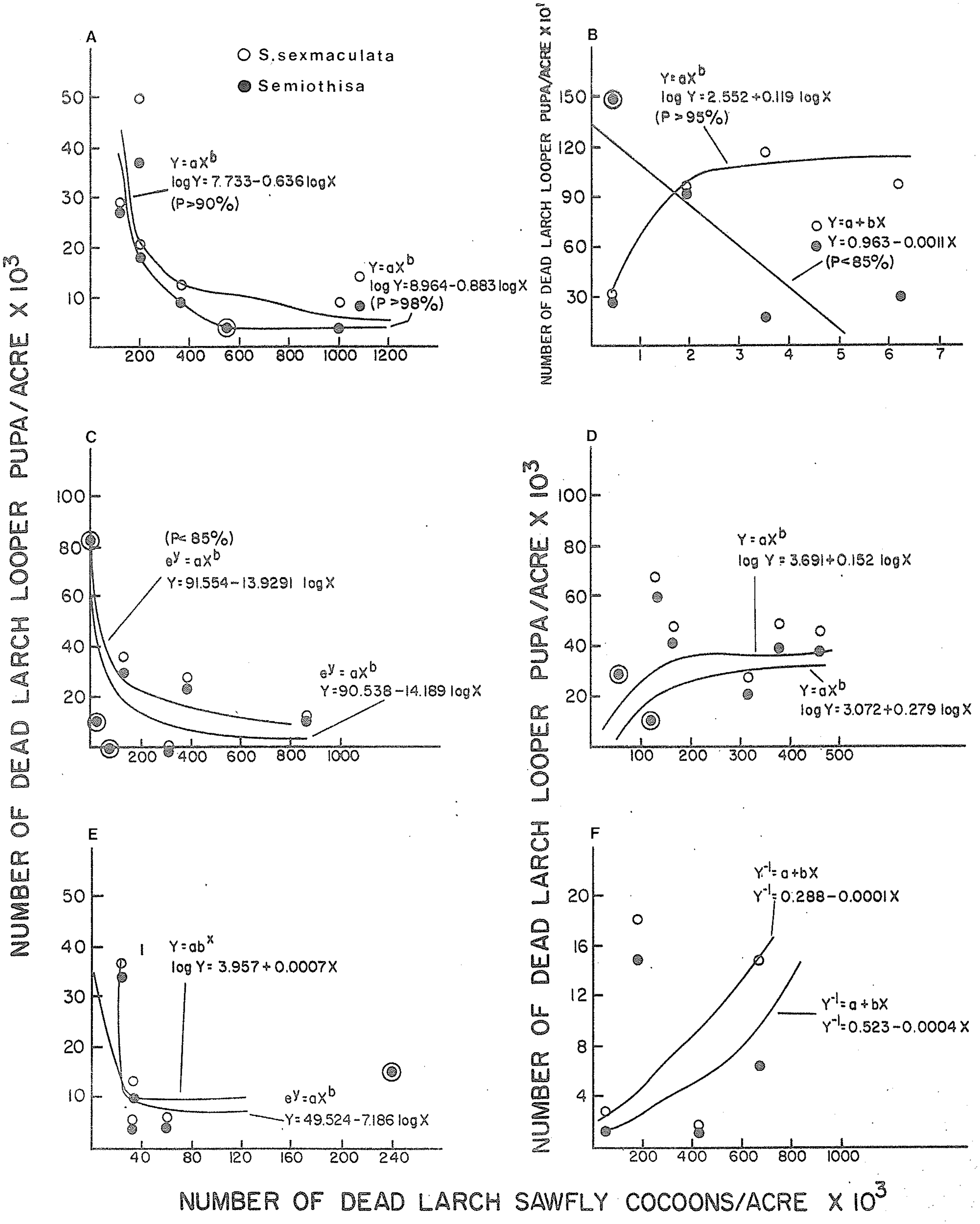
A
○ S. sexmaculata
● Semiothisa
Y=aX^b
log Y=7.733−0.636 log X
(P>90%)
Y=aX^b
log Y=8.964−0.883 log X
(P>98%)
B
Y=aX^b
log Y=2.552+0.119 log X
(P>95%)
○ Y=a+bX
● Y=0.963−0.0011X
(P<85%)
NUMBER OF DEAD LARCH LOOPER PUPA/ACRE X 10¹
C
(P<85%)
e^y=aX^b
Y=91.554−13.9291 log X
e^y=aX^b
Y=90.538−14.189 log X
D
Y=aX^b
log Y=3.691+0.152 log X
Y=aX^b
log Y=3.072+0.279 log X
NUMBER OF DEAD LARCH LOOPER PUPA/ACRE X 10³
E
Y=ab^X
log Y=3.957+0.0007X
e^y=aX^b
Y=49.524−7.186 log X
F
Y⁻¹=a+bX
Y⁻¹=0.288−0.0001X
Y⁻¹=a+bX
Y⁻¹=0.523−0.0004X
NUMBER OF DEAD LARCH LOOPER PUPA/ACRE X 10³
NUMBER OF DEAD LARCH SAWFLY COCOONS/ACRE X 10³

Figure 4. The small mammal populations of Manitoba bogs.

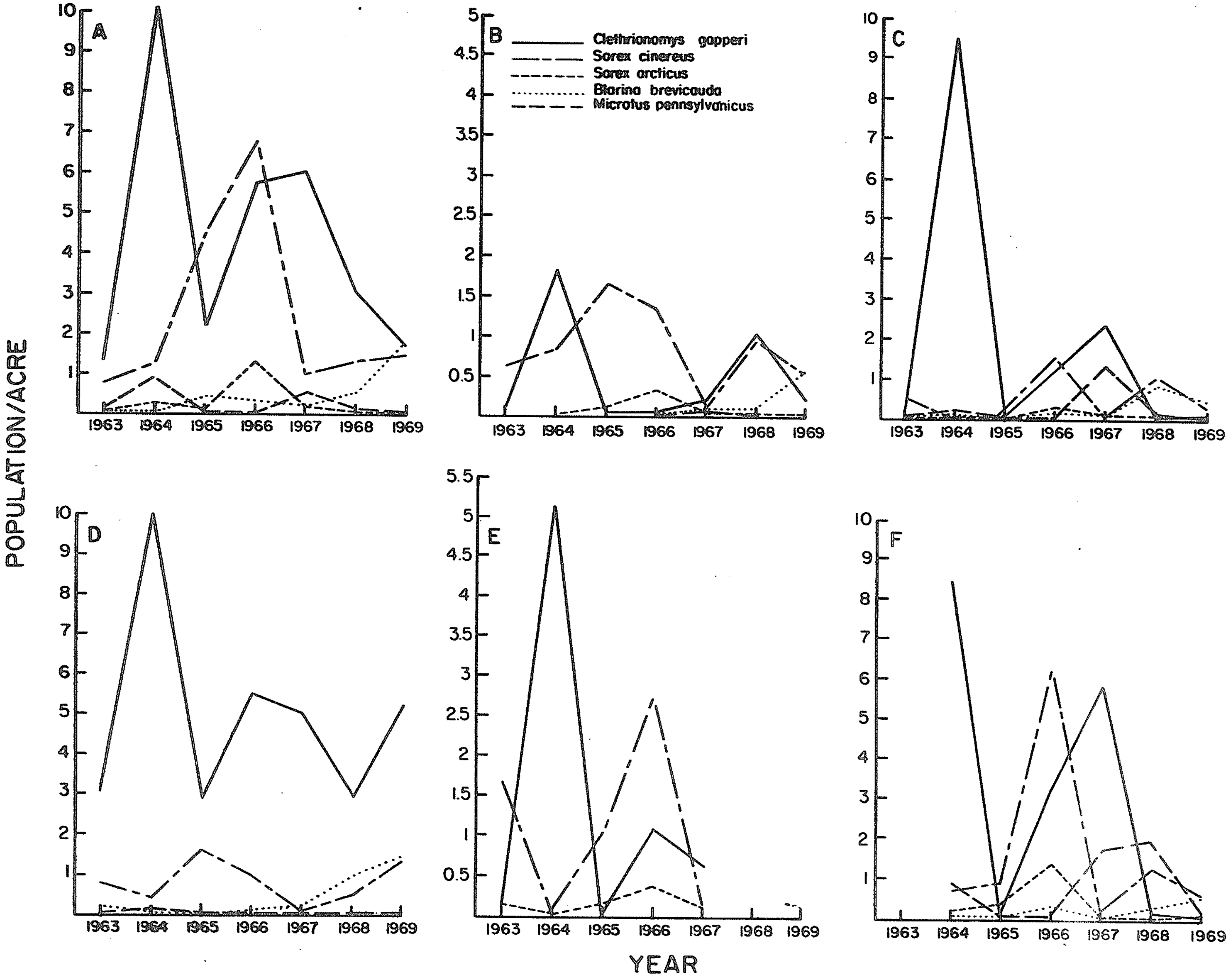
A
B
C
D
E
F
Clethrionomys gapperi
Sorex cinereus
Sorex arcticus
Blarina brevicauda
Microtus pennsylvanicus
POPULATION/ACRE
YEAR
1963
1964
1965
1966
1967
1968
1969
10
9
8
7
6
5
4
3
2
1
5.5
4.5
3.5
2.5
1.5
0.5

Figure 5. Larch looper populations in generation n+1 in relation to populations in generation n, with both expressed as common logarithms.

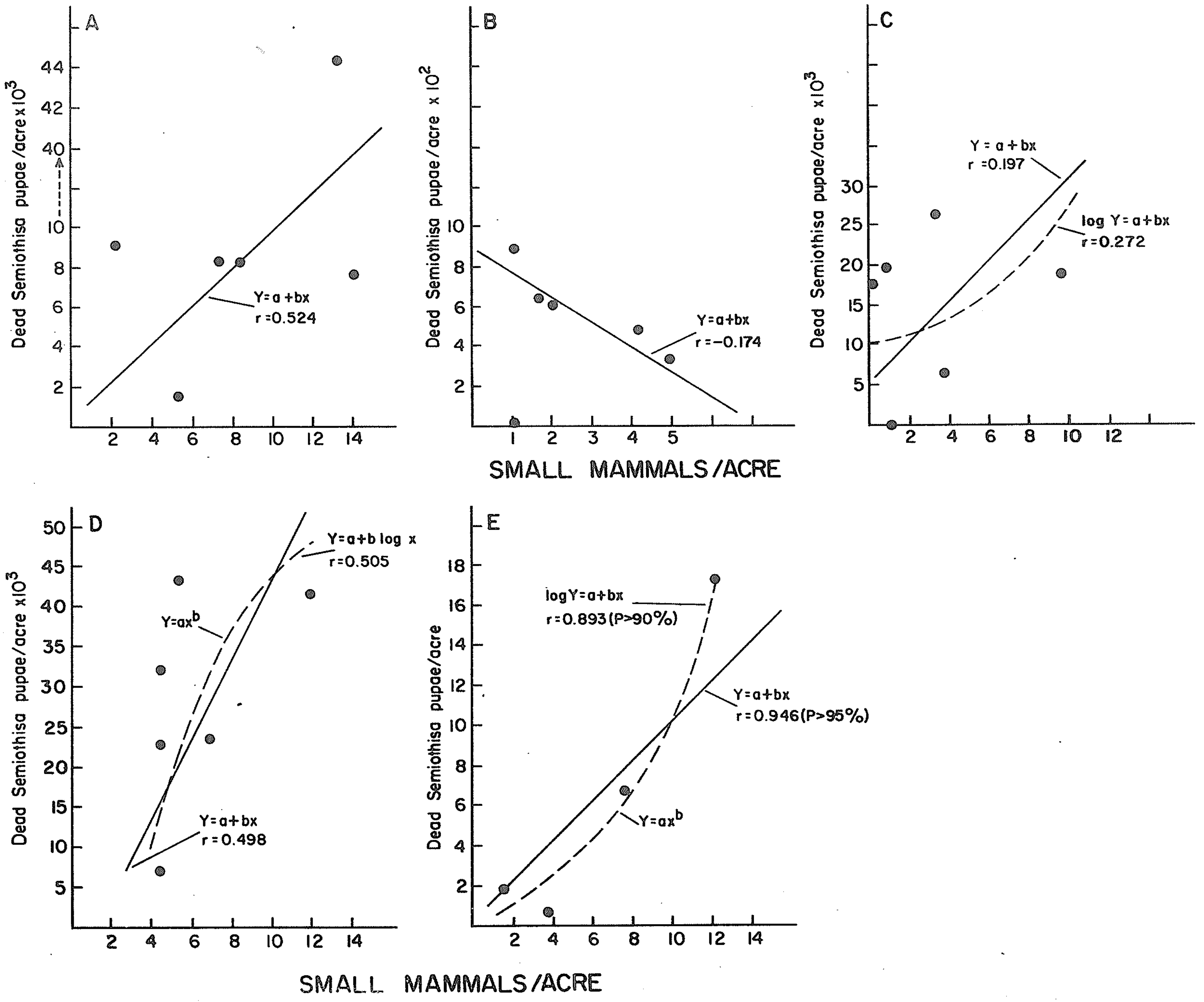
A
Dead Semiothisa pupae/acre x 10^3
44
42
40
10
8
6
4
2
2
4
6
8
10
12
14
Y=a+bx
r=0.524
B
Dead Semiothisa pupae/acre x 10^2
10
8
6
4
2
1
2
3
4
5
Y=a+bx
r=−0.174
C
Dead Semiothisa pupae/acre x10^3
30
25
20
15
10
5
2
4
6
8
10
12
Y = a + bx
r =0.197
log Y = a+bx
r=0.272
SMALL MAMMALS/ACRE
D
Dead Semiothisa pupae/acre x10^3
50
45
40
35
30
25
20
15
10
5
2
4
6
8
10
12
14
Y=a+b log x
r=0.505
Y=ax^b
Y=a+bx
r=0.498
E
Dead Semiothisa pupae/acre
18
16
14
12
10
8
6
4
2
2
4
6
8
10
12
14
log Y=a+bx
r=0.893(P>90%)
Y=a+bx
r=0.946(P>95%)
Y=ax^b
SMALL MAMMALS/ACRE

