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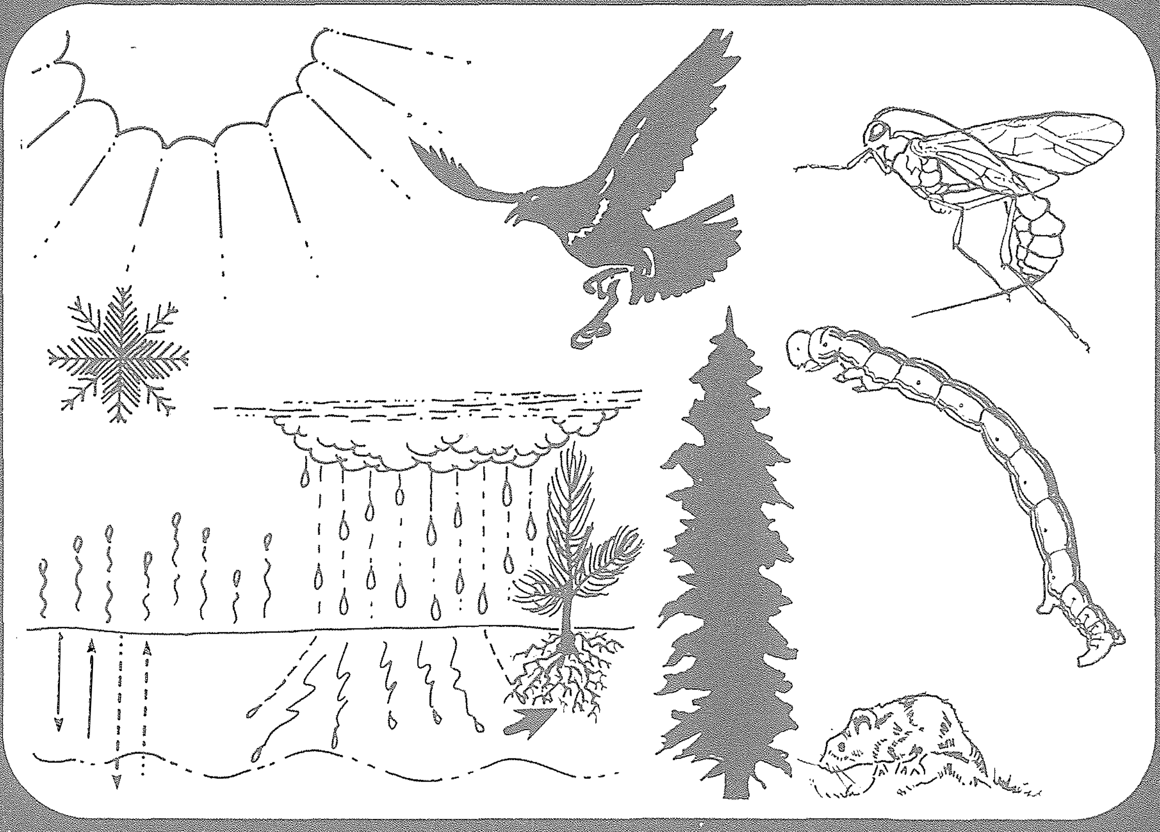
Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan, 1945-69



W.G.H. Ives

Northern Forest Research Centre • Edmonton, Alberta • Information Report NOR-X-233

ENVIRONMENTAL FACTORS AFFECTING 21 FOREST INSECT DEFOLIATORS IN MANITOBA AND SASKATCHEWAN, 1945-69

W.G.H. IVES

INFORMATION REPORT NOR-X-233
DECEMBER 1981

NORTHERN FOREST RESEARCH CENTRE
CANADIAN FORESTRY SERVICE
ENVIRONMENT CANADA
5320 - 122 STREET
EDMONTON, ALBERTA, CANADA
T6H 3S5

Ives, W.G.H. 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan, 1945-69. Environ. Can., Can. For. Serv., North. For. Res. Cent. Edmonton, Alberta. Inf. Rep. NOR-X-233.

ABSTRACT

Available outbreak histories are summarized for 21 species of forest insect defoliators commonly occurring in Manitoba and Saskatchewan. Data are presented on insect abundance and related weather conditions for 1945 to 1969. Literature on environmental factors affecting the abundance of the various insects is reviewed, and this study's data are analyzed to determine the main regulating mechanisms. In both cases, weather appears to be the principal factor determining the abundance of all 21 species of insects. Limited data on small mammals, birds, parasites, invertebrate predators, and diseases indicate that these factors may play important roles in particular circumstances.

RESUME

Compendium des historiques disponibles des invasions de 21 espèces d'insectes défoliateurs des forêts ordinairement relevés dans le Manitoba et la Saskatchewan. Des données sont présentées sur la pullulation de ces insectes et les conditions climatiques y associées pour la période de 1945 à 1969. La documentation sur les facteurs environnementaux qui affectent la pullulation des divers insectes est passée en revue et les données de la présente étude sont analysées en vue de déterminer les principaux mécanismes de régulation. Dans les deux cas, le climat semble être le principal facteur influant sur la pullulation de toutes les 21 espèces entomologiques. Des données succintes sur les petits mammifères, les oiseaux, les parasites, les prédateurs invertébrés et les maladies montrent que ces facteurs peuvent jouer des rôles importants dans des circonstances particulières.

PREFACE

This report is an attempt to summarize most of the information on forest insect defoliators in Manitoba and Saskatchewan that was collected between 1945 and 1969 by the Forest Insect and Disease Survey Unit, then located in Winnipeg, Manitoba. Not all defoliator species are covered, either because they were too uncommon or because the sampling of these species was not continuous enough to provide useful information on population trends. Similarly, the report does not cover areas that are primarily agricultural or those that were inaccessible during the period covered. Twenty-one species of insects are considered, of which only five are normally thought of as major pests. The remaining species have been included in the hope that an examination of fluctuations in their abundance may reveal clues that will eventually lead to a better understanding of factors determining the abundance of forest insects.

In this report I have not attempted to make an exhaustive review of the literature, which is rather voluminous because the abundance of insects is affected by so many factors. I have purposely avoided any technical discussions in the hope that the report will be of interest and use to anyone who is concerned about forest insects, particularly in the geographic areas discussed, but elsewhere as well. Although the reviews are nontechnical, I have attempted to present an adequate background for each topic. Parts of the reviews on small mammals and birds may seem irrelevant, but I believe that an understanding of the complex factors affecting the abundance of these animals is essential if one is to appreciate their role in insect population dynamics. Of necessity, most of the conclusions concerning the interrelationships between the various factors and insect population changes are primarily conjecture. I am hopeful that some of these conjectures may ultimately be tested experimentally, but that is beyond the scope of this report.

W.G.H. Ives

PREFACE

Le présent rapport est un essai de compilation de la plupart des données disponibles sur les insectes défoliateurs au Manitoba et en Saskatchewan, colligées entre 1945 et 1969 par le Relevé des insectes et des maladies des arbres forestiers, ayant alors son siège à Winnipeg (Manitoba). Toutes les espèces d'insectes défoliateurs ne sont pas considérées dans ce rapport, soit parce qu'elles n'étaient pas trop courantes dans les aires d'investigation soit parce que leur échantillonnage n'était pas assez continu pour fournir des informations utiles sur les tendances des populations. Pareillement, le rapport inaccessibles au cours de la période couverte. Des 21 espèces d'insectes considérées on pense que seulement 5 sont normalement des ravageurs importants. Les autres espèces ont été insérées au rapport dans l'espoir qu'une étude des fluctuations de leurs populations fournirait des indices susceptibles d'aboutir à une meilleure intelligence des facteurs qui déterminent le pullulement des insectes forestiers.

Dans ce rapport je n'ai pas cherché à faire la revue exhaustive de la documentation disponible sur le sujet qui est plutôt volumineux, étant donnée la pluralité des facteurs influant sur la population des insectes. J'ai sciemment évité toute discussion d'ordre technique, avec le ferme espoir que le rapport sera intéressant et utile pour toute personne s'occupant des insectes forestiers, particulièrement dans les aires géographiques qui y sont étudiées mais aussi bien ailleurs. Encore que ces études ne soient pas d'ordre technique, j'ai essayé de bien étayer chaque sujet. Certaines parties des considérations relatives aux petits mammifères et au oiseaux peuvent ne pas sembler pertinentes, mais je crois qu'il est essentiel de bien saisir les facteurs complexes qui conditionnent la population des insectes. Par la force des choses, la plupart des conclusions ayant trait aux correlations entre ces divers facteurs et les modifications survenant dans les populations d'insectes sont essentiellement d'ordre conjectural. J'espère que certaines de ces conjectures pourront être vérifées ultérieurement par l'expérience, mais c'est là une question qui déborde le cadre du présent rapport.

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INTRODUCTION

The material presented in this report is diverse, so to simplify presentation the report has been divided into a number of sections. Each section deals with a different topic and discusses only those insects for which there was sufficient information. The following are the 21 species of forest insect defoliators covered by this report:

Malacosoma disstria Hübner
Choristoneura conflictana (Walker)
Chrysomela crotchi Brown
Gonioctena americana Schaeffer
Orthosia hibisci (Guenée)
Campaea perlata Guenée
Pseudexentera oregonana Walsingham
Sciaphila duplex Walsingham
Enargia decolor Walker
Choristoneura fumiferana (Clemens)
Neodiprion abietis complex
Acleris variana (Fernald)
Choristoneura pinus pinus Freeman
Neodiprion nanulus nanulus Schedl
Neodiprion virginianus complex
Semiothisa bicolorata Fabricius
Zale duplicata largera Smith
Pristiphora erichsonii (Hartig)
Semiothisa sexmaculata Packard
Anoplonyx canadensis Harrington
Anoplonyx luteipes (Cresson)

Outbreak histories are presented for all 21 insects, and the influences of such environmental factors as weather, small mammals, birds, parasites, invertebrate predators, diseases, and competition from other defoliators are described for various species. Although these topics are interrelated to a degree and have a certain amount of unavoidable overlap, it was simpler to treat them separately. The literature for each topic has therefore also been reviewed separately and serves to introduce each section. To avoid undue repetition, this general introduction is limited to the presentation of a brief history of the Forest Insect Survey and to a discussion of why the Survey data have limited usefulness for quantitative analyses. Information on the history of the Survey has been obtained primarily from the annual reports of the Forest Insect (and Disease) Survey (Anonymous 1939-1973). The discussion on the limitations of Survey data is based on first-hand experience.

The Forest Insect Survey, initially based in Ottawa, was established in 1936 primarily to determine the distribution and abundance of the European spruce sawfly in Ontario and Quebec. After the first 2 years of operation it was felt that sufficient information had been obtained for this insect, and coverage was extended to include most forest insect pests or potential pests. Regional laboratories were opened at various centers across Canada, but the advent of World War II seriously curtailed development for a number of years.

After the war ended, staff and facilities gradually expanded, and forest insect surveys were begun on an organized basis. In 1945, surveys of the forested areas of the three prairie provinces by insect rangers from the Winnipeg laboratory plus samples sent in by cooperators throughout the three provinces resulted in 627 insect samples being processed. The Winnipeg laboratory remained responsible for surveys in the three prairie provinces until a laboratory was opened in Calgary in 1948.

From 1949 to 1969, which was the last complete year of operation for the Winnipeg laboratory, at least 3000 insect samples were processed annually. Usually the number was closer to 4000, and occasionally it was even more. Because nearly all of these samples contained more than one species of insect, it can readily be seen that the total volume of data increased rapidly.

In order to cope with the increasing volume of data and to improve access to the data, a Remington-Rand punched-card data system was adopted in 1958. At the Winnipeg laboratory, conversion of old records was successful for as far back as 1951. Earlier records were also converted, but the data were too fragmentary to be useful for population studies. Because of its ultimate domination, the IBM punched-card system was adopted in 1967, and all old data were subsequently converted to IBM format and stored on magnetic tape. These data for the Manitoba-Saskatchewan region have formed the basis of this report, although most of the data are of poor quality from a quantitative point of view. Some of the factors contributing to this poor quality are outlined below.

The primary objectives of the surveys conducted from the Winnipeg laboratory were to determine which species were forest pests, to gather information on the location and severity of infestations, and to obtain qualitative information on parasites affecting the various species. Consequently, very little attention was given to the establishment of permanent sampling plots and even less to the maintenance of continuity in sampling of those plots that might exist through fortuitous circumstances. Thus, although the data may appear to be voluminous, they are not necessarily continuous for a particular host tree and/or geographic area. The vagaries of staffing, funding, and so on all affected the coverage given in any particular year to any particular pest. If one then acknowledges that the conscientiousness and interest of the individual technician responsible for the data collection had a bearing on where and when the samples were collected, it is readily apparent that the resulting data are likely to be anything but robust.

In addition, there were a number of inherent weaknesses in both the sampling and rearing procedures. When received in the laboratory, all species were handled in much the same manner, especially as far as the storage and incubation of pupae or cocoons were concerned. This had the obvious advantage of making procedures simpler and easier to teach to temporary or new staff, but it often resulted in extremely poor rearing success. Adult emergence was usually not seriously affected among those species that did not go into eonymphal or pupal diapause, but very few host or parasite adults emerged from those species that overwintered in these stages. This meant that not only was a lot of potentially valuable information lost, but there were also serious doubts about the validity of any quantitative parasite records. In order to obtain meaningful estimates of the percentage parasitism, it was necessary to calculate them from the numbers of adults emerging, on the assumption that mortality was the same for parasitized and unparasitized host insects, which is a very questionable assumption. There was no reasonable alternative, however, except for dissection of the host insects. This was done with the larch sawfly for a number of years but was a time-consuming exercise. It also meant that parasites could no longer be positively identified, since only immature forms were available. It was therefore not a practical approach for most insect species.

Another problem, which also had a marked influence on rearing and overwintering success, was the length of time that the samples spent in transit, either in the technicians' vehicles or in the mail. Some insects are particularly vulnerable to high temperatures, and mortality during transit was a common problem, especially when samples were collected in remote areas. No completely satisfactory solution to the problem was found, although awareness on the part of the technicians and the use of first-class mail alleviated it somewhat.

Sampling problems were perhaps of even greater consequence. In the first place, not all insects responded equally to the beating procedures used, even if this was done conscientiously. Sawflies, for example, dropped fairly readily, especially in the later instars, but even these do not respond equally at all times. Last-instar larvae that have completed feeding will drop at the slightest disturbance, but those that are still actively feeding are much harder to dislodge. I also have a suspicion, unconfirmed by facts, that the larvae drop more readily when it is cool than when it is warm. It seems as if their grip on the foliage becomes more tenacious as the temperatures rise.

Other insects, such as the forest tent caterpillar, are extremely difficult to sample quantitatively by the beating-sheet method. While forest tent caterpillars are free-feeding insects (with no tents), they are also extremely mobile. When not feeding, they rest in masses on the trunks or limbs of the trees, and they are not easily dislodged. Even when feeding, they spin silk trails wherever they go and when disturbed usually lower themselves on these silken threads rather than falling free. What one collects, then, are usually those that have slipped, as it were, and these numbers may have little or no relationship to the numbers on the trees.

Another problem, affecting the data collected during 1966 to 1969, was the fact that different sizes of beating sheets were used. Prior to this, sheets measuring about 2.1 X 2.7 m (7 X 9 feet) were used. These were spread on the ground beneath the tree before beating began; however, it was usually impossible to sample an area consistently measuring 2.1 X 2.7 m. Beginning in 1966, hand-held sheets were used that measured 0.9 X 0.9 m (3 X 3 feet). Since these were supported by cross braces, the area sampled remained consistent, and in this respect they were a considerable improvement over the older method. Because of the variable area actually covered by the old sheets, conversion to a common basis did not seem feasible. Consequently, another source of variability entered into the data.

Another problem encountered was the apparent lack of randomness in the collection of the samples. This applied not only to the areas chosen (many technicians seemed to have their favorite collecting points, either because of easy access or because they knew there were insects in a particular area), but also to the trees selected within a given area. This was usually not a problem with minor species, whose presence could not be detected from the ground, but it very definitely seemed to be so for some of the common insects, especially the larch sawfly. Although there is no way of proving the point, there seemed to be a marked tendency to collect larvae from trees showing signs of larch sawfly defoliation, and a similar trend may have existed for other species as well. There is no way of knowing.

Yet another problem that was frequently encountered was the rather common practice of varying the number of trees sampled. When insects were scarce, numerous trees were often sampled; however, when the insects were abundant, perhaps only one tree was sampled. This inconsistency was partially removed during data editing by expressing all samples on a five-tree basis, but it did not solve the problem completely. If more than five trees had been sampled, it simply meant that the means had less variability than five-tree samples would have had. Because insect populations tend to show marked variation between trees, there was the distinct possibility that samples of less than five trees tended to inflate the estimates, especially if the technician selected a particular tree because it showed feeding damage and then terminated sampling after one or two trees because he had collected enough insects.

Perhaps one of the most serious problems with Forest Insect Survey data is the fact that the stage of larval development is not recorded, and there is often about 80% mortality from the time the eggs hatch until the larvae spin cocoons or pupate. Consequently, the time at which a sample is taken, in relation to the phenology of the insect concerned, has a marked influence on the number of insects in each sample. For example, if a sample is taken early in the season, when the larvae are small, it will usually contain more larvae than would a similar sample taken from the same area later in the season, simply because of natural mortality that had occurred in the interval between collection of the two samples. Thus, although the later sample may contain less insects than the earlier one, it does not represent a different population, merely normal attrition.

The reader who is familiar with Survey procedures could probably add to this list of shortcomings in the data, but I do not wish to belabor the point. Nevertheless, the above weaknesses are the primary reason why minimal statistical methodology has been used in the preparation of this report.

METHODS

This report is based upon data collected by the Forest Insect and Disease Survey; consequently, the methods used in field sampling and insectary or laboratory rearing were those employed by the Survey. They will not be elaborated upon here, except to state that only the beating samples were used, as other sampling methods were felt to be too subjective. In addition, seven of the more common defoliators caused enough damage from year to year in certain areas to warrant cartographic presentation in the annual district reports (Anonymous 1946-1970). Most of these maps were based upon aerial surveys of the affected area, supplemented by ground sampling.

This aerial survey information was coded and entered onto computer punched cards. A number of areas, each measuring 1 degree of longitude by 0.5 degree of latitude, were each divided into nine equal subareas (3 X 3 grid). The degree of known defoliation was recorded in each: subareas with light defoliation were coded as 3; moderate defoliation was coded as 5; and severe defoliation was coded as 7. A total of 484 of these areas (22 X 22 grid), each containing nine subareas, covered the two provinces (including a part of northwestern Ontario, which was not used). The areas in Manitoba and Saskatchewan were grouped into 15 larger areas, which were similar (for the forested areas at least) to those surveyed by each of the District Rangers (Fig. 1). Seven areas (numbered in Fig. 1) contained usable information on one or more of the major forest insect defoliators. The remaining areas were excluded from analyses, as the data were too fragmentary to be useful.

For each of the seven numbered areas, the mean annual infestation rating was calculated for each of the seven species, on the assumption that all subareas in each area that did not have a rating were actually zero. The resulting number was the infestation rating for that area and year. For each species and area, the largest of these annual ratings was equated to 100, and all others were expressed as percentages of the largest number, so values usually range from 0 to 100 for each species and area. If the data were too fragmentary, they were excluded from further analysis.

In the beating samples collected by staff from the Winnipeg laboratory, no distinction was made in the coded enclosure slip data between regular samples and large mass collections made for determining rates of parasitism. To screen out these samples, it was therefore necessary to examine the original enclosure slips for all samples of more than 50 insects and for all samples collected from more than five trees. Any mass collections (this was indicated in the remarks section on the enclosure slip) were then deleted from further analyses. The data were further edited by deleting the larger decoded numbers (50 or more) of insects per sample on records collected prior to 1966 and inserting the actual numbers in their place.

Beating samples were collected throughout the season, often without regard to the stage of insect development. This was particularly true for the nonpest species. Consequently, many of the samples were collected before or after the larval period of a number of species. In an attempt to remedy this situation, an average effective larval sampling period for each species was prepared by establishing a cumulative frequency distribution for the numbers of larvae collected on various dates. This was done for each of the 21 species of insects considered in this report. In the case of some insects that overwinter as partially-developed larvae, the fall period was not included. Usually, the numbers of such samples were too small and identifications too tenuous to make their inclusion worth while. All samples from the appropriate host were included if the dates fell within the prescribed period, but they were excluded if otherwise. An annual effective sampling date for each species, which varied from year to year and place to place, could (and perhaps should) have been used, but this was not practical, especially for the less common species. To compensate for the fact that some of the samples were collected outside of the insect's active feeding period, all estimates referred to in this report are the mean number of insects per positive sample (i.e., containing at least one insect of the species under consideration), except when none of the required species was present, in which case the number per sample was recorded as zero. The mean number per positive sample was edited to ensure that all sample estimates were expressed as the number of insects per five-tree sample. This was necessary because some samples were collected from more than five trees, others from less. Finally, the annual percentage of samples containing the designated species (for its effective sampling period) was calculated for each of the 21 species for each of the seven numbered areas shown in Fig. 1. This expression contains the inaccuracy introduced by

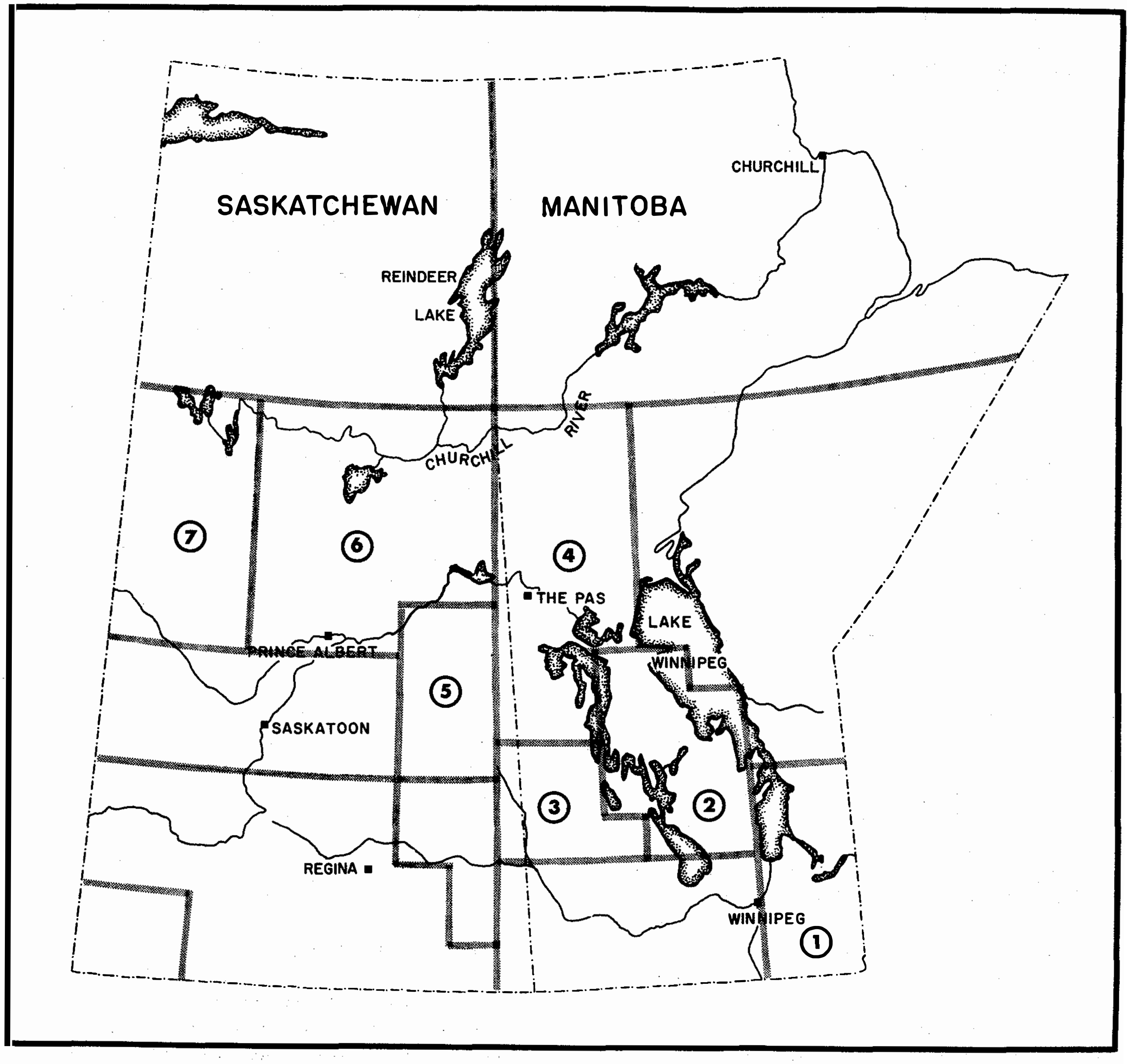

Figure 1. Outline of the 15 areas in Manitoba and Saskatchewan that were used for grouping the data.

poorly defined effective sampling periods, but no effective remedy could be found.

Total parasitism for each host species, based on adult emergence, was calculated for each of the seven areas whenever data were available, although estimates based on less than five individuals per rearing were not included. Three exceptions were made to this general rule: dipterous maggots that emerged from their host but did not survive to the adult stage were included; in the case of multiple parasitism, calculation of the percentage was based on the number of parasitized hosts killed rather than the number of parasite adults; and some of the larch sawfly parasitism records were based on dissections rather than rearings.

Records from weather stations operated by the Atmospheric Environment Service (one in each of the seven areas) were used to calculate a number of expressions summarizing seasonal weather conditions by 3-month periods. The periods used were August to October, November to January, February to April, and May to July for each generation of insects. Four summaries were prepared for some or all of the 3-month periods: total precipitation (all); heat units above 4.5°C (40°F) (all except November to January); heat units below -18°C (0°F) (November to January and February to April); and water deficits (May to July and August to October). The triangulation method (Lindsey and Newman 1956) was used to calculate the number of heat units because it was nearly as good an approximation as the sine curve (Arnold 1960) but the formulas were simple enough to be used on a programmable calculator. This meant that gaps in records could be filled in by making the calculations using data from substitute stations and without having to use a large computer. The water deficits were calculated from monthly precipitation and mean temperatures, assuming a saturated soil with a field capacity of 100 mm (4 in) at the beginning of May (Thornthwaite and Mather 1957).

After calculation, all of the above values were expressed as percentages of the range. For each variable, period, and area, the largest value during 1945 to 1969 was equated to 100%, the smallest value was equated to 0, and the remaining values ranged between these two extremes. This procedure simplified plotting and eliminated many of the differences between areas.

Additional data on bird and small mammal populations have also been summarized, although they are limited to only portions of the two provinces. Christmas bird counts in or adjacent to areas 5, 6, and 7 (Fig. 1) were available for 1945 to 1969 (Anonymous 1943-1977). All counts of black-capped and boreal chickadees and hairy and downy woodpeckers (the four insectivorous birds of any consequence) were expressed as numbers per party hour. For some of the earlier reports it was necessary to make some rather liberal assumptions in order to obtain this figure. Even so, because there were insufficient data for Area 7, it was discarded. Using the methods outlined by Kendeigh (1944), breeding bird censuses (which were of varying quality) were made for a number of years in four tamarack bogs in southeastern Manitoba during studies on the population dynamics of the larch sawfly. Small mammal population estimates were also made in the same bogs for a number of years. Live traps were used to catch mice and voles, while shrews were caught in tumble-in traps (Ives *et al.* 1968). Population figures were either total counts or were based on the Lincoln Index.[1]

Statistical manipulation of the data was relatively simple. For each of the seven districts shown in Fig. 1, and for each of the 21 species of insects, the population trends from year **t** to **t + 1** were grouped into one of four categories on the basis of the mean number of insects per positive sample and the percentage of samples that was positive (both being given equal weight): 1) insect absent; 2) insect present (no trend or trend unknown); 3) population increasing; and 4)

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[1] $$\text{Population} = \frac{\text{Number caught in last sample} \times \text{Total number marked}}{\text{Number of marked individuals in last sample}}$$

population decreasing. Some of the decisions concerning appropriate categories were somewhat arbitrary. For example, if the mean number of insects went up and the proportion that was positive went down, it was usually considered that no trend was evident. If both went up or both went down, there was no problem. There were, however, a number of cases in which one variable clearly went in one direction while the other displayed a slight trend in the other direction. Judgment had to be exercised in these instances.

These four categories were used to sort the weather records for the appropriate years, periods, and areas, and mean values (based on percentages of the range) were calculated for each. The differences between mean values for increasing populations and mean values for decreasing populations were then calculated, as were the differences between the present and absent categories.

Population trends for the forest tent caterpillar, the large aspen tortrix, and the spruce budworm were used to sort the appropriate Christmas bird counts for areas 5 and 6. A series of similar sorts, based on data for the larch sawfly and three other species of tamarack defoliators, was done with data collected during the breeding-bird and small-mammal censuses in the four tamarack bogs. Most of the population trends used for these sorts were determined from the larch sawfly population dynamics study records, as the Survey data were too fragmentary to be of much use.

Finally, simple correlations between the mean number of insects per positive sample were calculated for all possible combinations of pairs among the 21 species of insects for each area and for all seven areas combined (using the areas as replicates).

OUTBREAK HISTORIES

The economic importance of defoliating forest insects depends upon the amount of damage caused and the value of the resource affected. Evaluation on this basis is beyond the scope of the present report, but the frequency with which an insect species reaches infestation or outbreak levels[2] can be used as a measure of an insect's potential for causing economic damage.

This section will briefly review the literature on the major defoliators, in order to provide background on their importance. Information will also be presented on the frequency of occurrence of each of the 21 species in Manitoba and Saskatchewan between 1945 and 1969. This includes species that have not reached pest status, since an examination of changes in their abundance may reveal valuable clues concerning factors affecting insect abundance. Also presented are available information on total parasitism and a number of expressions intended to reflect various aspects of weather.

In the following review, and throughout the remainder of this report, the order in which the different species are discussed in each section will be the same as in Figs. 2-8, which are arranged by main host species. The grouping has no particular justification other than that it seemed a logical arrangement.

Malacosoma disstria[3]

The forest tent caterpillar is a native insect that frequently reaches outbreak proportions. Baird (1917) reported an outbreak in eastern North America as far back as 1791, and other outbreaks apparently occurred about 1820, 1828, 1840, and 1853. Later outbreaks had better documentation and occurred during 1866-70, 1874-78, 1883-84(?), 1887-89, 1897-99, and 1910-1914. Sippell (1962) reviewed the outbreaks in

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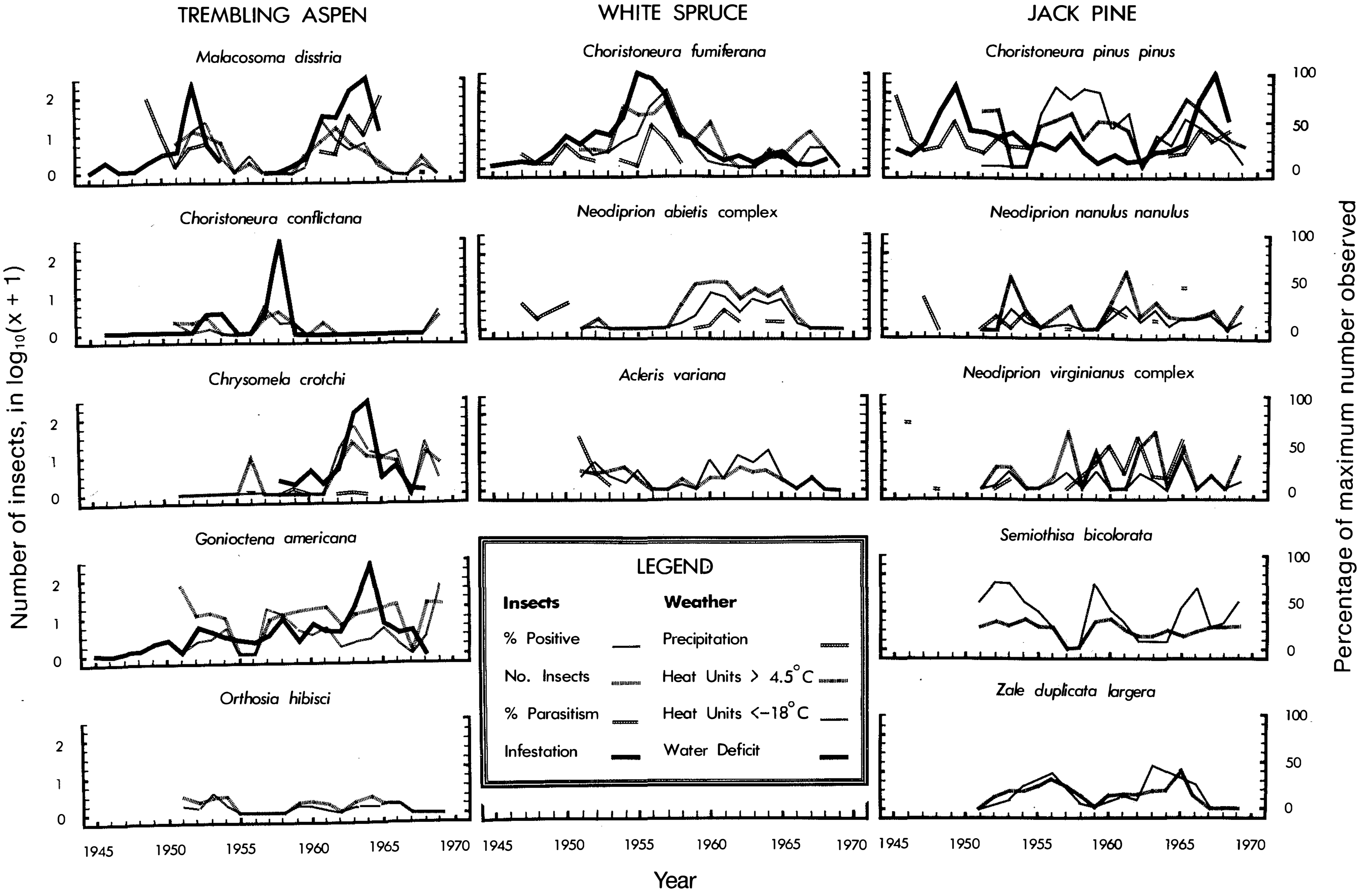
[2] Entomologists often refer to a localized upsurge in insect abundance as an infestation and to a number of discrete or coalesced infestations over a wider area as an outbreak.

[3] Lepidoptera: Lasiocampidae.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
Acleris variana
Neodiprion virginianus complex
Goniоctena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
LEGEND
Insects
Weather
% Positive
No. Insects
% Parasitism
Infestation
Precipitation
Heat Units > 4.5°C
Heat Units <-18°C
Water Deficit
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed
0
1
2
0
50
100
1945
1950
1955
1960
1965
1970
Year

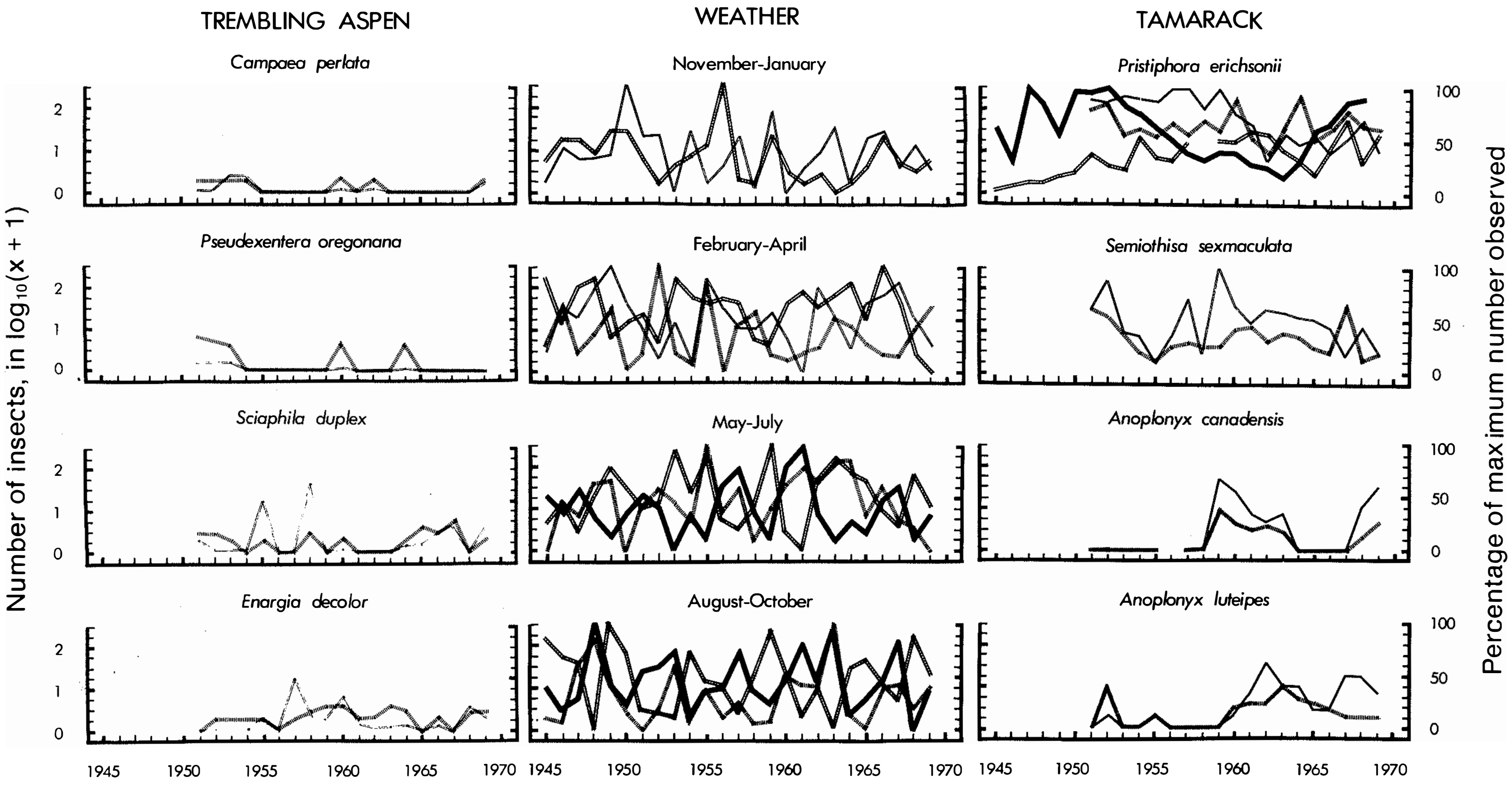
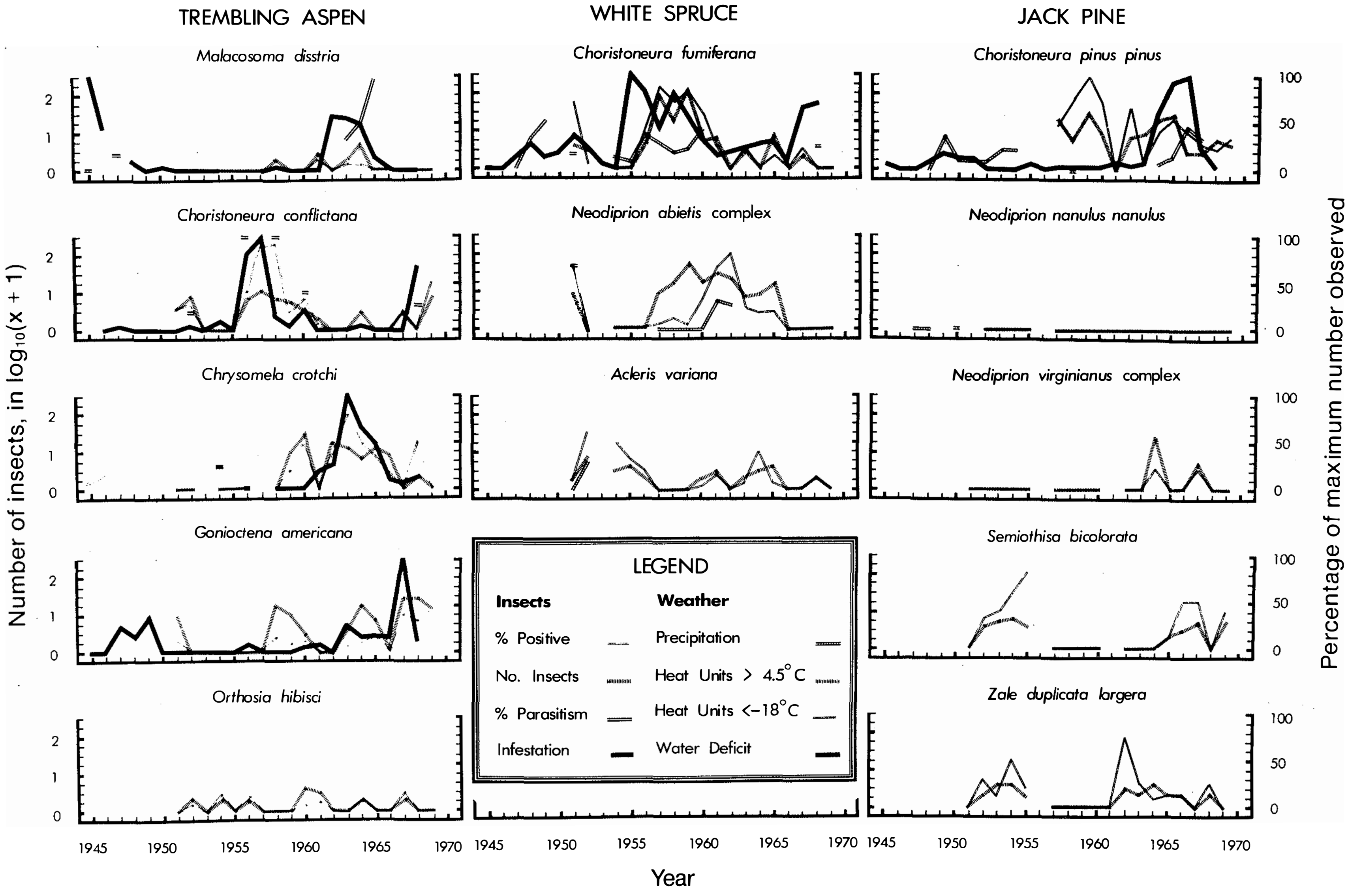