Table 1. The number of *Semiothisa* spp. larvae collected across Canada (after Prentice (ed.) 1963).

Year	No. larvae collected				Mean no. larvae/collection			
	sexmaculata	signaria	oweni	bicol.	sexmaculata	signaria	oweni	bicol.
1939	90	2027	11	0	6.0	4.6	1.6	0
1940	590	2343	138	0	5.6	3.4	5.2	0
1941	551	3387	19	0	7.0	3.1	1.2	0
1942	448	1483	10	0	2.9	2.2	1.4	0
1943	220	1133	2	0	4.1	2.2	1.0	0
1944	698	2025	18	57	5.4	2.8	3.0	9.5
1945	475	1490	22	2	4.1	2.9	7.3	1.0
1946	3042	2013	92	53	13.7	3.2	2.3	3.3
1947	1652	2052	140	10	8.7	2.7	4.4	1.0
1948	1366	2990	217	46	5.6	3.3	5.3	2.9
1949	3605	8823	72	10	7.9	4.6	3.0	2.5
1950	3441	7694	59	15	8.4	4.0	2.3	2.0
1951	2911	6150	78	127	5.9	3.5	2.2	2.1
1952	3156	3346	15	132	7.2	2.8	1.7	2.7
1953	3153	3177	35	182	7.7	2.3	1.6	2.7
1954	1650	2719	19	274	5.9	2.9	1.9	3.6
1955	4250	3966	7	62	16.3	3.2	1.0	1.7
1956	1269	3161	2	16	8.1	4.2	1.0	2.7
1957	701	413	1	0	6.9	1.7	1.0	0
1958	175	771	0	0	6.0	2.3	0	0

Table 2. The life table analysis of the green larch looper populations (*S.sexmaculata*).

a. Rennie

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$	S_x	minus form of log S_x	log l_x	k-value
1962	eggs	88012	52.4	.48	-0.32	4.945	.323
	larvae	41905	32.9	.67	-0.17	4.622	.173
	pupae	28120	95.9	.04	-1.40	4.449	1.402
	adults	1114				3.047	
				S_g=.0139	$\log S_g$=-1.89		K=1.898
1963	eggs	64896	54.1	.46	-0.34	4.812	.338
	larvae	29775	30.4	.70	-0.15	4.474	.158
	pupae	20713	90.0	.10	-1.00	4.316	.999
	adults	2075				3.317	
				S_g=.0322	$\log S_g$=-1.49		K=1.495
1964	eggs	137363	69.2	.31	-0.51	5.138	.512
	larvae	42249	11.8	.88	-0.06	4.626	.055
	pupae	37250	99.3	.01	-2.00	4.571	2.702
	adults	74				1.869	
				S_g=.0027	$\log S_g$=-2.57		K=3.269
1965	eggs	17667	31.0	.69	-0.16	4.247	.161
	larvae	12191	20.7	.79	-0.10	4.086	.100
	pupae	9672	99.3	.01	-2.00	3.986	2.153
	adults	68				1.833	
				S_g=.0055	$\log S_g$=-2.26		K=2.414

Table 2 a. Continued.

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1966	eggs	12586	43.4	.57	-0.24	4.100	.247
	larvae	7124	41.2	.59	-0.23	3.853	.231
	pupae	4185	93.4	.07	-1.15	3.622	1.181
	adults	276				2.441	
				S_g=.0235	$\log S_g$=-1.62		K=1.659
1967	eggs	22027	32.9	.67	-0.17	4.343	.173
	larvae	14788	43.7	.56	-0.25	4.170	.250
	pupae	8320	98.0	.02	-1.70	3.920	1.621
	adults	199				2.299	
				S_g=.0075	$\log S_g$=-2.12		K=2.044
1968	eggs	9890	45.6	.54	-0.27	3.995	.264
	larvae	5383	26.3	.74	-0.13	3.731	.132
	pupae	3968	99.4	.01	-2.00	3.599	2.237
	adults	23				1.362	
				S_g=.0040	$\log S_g$=-2.40		K=2.633
1969	eggs	8483	42.3	.58	-0.24	3.929	.239
	larvae	4898	30.4	.70	-0.15	3.690	.157
	pupae	3409	99.8	.01	-2.00	3.533	2.688
	adults	7				0.845	
				S_g=.0041	$\log S_g$=-2.39		K=3.084

b. Telford

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1962	eggs	7638	56.0	.44	-0.36	3.883	.356
	larvae	3363	51.7	.48	-0.32	3.527	.316
	pupae	1624	97.8	.02	-1.70	3.211	1.655
	adults	36				1.556	
				S_g=.0042	logS_g=-2.38		K=2.327
1963	eggs	1303	50.9	.49	-0.31	3.115	.309
	larvae	640	78.0	.28	-0.55	2.806	.657
	pupae	141	-----	---	-----	2.149	----
	adults	-				-----	
				S_g=-----	logS_g=-----		K=-----
1964	eggs	1454	48.1	.52	-0.28	3.163	.286
	larvae	754	62.2	.38	-0.42	2.877	.422
	pupae	285	94.4	.06	-1.22	2.455	1.161
	adults	16				1.294	
				S_g=.0119	logS_g=-1.92		K=1.869
1965	eggs	1586	39.6	.60	-0.22	3.200	.219
	larvae	958	66.2	.34	-0.47	2.981	.470
	pupae	324	93.2	.07	-1.15	2.511	1.169
	adults	22				1.342	
				S_g=.0143	logS_g=-1.84		K=1.858
1966	eggs	1595	45.5	.55	-0.26	3.203	.264
	larvae	869	71.3	.29	-0.54	2.939	.543
	pupae	249	70.3	.30	-0.52	2.396	.527
	adults	74				1.869	
				S_g=.0478	logS_g=-1.32		K=1.334

Table 2 b. Continued.

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1967	eggs	21296	50.3	.50	-0.30	4.328	.304
	larvae	10573	90.9	.09	-1.05	4.024	1.042
	pupae	960	97.7	.02	-1.70	2.982	1.640
	adults	22				1.342	
				S_g=.0009	$\log S_g$=-3.05		K=2.986
1968	eggs	13491	38.4	.62	-0.21	4.130	.210
	larvae	8313	92.6	.07	-1.15	3.920	1.131
	pupae	615	99.9	.01	-2.00	2.789	2.789
	adults	1*				0.000	
				S_g=.0004	$\log S_g$=-3.36		K=4.130
1969	eggs	13845	37.0	.63	-0.20	4.141	.201
	larvae	8717	99.9	.01	-2.00	3.940	3.940
	pupae	1*	----	---	-----	0.000	-----
	adults	-				-----	
				S_g=.0063	$\log S_g$=-2.20		K=4.141

* Transformation of 0 to (x+1).

c. Seddon's Corner

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1962	eggs	840324	55.3	.45	-0.35	5.924	.349
	larvae	375615	70.1	.30	-0.52	5.575	.610
	pupae	92250	00.0	1.00	0.00	4.965	.000
	adults	92250				4.965	
				S_g=.1350	$\log S_g$=-0.87		k=.959
1963	eggs	-----	----	----	-----	-----	----
	larvae	-----	----	----	-----	-----	----
	pupae	80360	99.8	.002	-2.70	4.905	2.805
	adults	126				2.100	
				S_g=-----	$\log S_g$=-----		K=----
1964	eggs	34592	36.0	.64	-0.19	4.539	.194
	larvae	22138	75.2	.25	-0.60	4.345	.243
	pupae	12636	95.0	.05	-1.30	4.102	1.303
	adults	630				2.799	
				S_g=.0080	$\log S_g$=-2.09		K=1.740
1965	eggs	93090	35.1	.65	-0.19	4.969	.188
	larvae	60413	47.6	.52	-0.28	4.781	.281
	pupae	31650	97.9	.02	-1.70	4.500	1.669
	adults	678				2.831	
				S_g=.0068	$\log S_g$=-2.17		K=2.138
1966	eggs	94802	36.4	.64	-0.19	4.977	.197
	larvae	60291	57.0	.43	-0.37	4.780	.373
	pupae	25285	97.5	.03	-1.52	4.403	1.590
	adults	650				2.813	
				S_g=.0083	$\log S_g$=-2.08		K=2.160

Table 2 c. Continued.

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1967	eggs	49253	67.7	.32	-0.49	4.692	.490
	larvae	15913	34.6	.65	-0.19	4.202	.185
	pupae	10413	99.4	.01	-2.00	4.017	2.191
	adults	67				1.826	
				S_g=.0021	logS_g=-2.68		K=2.866
1968	eggs	5459	45.1	.55	-0.26	3.737	.261
	larvae	2994	62.1	.38	-0.42	3.476	.421
	pupae	1136	00.0	1.00	0.00	3.055	.000
	adults	1136				3.055	
				S_g=.2090	logS_g=-0.68		K=0.682
1969	eggs	51847	41.9	.58	-0.24	4.715	.239
	larvae	29929	40.6	.59	-0.23	4.476	.226
	pupae	17789	98.2	.02	-1.70	4.250	1.743
	adults	322				2.507	
				S_g=.0068	logS_g=-2.17		K=2.208

d. Pine Falls

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1962	eggs	90868	56.2	.44	-0.36	4.958	.358
	larvae	39802	21.6	.78	-0.11	4.600	.106
	pupae	31188	95.1	.05	-1.30	4.494	1.311
	adults	1523				3.183	
				S_g=.0172	$\log S_g$=-1.77		K=1.775
1963	eggs	151001	41.3	.59	-0.23	5.179	.231
	larvae	88651	48.0	.52	-0.28	4.948	.284
	pupae	46104	91.9	.08	-1.10	4.664	1.090
	adults	3754				3.574	
				S_g=.0245	$\log S_g$=-1.61		K=1.605
1964	eggs	65987	37.8	.62	-0.21	4.819	.206
	larvae	41025	00.0	1.00	0.00	4.613	.000
	pupae	43918	89.1	.11	-0.96	4.613	.934
	adults	4773				3.679	
				S_g=.0682	$\log S_g$=-1.17		K=1.140
1965	eggs	43473	34.3	.66	-0.18	4.638	.024
	larvae	28568	00.0	1.00	0.00	4.614	.000
	pupae	28568	95.3	.05	-1.30	4.614	1.480
	adults	1261				3.134	
				S_g=.0330	$\log S_g$=-1.48		K=1.504
1966	eggs	89774	29.3	.43	-0.15	4.953	.315
	larvae	43451	43.4	.57	-0.20	4.638	.200
	pupae	27440	99.3	.01	-0.70	4.438	.687
	adults	5630				3.751	
				S_g=.0895	$\log S_g$=-1.05		K=1.202

Table 2 d. Continued.