Figure 2. Insect and seasonal weather data for southeastern Manitoba (Area 1 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.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Acleris variana
Neodiprion virginianus complex
Gonioctena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
LEGEND
Insects
% Positive
No. Insects
% Parasitism
Infestation
Weather
Precipitation
Heat Units > 4.5°C
Heat Units <−18°C
Water Deficit
Number of insects, in log10(x + 1)
Percentage of maximum number observed
Year
0
1
2
0
50
100
1945
1950
1955
1960
1965
1970

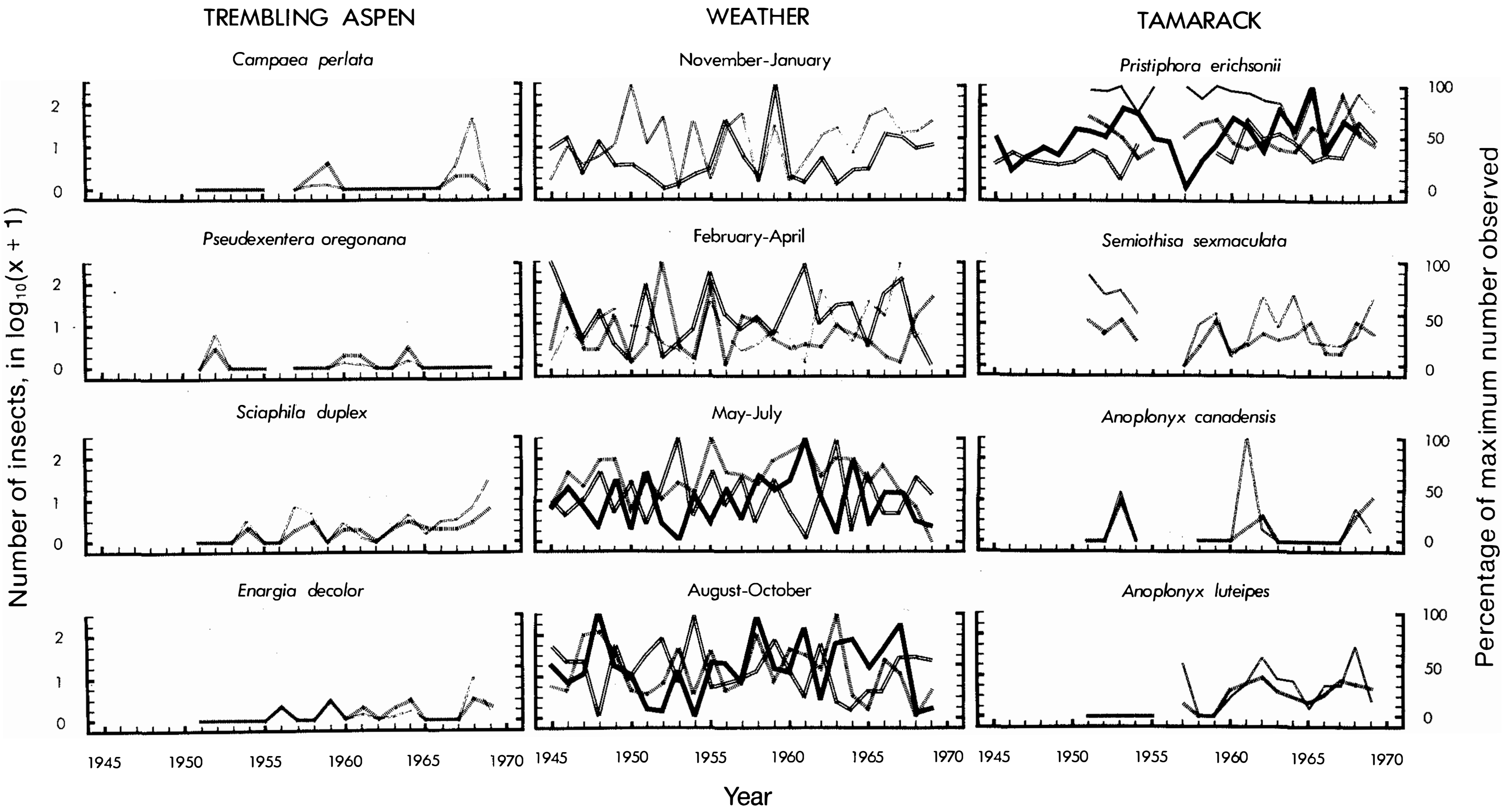
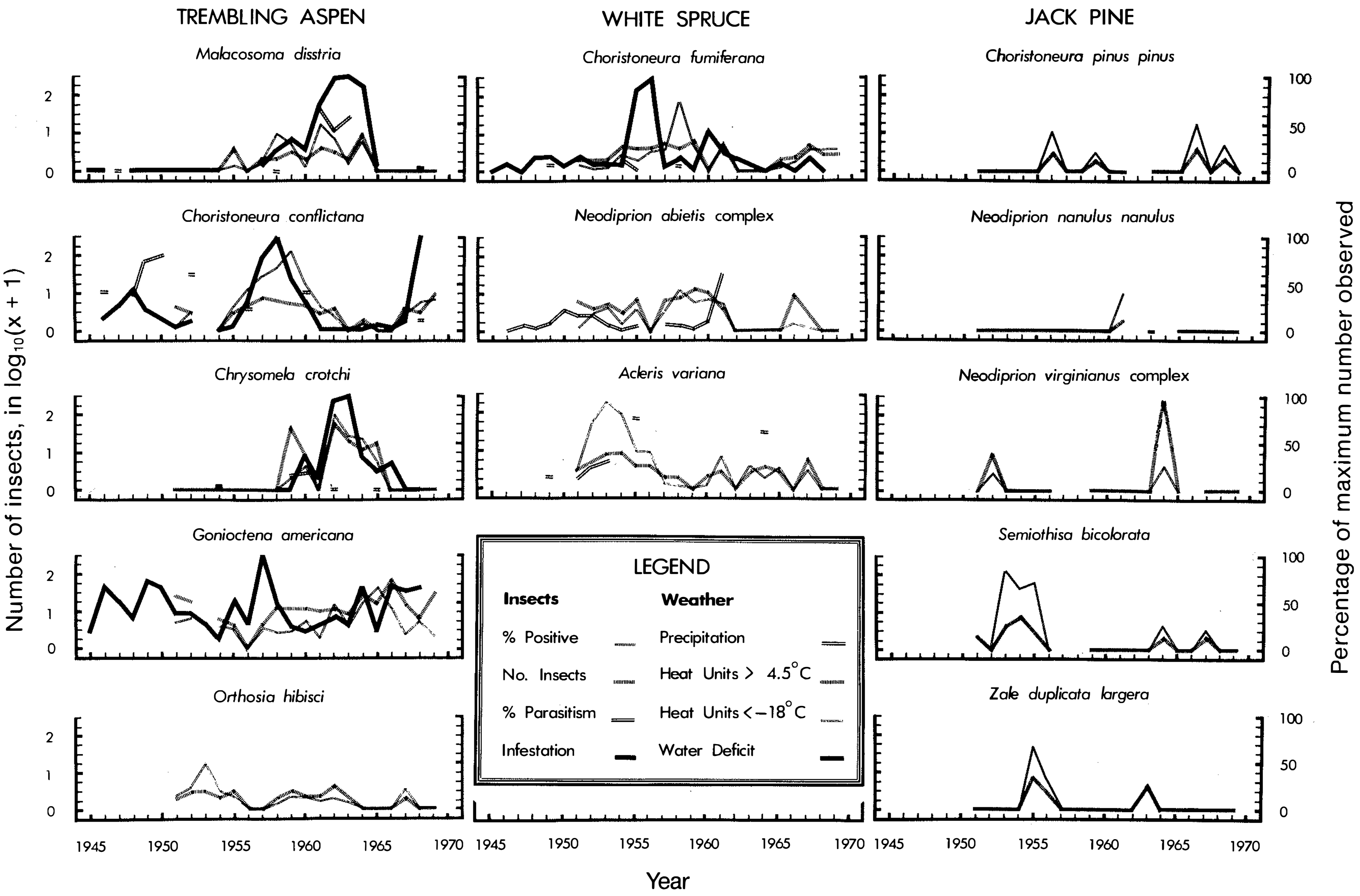


Figure 3. Insect and seasonal weather data for the Interlake and Westlake area of Manitoba (Area 2 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
Acleris variana
Neodiprion virginianus complex
Gonioctena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed
0
1
2
50
100
1945
1950
1955
1960
1965
1970
Year
LEGEND
Insects
Weather
% Positive
No. Insects
% Parasitism
Infestation
Precipitation
Heat Units > 4.5°C
Heat Units < −18°C
Water Deficit

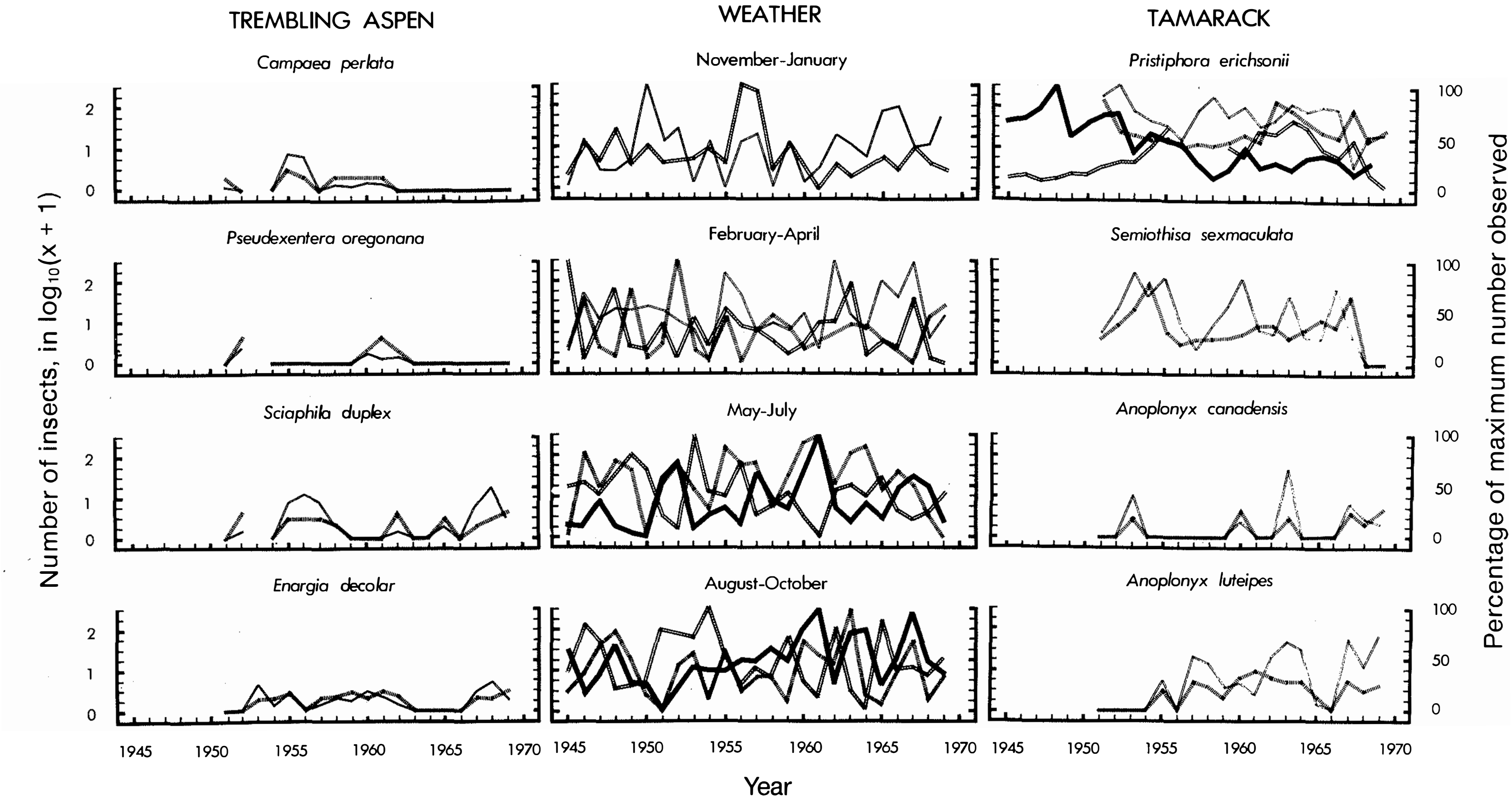
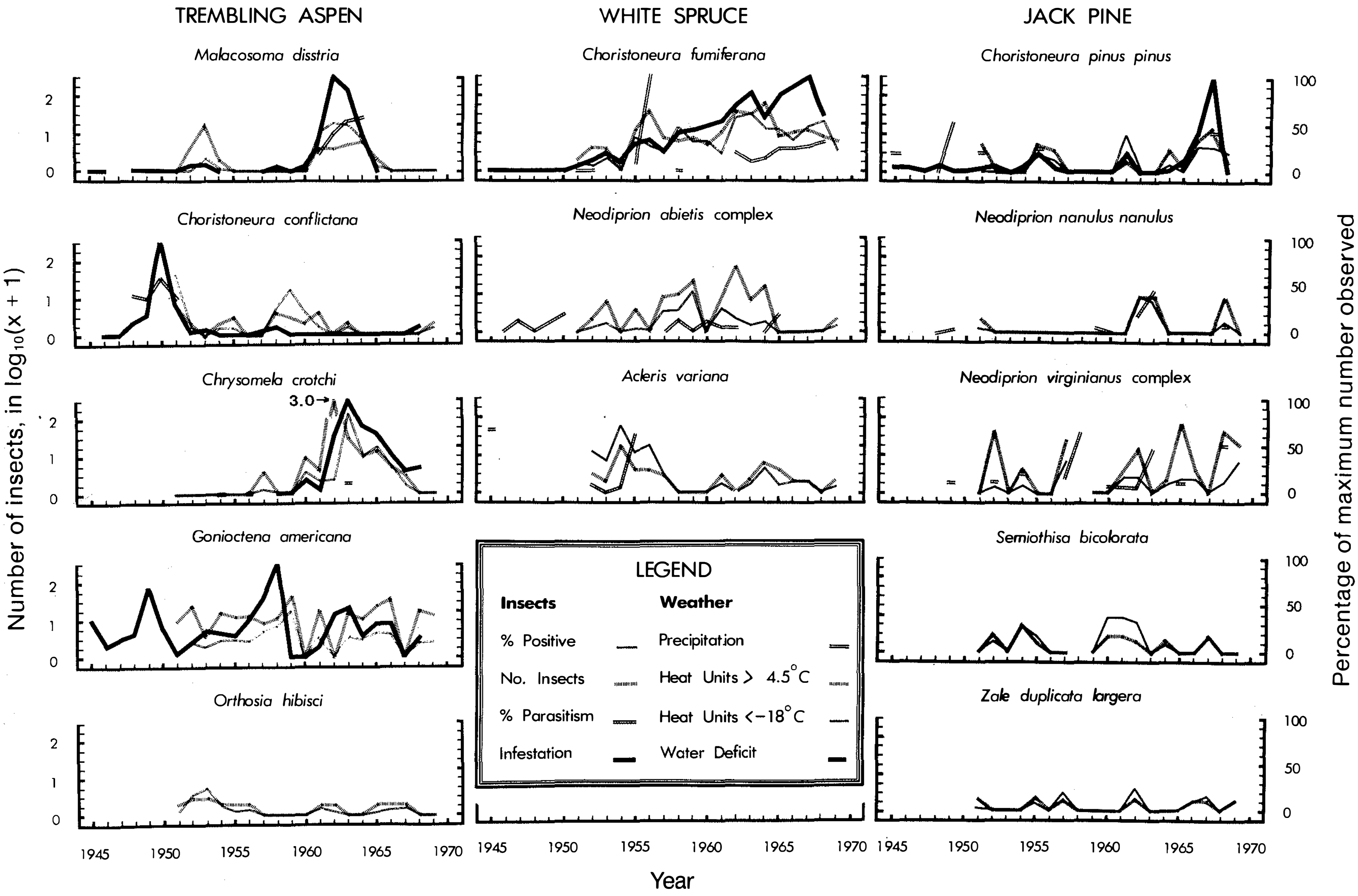


Figure 4. Insect and seasonal weather data for the Riding Mountain and Duck Mountain area of Manitoba (Area 3 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
3.0→
Acleris variana
Neodiprion virginianus complex
Goniactena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
LEGEND
Insects
Weather
% Positive
No. Insects
% Parasitism
Infestation
Precipitation
Heat Units > 4.5°C
Heat Units < −18°C
Water Deficit
0
1
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50
100
1945
1950
1955
1960
1965
1970
Year
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed