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1967	eggs	249750	57.4	.43	-0.37	5.397	.371
	larvae	106321	43.4	.57	-0.24	5.026	.246
	pupae	60210	99.3	.01	-2.00	4.780	.687
	adults	427				3.751	
				S_g=.0025	$\log S_g$=-2.61		K=2.767
1968	eggs	50225	77.3	.23	-0.64	4.701	.645
	larvae	11384	00.0	1.00	0.00	4.056	.000
	pupae	11384	95.6	.04	-1.40	4.056	1.359
	adults	498				2.697	
				S_g=.0092	$\log S_g$=-2.04		K=2.004
1969	eggs	65471	36.5	.64	-0.19	4.816	.197
	larvae	41560	44.0	.56	-0.25	4.619	.252
	pupae	23278	98.2	.02	-1.70	4.367	1.742
	adults	422				2.625	
				S_g=.0072	$\log S_g$=-2.14		K=2.191

e. Riverton

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1962	eggs	43495	46.7	.53	-0.28	4.639	.274
	larvae	23182	31.5	.69	-0.16	4.365	.164
	pupae	15876	98.9	.01	-2.00	4.201	1.968
	adults	171				2.233	
				S_g=.0037	$\log S_g$=-2.44		K=2.406
1963	eggs	16301	48.6	.51	-0.28	4.212	.289
	larvae	8382	42.9	.57	-0.24	3.923	.243
	pupae	4784	86.7	.13	-0.89	3.680	.876
	adults	637				2.804	
				S_g=.0393	$\log S_g$=-1.41		K=1.408
1964	eggs	67488	39.3	.61	-0.21	4.829	.216
	larvae	40978	74.5	.26	-0.58	4.613	.594
	pupae	10450	99.6	.004	-4.40	4.019	2.417
	adults	40				1.602	
				S_g=.0006	$\log S_g$=-5.19		K=3.227
1965	eggs	63236	40.6	.59	-0.23	4.801	.226
	larvae	37560	44.4	.56	-0.25	4.575	.255
	pupae	20898	----	---	-----	4.320	----
	adults	-----				-----	
				S_g=-----	$\log S_g$=-----		K=-----

Table 2 e. Continued.

	Columns						
	1 x	2 l_x	3 $100q_x$ (%)	4 S_x	5 minus form of log S_x	6 log l_x	7 k-value
1966	eggs	------	----	---	-----	-----	----
	larvae	------	----	---	-----	-----	----
	pupae	738978	----	---	-----	5.869	----
	adults	------				-----	
				S_g=-----	logS_g=-----		K=-----
1967	eggs	50106	30.4	.70	-0.15	4.700	.158
	larvae	34860	00.0	1.00	0.00	4.542	.000
	pupae	34860	99.8	.002	-4.70	4.542	2.722
	adults	66				1.820	
				S_g=.0014	logS_g=-4.85		K=2.880
1968	eggs	32753	41.5	.59	-0.23	4.515	.233
	larvae	19164	74.6	.25	-0.60	4.282	.594
	pupae	4872	99.9	.01	-2.00	3.688	3.688
	adults	1*				0.000	
				S_g=.0015	logS_g=-2.83		K=4.515
1969	eggs	125959	43.0	.57	-0.24	5.100	.244
	larvae	71846	99.9	.01	-2.00	4.856	4.856
	pupae	1*	----	---	-----	0.000	----
	adults	-				-----	
				S_g=.0057	logS_g=-2.24		K=5.100

* Transformation of 0 to (x+1).

f. Darwin

	Columns						
	1	2	3	4	5	6	7
	x	1_x	$100q_x$ (%)	S_x	minus form of log S_x	log 1_x	k-value
1964	eggs	171787	47.4	.53	-0.28	5.235	.279
	larvae	90362	23.4	.77	-0.11	4.956	.116
	pupae	69230	----	---	-----	4.840	----
	adults	-----				-----	
				S_g=-----	logS_g=-----		K=-----
1965	eggs	6324	38.4	.62	-0.21	3.801	.210
	larvae	3895	61.2	.39	-0.41	3.591	.411
	pupae	1512	94.2	.06	-1.22	3.180	1.240
	adults	87				1.940	
				S_g=.0145	logS_g=-1.84		K=1.861
1966	eggs	40864	44.8	.55	-0.26	4.611	.258
	larvae	22558	31.3	.69	-0.16	4.353	.163
	pupae	15486	98.6	.01	-2.00	4.190	1.844
	adults	222				2.346	
				S_g=.0038	logS_g=-2.42		K=2.265
1967	eggs	87727	14.2	.86	-0.07	4.943	.066
	larvae	75280	91.1	.09	-1.05	4.877	1.052
	pupae	6690	98.9	.01	-2.00	3.825	1.944
	adults	76				1.881	
				S_g=.0008	logS_g=-3.12		K=3.062

Table 2 f. Continued.

	Columns						
	1	2	3	4	5	6	7
	x	1_x	$100q_x$ (%)	S_x	minus form of log S_x	log 1_x	k-value
1968	eggs	10838	45.5	.55	-0.26	4.035	.263
	larvae	5910	70.2	.30	-0.52	3.772	.526
	pupae	1763	94.0	.06	-1.22	3.246	1.221
	adults	106				2.025	
				S_g=.0099	$\log S_g$=-2.00		K=2.010
1969	eggs	9934	40.1	.60	-0.22	3.997	.222
	larvae	5953	31.9	.68	-0.17	3.775	.167
	pupae	4054	99.5	.01	-2.00	3.608	2.330
	adults	19				1.278	
				S_g=.0041	$\log S_g$=-2.39		K=2.719

g. Hodgson

	Columns						
	1	2	3	4	5	6	7
	x	l_x	$100q_x$ (%)	S_x	minus form of log S_x	log l_x	k-value
1967	eggs	18723	44.4	.56	-0.25	4.272	.251
	larvae	10409	60.8	.39	-0.41	4.021	.410
	pupae	4080	98.9	.01	-2.00	3.611	1.968
	adults	44				1.643	
				S_g=.0022	$\log S_g$=-2.66		K=2.629
1968	eggs	2109	40.3	.60	-0.22	3.324	.224
	larvae	1260	82.5	.18	-0.74	3.100	.756
	pupae	221	48.4	.52	-0.28	2.344	.287
	adults	114				2.057	
				S_g=.0566	$\log S_g$=-1.24		K=1.267
1969	eggs	16047	41.1	.59	-0.23	4.205	.230
	larvae	9447	49.7	.50	-0.30	3.975	.298
	pupae	4754	99.9	.01	-2.00	3.677	3.677
	adults	1*				0.000	
				S_g=.0029	$\log S_g$=-2.53		K=4.205

* Transformation of 0 to (x+1).

Table 3. Relationships between 3 species of larch looper larvae as analysed by the correlation method (with larvae collected by sampling traps).

Type of analysis	r values						
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
S.sexmaculata(n) vs							
S.sexmaculata(n+1)	0.232	0.003	0.155	0.005	-0.077	-0.314	-----
S.signaria(n)	0.487	-0.496	0.176	0.562	0.638	0.693	0.881
S.signaria(n+1)	-0.191	-0.363	-0.583	0.449	-0.176	0.455	-----
S.oweni(n)	0.007	0.128	0.442	0.237	0.478	0.212	0.299
S.oweni(n+1)	-0.413	0.091	0.683^{+}	-0.456	0.771*	-0.001	-----
S.signaria(n) vs							
S.signaria(n+1)	-0.205	0.013	0.030	0.469	0.439	0.890*	-----
S.oweni(n)	0.221	0.280	-0.027	-0.354	0.113	-0.317	-0.189
S.oweni(n+1)	0.407	0.593	0.723^{+}	-0.104	0.816*	0.028	-----
S.oweni(n) vs							
S.oweni(n+1)	-0.241	0.416	0.500	-0.024	0.480	-0.299	-----

* Probability ⩾ 95 % level.
\+ Probability ⩾ 90 % level.

Table 4. Relationships between 3 species of larch looper pupae as analysed by the correlation method.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
S.sexmaculata pupae/acre(n) vs						
S.sexmaculata pupae/acre(n+1)	0.448	-0.266	0.609	-0.311	-0.118	-0.467
S.signaria pupae/acre(n+1)	0.136	-0.349	-0.109	0.053	-0.468	-0.155
S.oweni pupae/acre(n+1)	-0.481	-0.156	-0.485	-0.317	0.786*	-0.049
S.signaria pupae/acre(n)	0.642+	-0.383	-0.236	0.722*	-0.473	0.991**
S.oweni pupae/acre(n)	-0.150	0.027	-0.479	0.635+	-0.799*	-0.147
S.signaria pupae/acre(n) vs						
S.signaria pupae/acre(n+1)	-0.151	0.255	-0.171	0.475	0.938*	-0.299
S.oweni pupae/acre(n+1)	-0.036	0.568	0.529	0.128	-0.067	-0.045
S.oweni pupae/acre(n)	0.121	0.337	-0.480	-0.283	0.049	-0.192
S.oweni pupae/acre(n) vs						
S.oweni pupae/acre(n+1)	-0.283	0.215	0.022	-0.188	-0.247	-0.301

** Probability ⩾ 99 % level.
* Probability ⩾ 95 % level.
+ Probability ⩾ 90 % level.

Table 5. Relationships between the larch looper and larch sawfly larvae as analysed by the correlation method (with larvae collected by sampling traps).

Type of analysis	r values						
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
P.erichsonii(n) vs							
S.sexmaculata(n)	-0.344	0.631^{+}	0.080	0.497	-0.047	-0.270	0.325
S.sexmaculata(n+1)	-0.347	0.818^{*}	-0.507	0.150	-0.150	-0.467	-----
S.signaria(n)	0.479	-0.002	-0.372	0.905^{**}	0.265	-0.844^{*}	-0.162
S.signaria(n+1)	-0.306	0	-0.568^{++}	0.564^{++}	0.182	-0.676	-----
S.oweni(n)	0.558^{++}	-0.047	0.697^{+}	-0.339	-0.336	0.369	0.999^{*}
S.oweni(n+1)	0.655^{++}	0.420	0.103	-0.076	-0.081	-0.319	-----

** Probability > 99 % level.
* Probability > 95 % level.
\+ Probability > 90 % level.
\++ Probability > 85 % level.

Table 6. Relationships among the ground-inhabiting stages of larch looper and larch sawfly populations as analysed by the correlation method.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
P.erichsonii cocoons/acre(n) vs						
S.sexmaculata pupae/acre(n+1)	-0.539	0.018	-0.277	0.277	0.200	-0.505
S.signaria pupae/acre(n+1)	-0.456	0.324	-0.368	0.486	0.096	-0.721
S.oweni pupae/acre(n+1)	0.533	0.679^{+}	0.403	0.227	-0.619^{++}	-0.208
P.erichsonii cocoons/acre(n) vs						
S.sexmaculata pupae/acre (n)	-0.653^{+}	-0.464	-0.567	0.264	0.068	-0.498
S.signaria pupae/acre (n)	-0.105	0.155	-0.306	0.893^{**}	-0.289	-0.475
S.oweni pupae/acre (n)	0.581	-0.101	0.745^{*}	-0.272	-0.165	0.777

** Probability ≥ 99 % level.
* Probability ≥ 95 % level.
\+ Probability ≥ 90 % level.
++ Probability ≥ 85 % level.

Table 7. The percentage of larch sawfly cocoons destroyed by small mammals (after the 'Annual Report of Forest Research Technicians, Larch Sawfly Population Dynamics 1963-1970').

	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
Insectivores	31.5	21.0	7.5	3.0	23.5	----	----
Rodents	14.5	12.5	10.0	16.5	16.0	----	----
Total 1962-63	46.0	33.5	17.5	19.5	39.5	----	----
Insectivores	12.0	17.5	12.5	14.5	30.5	----	----
Rodents	29.0	5.5	10.5	23.5	5.5	----	----
Total 1963-64	41.0	23.0	23.0	38.0	36.0	----	----
Insectivores	50.0	68.2	41.0	44.0	46.0	28.6	----
Rodents	34.5	23.8	54.5	36.7	40.1	50.8	----
Total 1964-1965	84.5	92.0	95.5	80.7	86.2	79.4	----
Insectivores	50	33	42	42	43	42	----
Rodents	11	26	5	19	5	16	----
Total 1965-66	61	59	47	61	48	58	----
Insectivores	51	44	70	65	45	67	----
Rodents	24	9	12	16	39	25	----
Total 1966-67	75	53	82	81	84	92	----
Insectivores	34.9	70.8	41.6	52.2	35.5	6.4	----
Rodents	20.4	14.2	17.6	27.4	43.6	37.1	----
Total 1967-68	55.3	85.0	59.2	79.6	79.1	43.5	----
Insectivores	35	49	27	40	----	34	----
Rodents	2	17	7	27	----	9	----
Total 1968-69	37	66	34	67	----	43	----

Table 8. Relationships between the small mammal populations per acre and the estimated numbers of larch looper adults per acre as analysed by the correlation method.

Type of analysis	r avlues					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
C.gapperi/acre(n) vs						
S.sexmaculata/acre(n+1)	-0.483	-0.542	-0.079	0.544	-0.612	0.069
S.signaria/acre(n+1)	-0.544	-0.387	-0.284	0.670	-0.540	-0.695
S.oweni/acre(n+1)	-0.033	-0.611	-0.126	0.125	-0.091	0.213
S.cinereus/acre(n) vs						
S.sexmaculata/acre(n+1)	-0.295	0.324	0.434	0.151	0.984^{++}	0.908^{**}
S.signaria/acre(n+1)	-0.235	0.605	0.365	0	0.992^{+}	-0.229
S.oweni/acre(n+1)	0.726^{+}	0.702^{++}	-0.041	0.192	-0.705	0.988^{*}
S.arcticus/acre(n) vs						
S.sexmaculata/acre(n+1)	-0.210	0.843^{+}	0	0	0.726	0.948^{*}
S.signaria/acre(n+1)	-0.273	-0.202	-0.212	0	0.712	-0.376
S.oweni/acre(n+1)	0.868	0.383	0.538	0	-0.160	0.965^{*}
B.brevicauda/acre(n) vs						
S.sexmaculata/acre(n+1)	-0.455	-0.513	0.818^{*}	-0.457	0	0.815
S.signaria/acre(n+1)	-0.474	-0.519	0.930^{**}	-0.335	0	0.358
S.oweni/acre(n+1)	0.053	-0.490	-0.398	-0.140	0	0.725

Table 8. Continued.

Type of analysis	r values					
	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin
P.maniculatus/acre(n) vs						
S.sexmaculata/acre(n+1)	0	-0.084	0	0.699++	0	0.981*
S.signaria/acre(n+1)	0	-0.296	0	0.901*	0	-0.361
S.oweni/acre(n+1)	-0.274	-0.027	0	0	0	0.999**
M.pennsylvanicus/acre(n) vs						
S.sexmaculata/acre(n+1)	-0.266	-0.699	-0.540	0	0	-0.523
S.signaria/acre(n+1)	-0.407	-0.149	-0.258	0	0	0.519
S.oweni/acre(n+1)	-0.459	-0.152	0.075	0	0	-0.574

** Probability > 99 % level.
* Probability > 95 % level.
\+ Probability > 90 % level.
++ Probability > 85 % level.

Table 9. The estimated populations per acre of the green larch looper life stages (*S. sexmaculata* Pack.).

a. The estimated populations of adults.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	2260	616	19668	8519	1172	---	---
1963	1144	36	0	1523	171	---	---
1964	2075	-	126	3754	637	943	---
1965	74	16	630	4773	40	-	---
1966	68	22	678	1361	-	87	---
1967	276	74	650	5630	-	222	342
1968	169	22	67	427	66	76	44
1969	23	0	1306	498	0	106	114

b. The estimated egg populations.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	88012	7638	840324	90868	43495	-	-
1963	64896	1303	0	151001	16301	-	-
1964	137363	1454	34592	65987	67488	171787	-
1965	17667	1586	93090	43473	63236	6324	-
1966	12586	1595	94802	89774	0	40864	-
1967	22027	21296	49253	249750	50106	87727	18723
1968	9890	13491	5459	50225	32753	10838	2109
1969	8483	13845	51847	65471	125959	9934	16047

c. The gross number and percentage of eggs lost from the egg to the larval stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	46107	4275	464709	51066	20313	-	-
	52.4	55.9	55.9	56.2	46.7	-	-
1963	35121	663	—	62350	7919	-	-
	54.1	50.9	100.0	41.3	48.6	-	-
1964	95114	700	12454	24962	26510	81425	-
	69.2	48.1	36.0	37.8	39.3	47.4	-
1965	5476	628	32677	14909	25676	2429	-
	30.9	39.6	35.1	34.3	40.6	38.4	-
1966	5462	10726	34511	126323	—	18306	-
	43.4	45.5	36.4	29.3	100.0	44.8	-
1967	7239	10723	33340	143429	26264	12447	8314
	32.9	50.3	67.7	57.4	52.4	14.2	44.4
1968	4507	5178	2465	47306	13589	4928	849
	45.6	38.4	45.1	94.2	41.5	45.5	40.3
1969	3585	5128	21918	23911	54113	3981	6600
	42.3	37.0	41.9	36.5	42.9	40.1	41.1

d. The estimated populations of larvae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	41905	3363	375615	39802	23182	-	-
1963	29775	640	0	88651	8382	-	-
1964	42249	754	22138	41025	40978	90362	-
1965	12191	958	60413	28564	37560	3895	-
1966	7124	869	60291	43451	0	22558	-
1967	14788	10573	15913	106321	23842	75280	10409
1968	5383	8313	2994	2919	19164	5910	1260
1969	4898	8717	29929	41560	71846	5953	9447

e. The gross number and percentage of larvae lost from the larval to the pupal stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	13785	1739	263365	8614	7306	-	-
	32.9	51.7	70.1	21.6	31.5	-	-
1963	9062	499	0	42547	3598	-	-
	30.4	77.9	00.0	47.9	42.9	-	-
1964	4999	469	9502	0	30528	21132	-
	11.8	62.2	75.2	00.0	74.5	23.4	-
1965	2519	634	28763	0	16662	2383	-
	20.7	66.2	47.6	00.0	44.4	61.2	-
1966	2939	620	34356	16011	0	7072	-
	41.2	71.3	56.9	36.8	00.0	31.3	-
1967	6468	9613	5500	46111	0	68590	6329
	43.7	90.0	34.6	43.4	00.0	91.1	60.8
1968	1415	7698	1858	0	14292	4147	1039
	26.2	92.6	62.1	00.0	74.6	70.2	82.5
1969	1489	8717	12140	18282	71846	1899	4693
	30.4	100.0	40.6	43.9	100.0	31.9	49.7

f. The estimated populations of pupae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	28120	1624	92250	31188	15876	-	-
1963	20713	141	80360	46104	4784	-	-
1964	37250	285	12636	43918	10450	69230	-
1965	9672	324	31650	41151	20898	1512	-
1966	4185	249	25935	27440	738978	15486	-
1967	8320	960	10413	60210	34860	6690	4080
1968	3968	615	1136	11384	4872	1763	221
1969	3409	0	17789	23278	0	4054	4754

g. The gross number and percentage of pupae lost from the pupae to the adult stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	26976	1588	0	29665	15705	-	-
	95.9	97.8	00.0	95.1	98.9	-	-
1963	18638	----	80234	42350	4147	-	-
	89.9	----	99.8	91.9	86.7	-	-
1964	36976	269	12006	39145	10410	-	-
	99.3	94.4	95.0	89.1	99.6	-	-
1965	9604	302	30972	39790	-----	1425	-
	99.3	93.2	97.9	96.7	-----	94.2	-
1966	3909	175	25285	21810	-----	15264	-
	93.4	70.3	97.5	79.5	-----	98.6	-
1967	8151	938	10346	59783	34794	6614	4036
	97.9	97.7	99.4	99.3	99.8	98.9	98.9
1968	3945	615	0	10886	4872	1657	107
	99.4	100.0	00.0	95.6	100.0	93.9	48.4

h. The number of larvae collected in larvae sampling traps (oil drop funnels).

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	71	14	123	92	42	-	-
1963	65	3	41	136	16	-	-
1964	125	3	36	136	95	230	-
1965	39	3	150	129	86	24	-
1966	31	3	133	56	87	87	-
1967	52	20	89	135	60	117	30
1968	14	10	7	35	14	20	3
1969	18	22	51	53	93	18	38

Table 10. The estimated populations per acre of the brown larch looper life stages (*S. signaria dispuncta* Gn.).

a. The estimated populations of adults.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	258	0	640	0	0	-	-
1963	176	24	0	202	75	-	-
1964	813	--	73	773	208	160	-
1965	27	26	76	1295	12	---	-
1966	97	81	97	316	--	17	-
1967	106	0	22	167	--	11	11
1968	0	2	19	0	0	8	0
1969	22	0	589	85	0	47	9

b. The estimated egg populations.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	8677	0	27328	0	0	-	-
1963	9984	869	-----	19985	7132	-	-
1964	53846	485	20179	13586	22022	29129	-
1965	6342	2642	11171	11795	19853	6324	-
1966	17864	5848	13543	20840	-----	7985	-
1967	12284	0	1660	7400	0	4499	624
1968	0	1349	1560	0	0	1084	0
1969	8012	1259	23382	11118	10835	4415	1267

c. The gross number and percentage of eggs lost from the egg to the larval stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	4546 52.4	0 00.0	15113 55.3	0 00.0	0 00.0	- -	- -
1963	4850 48.6	442 50.9	----- -----	8233 41.2	3493 48.9	- -	- -
1964	37262 69.2	233 48.0	7265 36.0	5176 38.1	8625 39.2	14330 49.2	- -
1965	1966 31.0	1046 39.6	3921 35.1	4045 34.3	8061 40.6	2429 38.4	- -
1966	7753 43.4	2661 45.5	4930 36.4	10753 37.3	---- ----	3577 44.8	- -
1967	6056 49.3	0 00.0	833 50.2	4248 57.4	0 00.0	1939 43.1	277 44.4
1968	0 00.0	518 38.4	711 45.6	0 00.0	0 00.0	483 44.6	0 00.0
1969	3389 42.3	467 37.1	9889 42.3	4060 36.5	4655 42.9	1771 40.1	1052 93.4

d. The estimated populations of larvae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	4131	0	12215	0	0	-	-
1963	5134	427	0	11752	3659	-	-
1964	16584	252	12914	8410	13377	14799	-
1965	4376	1596	7250	7750	11792	3895	-
1966	10111	3187	8613	10087	0	4408	-
1967	6228	0	827	3152	0	2560	347
1968	0	831	855	0	0	591	0
1969	4623	792	13493	7058	6180	2644	745

e. The gross number and percentage of larvae lost from the larval to the pupal stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	1359	0	9214	0	0	-	-
	39.2	00.0	75.4	00.0	00.0	-	-
1963	1977	332	----	5656	1564	-	-
	38.5	77.7	----	48.1	42.7	-	-
1964	1981	157	5537	0	9955	3025	-
	11.9	62.3	42.9	00.0	74.4	20.4	-
1965	908	818	3445	0	5239	2388	-
	20.7	51.2	47.5	00.0	44.4	61.3	-
1966	4167	2277	4907	3713	----	1371	-
	41.2	71.4	56.9	36.8	----	31.1	-
1967	1597	----	374	1368	0	1220	211
	25.6	----	45.2	34.6	00.0	47.7	60.8
1968	0	770	530	0	0	415	0
	00.0	92.7	61.9	00.0	00.0	70.2	00.0
1969	1403	669	5471	3105	4636	617	370
	30.3	84.5	40.5	43.9	75.0	23.3	49.7

f. The estimated populations of pupae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	2772	0	3001	0	0	-	-
1963	3157	95	0	6096	2095	-	-
1964	14603	95	7377	9047	3422	11774	-
1965	3468	778	3805	11179	6553	1507	-
1966	5944	910	3706	6374	0	3037	-
1967	4631	0	453	1784	0	1340	136
1968	0	61	325	0	0	176	0
1969	3220	123	8022	3953	1544	2027	375

g. The gross number and percentage of pupae lost from the pupal to the adult stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	2596	0	0	0	0	-	-
	93.6	00.0	00.0	00.0	00.0	-	-
1963	2344	-	0	5323	1885	-	-
	74.2	-	00.0	87.3	89.9	-	-
1964	14576	69	7301	7752	3410	-	-
	99.8	72.6	98.9	85.7	99.6	-	-
1965	3369	697	3708	10863	----	1490	-
	97.1	89.6	97.4	97.2	----	98.9	-
1966	5838	910	3684	6207	----	3026	-
	98.2	100.0	99.4	97.4	----	99.6	-
1967	4631	0	434	1784	0	1332	136
	100.0	00.0	95.8	100.0	00.0	99.4	100.0
1968	0	61	0	0	0	129	0
	00.0	100.0	00.0	00.0	00.0	73.3	00.0

h. The number of larvae collected in larvae sampling traps (oil drop funnels).