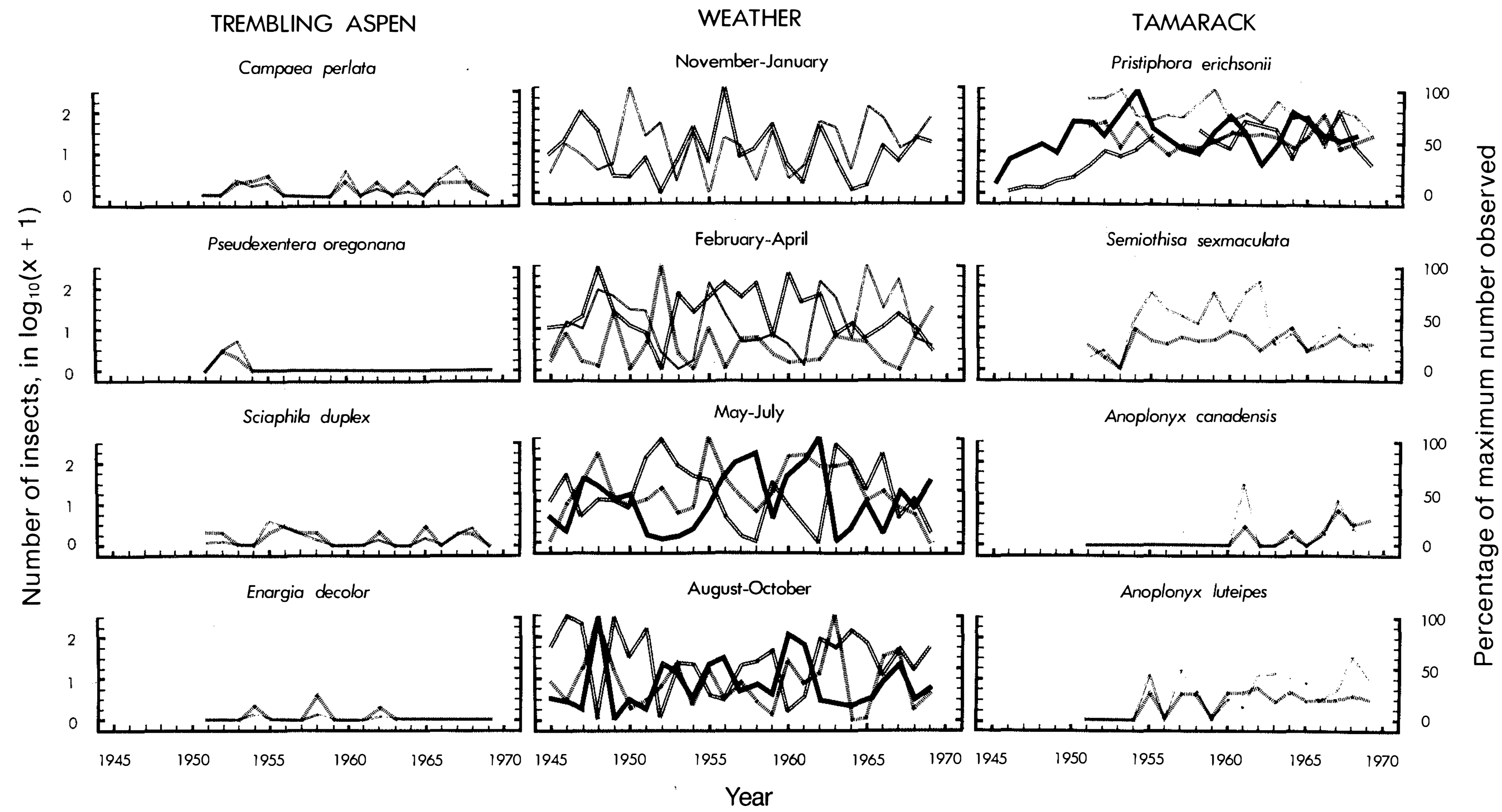
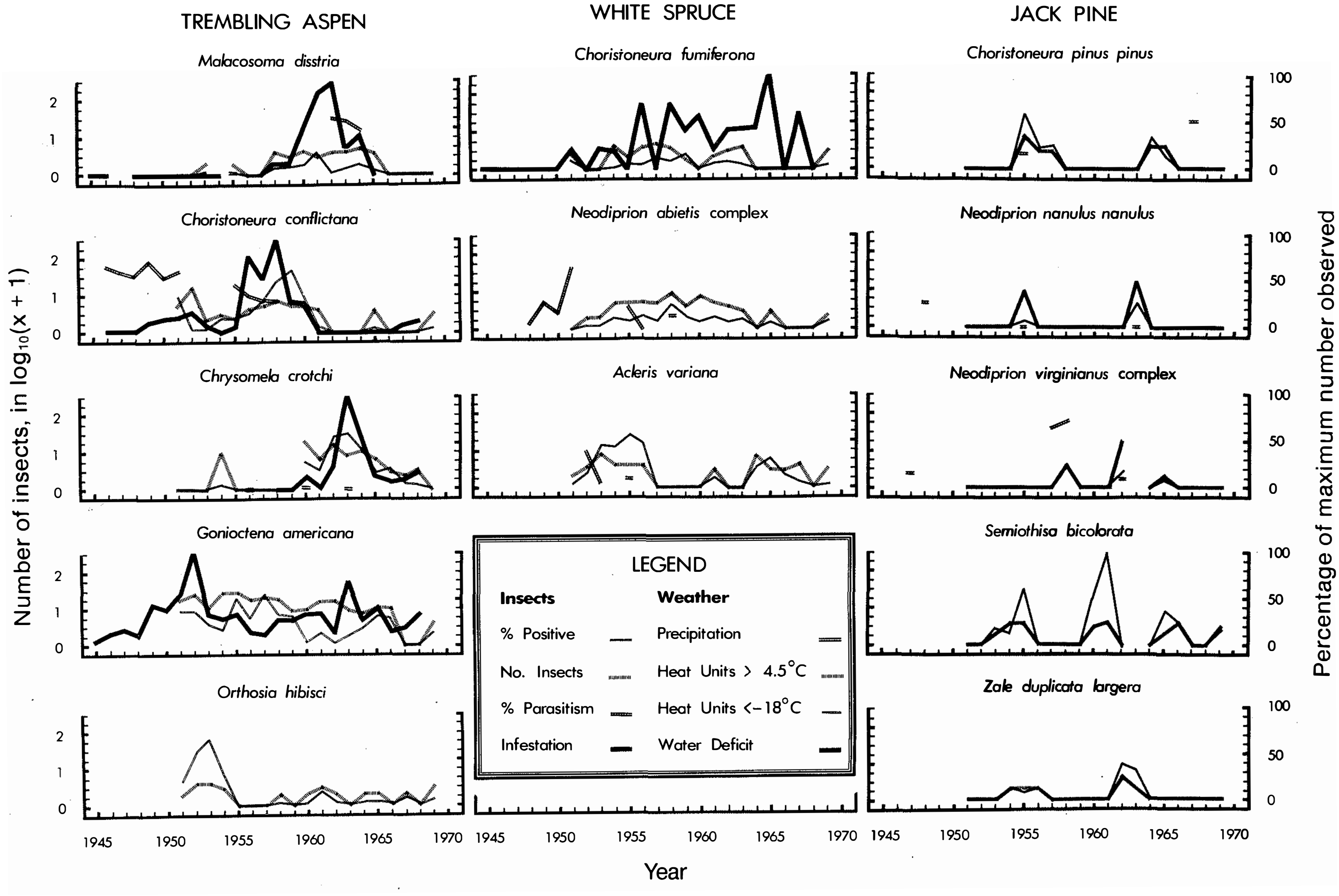


Figure 5. Insect and seasonal weather data for northwestern Manitoba (Area 4 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
Acleris variana
Neodiprion virginianus complex
Goniotena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
LEGEND
Insects
Weather
% Positive
No. Insects
% Parasitism
Infestation
Precipitation
Heat Units > 4.5°C
Heat Units <-18°C
Water Deficit
0
1
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50
100
1945
1950
1955
1960
1965
1970
Year
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed

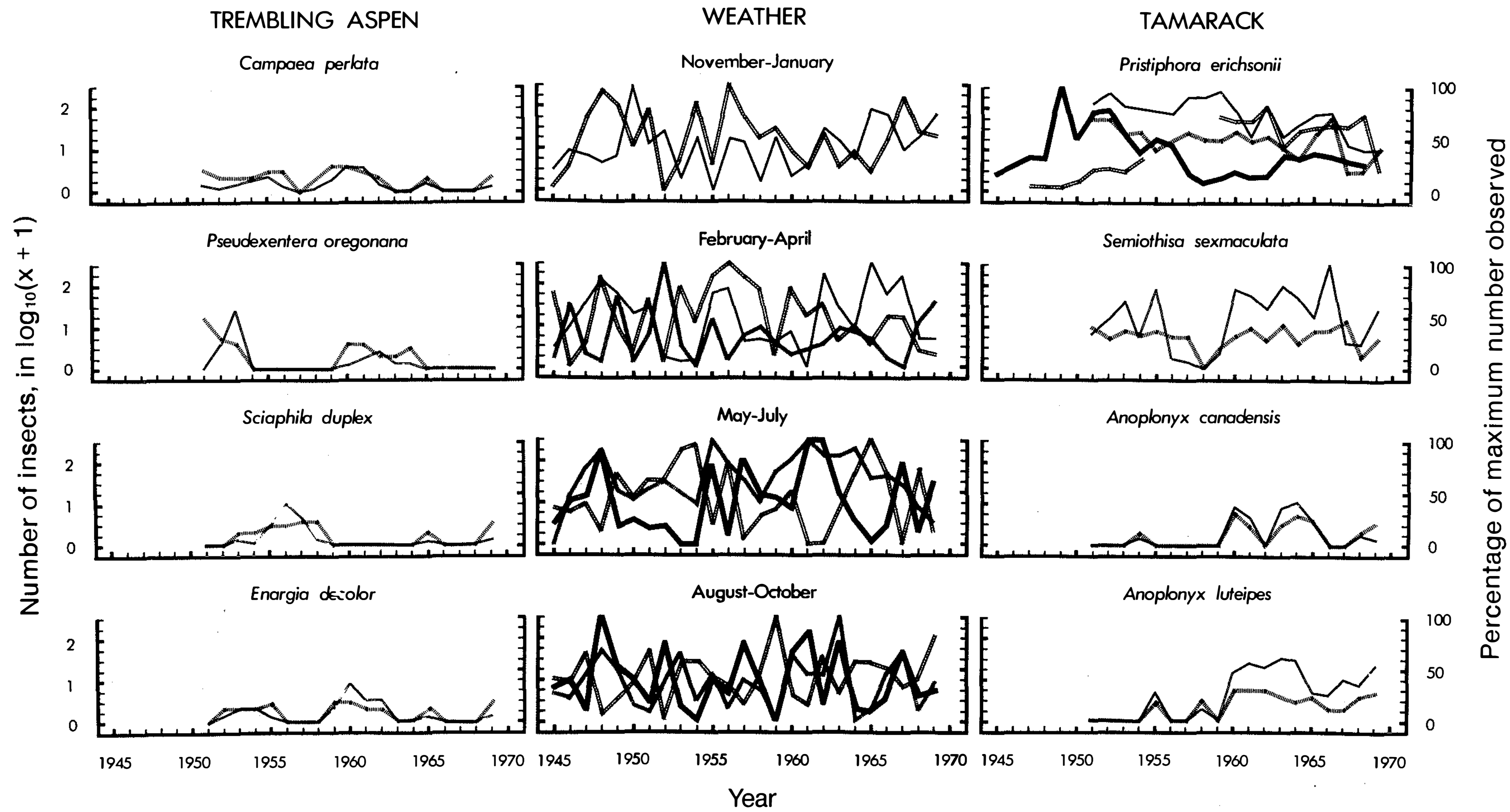
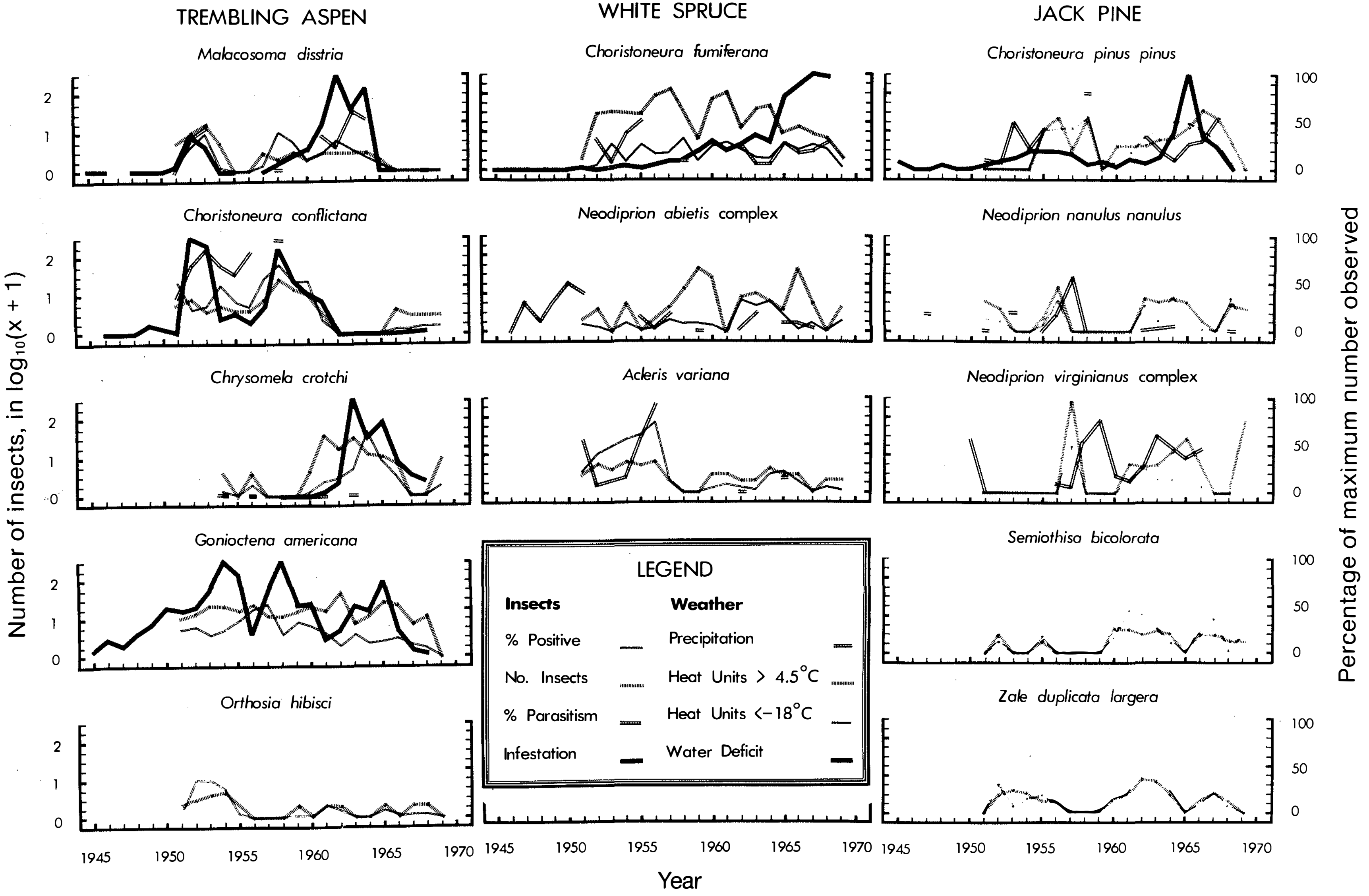


Figure 6. Insect and seasonal weather data for the Hudson Bay area of Saskatchewan (Area 5 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
Acleris variana
Neodiprion virginianus complex
Gonioctena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
LEGEND
Insects
Weather
% Positive
Precipitation
No. Insects
Heat Units > 4.5°C
% Parasitism
Heat Units <−18°C
Infestation
Water Deficit
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed
0
1
2
0
50
100
1945
1950
1955
1960
1965
1970
Year

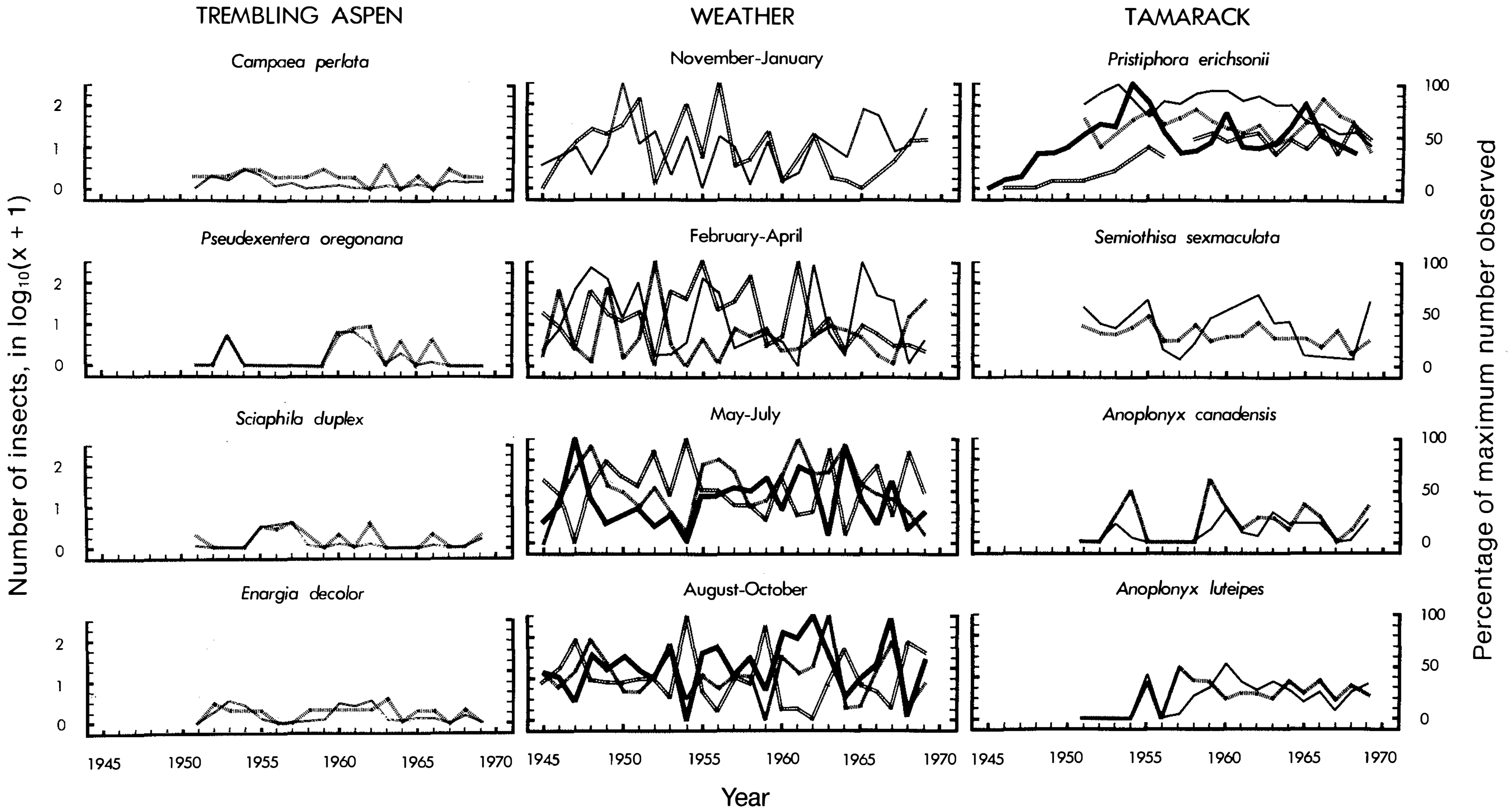
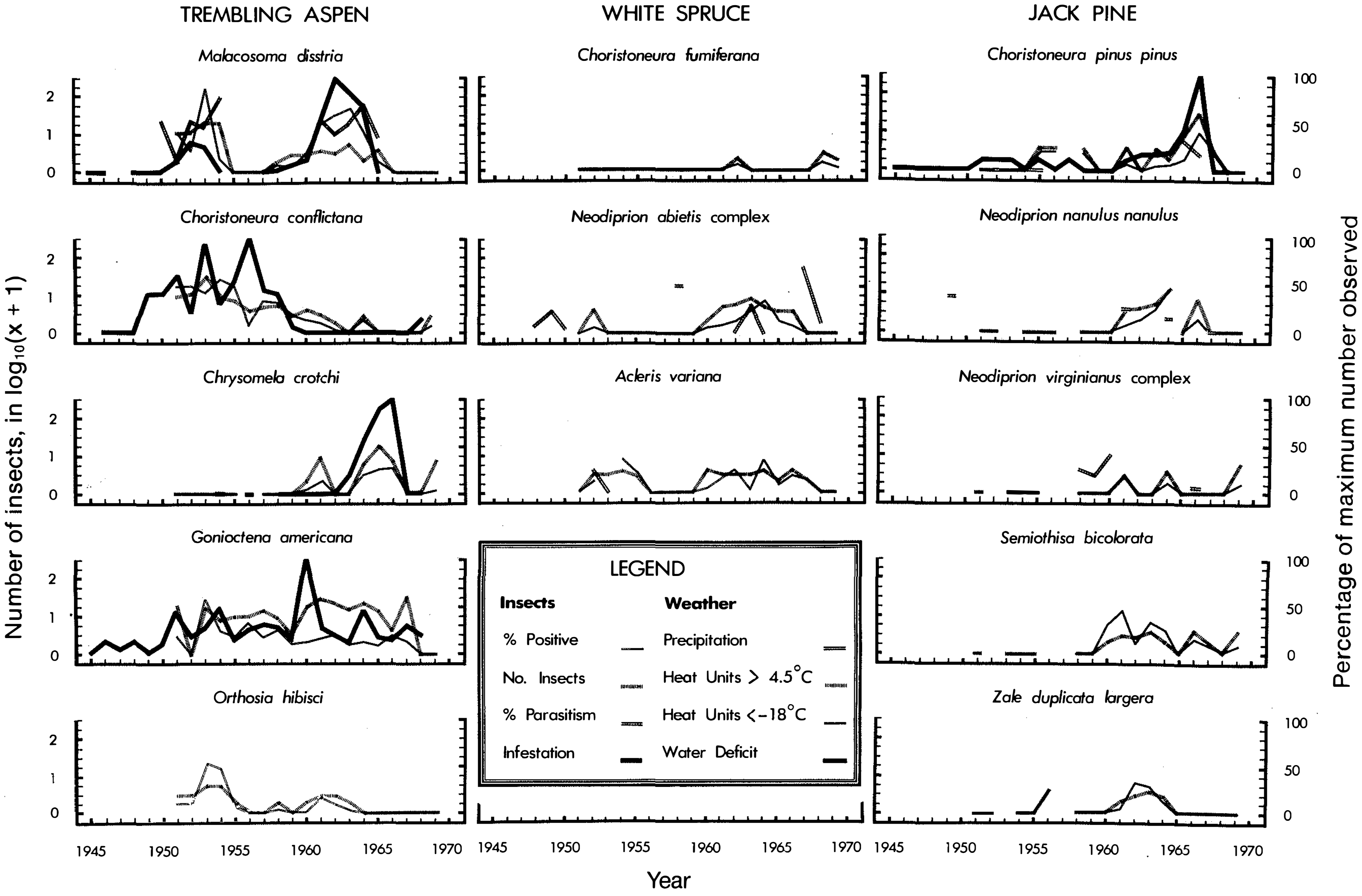


Figure 7. Insect and seasonal weather data for the Prince Albert area of Saskatchewan (Area 6 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the maximum value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.


TREMBLING ASPEN
WHITE SPRUCE
JACK PINE
Malacosoma disstria
Choristoneura fumiferana
Choristoneura pinus pinus
Choristoneura conflictana
Neodiprion abietis complex
Neodiprion nanulus nanulus
Chrysomela crotchi
Acleris variana
Neodiprion virginianus complex
Gonioctena americana
Semiothisa bicolorata
Orthosia hibisci
Zale duplicata largera
0
1
2
0
50
100
1945
1950
1955
1960
1965
1970
Year
Number of insects, in log₁₀(x + 1)
Percentage of maximum number observed
LEGEND
Insects
% Positive
No. Insects
% Parasitism
Infestation
Weather
Precipitation
Heat Units > 4.5°C
Heat Units <−18°C
Water Deficit

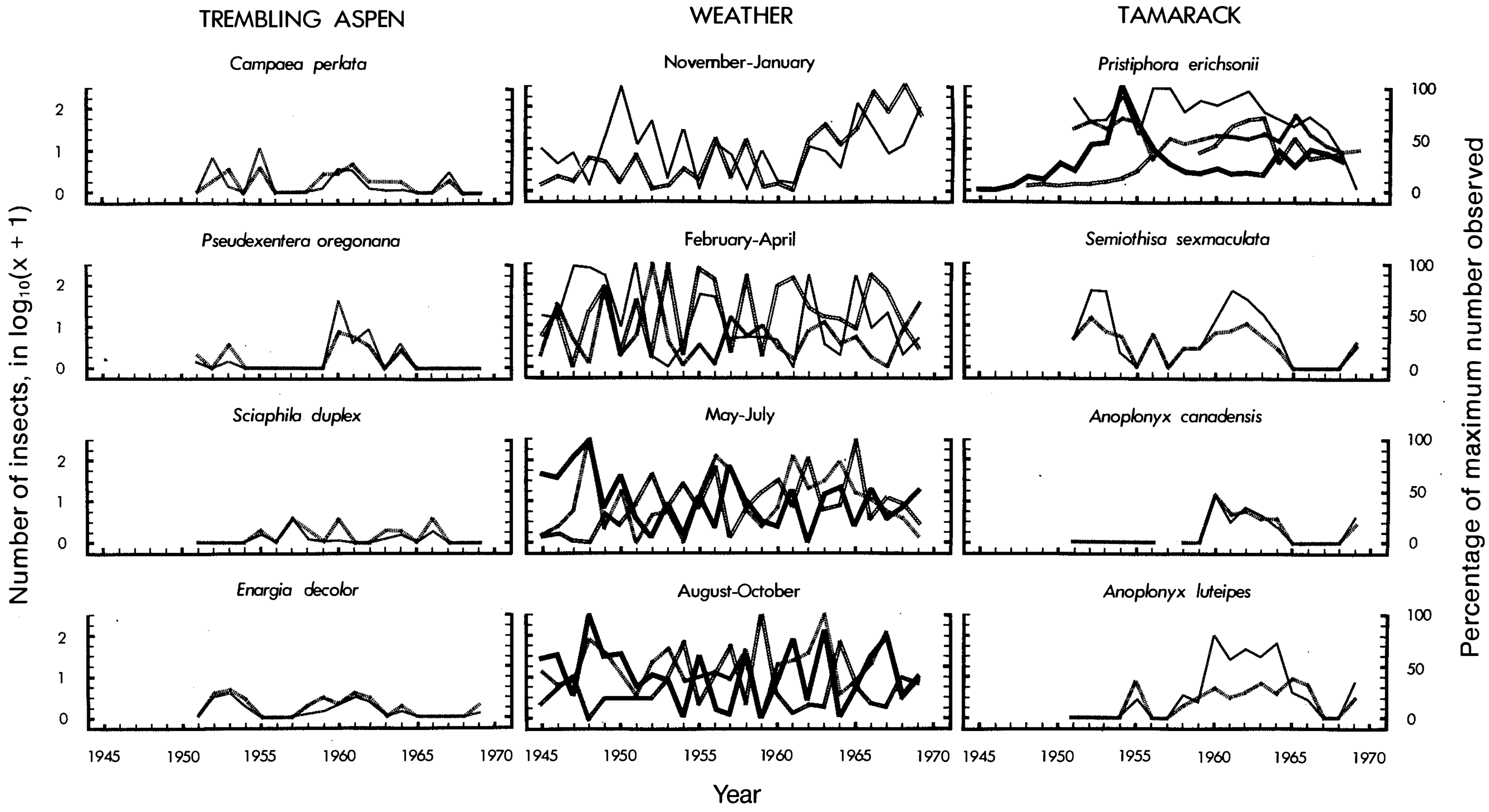


Figure 8. Insect and seasonal weather data for the Meadow Lake area of Saskatchewan (Area 7 in Fig. 1), 1945-69. Infestations are expressed as a percentage of the largest value observed for each insect. Seasonal weather data are expressed as a percentage of the range, i.e., the smallest value for each variable was equated to 0 and the largest to 100.

Ontario back to 1867. His figures differed only in minor details from those cited above. In addition, Sippell reported outbreaks in 1924-26, 1930-38, 1940-45, and 1948-56 and one starting in 1960. Brown (1938) discussed the 1931-38 Ontario outbreak in detail, while Hodson (1977) reviewed an outbreak in Minnesota that lasted from 1948 to 1959 and whose peak years were 1951-53. Sippell (1962) noted that the interval between the start of outbreaks in Ontario was about 10 years. A similar trend appeared to exist in Baird's (1917) early data as well.

The history of outbreaks in western Canada is less complete. Early reports (Baird 1917) indicated four outbreaks between 1890 and 1920, but these all appeared to be in British Columbia. Hildahl and Reeks (1960) reviewed the history of outbreaks in Manitoba and Saskatchewan and reported that the records indicated four sequences of infestations between 1923 and 1953. Because of the size of the area, however, there was always a location within it where the forest tent caterpillar was causing noticeable damage. The decision concerning the number of outbreaks was therefore not clear-cut. Ives (1969) gave a cartographic presentation of what appeared to be three outbreaks in Saskatchewan between 1938 and 1969. The first lasted from sometime prior to 1938 until 1945, the second was from 1951 to 1953, and the third occurred from 1958 to 1964. Ives (1971) presented a cartographic history of forest tent caterpillar infestations in Alberta between 1957 and 1970. A major outbreak occurred across much of the north-central part of the province between 1960 and 1964.

As the foregoing discussion shows, the forest tent caterpillar reaches outbreak levels at rather frequent intervals. In the usual pattern of infestation the period of extreme abundance is relatively short-lived. Sippell (1962) summarized the development of an outbreak as follows: 1) incipient period lasting 2 or 3 years, when populations and areas of defoliation were expanding; 2) period of excess lasting 1 or 2 years, when there was a marked excess in the numbers of insects required to strip the foliage from the trees; and 3) declining period usually lasting 1 year, leading to the collapse of the outbreak. The typical outbreak therefore lasts about 4 to 6 years. During most of this period there will be very little radial increment in the trees (Batzer 1955; Duncan and Hodson 1958), but there is little evidence of tree mortality directly attributable to forest tent caterpillar defoliation (Kulman 1971). Although there is some indication that the incidence of disease is greater among trees that have been weakened by forest tent caterpillar defoliation (Churchill *et al.* 1964; Duncan and Hodson 1958), the main loss is due to the reduction in radial increment during the period of defoliation. Duncan and Hodson (1958) stated that nearly 90% of the prospective radial growth was lost during the second and third year of heavy defoliation. Batzer (1955) estimated that the loss would amount to between 17 and 54 m^3/ha over 4 years. In addition, the large numbers of crawling larvae, especially prevalent during the period of excess, are extremely annoying to many people, particularly rural residents and campers.

Choristoneura conflictana[4]

The large aspen tortrix periodically reaches outbreak proportions, but these outbreaks tend to be short-lived and are often overshadowed by outbreaks of the forest tent caterpillar. Criddle (1918) reported what appeared to be a widespread outbreak in southwestern Manitoba (in association with the poplar leaf roller) that lasted from 1916 to 1918. Prentice (1955) reviewed the known outbreaks in Canada and reported two major outbreaks in Manitoba. Trembling aspen in parts of the Duck Mountain Provincial Forest were completely defoliated from 1946 to 1948. In 1948 an outbreak was detected in northern Manitoba, and by 1950 the area affected was approximately 26 000 km^2. The outbreak declined in 1951 and had collapsed by 1952. Ives (1969) gave a cartographic representation of infestations in Saskatchewan. Scattered pockets of moderate to severe defoliation occurred from 1948 to 1953 and again from 1956 to 1960. The years of heaviest infestation appeared to be 1952-53 and

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[4] Lepidoptera: Tortricidae.

1956-58. Wickman (1963) reported a small infestation that occurred in California in 1960 and 1961. Beckwith (1968) reported a major infestation in interior Alaska that affected an area of about 13 000 km^2 in 1966 and 1967.

Criddle (1918) reported that defoliation was responsible for much killing of the aspen, but otherwise there seems to have been little mortality that can be attributed directly to large aspen tortrix defoliation. The insects themselves are not as objectionable to most people as are forest tent caterpillars, but the extensive webbing during heavy defoliation (Beckwith 1973) can be extremely annoying, especially in campgrounds.

Chrysomela crotchi[5] and *Gonioctena americana*[6]

The aspen leaf beetle and the American aspen beetle both occur fairly frequently in Manitoba and Saskatchewan but appear to be relatively rare elsewhere. Elliot and Wong (1966) reported an outbreak of the aspen leaf beetle in Manitoba and Saskatchewan that reached a peak area of 189 000 km^2 in 1963. Ives (1969) showed that these two insects caused more or less continuous but spotty defoliation in Saskatchewan between 1947 and 1965. The periods of heaviest defoliation were 1950-53 and 1959-63, although light defoliation occurred until 1965. A perusal of the Annual Forest Insect and Disease Survey Reports (Anonymous 1939-1973) indicated that most of the earlier damage was probably attributable to the American aspen beetle, while the aspen leaf beetle caused most of the damage in the later outbreak. Apart from severe skeletonizing of the foliage, little real damage to the trees seems to have occurred.

Orthosia hibisci[7], *Campaea perlata*[8], *Pseudexentera oregonana*[9], *Sciaphila duplex*[10], and *Enargia decolor*[11]

This group of lepidopterous defoliators are fairly common on trembling aspen but seldom cause any significant amount of defoliation. This does not mean that they cannot do so if conditions are favorable to the insect. For example, Sippell *et al.* (1971) summarized the abundance of *E. decolor* in Ontario between 1955 and 1970. It caused widespread defoliation on three occasions: in northwestern Ontario in 1959 and 1960; in an area east of Lake Superior from 1960 to 1963; and in northeastern Ontario in 1969 and 1970. Similarly, *S. duplex* (the poplar leaf roller) has reached infestation levels a number of times in various parts of Canada, and an area of about 100 000 ha was infested in 1962 at the peak of an outbreak in western Wyoming, Utah, and southeastern Idaho (McGregor 1967).

Choristoneura fumiferana[12]

The spruce budworm is probably the most important forest insect in eastern Canada; consequently, a large amount of effort has been expended studying this insect and documenting its epidemics. Blais (1965) examined basal discs of old white spruce trees cut in the Laurentide Park in Quebec, and on the basis of growth suppression he was able to detect spruce budworm outbreaks as early as 1704. Other outbreaks started about 1748, 1808, 1834, 1910, and 1947. Bean and Waters (1961) reported outbreaks in Maine starting about 1807, 1878, 1910, and 1944. Blais (1954) was able to trace the development of an outbreak that started in about 1866 in the Lac Seul area of northwestern Ontario, which is much the same area in which an outbreak started about 1940. Blais (1968) gave a comprehensive summary of past outbreaks in western and central Ontario, in central and eastern Quebec, and in southern Quebec, New Brunswick, and Maine. He was able to show that the outbreaks were not synchronous over eastern North America: populations in some areas reached outbreak proportions, while those in other areas remained at endemic levels. These differences he attributed to climate and forest composition. In parts of the area the occurrence of outbreaks was limited by cool weather in the summer.

[5, 6] Coleoptera: Chrysomelidae.
[7, 11] Lepidoptera: Noctuidae.
[8] Lepidoptera: Geometridae.
[9, 10] Lepidoptera: Olethreutidae.
[12] Lepidoptera: Tortricidae.

In other parts there was not enough balsam fir to support a budworm outbreak. In still other areas severe budworm outbreaks destroyed most of the balsam fir, and further outbreaks did not develop until the balsam fir once again approached maturity.

Outbreaks in eastern Canada during the current century have been outlined by a number of workers. De Gryse (1947) traced the generalized history of outbreaks in Ontario and Quebec from 1909 to 1944. Brown (1970) extended the area to include all of eastern Canada and updated the history to 1966. Detailed histories of budworm outbreaks in various parts of eastern Canada have also been given by several authors: Blais (1964)--Laurentide Park region; Blais and Martineau (1960)—Lower St. Lawrence region and Gaspé Peninsula; Elliot (1960)—northwestern Ontario; Otvos and Moody (1968)—Newfoundland; and Webb *et al.* (1961)—Atlantic region.

Less information is available on outbreak history in western Canada. Hildahl and DeBoo (1974) reviewed the rather sketchy information on the history of the insect in Manitoba. Apparently an outbreak occurred in the central part of the province about 1907, and another occurred around Lake Winnipeg about 1927. Since then, outbreaks have been recorded in the Spruce Woods Provincial Forest starting in 1940, in the Namew Lake area starting in 1951, and east of Lake Winnipeg starting in 1953. Ives (1969) outlined the known history of the spruce budworm in Saskatchewan from 1938 to 1967. Apart from a small area in the Cypress Hills, the main outbreak appeared to be a gradual extension of the Namew Lake infestation. At its peak (1965 to 1967) the infested area in Saskatchewan stretched along much of the Churchill River system.

There are two obvious differences between outbreaks of the spruce budworm and those of the aspen defoliators, particularly the forest tent caterpillar, that have been discussed previously. The forest tent caterpillar frequently reaches outbreak proportions but usually causes very little tree mortality. On the other hand, the spruce budworm reaches outbreak levels less frequently, but when outbreaks do occur, the results are usually much more devastating.

The amount of timber loss attributed to the spruce budworm is staggering. The losses between 1909 and 1946 were very effectively summarized by de Gryse (1947):

> One outbreak after another has occurred in an uninterrupted series. As previously stated, about 250,000,000 cords of spruce and balsam have fallen prey to the budworm between 1909 and 1946. Statistics of this kind make little or no impression on our imagination. Let us put it another way. Suppose that all the spruce and balsam killed in Canada by the budworm in the past 37 years were sawn into 4-ft. logs. Suppose also that, after fashion of piling cord measure, we attempted to heap this wood into lots 8 feet long, 4 feet wide and 4 feet high, each pile being contiguous with the next. When our job is finished we would have a band of wood 4 feet in height and 60 feet in width, completely encircling the earth at the equator.

This statement, based on crude loss estimates, clearly indicates why the spruce budworm is considered to be the major forest pest in eastern Canada. More-detailed studies confirm the serious losses caused by this insect. Turner (1952) presented extensive tables on losses attributable to budworm attack on white spruce and balsam fir stands. Generally speaking, losses were higher among the balsam fir than among the white spruce. This was confirmed by Elliot (1960) when he studied the effects of continuous defoliation on these two tree species in two different areas in northwestern Ontario. Both species started to show light mortality after 5 years of continuous defoliation. After 7 years, mortality of balsam fir ranged from about 40% to 50%, while mortality of white spruce was only 20% to 30%. After 9 years the corresponding figures were 85-90% for balsam fir and 40-55% for white spruce. All of the balsam fir were dead after 11 years of continuous defoliation, but only about 70% of the white spruce had died. Elliot (1960) estimated that about 1.14 million ha in the Lac Seul area and another 2.14 million ha in the Lake Nipigon area were affected by the 1944-55 outbreak in northwestern Ontario. He estimated that the losses were 28.3 million m^3 balsam fir, 18.3 million m^3 white spruce, and 16.4 million m^3 black spruce, for a total loss of about 63 million m^3 of wood. The most direct, and perhaps best, assessment of the effects of budworm defoliation was made in Minnesota (Batzer 1973). A number of plots were protected from budworm defoliation by annual spraying with DDT, while budworm populations were allowed to develop unchecked in a series of similar plots that were not sprayed. When the outbreak ended 5 years later, the volume of the timber on the unsprayed areas was about 28 m^3/ha less than on the sprayed areas. The effects of defoliation continued after the outbreak ended, and the difference between the volumes on the sprayed and unsprayed plots had increased to 71 m^3/ha in another 5 years. It is easy to see why the spruce budworm is of major concern to forest managers.

Neodiprion abietis complex[13]

Bird (1929) reviewed the early literature on this group of insects and found that outbreaks have occurred over a wide area of eastern North America, but those with injurious numbers have been mostly localized in nature. There are a number of strains (or perhaps subspecies) within this complex, each feeding on different hosts (Knerer and Atwood 1972). Struble (1957) reported an outbreak of *N. abietis* on white fir in California that started about 1951, peaked in 1953, and collapsed in 1955. By 1954, several infestations, ranging in size from a few hundred to a few thousand hectares, had been reported. The largest affected area covered about 4000 ha. Hildahl and Peterson (1972) reported an outbreak of *N. abietis* in the Interlake area of Manitoba that occurred between 1960 and 1965 and affected an area of about 9300 km^2. Ives (1969) presented maps showing that damage by *N. abietis* had been reported across central Saskatchewan in most years between 1950 and 1967. The most severe damage occurred between 1961 and 1965, along the Churchill River.

The damage caused by this insect is usually not too injurious to the trees, but if defoliation is prolonged and severe it will cause tree mortality. This occurred in the Interlake area of Manitoba, where heavy mortality of balsam fir occurred during the 1960-65 outbreak (Hildahl and Peterson 1972).