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	7	0	4	0	0	-	-
1963	10	2	7	18	7	-	-
1964	49	1	21	28	31	39	-
1965	14	5	18	35	27	24	-
1966	44	11	19	13	9	17	-
1967	29	0	3	4	0	6	1
1968	0	1	2	0	0	2	0
1969	17	2	23	9	8	8	3

Table 11. The estimated populations per acre of S.oweni Swett. life stages.

a. The estimated populations of adults.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
1963	0	0	0	0	0	-	-
1964	17	0	0	0	0	4	-
1965	0	0	4	37	3	-	-
1966	0	7	15	0	-	0	-
1967	58	4	15	584	-	61	46
1968	0	2	10	37	9	0	0
1969	3	0	0	26	28	0	0

b. The estimated egg populations.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
1963	0	0	0	0	0	-	-
1964	1099	0	0	0	0	747	-
1965	0	0	621	337	4412	527	-
1966	0	532	2138	0	0	0	-
1967	4660	1065	1107	25900	3340	23994	2496
1968	0	1349	780	4305	4679	0	0
1969	943	0	0	1235	4063	0	0

c. The gross number and percentage of eggs lost from the egg to the larval stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0 00.0	0 00.0	0 00.0	0 00.0	0 00.0	- -	- -
1963	0 00.0	0 00.0	0 00.0	0 00.0	0 00.0	- -	- -
1964	761 69.2	0 00.0	0 00.0	0 00.0	0 00.0	368 49.3	- -
1965	0 00.0	0 00.0	218 35.1	116 34.4	1792 40.6	202 38.3	- -
1966	0 00.0	242 45.5	778 36.4	0 00.0	0 00.0	0 00.0	- -
1967	2298 49.3	536 50.3	556 50.2	14866 57.4	1747 52.3	10352 43.1	1067 42.7
1968	0 00.0	518 38.4	352 45.0	4055 94.2	1941 41.5	0 00.0	0 00.0
1969	404 42.8	0 00.0	0 00.0	451 36.5	1746 42.9	0 00.0	0 00.0

d. The estimated populations of larvae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
1963	0	0	0	0	0	-	-
1964	338	0	0	0	0	379	-
1965	0	0	403	221	2620	325	-
1966	0	290	1360	0	0	0	-
1967	2362	529	551	11034	1593	13652	1429
1968	0	831	428	250	2738	0	0
1969	539	0	0	784	2317	0	0

e. The gross number and percentage of larvae lost from the larval to the pupal stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0 00.0	0 00.0	0 00.0	0 00.0	0 00.0	- -	- -
1963	0 00.0	0 00.0	0 00.0	0 00.0	0 00.0	- -	- -
1964	40 11.8	0 00.0	0 00.0	0 00.0	0 00.0	77 20.3	- -
1965	0 00.0	0 00.0	190 47.1	0 00.0	1164 44.4	199 61.2	- -
1966	0 00.0	207 71.4	1301 95.7	0 00.0	0 00.0	0 00.0	- -
1967	605 25.6	481 90.9	249 45.2	4787 43.3	0 00.0	6507 47.7	885 61.9
1968	0 00.0	770 92.7	260 60.7	146 58.4	2042 74.6	0 00.0	0 00.0
1969	160 29.7	0 00.0	0 00.0	345 47.8	1738 75.0	0 00.0	0 00.0

f. The estimated populations of pupae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
1963	0	0	0	0	0	-	-
1964	298	0	0	0	0	302	-
1965	0	0	213	319	1456	126	-
1966	0	83	59	0	0	0	-
1967	1757	48	302	6247	2323	7145	544
1968	0	61	162	104	696	0	0
1969	379	0	0	439	579	0	0

g. The gross number and percentage of pupae lost from the pupal to the adult stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
	00.0	00.0	00.0	00.0	00.0	-	-
1963	0	0	0	0	0	-	-
	00.0	00.0	00.0	00.0	00.0	-	-
1964	298	0	0	0	0	-	-
	100.0	00.0	00.0	00.0	00.0	-	-
1965	0	0	198	319	-	126	-
	00.0	00.0	92.9	100.0	----	100.0	-
1966	0	79	44	0	0	0	-
	00.0	95.2	74.6	00.0	00.0	00.0	-
1967	1757	46	292	6210	2314	7145	544
	100.0	95.8	96.7	99.4	99.6	100.0	100.0
1968	0	61	162	78	668	0	0
	00.0	100.0	100.0	75.0	95.8	00.0	00.0

h. The number of larvae collected in larvae sampling traps (oil drop funnels).

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	0	0	0	0	0	-	-
1963	0	0	0	0	0	-	-
1964	1	0	0	0	0	1	-
1965	0	0	1	1	6	2	-
1966	0	1	3	0	6	0	-
1967	11	1	2	14	4	32	4
1968	0	1	1	3	2	0	0
1969	2	0	0	1	3	0	0

Table 12. The estimated populations per acre of the larch sawfly (*P. erichsonii* Htg.) life stages (after the 'Annual Report of Forest Research Technicians, Larch Sawfly Population Dynamics 1962-70'.).

a. The estimated populations of adults.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	11979	220	1439	19173	18014	-	-
1963	11543	83	75	6970	2178	-	-
1964	10890	-	218	43342	1960	653	-
1965	2831	218	2831	45738	218	-	-
1966	16988	331	11107	16553	-	1089	-
1967	36808	165	42253	12850	-	6752	21997
1968	23740	165	19384	4575	436	18949	5663
1969	2831	0	19384	2831	0	10019	1307

b. The estimated egg populations.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	402981	2728	61487	204459	667935	-	-
1963	654949	3040	5281	688400	206823	-	-
1964	721964	3392	59573	761802	208865	118015	-
1965	686714	22195	421990	416897	347044	206563	-
1966	3084347	23920	1555240	1091723	105243	501655	-
1967	2916831	47916	3195473	569815	37580	2646028	1203230
1968	1381001	99837	1577638	538135	215238	2682078	272068
1969	1014273	156704	770613	371828	107000	932133	183700

c. The estimated populations of Vth. instar larvae.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	191819	1201	27484	89555	356010	-	-
1963	336771	1496	2905	404799	106100	-	-
1964	222364	1761	38126	471555	126868	59950	-
1965	473873	13406	273871	273901	206144	127243	-
1966	1745741	13036	989132	528393	53989	276913	-
1967	1478833	23814	1591345	242741	17926	1505591	668996
1968	751731	61515	865186	327530	125938	1462338	162547
1969	585902	98652	444840	236044	61031	558986	108151

d. The estimated populations of cocoons.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	128720	579	6752	73399	244154	-	-
1963	207128	331	1960	209959	60766	-	-
1964	195802	662	21780	507256	32452	47698	-
1965	375487	6535	143748	395089	114563	49223	-
1966	1026274	3722	425581	333887	8494	190793	-
1967	1099672	2178	872507	137432	26136	788000	262013
1968	554083	4550	328442	121968	32017	436253	28532
1969	407504	15303	264409	132205	15246	427977	54450

e. The gross number and percentage of cocoons lost from the cocoon to the adult stage.

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	117177 91.0	496 85.7	6677 98.9	66429 90.5	241976 99.1	- -	- -
1963	196238 94.7	--- ----	1742 88.9	166617 79.3	58806 96.8	- -	- -
1964	192971 98.5	444 67.1	18949 87.0	461518 90.9	32234 99.3	- -	- -
1965	358499 95.5	6204 94.9	132641 92.3	378536 95.8	----- ----	48134 97.8	- -
1966	989466 96.4	3557 95.6	383328 90.1	321037 96.1	----- ----	184041 96.5	- -
1967	1075932 97.8	2013 92.4	853123 97.8	132858 96.7	25700 98.3	769051 97.6	256350 97.8
1968	551252 99.5	4550 100.0	308058 93.8	119137 97.7	32017 100.0	426234 97.7	27225 95.4

f. The number of larvae collected in larvae sampling traps (oil drop funnels).

Year	Rennie	Telford	Seddon's Corner	Pine Falls	Riverton	Darwin	Hodgson
1962	325	5	9	207	645	–	–
1963	656	7	0	620	203	–	–
1964	657	7	62	1570	294	158	–
1965	1516	42	680	1237	472	784	–
1966	7597	45	2182	681	0	1068	–
1967	6886	45	5774	308	45	3529	1928
1968	1955	74	2023	375	92	4949	387
1969	2152	249	758	301	79	1689	435

Table 13. Small mammal populations per acre (after the 'Annual Report of Forest Research Technicians, Larch Sawfly Population Dynamics 1962-70'.).

a. *Clethrionomys gapperi loringi.*

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	1.38	10.5	2.23	5.74	6.06	3.19	1.70
Telford	0.11	1.81	0.00	0.00	0.21	1.06	0.21
Seddon's Corner	0.19	9.45	0.09	1.28	2.39	0.00	0.09
Pine Falls	3.08	10.7	2.87	5.53	5.00	2.98	5.32
Riverton	0.09	5.14	0.09	1.10	0.64	----	----
Darwin	----	8.51	0.21	3.19	5.74	0.21	0.00
Hodgson	----	----	----	----	4.36	0.43	6.38

b. *Peromyscus maniculatus bairdii.*

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	0.00	0.25	0.00	0.00	0.00	0.00	0.08
Telford	0.00	0.00	0.00	0.00	0.17	0.00	0.00
Seddon's Corner	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pine Falls	0.33	0.74	0.00	0.17	0.00	0.00	0.00
Riverton	0.00	0.00	0.00	0.00	0.00	----	----
Darwin	----	1.49	0.00	0.66	0.00	0.00	0.33
Hodgson	----	----	----	----	0.00	0.00	0.08

Table 13. Continued.

c. Microtus pennsylvanicus.

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	0.00	0.95	0.00	0.00	0.59	0.12	0.00
Telford	0.35	2.35	0.35	0.00	0.47	2.00	0.00
Seddon's Corner	0.11	0.20	0.00	0.00	1.33	0.10	0.00
Pine Falls	0.00	0.12	0.00	0.00	0.00	0.00	0.00
Riverton	0.00	0.00	0.00	0.10	0.00	----	----
Darwin	----	0.94	0.12	0.12	1.76	2.00	0.00
Hodgson	----	----	----	----	0.24	0.00	0.12

d. Sorex cinereus cinereus.

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	0.80	1.28	4.56	6.80	1.04	1.36	1.52
Telford	0.64	0.80	1.68	1.36	0.16	0.96	0.56
Seddon's Corner	0.58	0.07	0.00	1.57	0.00	1.16	0.34
Pine Falls	0.80	0.48	1.60	1.04	0.16	0.56	1.28
Riverton	1.71	0.14	1.03	2.74	0.27	----	----
Darwin	----	0.72	0.88	6.32	0.24	1.28	0.48
Hodgson	----	----	----	----	0.00	0.00	0.88

Table 13. Continued.

e. *Sorex arcticus*.

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	0.00	0.31	0.16	1.33	0.31	0.08	0.00
Telford	0.00	0.00	0.08	0.31	0.00	0.08	0.00
Seddon's Corner	0.00	0.00	0.00	0.27	0.00	0.00	0.00
Pine Falls	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Riverton	0.20	0.00	0.13	0.40	0.13	----	----
Darwin	----	0.23	0.39	1.41	0.00	0.08	0.08
Hodgson	----	----	----	----	0.00	0.00	0.00

f. *Blarina brevicauda manitobensis*.

Plot	1963	1964	1965	1966	1967	1968	1969
Rennie	0.00	0.00	0.45	0.36	0.27	0.54	1.71
Telford	0.00	0.00	0.00	0.00	0.09	0.09	0.54
Seddon's Corner	0.00	0.08	0.00	0.23	0.08	0.86	0.55
Pine Falls	0.27	0.09	0.00	0.18	0.27	0.99	1.44
Riverton	0.00	0.00	0.00	0.08	0.00	----	----
Darwin	----	0.19	0.00	0.36	0.00	0.27	0.45
Hodgson	----	----	----	----	0.00	0.00	0.18

Table 14. The abundance of small mammal populations based on a 200 trap-night period.