Acleris variana[14]

The eastern black-headed budworm is a widely-distributed species. Outbreaks have occurred at intervals of 10 to 15 years in Newfoundland and the Maritime Provinces, and one infestation has been reported in Quebec (McNamee 1979). Outbreaks have not occurred in the rest of Canada, although widespread epidemics of the closely related western black-headed budworm, *Acleris gloverana* Walsingham[15], have been reported in the Pacific Northwest, British Columbia, and Alaska (Schmiege and Crosby 1970). *A. gloverana* infestations appear to last long enough to cause serious damage to the trees (Hard 1974), but it seems that infestations of *A. variana* ususally subside before serious injury occurs (Morris 1959). Inasmuch as this insect has not yet occurred in outbreak proportions in Manitoba or Saskatchewan (McNamee 1979; Prentice and Hildahl 1955), it seems safe to assume that it does not pose a major threat to the forests of this area.

Choristoneura pinus pinus[16]

The jack pine budworm is a major native pest of jack pine and other pines in the Lake States, northwestern Ontario, Manitoba, and to a lesser extent Saskatchewan; however, it was not recognized as a separate species until fairly recently. The first recorded outbreak occurred in Minnesota from about 1923 to 1926 (Graham 1935), and additional infestations were recorded in Minnesota and Michigan during the early 1930s. Since then, the insect has continued to cause periodic damage in this area at intervals of 6 to 8 years (Dixon and Benjamin 1963). In Canada it has caused moderate to severe defoliation in northwestern Ontario in 1937-50, 1953-56, and 1959-67 (DeBoo and Hildahl 1968). The outbreak periods were similar in Manitoba: 1936-50, 1954-57, and 1963 or 1964 to 1966. Outbreaks were recorded in Saskatchewan in 1939-45 and 1963-66. Ives (1969) also showed these two outbreak periods for Sas-

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[13] Hymenoptera: Diprionidae.

[14], [15], [16] Lepidoptera: Tortricidae.

katchewan and indicated a minor upsurge in populations from 1954 to 1957. A detailed cartographic history of this insect in Manitoba and Saskatchewan from 1938 to 1967 was given by Brandt and McDowall (1968).

Most of the damage to jack pine that is attributable to the jack pine budworm consists of reduced increment and top-killing, although tree mortality may also occur (DeBoo and Hildahl 1968). In Minnesota, Kulman *et al.* (1963) found that the production of both springwood and summerwood was reduced by as much as 99% by very heavy defoliation. Even moderate defoliation reduced the summerwood by 60% and the springwood the following year by 76%. Kulman *et al.* (1963) also found that from 29% to 44% of severely defoliated trees died. Brandt and McDowall (1968) found that mortality was much higher among the smaller, suppressed trees than among the intermediate, codominant or dominant trees. Their mortality figures for various-sized trees were 5.1 cm—56%, 7.6 cm—42%, 10.2 cm—10%, and ⩾12.7 cm—2%. These figures clearly indicate that the mortality among the larger trees is minimal. If the drought that tends to coincide with outbreaks of this insect is severe, however, the lack of moisture will further damage the trees, and the combined effects of drought and defoliation may cause stagnation of the stand, from which even the larger trees may not recuperate (MacAloney 1944). MacAloney therefore recommended that jack pine stands be managed on a short rotation (70-80 years), especially on the poorer, droughty sites, and this recommendation is probably still sound.

Neodiprion nanulus nanulus[17], *Neodiprion virginianus* complex[18], *Semiothisa bicolorata*[19], and *Zale duplicata largera*[20]

These four insects are fairly common on jack pine, but only the two *Neodiprion* species have been known to cause any significant damage. Kapler and Benjamin (1960) reported an infestation of the red pine sawfly, *N. nanulus nanulus*, that caused severe defoliation of red pine in a 13.4-ha plantation in Wisconsin during 1955 and 1956. Wilkinson *et al.* (1966) reported that *Neodriprion rugifrons* Middleton (a species within the redheaded jack pine sawfly, *N. virginianus*, complex) had defoliated and killed small jack pine planted at two locations in Wisconsin in 1957 and again in 1962 and 1963. No mention was made of the number of trees involved. Martineau (1959) reported two small areas of light to moderate defoliation by larvae of *N. virginianus* complex in Quebec during 1957 and 1958.

Infestations of *N. nanulus nanulus* were reported in 1947 near Hudson Bay, Saskatchewan, and in the Moosehorn-Fairford area of Manitoba (Anonymous 1939-1973). The infestation near Moosehorn lasted until 1949, and as many as 40 ha of pine may have been affected. Pine-infesting sawflies (probably including *N. nanulus nanulus* and *N. virginianus* complex) were also reported in 1957 on about 16 ha of young jack pine in the Freshford area of northern Manitoba. Larvae of the *N. virginianus* complex also destroyed up to 90% of the old foliage on jack pine in the Nisbet Provincial Forest in Saskatchewan in 1957, but no mention was made concerning the size of the area involved.

From the foregoing discussion it is apparent that none of these four species pose a major threat to pine forests in the region. Because they have the potential to cause severe damage, however, the forest manager should be on the lookout especially for larvae of both *N. nanulus nanulus* and the *N. virginianus* complex.

Pristiphora erichsonii[21]

The origin of the larch sawfly in North America is somewhat obscure. According to one school of thought it was introduced in historic times; the other school of thought believes that it is native (Coppel and Leius 1955).

[17, 18] Hymenoptera: Diprionidae.

[19] Lepidoptera: Geometridae.

[20] Lepidoptera: Noctuidae.

[21] Hymenoptera: Tenthredinidae.

The insect was first noted in Brookline, Massachusetts, in 1880 (Fyles 1892) and at that time was believed to have been brought over on European larch. Fyles (1906) later speculated that it may have been introduced with young Norway spruce. Turnock (1972) referred to the introduction of *Mesoleius tenthredinis* (Morley)[22] into North America and examined the effect that this had on the population patterns and life systems of the larch sawfly:

> The influence of human activities on larch sawfly populations has been more direct in North America than in Europe. The presence or absence of larch sawfly populations in North America prior to the 19th Century remains a matter for speculation, but there seems little doubt that the origin of the first recorded permanent population was from the introduction of the larch sawfly from Europe to New England shortly before 1880. The deliberate introduction of *M. tenthredinis*, from 1910 to 1913, led to the development of the temporary type of population pattern which still persists in cordilleran North America and Newfoundland. The temporary type reverted to the recent permanent type as the susceptible strain of larch sawfly was replaced by the resistant strain, beginning in Manitoba about 1938 and spreading from that focus. The resistant strain may have arisen in Manitoba by mutation but the absence of quarantine precautions when *M. tenthredinis* was introduced in 1910-13 makes it possible that the resistant strain was introduced at this same time. If this is true, a period of nearly 30 years elapsed before the resistant strain became dominant in the Manitoba populations.

More recently, however, Wong (1974) recognized morphological differences among sawflies from different areas and identified five strains. He pointed out that

> Aweme and Fernie strains occur only in North America and Salzburg strain is confined to Eurasia. Two Eurasian strains, Ambleside and Thirlmire, were accidentally introduced into Canada from England by 1913 among cocoons shipped for the release of the parasite *Mesoleius tenthredinis* Morley. It is postulated that the ancestors of Aweme-Salzburg strains [and] Fernie-Thirlmire strains dispersed across the Bering Land Bridge into North America some time in the Miocene. These phyletic lines evolved into distinct Eurasian and North American strains. Early infestations in North America apparently consisted of North American strains, while later outbreaks have consisted primarily of the recently introduced Eurasian strains.

Graham (1956) also believed that the larch sawfly is native to North America. On the basis of annual increments on the basal disc of an old tamarack cut in Minnesota, Graham suggested that outbreaks may have occurred during the following years: 1734-41; 1745-49; 1752-54(?); 1781-86; 1791-99; 1819-23(?); 1835-41; 1849-54; 1864-67; 1877-85; 1906-13; and 1917-27. The last three outbreak periods have been substantiated by other evidence, but the earlier records are based solely on suppression of the annual increment. Naim *et al.* (1962) found that there was

> no difference between the alterations of the characteristic growth curves of trees subjected to severe defoliation and those of trees that have been severely flooded. No means has yet been determined of recognizing growth reductions due to insect attack in this region from those due to other adverse factors without corroborative knowledge of outbreak history . . . .

Graham's (1956) figures may therefore have been reflecting growth reductions due to wet years rather than to larch sawfly outbreaks.

Drooz (1960) reviewed the history of larch sawfly outbreaks in Europe, Great Britain, Siberia, and North America. (It may be

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[22] Hymenoptera: Ichneumonidae.

significant that the first outbreak in Europe was not reported until 1838.) In Canada, outbreaks occurred in Quebec from 1883 to 1891, and defoliation in 1885 extended from Ottawa to New Brunswick. Infestations continued to spread westward, reaching the Lakehead area in Ontario by 1908, Winnipeg in Manitoba by 1909, and Battleford in Saskatchewan by 1910. Nairn *et al.* (1962) reviewed the history of larch sawfly outbreaks in Manitoba and Saskatchewan and found they occurred in 1908-19, 1924-27, and 1938-59. Infestations in individual stands usually lasted no longer than 4 years. Ives (1969) summarized the outbreak history in Saskatchewan from 1941 to 1967. The insect was present thoughout this period, but the heaviest infestations appear to have been in 1949-53 and 1958-60.

Regardless of its origin, the early outbreaks of this insect in North America were particularly devastating. Fyles (1892) revisited an area in Quebec in which he had observed the larch sawfly to be present in vast numbers 8 years earlier. He gave the following account of his second visit:

> The tamarack swamps of the Township of Bury occupy about one tenth of its surface, or 640 acres, and show on an average forty marketable trees to the acre. The largest of these trees are about 2 feet 6 inches in diameter at the butt—one was found having a diameter of 2 feet 9 inches. The usual size is 2 feet. This represents a growth of 200 years. Two hundred and twenty rings of annual growth was the actual record on the butt of one tree. Besides these marketable trees there are numerous others, in every stage of growth, which, under favourable circumstances, would, in successive years, have attained to marketable value. Of all these trees 98 per cent are dead and the remainder dying . . . .
>
> As we have seen, there are in Bury 640 acres of tamarack giving on the average forty marketable trees to the acre, or 25,600 such trees in all. Every tree contains at least 400 feet, board measure, of lumber. This gives for the whole forest 10,240,000 feet, which, in a sound condition, would have been worth $30,720, and which left standing would, under favourable circumstances, have been increasing in value . . . . besides the value of the younger trees which would have been a source of income in future years, as they successively attained perfection.

Very little information is available on mortality of tamarack during the early outbreaks in Manitoba or Saskatchewan. Nairn *et al.* (1962) reported that mature tamarack were dying in various parts of Manitoba from 1911 to 1920, but he gave no details. Experimental defoliation of young tamarack (Graham 1931; Ives and Nairn 1966b) showed that young trees died after 2 or 3 years of complete artificial defoliation. No mortality occurred after 4 years of 70% defoliation, but the increment was reduced in proportion to the amount of defoliation.

The available information clearly indicates that the larch sawfly is a major pest of tamarack. It may well be one of the principal reasons why there is currently so little merchantable tamarack in North America.

Semiothisa sexmaculata[23], *Anoplonyx canadensis*[24], and *Anoplonyx luteipes*[25]

These defoliators of tamarack—the green larch looper, the onelined larch sawfly, and the threelined larch sawfly—are sometimes fairly common (Bergeron 1973; Ives 1977) but have never been reported to cause appreciable damage. They should therefore pose no threat to tamarack stands in the region.

SUMMARY OF MANITOBA AND SASKATCHEWAN DATA

Data on insect population trends and associated weather information for Manitoba and Saskatchewan, summarized by districts,

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[23] Lepidoptera: Geometridae.

[24, 25] Hymenoptera: Tenthredinidae.

are shown graphically in Figs. 2-8. Portions of the entomological data are also listed numerically in Appendix 1. Most of these data are extremely variable, particularly those relating to seasonal weather, and any trends that may exist are difficult to detect visually. Inasmuch as the interrelationships between these data form the basis of the remainder of this report, they will not be discussed in detail here. The infestation ratings are not mentioned later, however, so a brief discussion of them is warranted here.

One of the reasons why the infestation ratings were not examined in detail was their crudeness. They were obtained from small-scale maps that were subject to considerable error in plotting and were based on historic reports, so that omissions could not be detected. Nevertheless, the results probably give an unbiased picture of the infestation patterns of those insects causing enough damage to warrant mapping. It must be kept in mind that some of the irregularities in the graphs may well be due to differences in thoroughness of coverage from year to year, rather than to changes in insect density. A table summarizing the more pertinent results has been prepared (Table 1) because comparisons between the various graphs are rather difficult.

There is considerable variation among the seven districts for the years in which major infestations of the various insects occurred, and this suggests that localized factors played a role in determining insect abundance. There is also, however, a large degree of similarity in the infestation histories of the two provinces, and this suggests that a factor operating over a large area, such as seasonal weather, may play the major role in determining insect abundance in the area. The information in the following section on environmental factors tends to confirm this supposition.

INFLUENCE OF ENVIRONMENTAL FACTORS

In the preceding section it was shown that the insect species did not all reach high population levels during the same periods. This section will examine these insect populations (or trends in populations) to determine, if possible, which factors appear to be affecting the abundance of each species.

The fact that insect populations are under some form of regulation was apparently first recognized by Howard and Fiske (1911). Thompson (1924, 1939) and Nicholson (1933, 1954) and Nicholson and Bailey (1935) outlined two opposing theories of population regulation. Although it is risky to summarize these theories briefly because of the danger of misinterpretation, an attempt will nevertheless be made. Thompson believed that climatic and edaphic factors are the primary extrinsic factors responsible for natural control and that density-dependent mechanisms are only involved on rare occasions. In his opinion, populations are not really regulated, but merely fluctuate. Nicholson, on the other hand, believed that populations are self-regulating. He was willing to concede that weather caused heavy mortality on occasion, but he considered that this mortality simply changed the level about which the population density fluctuated. He insisted that, without regulation, populations would, in the long run, either increase infinitely or become extinct.

The points of view expressed by Thompson and Nicholson appear to have much in common, especially when one considers the meaning of the word edaphic. One usually thinks of this word in relation to soil, but it also means autochthonous, which in turn means indigenous or native. This interpretation of edaphic would therefore include such things as native parasites and predators. Whether these are density-dependent depends upon circumstances: in many cases they appear to be density-independent. One of the main differences between the two points of view, therefore, seems to be semantic. Nevertheless, a great deal of controversy has arisen over the two theories (Bakker 1964; Kuenen 1958), and this is perhaps best exemplified in the papers written by Thompson (1956) and Nicholson (1958). Although ostensibly review papers, they consist mainly of vituperative

Table 1. Years in which the infestation ratings for each of seven insect species equalled or exceeded 50% of the insect's maximum rating between 1945 and 1968 in each of seven forested areas in Manitoba and Saskatchewan (see Fig. 1)

Insect species	Southeastern Manitoba	Interlake and Westlake	Riding and Duck mountains	Northwestern Manitoba	Hudson Bay area	Prince Albert area	Meadow Lake area
Malacosoma disstria	1952	1945					
	1961-64	1962-64	1961-64	1962-63	1961-62	1962-64	1962-64
Choristoneura conflictana				1950		1952-53	1951, 1953
	1958	1956-57	1957-59		1956-58	1958-59	1955-56
		1968	1968				
Chrysomela crotchi	1963-64	1963-64	1962-63	1962-65	1963	1963-65	1964-66
Gonioctena americana			1946-47				
			1949-50	1949	1951-52	1953-55	
			1957	1957-58		1957-60	1960
	1964		1964	1963	1963	1963, 1965	
		1967	1966-68				
Choristoneura fumiferana	1954-57	1955-59	1955-56		1956, 1958		-
				1961-68	1960		
		1967-68			1965, 1967	1965-68	
Choristoneura pinus pinus	1948-49		-		-		
	1966-68	1964-66		1967		1965	1966
Pristiphora erichsonii	1945		1945-52				
	1947-56	1950-55	1954	1950-55	1949-53	1951-56	1954-55
		1960-61		1959-61		1960	
	1965-68	1963-65		1963-68		1964-66	
		1967-68					

verbiage attacking each other's point of view and really did very little to clarify the situation.

The relative merits of either point of view have been discussed by a number of authors, most of whom tend to side with one or the other. Those that do not take sides usually have put forth theories of their own, so that the literature has become quite extensive. An exhaustive review would occupy too much space, but reference to some of the papers should be made. Solomon (1949) and Thompson (1939) discussed the different theories and gave excellent reviews of early work. The interested reader can use these papers as a starting point to delve more deeply into the historical aspect of the topic.

Andrewartha and Birch (1954) discussed a large body of data on animal populations and factors affecting them. They disagreed with Nicholson on the basis that his underlying assumptions are rarely, if ever, met in nature and hence his formulas do not reflect events as they occur in the field. Their ideas of factors affecting population fluctuations appear to be very similar to those expressed by Thompson.

A number of reviewers (Clark *et al.* 1967; Solomon 1957; Varley and Gradwell 1970; and Varley *et al.* 1973) appeared to favor the views expressed by Nicholson. Klomp (1962, 1964) was perhaps one of the most avid of the Nicholson supporters. In his 1962 paper he suggested that "In fact weather does not regulate the number of animals, but determines the number of suitable habitats .... It is the regulation per unit of suitable habitat ... which interests us, but not the total quantity of suitable habitat, how[ever] interesting the latter question may be from the viewpoint of the forester." This is in direct contrast to Thompson (1956), who pointed out that the economic entomologist cannot be unduly concerned about whether or not population reduction is related to density but must be concerned about immediate results:

> **For example if I spray my clothes-closet with an insecticide to kill clothes-moths, a 99 per cent kill will be satisfactory to me, even though I thus reduce the competition among clothes-moths and relax intraspecific pressure, thus giving the clothes-moth population an opportunity to build up again. If a fruit grower sprays his orchard for codling moth and saves 95 per cent of the crop, thus making a substantial addition to his income, the percentage mortality he has obtained will, to him, be the important index of the controlling factor of the spray he has used. If low temperature or heavy rain wipes out an injurious insect at an early stage in its development, reducing economic damage to a minimum, the agriculturist who has benefited from the action of this factor will not care whether it is "reactive" or not. He will consider that the percentage mortality has been the real index of its importance and in this view he will be perfectly correct. Economic entomologists and agriculturists in general work season by season or, if you like, generation by generation, and it is only with respect to a fairly extended period of time or a series of generations that the principle laid down by Nicholson applies. The ecologist who is studying the variation in population and the causes of mortality that operate throughout the life-cycle is obliged to adopt the same viewpoint. If he finds that in a certain generation of insects, unfavourable weather has wiped out a large part of the population, he is obliged to recognize that weather has been one of the important factors determining population density. If he is then told by Nicholson and his adherents that nevertheless such factors do not control density and that, to control density, density-dependent factors are required, he can only reply that at all events density independent factors really determine density even if they do not "control" it in the sense that they "regulate" it. We are in fact struggling here again, with pseudo-problems, arising partly from semantic difficulties. Nicholson does not deny that density independent factors have a determining influence on density. Climate, he says, has a profound effect on density. Climate also limits the distribution of species. It seems clear that if by climatic influences a species is excluded**

> from certain areas we can say that in these areas the density of the species is reduced to zero. The word reduction is not improper in this connection because as a result of the fact that climatic conditions often change very drastically a species might occupy a certain habitat for a time and then be exterminated, as would individuals who happen for various reasons to wander into the habitat or are carried into it.
>
> In my 1939 paper I said that the discontinuity and variability in habitats produced by the physical factors is undoubtedly the primary extrinsic factor of natural control. It will now be amply clear that the argument in which we are engaged turns to an important extent on the meaning of the word "control." By control Nicholson means regulation or government, whereas control in my view simply refers to the fact that no organism increases without limit. To this Nicholson has replied that the discontinuity and variability of habitats does not inconvenience organisms to any extent; "most species," he says "are well adapted to cope with such fragmentation." These adaptations, in his view, enable animals to occupy fully all favourable sites, and in these sites the populations are governed by density reactions .... the views of Nicholson and myself are in many ways similar, because we are both anxious to take all the available facts into account, and yet they differ in certain subtle but extremely important respects. The difference is, I think, not just what might have been expected from the general trend of the arguments on both sides. It is, that when all is said and done the factor of chance plays a much greater part in the world as I see it, than it does as in the world as Nicholson sees it. It is true that I have frequently stressed the adaptive abilities of animals more than has Nicholson. I feel indeed that the adaptive abilities of animals are extremely remarkable. Nevertheless, I am convinced that in spite of these abilities many of them find it extremely difficult to survive because their possibilities of existence are quite restricted by the specificity of their requirements and by the great diversity and fragmentation of their habitats, both in space and time. They have to move through a network of random events.