	27-7-70	27-7-70	9-8-70	9-8-70	23-8-70	23-8-70	14-9-70	13-10-70	23-2-71	23-2-71	23-2-71	22-3-71	22-3-71	24-4-71	24-4-71	31-5-71	31-5-71	28-6-71	7-9-71	7-9-71	13-9-71	13-9-71	13-10-71	TOTAL
S.cinereus	11	1	2	2	4	1	2	2	3	4	17	0	9	0	16	0	1	2	17	14	6	4	0	118
S.arcticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M.hoyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B.brevicauda	13	6	6	3	1	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37
C.gapperi	4	7	0	0	3	7	0	9	8	3	9	2	2	3	5	3	1	4	10	4	5	3	14	106
M.pennsylvanicus	1	3	0	0	11	2	0	0	0	0	0	1	0	0	0	0	3	1	1	0	0	1	0	24
Z.hudsonius	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sy.cooperi	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	3
Total	29	17	8	6	19	13	7*	11*	12	7	26	3	12*	3	21	3	5	7	28	19	11	8	14	275

* Number caught after a 150 trap-night period.

Table 15. Food preferences showed by masked shrews (<u>Sorex cinereus</u>) between healthy larch looper pupae and healthy larch sawfly cocoons.

Animal characteristics		Food preferences	
age	sex	larch looper pupae	larch sawfly cocoon
A	m	93(32**-61) *	136(43-93)
A	m	7(6**-1**)	32(20-12)
A	m	49(16**-11-6-10-6**)	40(18-9-3-8-2)
A	f	11(0**-2-4-3-2**)	96(0-26-64-5-1)
A	-	93(26*-55-12)	24(0-24-0)
A	-	0(0**-0**)	4(2-2)
A	f	72(35**-24-13**)	106(49-48-9)
A	f	184(26**-144-14**)	106(24-67-15)
A	f	35(18**-17**)	49(14-35)
A	m	319(29**-48**-174-68**)	366(59-40-176-91)
A	m	69(28-34-7*)	31(29-1-1)
A	m	51(20**-23-8**)	61(25-29-7)
A	f	142(50**-60-32**)	135(68-46-21)
A	m	84(34**-50**)	0(0-0)
A	f	0(0**-0-0**)	0(0-0-0)
A	m	18(3**-4-11**)	107(24-53-30)
A	m	1(1**-0-0**)	4(3-0-1)
A	f	45(7**-29-19**)	3(3-0-0)
A	f	3**	10
A	m	0**	5
A	f	93(33**-43-17**)	29(0-29-0)
A	m	17(15**-2-0**)	52(29-22-1)
A	m	148(0**-80-68**)	126(0-71-56)
A	f	10(4**-5-1**)	22(2-6-14)
A	m	52(20**-32**)	43(25-18)

A-adult
m-male
f-female

* Numbers in parentheses refer to the daily number of visits.

** Visits cumulated over a half-day period.

Table 16. Food preferences showed by other shrew species between healthy larch looper pupae and healthy larch sawfly cocoons.

Animal characteristics			Food preferences	
species	age	sex	larch looper pupae	larch sawfly cocoon
S.arcticus	A	f	14(6**-3-1-3-1**)	38(9-7-5-12-5)
	A	m	19(5**-12-2**)	51(20-30-1)
M.hoyi	A	m	57**	23
	A	m	63(0**-1-35-26-1**)	0(0-0-0-0-0)
	A	m	72(44**-10-18**)	162(73-61-28)
	A	f	20(16**-2-2**)	103(34-31-38)
	A	m	1(1**-0-0**)	12(0-5-7)
B.brevicauda	A	f	79(6**-10-11-19-25-8**)	87(0-7-15-19-40-6)
	A	m	45(12**-14-6-7-6**)	20(0-5-11-4-0)
	A	f	15(9**-2-2-2-0**)	90(41-31-8-6-4)
	A	m	65(4**-3-14-1**-22-21**)	53(3-11-18-4-15-2)
	A	-	98(15**-26-9**-27-15-6**)	87(12-13-5-24-27-6)

A-adult
m-male
f-female

* Numbers in parentheses refer to the daily number of visits.
** Visits cumulated over a half-day period.

Table 17. Food preferences of 24 redback voles between healthy larch looper pupae and healthy larch sawfly cocoons.

Animal characteristics			Food preferences	
age	sex	weight(g)	larch looper pupae	larch sawfly cocoon
Sa	m	19.2	118(25-69-14-8-2)*	171(26-129-12-4-1)
Sa	m	18.2	237(102-64-39-20-12)	246(120-82-15-14-15)
A	m	21.7	12(6-4-2-0-0)	22(12-5-2-1-2)
A	m	20.5	14(13-0-0-1-0)	227(129-64-23-4-7)
A	f	22.3	24(2-0-3-11-8)	9(5-1-0-3-0)
Sa	f	19.1	125(31-34-16-18-26)	126(44-35-15-18-14)
Sa	f	19.1	58(14-13-19-11-1)	70(23-25-13-8-1)
A	f	24.8	182(58-39-27-44-14)	128(23-36-25-37-7)
A	m	23.6	56(4-26-11-15)	138(57-47-17-17)
A	m	22.0	15(0-5-5-5)	10(0-2-7-1)
A	m	22.3	9(2-1-0-6)	4(0-1-2-1)
Sa	m	15.9	1(0-1-0-0)	0
A	m	30.0	0	6(5-1-0-0)
A	m	21.7	2(0-1-0-1)	75(19-24-20-12)
A	f	24.1	65(16-38-8-3)	99(12-73-6-8)
Sa	f	19.1	126(56-41-20-9)	12(7-2-2-1)
Sa	m	19.2	51(22-29)	38(23-15)
Sa	f	15.6	39	18
Sa	f	17.2	34(8-26)	218(45-173)
Sa	f	14.4	73(26-32-7-8)	138(48-65-21-4)
Sa	f	16.9	68(29-25-14-0)	44(12-14-18-0)
A	m	21.1	29(6-13-8-2)	65(19-33-7-6)
Sa	f	19.7	40(8-27-3-2)	19(3-16-0-0)
A	f	23.7	75(34-29-11-1)	29(10-10-9-0)

* The numbers in parentheses refer to the daily number of visits.

Sa-subadult
A-adult
m-male
f-female

Table 18. Food preferences of 24 redback voles between healthy larch looper pupae and parasitized larch sawfly cocoons.

Animal characteristics			Food preferences	
age	sex	weight(g)	larch looper pupae	larch sawfly cocoon
Sa	m	19.2	46(3-11-19-13)*	66(4-24-16-22)
Sa	m	18.2	57(15-20-20-2)	53(7-19-22-5)
A	m	21.7	10(0-8-1-1)	2(0-1-1-0)
A	m	20.5	21(3-2-9-7)	21(2-19-0-0)
A	f	22.3	21(3-7-4-7)	8(3-2-2-1)
Sa	f	19.1	131(43-39-45-4)	78(9-24-36-9)
Sa	f	19.1	22(2-10-7-3)	17(2-4-9-1)
A	f	24.8	32(7-11-11-3)	90(14-25-39-12)
A	m	23.6	196(60-56-46-34)	104(53-24-25-12)
A	m	22.0	69(22-35-11-1)	50(36-9-4-1)
A	m	22.3	11(9-1-1-0)	8(5-3-0-0)
Sa	m	15.9	111(103-8-0-0)	6(6-0-0-0)
A	m	30.0	7(4-0-2-1)	2(1-0-1-0)
A	m	21.7	102(30-15-50-7)	40(13-17-9-1)
A	f	24.1	249(40-93-40-76)	220(39-65-55-61)
Sa	f	19.1	8(7-1-0-0)	130(40-62-22-6)
Sa	f	14.4	21(0-15-4-2)	19(2-7-10-0)
Sa	f	16.9	18(1-8-4-5)	4(0-0-4-0)
A	m	21.1	36(4-22-3-7)	84(10-39-14-21)
Sa	f	19.7	0	4
A	f	23.7	18(5-5-6-2)	35(6-12-12-5)
Sa	m	18.8	126(86-40)	120(58-62)
Sa	f	18.9	3(0-1-1-1)	13(1-1-2-9)
Sa	f	18.4	98(19-23-32-24)	15(5-5-4-1)

* The numbers in parentheses refer to the daily number of visits.

Sa-subadult
A-adult
m-male
f-female

Table 19. Food preferences of 23 redback voles between healthy larch looper pupae and a concentration of larch sawfly cocoons.

Animal characteristics			Food preferences	
age	sex	weight(g)	larch looper pupae	larch sawfly cocoon
Sa	m	19.2	32(6-8-17-1)*	43(4-18-16-5)
Sa	m	18.2	33(5-14-9-5)	78(4-2-51-21)
A	m	21.7	1(0-1-0-0)	10(2-4-2-2)
A	m	20.5	5(2-0-0-3)	17(0-5-4-8)
A	m	22.3	2(1-1-0-0)	11(4-3-0-4)
Sa	f	19.1	7(0-3-3-1)	32(2-14-1-15)
Sa	f	19.1	12(1-6-5-0)	10(3-4-3-0)
A	f	24.8	75(21-12-29-13)	18(6-6-5-1)
A	m	23.6	162(4-36-92-30)	161(17-32-85-27)
A	m	22.0	14(2-4-6-2)	64(1-30-17-16)
A	m	22.3	44(8-24-9-3)	78(9-24-39-6)
Sa	m	15.9	0	0
A	m	30.0	2(0-2-0-0)	1(0-0-1-0)
A	m	21.7	25(4-11-9-1)	5(1-1-2-1)
A	f	24.1	15(0-6-6-3)	16(2-6-7-1)
Sa	f	19.1	20(2-10-5-3)	147(24-86-26-11)
Sa	f	14.4	11(3-7-1-0)	22(8-7-6-1)
Sa	f	16.9	42(15-24-2-1)	52(20-23-5-4)
A	m	21.1	47(2-11-17-17)	10(2-3-4-1)
Sa	f	19.7	2(0-0-1-1)	0
A	f	23.7	58(15-32-6-5)	16(6-7-2-1)
Sa	f	18.9	9(1-8-0-0)	1(0-1-0-0)
Sa	f	18.4	71(2-60-7-2)	162(17-135-7-3)

* The numbers in parentheses refer to the daily number of visits.

Sa-subadult
A-adult
m-male
f-female

Table 20. Food preferences of 22 redback voles between a concentration of healthy larch looper pupae and one healthy sawfly cocoon.

Animal characteristics			Food preferences	
age	sex	weight(g)	larch looper pupae	larch sawfly cocoon
Sa	m	19.2	68(15-30-16-7)*	29(3-11-10-5)
Sa	m	18.2	96(25-52-14-5)	64(18-18-19-9)
A	m	21.7	4(1-0-3-0)	1(1-0-0-0)
A	m	20.5	21(2-5-8-6)	24(4-16-4-0)
A	m	22.3	15(4-3-7-1)	3(0-0-3-0)
Sa	f	19.1	56(1-34-10-2)	15(1-6-7-1)
Sa	f	19.1	9(2-5-1-1)	8(0-5-2-1)
A	f	24.8	10(3-2-4-1)	55(11-17-19-8)
A	m	23.6	103(27-30-25-21)	121(35-43-23-20)
A	m	22.0	29(5-10-10-4)	49(6-18-18-7)
A	m	22.3	35(22-6-3-4)	6(0-6-0-0)
A	m	30.0	2(1-1-0-0)	2(0-1-0-1)
A	m	21.7	39(0-0-19-20)	148(3-11-90-39)
A	f	24.1	34(1-9-15-9)	110(3-11-59-37)
Sa	f	19.1	341(26-59-94-162)	86(16-19-25-26)
Sa	f	14.4	26(1-9-12-4)	1(0-0-1-0)
Sa	f	16.9	5(2-2-1-0)	1(0-1-0-0)
A	m	21.1	10(1-4-4-1)	38(7-14-14-3)
Sa	f	19.7	0	8(3-4-1-0)
A	f	23.7	3(2-0-1-0)	17(2-6-8-1)
Sa	f	18.9	2(0-1-1-0)	3(1-1-0-1)
Sa	f	18.4	115(15-31-56-13)	26(3-14-9-0)

* The numbers in parentheses refer to the daily number of visits.