This somewhat lengthy quotation clearly indicates Thompson's views, which to me, as a practicing ecologist, seem eminently reasonable.

Part of the problem, as indicated by Richards (1961), lies in the field of interest of the researcher: some are primarily interested in explaining the phenomena of balance, while others are more interested in explaining fluctuations. As Andrewartha and Birch (1954) pointed out, steady density (about which populations are supposed to balance) is a conceptual idea, the existence of which has yet to be proven under field conditions. Similar statements were made by Uvarov (1931). This leaves the practicing ecologist with little choice but to look for factors that he can associate with population change, for only by so doing will he gain an understanding of what is causing population change. If the only important factors, according to the pro-Nicholson school of thought, are so abstract that they can never be recognized as being important in the field, there seems to be little point in pursuing the matter under field conditions because of all of the complexities that are almost certainly to be encountered. On the other hand, laboratory experiments conducted under controlled conditions are so removed from natural conditions, according to the pro-Thompson school of thought, that they do very little to clarify the understanding of factors responsible for population fluctuations under natural conditions.

Some workers have attempted to develop theories of their own to overcome this dilemma. Schwerdtfeger (1941, 1958, 1968) and Reddingius (1971) both seem to have similar ideas, in which a combination of environmental factors interacting with one another are primarily responsible for determining the population trend for any given species. Schwerdtfeger concedes that the so-called density-dependent factors may occasionally come into play, especially if populations explode and deplete their food supply. Den Boer (1968) proposed a similar idea when he advanced his spreading-of-risk theory to explain population fluctuations. Glen (1954) and Milne (1957a, 1957b) appeared to share similar views and felt that Thompson's interpretation was probably close to the truth, except for the fact that he did not place enough emphasis on density-dependent factors. All these ideas seem interesting, but they are very similar to Thompson's view and hence do little to clarify the situation.

Perhaps the best summation of the current status of population dynamics was given by Watt (1962):

> In physics, theoretical developments have typically been stimulated by the desire to make sense out of data which were already collected .... In population dynamics, on the other hand, all classical theories are *a priori*, not *a posteriori*, deductive models. The distinction is subtle but very important. The essence of the modern ... scientific tradition is that in the last analysis it is *a posteriori*. The theories of modern science are elaborated by deduction, but the basic assumptions are obtained by observation, not abstract reasoning. Prospective critics of my opinion that classical population models are *a priori* will need to arm themselves with actual quantitative data from the early theoretical writings .... Such data will not be found .... The historical development of physics has been characterized by a high degree of integration between theory and experiment. In quantum mechanics, for example, the closeness of this integration in the last few decades has been amazing. On the other hand, many writers have noticed the lack of such integration in population ecology. This is an extremely important point, since the single factor most necessary for rapid evolution of a branch of science is this close integration of theory and empirical work. It is clear that sophisticated theory by itself is not adequate since population ecology has had such theories for about four decades. These theories have never had an impact on the rate of scientific evolution like that of the physical theories which have often been tested weeks and even hours after they were published. It is also clear that elaborate experimental and observational studies, not directed and interpreted by theories, do not greatly advance a science.

Concerning the Lotka-Volterra model, Watt commented that

> all early mathematical population theories minimized the importance of climate in population regulation. As noted elsewhere, for some populations at least, factors such as climate may never allow a population to become dense enough for density-dependent factors to be brought into play. Unfortunately, there are only a few bodies of population data available which cover enough years to support this position adequately.

Watt considered Volterra's approach sound for a favorable environment that is stable: "all the conclusions which Volterra draws out in a very thorough monograph are perfectly valid deductions from the assumptions he makes. However, the assumptions are not drawn from biological reality." Watt also discussed the Nicholson-Bailey model:

> The difficulty is not so much that the assumptions made are incorrect, as that an inadequate number of assumptions are made .... For example, it could not have been expected to occur to anyone, including Nicholson & Bailey, that the efficiency of parasites per female decreases as the parasite population density increases. As additional experimental work is done, newly discovered facts will make *a priori* models seem even further removed from biological reality.

Watt refers to other *a priori* models as well; the interested reader should refer to the original papers for details.

Finally, the discussion by Richards and Southwood (1968), based on a concept developed by Huffaker and Messenger (1964), probably gives the most succinct summation of the relative roles of what they call "disturbing" and "regulating" processes. By means of a simple figure, they show that for populations at the center of the species range, in stable or permanent habitats, the regulating processes play a dominant role in determining abundance. As one moves toward populations on the edge of a species range, into unstable or temporary habitats, the disturbing processes assume a dominant role and regulating processes become of minor importance.

The populations examined in this study probably approach the latter situation. Almost certainly, because of the harshness of the climate, especially during the winter, one can expect weather to play a role in determining species abundance. The vulnerability of a particular insect to any given environmental factor depends upon the degree to which it is susceptible to that factor, however, and this is influenced by the insect's life cycle. Brief descriptions of the life cycles of all 21 species are therefore given in Table 2. Other factors that might also influence population change include predation by small mammals, birds, and invertebrates (including parasitism); diseases; and competition with other species of insects.

Each of these topics will be discussed separately. Particular emphasis will be placed upon the effects of seasonal weather because complete weather records are available for the areas and periods under consideration. For the sake of completeness, however, the more-limited data relating to the other factors will be discussed as well. For each factor the available literature on each insect species will be reviewed, and the available data for this study will be compared with these results to determine what agreement, if any, exists. The literature on some species is voluminous, so little new information is likely to be presented for these species in this paper. However, if the results are in general agreement for the common insects, it should give more credence to suggested relationships for the less-common species, for which there is little or no information in the literature.

WEATHER

Entomologists have long recognized that weather has a marked influence on insect survival. Uvarov (1931) reviewed over 1150 papers written in 11 languages, all dealing with the effects of various aspects of weather upon insects. He did not consider even this number of papers to be an exhaustive review and rejected many articles, either because they made only brief reference to weather or because their inclusion would have introduced undesirable duplication of results. Uvarov recognized that overwintering weather often caused severe mortality, but that cold winters were not necessarily the most damaging; variable weather conditions sometimes caused even higher mortality. He acknowledged the importance of the amount of snow cover in determining the survival of hibernating insects. Uvarov also believed that warm dry weather favored the buildup of outbreaks for a number of insects, including the pine noctuid, *Panolis flammea* Schiffermüller[26], and the oak leaf roller, *Tortrix viridana* Linnaeus[27]. Drought conditions appeared to favor bark beetles, cutworms, and grasshoppers.

Although much research has been conducted in the 50 years since Uvarov conducted his review, the thoroughness with which he covered the field and the depth of his perception seem to warrant repetition:

> It is usually assumed that the numbers of an insect species, while increasing during a gradation, return in the intervals to what is called the normal number, which is considered to be more or less constant. There is no evidence, however, that this is actually so. Indeed, it appears that the conception of a normal number is a fiction, since the total population of a given area and habitat is never stabilized and the ratio of its component species fluctuates continually, though the smaller fluctuations cannot be observed except by quantitative methods of study ... throughout the years. There is, of course, always a certain *average* relative number of each species, but this is only a mathematical average, not actually existent in nature . . . .
>
> The theory that all living organisms are in stable equilibrium so far as their relative numbers are concerned is widely

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[26] Lepidoptera: Noctuidae.

[27] Lepidoptera: Tortricidae.

Table 2. Abbreviated life histories for 21 species of forest insects[1]

Insect species	Larval period	Adult period	Overwintering stage	Remarks	References
Malacosoma disstria	19 May - 12 July	Late June and July	Pharate larvae in egg masses on twigs	-	Witter *et al.* 1972
Choristoneura conflictana	19 May - 30 June	Late June to early July	II-instar larvae in hibernaculae under moss at base of tree or under loose bark	I-instar larvae feed from early July to late August	Beckwith 1968; Powell 1964; Prentice 1955; Wickman 1963
Chrysomela crotchi	7 July - 6 September	Fall and spring	Sexually immature adults in duff	Only one generation in this area	Brown 1956; Smereka 1965
Gonioctena americana	19 May - 30 June	Mid-July and early spring	Sexually immature adults in duff	Adults lay eggs that hatch almost immediately	Rose and Smereka 1959
Orthosia hibisci	16 May - 6 July	Spring	Pupae in soil	-	Furniss and Carolin 1977
Campaea perlata	19 May - 24 June	Late July to late August	Partly grown larvae	Larvae feed in late summer and complete development in the spring	Kusch 1979, pers. commun.; Prentice 1963
Pseudexentera oregonana	19 May - 24 June	Late March to early April	Pupae in soil	-	Wong and Melvin 1967
Sciaphila duplex	19 May - 30 June	Early June to early July	II-instar larvae in hibernaculae in conks, bark crevices,or fallen leaves	I-instar larvae feed until trees lose their leaves	McGregor 1967; Prentice 1965
Enargia decolor	25 May - 6 July	Late July to late August	Eggs in masses in bark crevices on trunk	Larvae feed between leaves fastened together	Cameron 1977, pers. commun.; Smereka 1970; Wong and Melvin 1976

Table 2 continued.

Insect species	Larval period	Adult period	Overwintering stage	Remarks	References
Choristoneura fumiferana	25 May - 18 July	Early July to early August	II-instar larvae in hibernaculae on branches under bark scales or lichens	-	Atwood 1944; Bean and Waters 1961; Cerezke 1979, pers. commun.; Graham and Orr 1940; Hewitt 1911; Morris 1963b; Morris and Miller 1954; Swaine *et al.* 1924
Neodiprion abietis complex	13 June - 12 August	Late July to early September	Eggs in foliage	-	Bird 1929; Brown 1953; Hildahl and Peterson 1972; Struble 1957
Acleris variana	1 June - 31 July	August-September	Eggs on foliage	-	Baker 1972; Miller 1966
Choristoneura pinus pinus	1 June - 24 July	Early July to early August	II-instar larvae in hibernaculae under bark scales or between needles	-	Allen 1968; Baker 1972; Graham 1935
Neodiprion nanulus nanulus	13 June - 24 July	Late August to early October	Eggs on foliage	Winter is passed as a well-developed embryo	Atwood and Peck 1943; Cerezke 1979, pers. commun.; Kapler and Benjamin 1960
Neodiprion virginianus complex	13 July - 30 August	June and July	Cocoons in soil	-	Atwood and Peck 1943; Cerezke 1979, pers. commun.; Martineau 1959; Wilkinson *et al.* 1966; Schedl 1938
Semiothisa bicolorata	13 July - 12 September	Mid-July to mid-August	Pupae in soil	-	McGuffin 1972; Prentice 1963
Zale duplicata largera	19 June - 12 August	Late May	Pupae in soil	-	Prentice 1962

Table 2 concluded.

Insect species	Larval period	Adult period	Overwintering stage	Remarks	References
Pristiphora erichsonii	25 May - 24 August	Late May to late July	Eonymphs in cocoons in moss	-	Drooz 1960; Hewitt 1911; Graham 1956; Lejeune *et al.* 1955; Turnock 1960
Semiothisa sexmaculata	19 July - 6 September	July to August	Pupae in moss	-	Bergeron 1973; McGuffin 1972; Prentice 1963
Anoplonyx canadensis	1 August - 18 September	Late May to early July	Cocoons in moss	Larvae present until mid-October	Ives 1977; Wong 1955
Anoplonyx luteipes	25 June - 24 August	May to June	Cocoons in moss	-	Ives 1977; Wong 1955

[1] The larval period is based on sampling data. The remainder of the information was obtained from the cited literature.

> recognized today. When this theory is applied to the fluctuations in numbers of an insect species the process is presented as follows. If the environmental (i.e. climatic) conditions are at all favorable for the insect, it begins to increase in numbers, with the result that there is more food for its predators, parasites, and disease-producing organisms, while the amount of food available for the insect itself decreases and the competition between its individuals becomes more acute. An increase in the numbers of all the natural enemies of the insect follows. They gain ascendancy over the insect and cause a decrease in its numbers, leading to shortage of food for the natural enemies and the reduction of their numbers. The insect then again begins to multiply. The process is usually compared with the movements of a pendulum, the vertical line representing the average or normal condition.
>
> This theory of a stable equilibrium in nature is, however, in direct contradiction of the facts. While it is true that an increase in number of a species is usually only temporary, and that a decrease will, sooner or later, follow, there are no proofs that the fluctuations in the two directions are of an approximately equal magnitude, as in the case of a pendulum. Nor is the so-called normal number a constant. We know that some species become gradually more numerous or expand their area of distribution, while others die out .... To speak of a stable equilibrium in nature, and to compare the fluctuations in numbers of organisms with the regular movements of a pendulum, always returning to a non-existent "normal condition", is contrary to common sense and a denial of evolution.
>
> No one will deny the controlling values of these (density-dependent) factors, but the evidence collected in this section, as well as in the whole of this paper, should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms. These factors cause a regular elimination of an enormous percentage of individuals under so-called normal conditions, which in fact are such that insects survive them, not because they are perfectly adapted to them, but only owing to their often fantastically high reproductive abilities. Any temporary deviations in the climatic factors, however slight they may be, affect the percentage survival, either directly, or indirectly (through natural enemies or food plants), and thus influence abundance.

Fifty years later, one wonders how much can be added to this summation.

Microclimatic Differences

One of the problems in determining the effects of weather upon insect outbreaks, especially from the examination of historical records, is the fact that one is forced to use standard meteorological records from whatever meteorological stations were in operation for the area and period under consideration. In many cases, the stations are some distance from the forested areas and thus do not necessarily give an accurate reflection of weather conditions in the forest. In addition, differences in topography, elevation and aspect may have a marked influence on the microclimate (MacHattie and McCormack 1961; Powell 1970).

An even greater problem, however, is that standard weather records may have very little relationship to the microenvironment in which the insects are living. Wellington (1950) discussed the difficulty of relating standard air temperatures to temperatures in insectan habitats and showed that vegetative temperatures in the summer may exceed air temperatures by as much as 8° C during the day and may drop to as much as 3°C below air temperature at night. Ives (1964) found that exposed bark temperatures on tamarack were commonly 10-13° C higher than air temperatures, and on one occasion the temperature on the upper surface of a large branch was 17° C higher than the corresponding air temperature. Depending upon circumstances, these types of differences may affect the survival or phenology of the insect.

Ives (1960), for example, encountered high mortality (on one occasion) when studying the developmental rates of *Pristiphora* *erichsonii* larvae in field shelters. Normally, temperatures in the shelters approximated Stevenson screen temperatures reasonably well, although there was a slight time lag and maximum temperatures were slightly higher. On the occasion mentioned, however, the thermograph recorded a maximum of 38°C (100°F), its upper limit, and most of the larvae in the shelters at the time were killed. The maximum temperature recorded in a Stevenson screen about 3 km away was 32° C, which is not unusually hot for summer temperatures in that area. Larvae could therefore be exposed to lethal temperatures during unusually hot weather, especially if the trees were severely defoliated and the larvae were wandering in search of food. Baltensweiler (1966a) found that varying amounts of radiation affected the phenology of the larch bud moth, *Zeiraphera griseana* Hübner[28]. He compared the hatching dates of eggs under lichens exposed to radiation to those in shaded locations and found that there were no elevational differences in the dates when the spring was cold and late. When the spring was early and warm the exposed eggs hatched progressively earlier than the shaded ones as the altitude increased. At the lowest elevation there were no differences, but at the highest elevation the exposed eggs hatched about 2 weeks earlier than the shaded ones. Consequently, as pointed out by Uvarov (1931), standard weather data "bear only a very distant and indirect relation to the ecoclimate and the microclimate of the actual habitat of the insect".

Data from Other Countries

In spite of the limitations inherent in the available weather data, a number of workers, particularly in Europe, have demonstrated apparent relationships between weather and insect population fluctuations. Cramer (1962) examined outbreaks of five species of forest insects in the Schwetzingen forest district in southwestern Germany in relation to weather records from Karlsruhe, about 40 km away, for 1841 to 1950 and concluded that

1. Sawfly outbreaks (probably mostly the pine sawfly, *Diprion pini* Linnaeus[29]) have occurred whenever the mean monthly temperatures from March to October have added up to more than 109°C and precipitation did not exceed 550 mm.
2. Outbreaks of the pine moth, *Dendrolimus pini* Linnaeus[30], were likely to occur if the sums of the mean monthly temperatures for May to October and March-April of the following year averaged more than 77.0°C over a 3-year period and the total precipitation for July to September and March-April averaged less than 340 mm. More moderate, but comparable, conditions over a longer period also appeared to have comparable effects.
3. An outbreak of the European pine looper, *Bupalis piniarius* Linnaeus[31], occurred when below-average precipitation occurred in both May and June for 3 consecutive years. A minor outbreak also occurred in 1850. On this occasion the June 1848 precipitation reached average levels. Precipitation for May 1848 and for May and June in 1849 was below normal.
4. Outbreaks of the pine noctuid, *Panolis flammea*, seemed likely if the mean monthly temperature for May was at least 17° C and precipitation was not above normal or whenever temperatures exceeding 15.5°C and precipitation less than 30 mm in May recurred in a few years close together. Outbreaks usually occurred 2 years later.
5. Outbreaks of the nun moth, *Lymantria monacha* Linnaeus[32], seemed probable if the sums of the mean monthly temperatures for May and June averaged more than 32.5°C in 3 consecutive years and the average total precipitation during May in the same 3 years was less than 80 mm.

All of these relationships are circumstantial; however, there are two points in their favor: observations spanned a period of 110 years, and the life history of each insect was taken into consideration when looking for relationships between outbreaks and weather.

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[28] Lepidoptera: Tortricidae.

[29] Hymenoptera: Diprionidae.

[30] Lepidoptera: Lasiocampidae.

[31] Lepidoptera: Geometridae.

[32] Lepidoptera: Lymantriidae.

Baltensweiler (1966b) suggested that optimum conditions for increases in populations of the larch bud moth, *Zeiraphera griseana*, are 1) cool weather when the eggs are young (July to September); 2) cold during overwintering of eggs (December to March); and 3) spring weather not too dry and, most importantly, uniformly warm during development of eggs (after the completion of diapause) until the young larvae establish feeding sites on new shoots (March to June). He speculated that outbreaks of this insect in central Europe were triggered by long-term climatic swings. Major outbreaks apparently require two conditions: 1) a period of approximately 10 years during which weather conditions favorable to the population are concentrated above average levels; and 2) a minimum of four consecutive favorable weather situations, so that generation mortality is low.

Bejer-Peterson (1972) found an apparent relationship between weather and outbreaks of the pine shoot moth, *Rhyacionа buoliana* Schiffermüller[33], in Denmark. Years with marked increases in the abundance of the insect were preceded by rising average temperatures for June to August the year before, coincident with a decline in the September (and to a lesser extent July to September) precipitation. During 1935 to 1968 there were no years with this climatic pattern that were not accompanied by a rise in *R. buoliana* damage.

In China, Hsiao and Yen (1964) found that weather affected survival of the pine caterpillar, *Dendrolimus punctatus* Walker[34]. They found that cool moist conditions during eclosion of first-generation eggs in May were beneficial; similar conditions during August favored the second generation. Hot dry weather during the summer and temperatures below 10°C in February and March were unfavorable.

All except the last-mentioned species of insect were favored by warm dry weather during at least part of their life cycle. Apart from the obvious direct benefit to the insect, the warm dry weather may have indirect benefits as suggested by Uvarov (1931). House (1965) suggested that the degree of succulence and the concentration of nutrients in plant tissues may affect the degree of destruction caused by phytophagous insects. Auclair *et al.* (1957) found that varieties of peas resistant to the pea aphid *Acyrthosiphon pisum* (Harris)[35] had lower concentrations of amino acids than did susceptible varieties. In related findings, Maltais and Auclair (1957) also found that there were lower concentrations of both total and soluble nitrogen in the resistant varieties.