Sa-subadult
A-adult
m-male
f-female

Table 21. Food preferences showed by other voles and mice between healthy larch looper pupae and healthy larch sawfly cocoons.

Animal characteristics			Food preferences	
species	age	sex	larch looper pupae	larch sawfly cocoon
M.pennsylvanicus	A	f	162(30**-66-48-18**)*	136(25-52-42-17)
	A	f	0(0**-0-0-0-0**)	3(1-1-1-0-0)
	A	m	54(23**-25-5-0-1**)	1(1-0-0-0-0)
	A	m	50(7**-31-8-2-2**)	142(0-22-63-45-12)
	A	m	64(22**-24-9-3-6**)	35(9-19-4-0-3)
	Sa	m	0(0**-0-0-0-0**)	84(27-40-9-6-2)
	A	m	55(17**-11-10-4-9-4**)	6(5-1-0-0-0-0)
	Sa	m	12(7**-3-1-1-0-0**)	51(18-20-6-4-3-0)
	A	f	55(7**-1-4-11-19-13**)	16(11-0-1-2-2-0)
	A	m	0(0**-0-0-0-0-0**)	75(4-3-18-34-11-5)
P.maniculatus	A	f	235(38**-2475-81-17**)	70(17-29-4-16-4)
	Sa	f	33(8**-10-4-10-1**)	90(21-26-17-23-3)

* Numbers in parentheses refer to the daily number of visits.

** Visits cumulated over a half-day period.

Sa-subadult
A-adult
m-male
f-female

Table 22. Mean values of oxygen consumption and carbon dioxide production of redback voles (analysed by age and sex).

Temperature (°F)	Oxygen (cc)						Carbon dioxide (cc)					
	males			females			males			females		
	Sa	Mean	A	Sa	Mean	A	Sa	Mean	A	Sa	Mean	A
69-72	83.6(8)*	90.5(12)	104.3(4)	68.4(4)	85.7(8)	102.9(4)	51.6(8)	56.0(12)	64.6(4)	46.7(4)	55.8(8)	63.2(4)
62-64	109.4(10)	114.1(13)	128.2(3)	88.0(5)	106.0(8)	136.1(3)	63.6(9)	66.0(12)	73.2(3)	67.8(5)	69.0(8)	70.9(3)
53-57	122.5(9)	123.0(13)	124.2(4)	100.4(3)	113.4(8)	121.4(5)	78.3(9)	80.0(13)	83.9(4)	69.5(3)	76.8(8)	81.2(5)

* The numbers in parentheses refer to the number of animals tested at a given temperature.

Sa-subadult
A-adult

Table 23. Relationships between the oxygen consumption (x) and the carbon dioxide production (y) of 20 redback voles.

Temperature (°F)	cc O_2/hr vs cc CO_2/hr		cc O_2/g-hr vs cc CO_2/g-hr	
	r	Y	r	Y
69-72	0.725**	2.56+0.34X	0.674**	1.47+0.31X
62-64	0.421[1]	4.76+0.17X	0.285[2]	2.48+0.19X
53-57	0.852**	2.92+0.42X	0.863**	1.38+0.44X

** Probability > 99 % level.
[1] Probability > 93 % level.
[2] Probability > 78 % level.

Table 24. The daily urinary-nitrogen excretion of redback voles (mg/g-day).

	Temperatures (°F)											
	54	54	55	58	66	68	69	70	71	72	72	75
f	0.874	2.808	9.024	0.849	-----	-----	-----	-----	-----	-----	-----	-----
f	6.624	3.144	1.392	0.998	3.576	5.256	4.080	2.664	1.838	2.496	3.144	0.838
m	2.832	2.808	0.463	0.749	2.335	2.712	0.802	2.664	0.127	1.435	1.361	0.823
f	2.004	0.559	1.121	0.475	1.013	3.436	1.411	3.168	1.834	1.226	1.073	0.252
f	-----	-----	-----	-----	1.802	2.359	3.792	2.592	0.703	1.418	1.632	3.000
Mean	3.084	2.330	3.000	0.768	2.182	3.441	2.521	2.772	1.126	2.627	1.803	1.228
		2.805			2.182				2.802			
Mean weight of voles (g)		21.2			20.2				21.0			
Daily nitrogen excretion (mg/vole)		59.35			44.14				43.70			

m-male
f-female

Table 25. The metabolic requirements of redback voles using the calorific conversion of oxygen and RQ values.

Temperature (°F)	Maximum RQ	Daily O_2 consumption (liter)	Calorific conv. (kcal)
69-72	.78	2.126	10.15
62-64	.76	2.688	12.77
53-57	.74	2.856	13.50

Table 26. The trapping record of small mammals caught on 13 tamarack bogs of Manitoba

Plot	Trapping period	Trap-nights	Species and numbers caught
A	27-7-70	250	16 Sc, 16 Bb, 5 Cg
B	27-7-70	250	2 Sc, 8 Bb, 8 Cg, 5 Mp
C	9-8-70	250	2 Sc, 9 Bb
D	9-8-70	250	3 Sc, 4 Bb, 1 Zh
E	23-8-70	250	6 Sc, 3 Bb, 3 Cg, 12 Mp
F	23-8-70	250	2 Sc, 4 Bb, 1 Sa,9Cg,3Mp
G	14-9-70	150	2 Sc, 5 Bb
H	12-10-70	150	2 Sc, 9 Cg
FFS1	23-2-71	200	3 Sc, 8 Cg, 1 Syc
FFS2	23-2-71	200	4 Sc, 3 Cg
Rennie	23-2-71	150	17 Sc, 9 Cg
Meditation lake	22-3-71	200	2 Cg, 1 Mp
Rennie	22-3-71	200	9 Sc, 2 Cg, 1 Syc
Meditation lake	25-4-71	200	3 Cg
Rennie	25-4-71	200	16 Sc, 5 Cg
B	31-5-71	200	5 Cg
C	31-5-71	200	1 Sc, 1 Cg, 3 Mp
A	29-6-71	200	2 Sc, 4 Cg, 1 Mp
A	7-9-71	200	17 Sc, 19 Cg, 1 Mp
B	7-9-71	200	14 Sc, 4 Cg, 1 Syc
C	13-9-71	200	4 Sc, 3 Cg, 1 Mp
F	13-9-71	200	6 Sc, 5 Cg
Seddon's Corner	13-10-71	200	14 Cg

Sc, Sorex cinereus
Sa, Sorex arcticus
Bb, Blarina brevicauda
Cg, Clethrionomys gapperi
Mp, Microtus pennsylvanicus
Syc, Synaptomys cooperi
Zh, Zapus hudsonius

FFS, Forestry Field Station

Table 27. The mean volume of small mammal stomach contents analysed by plot, species, age and sex.

Plot-Time	Species	Volume of contents (cc)			
		Sa male	Sa female	A male	A female
A 27-7-70	S.cinereus	--	--	0.09 (10)*	0.04 (6)
	B.brevicauda	0.05 (1)	--	0.27 (8)	0.26 (7)
	C.gapperi	0.15 (1)	--	1.15 (1)	2.32 (2)
	M.pennsylvanicus	0.60 (1)	--	--	--
B 27-7-70	S.cinereus	--	--	0.15 (1)	0.03 (1)
	B.brevicauda	0.03 (2)	0.59 (2)	0.67 (3)	0.25 (1)
	C.gapperi	--	0.65 (1)	0.98 (6)	0.75 (1)
	M.pennsylvanicus	0.92 (3)	--	0.70 (1)	1.00 (1)
C 9-8-70	S.cinereus	--	--	0.02 (1)	0.07 (1)
	B.brevicauda	0.25 (1)	0.45 (3)	0.41 (4)	0.20 (1)
D 9-8-70	S.cinereus	--	--	0.03 (2)	0.03 (1)
	B.brevicauda	--	--	0.05 (1)	0.83 (3)
	Z. hudsonius	--	--	0.35 (1)	--
E 23-8-70	S.cinereus	--	--	0.03 (1)	0.04 (5)
	B.brevicauda	--	--	0.47 (2)	--
	C.gapperi	0.85 (1)	1.35 (1)	0.95 (2)	--
	M.pennsylvanicus	0.75 (4)	0.71 (4)	1.15 (1)	--
F 23-8-70	S.cinereus	--	--	--	0.07 (2)
	S.arcticus	--	--	--	0.05 (1)
	B.brevicauda	--	0.30 (1)	0.30 (1)	0.32 (2)
	C.gapperi	0.84 (4)	0.52 (2)	0.82 (2)	0.90 (1)
	M.pennsylvanicus	0.97 (2)	--	0.80 (1)	--

Table 27. Continued.

Plot-Time	Species	Volume of contents (cc)			
		Sa male	Sa female	A male	A female
G 19-9-70	S.cinereus	--	--	0.10 (1)	0.00 (1)
	B.brevicauda	--	--	0.34 (4)	0.50 (1)
H 12-10-70	S.cinereus	--	--	0.05 (1)	0.05 (1)
	C.gapperi	1.00 (1)	0.30 (1)	0.60 (4)	0.50 (3)
FFS1 23-2-71	S.cinereus	--	--	0.08 (3)	--
	C.gapperi	--	--	0.83 (5)	0.50 (3)
	Sy.cooperi	0.05 (1)	--	--	--
FFS2 23-2-71	S.cinereus	--	--	0.06 (3)	0.10 (1)
	C.gapperi	--	--	--	0.55 (3)
Rennie 23-2-71	S.cinereus	--	--	0.06 (9)	0.05 (8)
	C.gapperi	--	--	0.91 (2)	1.01 (6)
Meditation 22-3-71 lake	C.gapperi	0.35 (1)	--	1.65 (1)	--
	M.pennsylvanicus	--	--	1.10 (1)	--
Rennie 22-3-71	S.cinereus	--	--	0.10 (3)	0.05 (5)
	C.gapperi	--	--	0.15 (1)	1.00 (1)
	Sy.cooperi	--	--	0.28 (1)	--
Meditation 25-4-71 lake	C.gapperi	--	--	0.77 (2)	0.75 (1)
Rennie 25-4-71	S.cinereus	--	--	0.17 (10)	0.11 (6)
	C.gapperi	--	--	1.02 (3)	0.55 (2)

Table 27. Continued.

Plot-Time	Species	Volume of contents (cc)			
		Sa male	Sa female	A male	A female
B 31-5-71	C.gapperi	--	--	1.35 (2)	3.40 (1)
C 31-5-71	S.cinereus	--	--	--	0.75 (1)
	C.gapperi	--	--	1.85 (1)	--
	M.pennsylvanicus	--	0.15 (1)	1.17 (2)	--
A 29-6-71	S.cinereus	--	--	0.07 (1)	0.00 (1)
	C.gapperi	--	--	0.82 (2)	0.90 (1)
	M.pennsylvanicus	0.70 (1)	--	--	--
A 7-9-71	S.cinereus	--	--	0.07 (12)	0.07 (4)
	C.gapperi	--	--	1.13 (5)	0.66 (5)
B 7-9-71	S.cinereus	--	--	0.09 (8)	0.05 (6)
	C.gapperi	--	--	0.74 (2)	1.17 (2)
C 13-9-71	S.cinereus	--	--	0.03 (1)	0.04 (3)
	C.gapperi	--	0.90 (1)	1.75 (1)	0.50 (1)
F 13-9-71	S.cinereus	--	--	0.05 (4)	0.04 (2)
	C.gapperi	0.80 (1)	1.10 (1)	0.90 (2)	0.85 (1)

* The numbers in parentheses refer to the number of stomachs analysed.

FFS, Forestry Field Station
Sa, Subadult
A, Adult

Table 28. The mean volume of intestinal contents of small mammals analysed by plot, species, age and sex.

Plot-Time	Species	Volume of contents (cc)			
		Sa male	Sa female	A male	A female
A 27-7-70	S.cinereus	--	--	0.14 (10)*	0.15 (6)
	B.brevicauda	0.85 (1)	--	1.33 (8)	1.43 (7)
B 27-7-70	S.cinereus	--	--	0.20 (1)	0.20 (1)
	B.brevicauda	0.62 (2)	0.82 (2)	1.43 (3)	1.10 (1)
C 9-8-70	S.cinereus	--	--	0.10 (1)	0.20 (1)
	B.brevicauda	1.00 (1)	0.92 (3)	1.47 (4)	1.20 (1)
D 9-8-70	S.cinereus	--	--	0.20 (2)	0.30 (1)
	B.brevicauda	--	--	1.05 (1)	1.37 (3)
E 23-8-70	S.cinereus	--	--	0.10 (1)	0.12 (5)
	B.brevicauda	--	--	1.17 (2)	--
F 23-8-70	S.cinereus	--	--	--	0.15 (2)
	S.arcticus	--	--	--	0.30 (1)
	B.brevicauda	--	0.60 (1)	0.55 (1)	0.80 (2)
H 12-10-70	S.cinereus	--	--	0.03 (1)	0.05 (1)
FFS1 23-2-71	S.cinereus	--	--	0.09 (3)	--
FFS2 23-2-71	S.cinereus	--	--	0.14 (3)	0.05 (1)
Rennie 23-2-71	S.cinereus	--	--	0.14 (9)	0.13 (8)

Table 28. Continued.

Plot-Time	Species	Volume of contents (cc)			
		Sa male	Sa female	A male	A female
Rennie 22-3-71	S.cinereus	--	--	0.08(3)	0.14(5)
Rennie 25-4-71	S.cinereus	--	--	0.19(10)	0.16(6)
C 31-5-71	S.cinereus	--	--	--	0.40(1)
A 29-6-71	S.cinereus	--	--	0.07(1)	0.05(1)
A 7-9-71	S.cinereus	--	--	0.15(12)	0.10(4)
B 7-9-71	S.cinereus	--	--	0.20(8)	0.15(6)
C 13-9-71	S.cinereus	--	--	0.15(1)	0.17(3)
F 13-9-71	S.cinereus	--	--	0.20(4)	0.19(2)

* The numbers in parentheses refer to the number of intestinal analyses.

FFS, Forestry Field Station
Sa, Subadult
A, Adult

Table 29. The mean percentage of small mammal stomach contents analysed by plot, species and time of the year.

Plot-Time	Species	Mean percentage				
		looper	sawfly	other-insects	plant	miscell.
A 27-7-70	S.cinereus(16)*	--	49.8	48.8	1.4	--
	B.brevicauda(16)	--	67.6	30.4	2.0	--
	C.gapperi(4)	--	18.1	0.1	81.8	--
	M.pennsylvanicus(1)	--	0.2	--	99.8	--
B 27-7-70	S.cinereus(2)	--	50.0	50.0	--	--
	B.brevicauda(8)	6.1	19.8	66.7	--	7.4
	C.gapperi(8)	--	0.2	0.2	99.6	--
	M.pennsylvanicus(5)	--	--	--	100	--
C 9-8-70	S.cinereus(2)	--	50.0	50.0	--	--
	B.brevicauda(9)	7.8	28.0	52.0	1.1	11.1
D 9-8-70	S.cinereus(2)	--	5.0	95.0	--	--
	B.brevicauda(5)	--	26.5	73.3	0.2	--
	Z.hudsonius (1)	--	--	1.0	99.0	--
E 23-8-70	S.cinereus(6)	--	--	100	--	--
	B.brevicauda(2)	--	--	99.9	0.1	--
	C.gapperi(4)	--	--	1.1	98.9	--
	M.pennsylvanicus(10)	--	+	0.3	99.7	--
F 23-8-70	S.cinereus(2)	--	--	100	--	--
	S.arcticus(1)	--	--	100	--	--
	B.brevicauda(4)	--	--	99.3	0.7	--
	C.gapperi(9)	+	--	0.4	99.6	--
	M.pennsylvanicus(3)	--	--	+	100	--

Table 29. Continued.

Plot-Time	Species	Mean percentage				
		looper	sawfly	other-insects	plant	miscell.
G 14-9-70	S.cinereus(2)	--	22.4	77.6	--	--
	B.brevicauda(5)	2.0	2.0	75.4	1.2	19.4
H 12-10-70	S.cinereus(2)	--	0.1	99.9	--	--
	C.gapperi(9)	--	+	0.4	99.6	--
FFS1 23-2-71	S.cinereus(3)	--	--	97.6	1.7	0.7
	C.gapperi(8)	--	--	0.2	99.6	0.2
	Sy.cooperi(1)	--	--	--	100	--
FFS2 23-2-71	S.cinereus(4)	--	--	80.0	--	20.0
	C.gapperi(3)	--	--	--	100	--
Rennie 23-2-71	S.cinereus(17)	--	24.4	64.4	8.6	2.6
	C.gapperi(9)	--	--	0.2	99.8	--
Meditation lake 22-3-71	C.gapperi(2)	--	--	0.1	99.9	--
	M.pennsylvanicus(1)	--	--	--	100	--
Rennie 22-3-71	S.cinereus(8)	--	35.6	62.8	1.6	--
	C.gapperi(2)	--	--	--	100	--
	Sy.cooperi(1)	--	--	--	100	--
Meditation lake 25-4-71	C.gapperi(3)	--	--	--	100	--
Rennie 25-4-71	S.cinereus(16)	8.4	+	91.6	--	--
	C.gapperi(5)	--	+	0.4	99.6	--
B 31-5-71	C.gapperi(3)	--	--	0.8	99.2	--

Table 29. Continued.

Plot-Time	Species	Mean percentage				
		looper	sawfly	other-insect	plant	miscel.
C 31-5-71	S.cinereus(1)	--	--	100	--	--
	C.gapperi(1)	--	--	1.0	99.0	--
	M.pennsylvanicus(3)	--	--	--	100	--
A 29-6-71	S.cinereus(2)	--	--	100	--	--
	C.gapperi(3)	--	--	0.1	99.9	--
	M.pennsylvanicus(1)	--	--	--	100	--
A 7-9-71	S.cinereus(17)	--	22.0	78.0	--	--
	C.gapperi(10)	--	0.1	--	99.9	--
B 7-9-71	S.cinereus(14)	--	0.1	99.9	--	--
	C.gapperi(4)	--	+	--	100	--
C 13-9-71	S.cinereus(4)	--	--	100	--	--
	C.gapperi(3)	--	--	--	100	--
F 13-9-71	S.cinereus(6)	--	--	100	--	--
	C.gapperi(5)	--	--	0.4	99.6	--
Seddon's Corner 13-10-71	C.gapperi(14)	--	--	--	100	--

* The numbers in parentheses refer to the number of stomach analyses.

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Table 30. The mean percentage of small mammal intestinal contents analysed by plot, species and time of the year.

Plot-Time	Species	Mean percentage				
		looper	sawfly	other-insect	plant	miscell.
A 27-7-70	S.cinereus(16)*	--	57.9	42.1	--	--
	B.brevicauda(16)	0.3	73.5	26.2	--	--
B 27-7-70	S.cinereus(2)	--	49.3	50.7	--	--
	B.brevicauda(8)	0.7	37.6	50.9	5.8	5.0
C 9-8-70	S.cinereus(2)	--	50.0	50.0	--	--
	B.brevicauda(9)	3.3	29.3	55.2	4.0	8.2
D 9-8-70	S.cinereus(2)	--	2.0	98.0	--	--
	B.brevicauda(5)	--	21.7	77.7	0.6	--
E 23-8-70	S.cinereus(6)	--	1.7	98.3	--	--
	B.brevicauda(2)	--	--	100	--	--
F 23-8-70	S.cinereus(2)	3.2	--	96.8	--	--
	S.arcticus(1)	--	--	100	--	--
	B.brevicauda(4)	--	3.1	96.7	0.2	--
G 14-9-70	S.cinereus(2)	2.0	16.6	81.4	--	--
	B.brevicauda(5)	7.5	9.9	80.2	1.2	1.2
H 12-10-70	S.cinereus(2)	8.4	2.5	89.1	--	--
FFS1 23-2-71	S.cinereus(3)	--	3.7	68.5	27.8	--
FFS2 23-2-71	S.cinereus(4)	--	--	93.8	6.2	--

Table 30. Continued.

Plot-Time	Species	Mean percentage				
		looper	sawfly	other-insect	plant	miscel.
Rennie 23-2-71	S.cinereus(17)	--	24.7	59.0	10.4	5.9
Rennie 22-3-71	S.cinereus(8)	--	27.3	60.1	12.6	--
Rennie 25-4-71	S.cinereus(16)	7.3	4.7	87.7	0.3	--
C 31-5-71	S.cinereus(1)	--	--	100	--	--
A 29-6-71	S.cinereus(2)	--	--	100	--	--
A 7-9-71	S.cinereus(17)	--	10.1	89.9	--	--
B 7-9-71	S.cinereus(14)	--	7.1	92.9	--	--
C 13-9-71	S.cinereus(4)	--	--	100	--	--
F 13-9-71	S.cinereus(6)	--	--	100	--	--

* The numbers in parentheses refer to the number of intestinal analyses.

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Table 31. The estimations of larch looper larvae and pupae populations of 17 tamarack bogs of Manitoba.

Plot	No. trees/acre	No. larvae/acre	No. pupae/acre
1970			
A	640	90605	48293
B	360	7465	3979
C	850	11475	6116
D	570	7695	4101
E	760	10260	5469
F	310	4185	2231
G	236[+]	0	500[+++]
H	491[++]	32858	17513
Rennie	267	33448	17828
Telford	236	0	500[+++]
Seddon's Corner	491	32858	17513
Darwin	178	30643	16333
1971			
A	640	16192	8631
B	360	21600	11513
C	850	15725	8381
F	310	1500	800
Seddon's Corner	491	12586	6708

[+] Based on the number of trees of Telford plot.

[++] Based on the number of trees of Seddon's Corner plot.

[+++] Introduced 50 pupae on a 0.1 acre surface = 500 pupae per acre.

Table 32. Populations of small mammals per 1000 trap-nights.

Plot	Species								
	Sc	Sa	Bb	Cg	Mp	Syc	Zh	Th	Me
1970									
A	64	0	64	20	0	0	0	0	0
B	8	0	32	32	20	0	0	0	0
C	8	0	36	0	0	0	0	0	0
D	12	0	16	0	0	0	4	0	0
E	24	0	8	12	48	0	0	0	0
F	8	4	16	36	12	0	0	0	0
G	13	0	33	0	0	0	0	0	0
H	13	0	0	60	0	0	0	0	0
Rennie	8	2	12	99	0	0	0	0	0
Telford	6	0	34	3	0	0	0	2	3
Seddon's Corner	16	3	2	108	8	0	0	2	0
Darwin	8	2	6	50	8	0	0	0	0
1971									
A	85	0	0	50	5	0	0	0	0
B	70	0	0	20	0	5	0	0	0
C	20	0	0	15	5	0	0	0	0
F	30	0	0	25	0	0	0	0	0
Seddon's Corner	0	0	0	70	0	0	0	0	0

Sc,	Sorex cinereus
Sa,	Sorex arcticus
Bb,	Blarina brevicauda
Cg,	Clethrionomys gapperi
Mp,	Microtus pennsylvanicus
Syc,	Synaptomys cooperi
Zh,	Zapus hudsonius
Th,	Tamiasciurus hudsonicus
Me,	Mustela erminae

Table 33. Densities and recovery rates of larch looper pupae 'planted' in tamarack bogs.

Plot	Density 'planted'	Recovery rate (%)
1970		
A	25	88
B	25	100
C	25	100
D	25	88
E	25	96
F	25	100
G	50	100
Rennie	50	96
Telford	50	90
Seddon's Corner	50	94
Darwin	50	80
H	75	88
1971		
B	75	100
A	100	100
C	125	100
F	150	98.6
Seddon's Corner	175	99.4

Table 34. The fate of larch looper pupae 'planted' in tamarack bogs.

Plot	% eaten		% not eaten		
	On-location	hoarded	healthy	diseased	emerged
1970					
A	80	12	8	--	--
B	80	--	20	--	--
C	56	--	32	4	8
D	80	12	8	--	--
E	76	4	8	4	8
F	56	--	20	20	4
G	90	--	4	6	--
H	85	12	3	--	--
Rennie	78	4	16	2	--
Telford	78	10	8	4	--
Seddon's Corner	88	6	6	--	--
Darwin	74	20	2	4	--
1971					
A	96	--	4	--	--
B	75	--	24	1	--
C	70	--	28	2	--
F	96	1	3	--	--
Seddon's Corner	81	1	15	3	--

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