White (1969) devised a stress index based on soil water relationships that induce water deficits in plant tissues in Australia (high winter precipitation followed by summer drought) and showed that this index was related to outbreaks of the psyllid *Cardiaspina densitexta* Taylor[36] on eucalyptus. He then extended the concept to looper larvae (White 1974) and found that outbreaks of *Selidosema suavis* Butler[37] in a plantation of Monterey pine at Eyrewell in New Zealand were also related to the stress index. Each outbreak of the insect in the Eyrewell plantation started in the area under greatest stress due to winter flooding (attributable to a hard pan layer close to the surface and a concentration of old water races that tended to flood the area) followed by summer droughts (attributable to poor water storage capacity of the soil). White then related outbreaks of other insects to the stress index: two outbreaks of the looper *Neocleora herbuloti* Fletcher[38] in plantations of exotic pines and eucalyptus in South Africa followed a series of years with increasing values of the stress index; and good correlations were also shown between the stress index and larval populations of the

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[33] Lepidoptera: Olethreutidae.

[34] Lepidoptera: Lasiocampidae.

[35] Homoptera: Aphididae.

[36] Homoptera: Psyllidae.

[37, 38] Lepidoptera: Geometridae.

European pine looper, *Bupalis piniarius*, in the Netherlands. There were also relationships between the stress index and outbreaks of the phantom hemlock looper, *Nepytia phantasmaria* (Strecker)[39], on Douglas-fir in California and between the index and outbreaks of the mountain mahogany looper, *Anacamptodes clivinaria* (Barnes and McDunnough)[40], on mountain mahogany in Idaho. Although no index was calculated, the well-known association between periods of warm dry summer weather and outbreaks of the eastern spruce budworm, *Choristoneura fumiferana*, on balsam fir in the Maritimes also fits the concept of stress, since increased staminate flower production is often a reflection of stress.

White (1976) then went on to apply the concept to various acridids throughout the world and suggested that it may have a widespread applicability to understanding the ecology of herbivorous animals. Under normal conditions, most of the food may be too dilute for good survival of the very young, and only under stress conditions do the plant tissues contain a high-enough concentration of essential amino acids to allow an increase in survival and hence a buildup in populations. It is an interesting concept that may help to explain the widespread association between drought and insect outbreaks.

Canadian Survey Data

The extensive data on forest insects that have been collected by the Forest Insect and Disease Survey have been examined previously by Watt (1967). Watt recognized the poor quality of the Survey data, in terms of both precision and accuracy, and devised rather sophisticated procedures to cope with this. Of the 989 species of forest lepidopterans listed by McGugan (1958) and Prentice (1962, 1963, 1965), Watt selected those species that had at least 100 specimens collected annually for at least 10 years. He then selected 11 major weather stations across Canada and for each station used the mean monthly temperatures over an 18-year period to calculate an 18-year mean and standard error. Four major climatic zones were recognized. For each of these zones he examined population counts in year t for each insect species in relation to mean monthly temperatures for January to December in year t-1 and for January to July in year t. From these 19 variates the computer selected the two that gave the highest correlations in a multiple regression analysis. Conventional statistics were useless for evaluating the results. This problem was overcome by repeatedly running the same analyses, with weather from the same stations, at various numbers of years into the future. F-values so generated were used to construct frequency tables against which the calculated values could be evaluated for actual relationships. On the basis of these analyses, Watt concluded that 1) the standard error of the logarithms of the counts varied more in milder climates (because the populations in maritime areas fluctuated around lower levels), and 2) insects with limited distribution were much more sensitive to differences in temperatures between years than were those with widespread distributions (because species normally under density-dependent control are very sensitive to weather differences that may occur, while those normally under control of density-independent factors are rather insensitive to changes in weather). If this last explanation is correct, any demonstrated relationships for forest insect populations in Manitoba and Saskatchewan should indicate that the factor involved is of major importance in determining population trends. Otherwise, according to Watt's interpretation, it should be difficult to show that a relationship exists.

In contrast to the sophisticated computer programming used by Watt, the approach adopted in this study seems over-simplified. As outlined in the methods, the insect sampling data were used primarily to sort the seasonal weather data into four categories based on insect abundance: present (no detectable or known trends from the previous year); absent; increasing (in relation to the previous year); and decreasing. The first two categories were used only for one species (Appendix 3). Evaluations of the effects of seasonal weather are therefore based on values observed during increases and decreases in populations of the insect under consideration. No statistical tests were conducted, for three principal reasons: 1) The same data were

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[39, 40] Lepidoptera: Geometridae.

sorted 21 times (once for each insect species) and these sorts are probably not independent, so the usual statistical tests would be invalid and therefore meaningless; 2) The weather variables are nothing more than indices of conditions experienced by the various species of insects, and there is no way of knowing what the degree of relationship is for each species from available information; and 3) The aim of the study is to determine possible relationships that may be biologically (rather than statistically) significant.

As mentioned in the introduction to this section, the credibility of any apparent relationships is dependent entirely upon the degree with which the present analyses agree with the findings of other workers. Each species will therefore be discussed separately, in the order presented in Figs. 2-8. Available literature on the effects of weather will be reviewed briefly, and then the current results will be given.

To simplify discussion, a step-wise procedure has been adopted in condensing the data. The original seasonal weather data summaries, before conversion to percentages, are presented in Appendix 2. The mean values, in percentages of the range, after sorting into the four categories (present, absent, increasing, and decreasing) are given in Appendix 3. The differences between these mean values (increasing minus decreasing) are summarized in numerical terms in Table 3 and in descriptive terms in Table 4. Mean differences of 5 or more in Table 3 have been considered to be meaningful, as most means in Appendix 2 are based on 20 or more observations. This difference was selected intuitively. Obviously, a larger value would have reduced the number of meaningful differences, while a smaller one would have produced a plethora of differences. The selected value represented a compromise between the two extremes, nothing more.

For simplicity, the following discussion will be confined to Table 4. The interested reader can retrace the steps outlined in the preceding paragraph to determine the relative or absolute numerical differences.

Malacosoma disstria

This insect and some of its close relatives have been the subject of numerous studies. In reviewing the parasites and predators of the genus *Malacosoma*, Witter and Kulman (1972b) found that more than 500 papers had been published on this group of insects during the past 150 years. Obviously, it is impractical to cite more than a fraction of these. Major contributions have been made by Hodson and his associates (Hodson 1939, 1941, 1977; Hodson and Weinman 1945) and by Witter and his associates (Witter and Kulman 1972a, 1972b; Witter *et al.* 1972, 1975) during long-term studies in the Lake States.

More-limited studies were conducted by a number of workers. Wellington (1952) studied the air-mass climatology in Ontario north of Lake Superior and concluded that the best conditions for tent caterpillar development appear to be humid, partly cloudy weather throughout the greater part of the larval stage, although direct sunshine is required in early larval life if the air is cool. Ives (1973) examined outbreaks in the prairie provinces and Ontario and found that all known infestations in 10 geographical areas were preceded by a single year (2 to 4 years earlier) with a relatively cool winter and an unusually warm spring.

The cold-hardiness of overwintering pharate larvae was evaluated by Hanec (1966). He found that the lowest supercooling temperatures occurred from November to April, when they ranged from -32.6°C to -40.8°C. Witter *et al.* (1975) found that the highest mortality of pharate larvae in the field occurred when the coldest overwintering temperatures exceeded -40.8°C. Gorham (1923) reported what appeared to be overwintering mortality due to low temperatures in New Brunswick, and Prentice (1954) noted high overwintering mortality in Saskatchewan following a winter in which unusually low temperatures occurred. Hodson (1941), however, noted that pharate larvae did not appear to be adversely affected by temperatures of -46.7°C. Wetzel *et al.* (1973) found that egg masses nearing anticipated hatching dates were able to withstand temperatures as low as

Table 3. **Mean differences in weather variables for increasing vs. decreasing populations based on sampling sort of data for the years 1951 to 1969. Absolute values ⩾5 are underlined for emphasis. Each weather variable was expressed as a percentage of its range in each of seven areas (see Fig. 1) between 1945 and 1969: i.e., the smallest value was equated to 0 and the largest to 100. Mean differences were calculated from sorted data for the interval 1952 to 1969.**

	Precipitation				Heat units <-18°C		Heat units >4.5°C			Water deficits	
Insect species	Nov.-Jan.	Feb.-April	May - July	Aug.-Oct.	Nov.-Jan.	Feb.-April	Feb.-April	May - July	Aug.-Oct.	May - July	Aug.-Oct.
Malacosoma disstria	-2.6	3.2	-17.2[1]	-14.6	-18.8	-35.1[1]	9.0	7.5	13.6	16.9[1]	11.5
Choristoneura conflictana	13.9	-13.8	-0.6	-3.4	11.1	-4.8	10.7	-22.4[1]	-5.9	-9.3	-4.8
Chrysomela crotchi	6.5	2.3	7.7	-1.9	-2.6	-4.2	4.7	2.3	-7.6	-2.2	9.8
Gonioctena americana	-14.4	-5.2	2.5	4.5	3.2	-8.4	8.3	1.6	-0.9	0.3	-3.0
Orthosia hibisci	-22.9	-16.0	2.3	-7.9	-5.0	-28.6[1]	24.0	-16.2[1]	-14.5	-3.3	7.9
Campaea perlata	-21.8[1]	9.5	20.2	5.5	-25.0	-8.4	-9.1	-11.1[1]	-2.6	-21.8[1]	-0.9
Pseudexentera oregonana[2]	-15.9	7.9	-3.4	-9.4	-11.8	-11.4	4.6	14.6	10.2	7.2	12.2
Sciaphila duplex	-2.8	14.7	1.0	20.8	-6.9	14.6	6.2	5.9	8.7	3.5	-16.9[1]
Enargia decolor	-19.0	-11.8	-9.8	1.6	-2.9	-20.4[1]	21.1	-12.9[1]	-18.6	8.2	-3.8
Choristoneura fumiferana	12.0	13.6	-1.9	-7.4	5.6	-0.1	-12.8	10.4	7.1	4.0	5.4
Neodiprion abietis complex	-1.6	-2.0	-0.2	-6.6	-6.0	-17.5[1]	9.7	-3.2	-5.6	-2.1	-3.7
Acleris variana	-18.2	-12.2	13.7	8.7	-4.1	-19.0[1]	14.2[1]	7.0	8.9	-7.6	-4.0
Choristoneura pinus pinus	-4.9	12.5	6.4	3.9	-10.3	12.0	-0.8	21.5	7.0	-0.5	-3.3
Neodiprion nanulus nanulus	17.9	13.8	-21.7[1]	6.2	-8.4	1.6	-11.7	10.9	1.5	23.0[1]	-6.6

Table 3 concluded.

Insect species	Precipitation Nov.-Jan.	 Feb.-April	 May - July	 Aug.-Oct.	Heat units <-18°C Nov.-Jan.	 Feb.-April	Heat units >4.5°C Feb.-April	 May - July	 Aug.-Oct.	Water deficits May - July	 Aug.-Oct.
Neodiprion virginianus complex	0.1	-1.5	-8.8	0.1	8.2	-11.8[1]	7.3	1.2	-0.5	10.0	-4.4
Semiothisa bicolorata	-15.9	2.6	1.7	5.5	-4.6	-20.2[1]	-2.3	-9.2	-22.3[1]	-7.9	-18.7[1]
Zale duplicata largera	-9.6	2.5	-3.6	-2.6	-9.8	-0.7	1.5	4.4	-9.1	1.2	3.3
Pristiphora erichsonii	8.2	-3.3	4.3	-1.7	14.4	24.4	-0.2	-7.0	-15.9[1]	-5.0	4.6
Semiothisa sexmaculata	-7.2	-7.8	-13.5[1]	10.1	-3.6	-8.7	3.9	1.8	-5.8	10.6[1]	-8.0
Anoplonyx canadensis	8.7	-13.8	7.8	8.3	6.4	-1.3	6.0	-25.9[1]	-12.3	-17.4[1]	-5.2
Anoplonyx luteipes	5.3	15.2	-10.6	4.7	-11.1	-4.1	-3.0	7.1	0.1	14.4	2.1

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[1] The extreme values during decreasing populations may be harmful.

[2] The categories present-absent were used instead of increasing-decreasing.

Table 4. Summary of weather conditions that appear to be favorable or unfavorable for 21 forest insect defoliators

Insect species	Favorable weather		Unfavorable weather	
	Condition	Period	Condition	Period
Malacosoma disstria	Mild	Nov. - April	Cold	Nov. - April
	Warm and dry	May - Oct.	Wet	May - July
Choristoneura conflictana	Cold with heavy precipitation	Nov. - Jan.	Hot	May - July
	Mild with light precipitation	Feb. - April		
	Cool	May - July		
Chrysomela crotchi	Heavy precipitation	Nov. - Jan.	-	-
	Warm and wet	May - July		
	Cool and dry	Aug. - Oct.		
Gonioctena americana	Light precipitation	Nov. - Jan.	-	-
	Mild with light precipitation	Feb. - April		
Orthosia hibisci	Mild with light precipitation	Nov. - April	Cold	Feb. - April
	Cool and dry	Aug. - Oct.	Hot	May - July
Campaea perlata	Mild	Nov. - Jan.	Heavy precipitation	Nov. - Jan.
	Cool (low heat units >4.5°C)	Feb. - April	Hot and dry	May - July
Pseudexentera oregonana	Mild with light precipitation	Nov. - Jan.	-	-
	Mild with heavy precipitation	Feb. - April		
	Warm and dry	May - Oct.		
Sciaphila duplex	Mild	Nov. - Jan.	Dry	Aug. - Oct.
	Cold with heavy precipitation	Feb. - April		
	Warm	May - Oct.		
Enargia decolor	Light precipitation	Nov. - Jan.	Cold	Feb. - April
	Mild with light precipitation	Feb. - April	Hot	May - July
	Cool and dry	May - July		
	Cool	Aug. - Oct.		

Table 4 continued.

Insect species	Favorable weather		Unfavorable weather	
	Condition	Period	Condition	Period
Choristoneura fumiferana	Cold with heavy precipitation	Nov. - Jan.	-	-
	Cool (low heat units >4.5°C) with heavy precipitation	Feb. - April		
	Warm	May - July		
	Warm and dry	Aug. - Oct.		
Neodiprion abietis complex	Mild	Nov. - April	Cold	Feb. - April
	Cool and dry	Aug. - Oct.		
Acleris variana	Light precipitation	Nov. - Jan.	Cold	Feb. - April
	Mild with light precipitation	Feb. - April		
	Warm and wet	May - Oct.		
Choristoneura pinus pinus	Mild	Nov. - Jan.	-	-
	Cold with heavy precipitation	Feb. - April		
	Hot	May - July		
	Warm	Aug. - Oct.		
Neodiprion nanulus nanulus	Mild with heavy precipitation	Nov. - Jan.	Wet	May - July
	Cool (low heat units >4.5°C)	Feb. - April	Warm (high heat units >4.5°C)	Feb. - April
	Warm and dry	May - July		
Neodiprion virginianus complex	Cold	Nov. - Jan.	Cold	Feb. - April
	Mild	Feb. - April		
	Dry	May - July		
Semiothisa bicolorata	Light precipitation	Nov. - Jan.	Cold	Feb. - April
	Mild	Feb. - April	Warm and dry	May - Oct.
	Cool and wet	May - Oct.		
Zale duplicata largera	Mild with light precipitation	Nov. - Jan.	-	-
	Cool	Aug. - Oct.		

Table 4 concluded.

Insect species	Favorable weather		Unfavorable weather	
	Condition	Period	Condition	Period
Pristiphora erichsonii	Cold with heavy precipitation	Nov. - Jan.	Warm	Aug. - Oct.
	Cold	Feb. - April		
	Cool and wet	May - July		
	Cool	Aug. - Oct.		
Semiothisa sexmaculata	Light precipitation	Nov. - Jan.	Wet	May - July
	Mild with light precipitation	Feb. - April		
	Dry	May - July		
	Cool and wet	Aug. - Oct.		
Anoplonyx canadensis	Cold with heavy precipitation	Nov. - Jan.	Hot and dry	May - July
	Mild with light precipitation	Feb. - April		
	Cool and wet	May - Oct.		
Anoplonyx luteipes	Mild with heavy precipitation	Nov. - Jan.	-	-
	Heavy precipitation	Feb. - April		
	Warm and dry	May - July		

-15°C, while lower temperatures caused appreciable mortality. Hanec (1966) found that most newly hatched larvae were able to survive temperatures ranging from -1°C to 15°C for 10 days without food.

Raske (1975) found that little mortality occurred unless the larvae were subjected to temperatures of at least -7°C for 14 days. He concluded that low spring temperatures were unlikely to be a factor in forest tent caterpillar mortality. Nevertheless, mortality attributed to adverse spring weather has been reported by several workers. Tothill (1918) reported that in the spring of 1915 in Nova Scotia there were enough eggs on the poplar trees to bring about wholesale defoliation. The eggs hatched well, but a light frost killed most of the first-instar larvae, and no tent caterpillar larvae could be found the following spring. Sweetman (1940) also believed that spring weather was probably the most important natural check for the pests and that weather was probably the dominant factor in the production of the cyclic abundance of these insects. Blais *et al.* (1955) thoroughly documented a collapse of forest tent caterpillar populations in northwestern Ontario that definitely appeared to be due to adverse spring weather. It therefore seems reasonably certain that unfavorable spring weather does have a detrimental effect on field populations. The larvae may not be killed directly by the frost, but if they are dislodged or deprived of their food and starve to death the end result is much the same. Witter *et al.* (1972) concluded that the factors that appear most likely to affect outbreaks (in Minnesota) are pharate larval mortality, spring frosts that kill first-stage larvae and/or foliage, and pupal parasitism by *Sarcophaga aldrichi* Parker[41]

The results of the present study (Table 4) agree with most of the preceding findings. Cold weather during both early and late winter (November to January, February to April) was unfavorable, indicating a lack of complete cold hardiness in the overwintering pharate larvae. Wet weather during May to July was also unfavorable. This appears to disagree somewhat with Wellington's (1952) findings; however, partly cloudy, humid weather is not necessarily the same as wet weather. It may be that wet summers tend to be cool, and Hodson (1941) has shown that very little feeding takes place below 15°C. Prolonged periods of cool, cloudy weather could therefore limit the rate of development and cause an increase in mortality either directly or by increasing the time during which the larvae are exposed to other mortality agents. Mild winters (low heat units <0° C) were favorable, a corollary to the adverse effects of cold winters already noted. Warm dry weather during May to July and August to October was favorable. The highly mobile larvae are probably able to avoid the adverse effects of high temperatures by seeking shade during the hottest part of the day. Although their periods of feeding might be limited during warm weather, the more-rapid development apparently more than compensated for this. Warm dry weather during the summer probably shortened the pupal period, thus reducing exposure to *S. aldrichi*. It probably also favored mating and oviposition, provided temperatures did not become as extreme as they did in the 1930s when excessively hot temperatures probably killed forest tent caterpillar eggs in the Lake States (Hodson 1941).

Choristoneura conflictana

Relatively little work has been done on mortality factors affecting populations of *C. conflictana*. Wickman (1963) and Beckwith (1968, 1973) both thought that starvation was a major factor causing population collapses. High larval populations caused stripping of the trees before larval development was completed. Many of the larvae died, and undernourished females that survived laid less eggs than normal. In addition, the defoliation reduced or eliminated most of the aspen foliage, and the females were forced to lay their eggs elsewhere. The fate of larvae hatching from these eggs was not known, but it was unlikely that many survived. Low temperatures during the winter appeared to have minimal adverse effects on survival. Temperatures were in the -40s (°C), but second-instar larvae emerged successfully from twigs collected above the snow line in February, indicating

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[41] Diptera: Sarcophagidae.

that the hibernating larvae had survived the cold spell (Beckwith 1968).

In this study, cold weather with heavy precipitation in the early winter (November to January) followed by mild weather and light precipitation in the late winter (February to April) appeared to favor survival (Table 4). The heavy precipitation in early winter would tend to protect those larvae hibernating near the base of the trees or under loose bark on deadfall. The cold weather would ensure that hibernating larvae above the snow line were not subjected to excessive amounts of freezing and thawing. The light precipitation and mild temperatures in late winter would probably mean that development would start fairly early in the spring. Premature emergence would not necessarily be detrimental, as the larvae mine the buds (Beckwith 1968, 1973; Prentice 1955; Wickman 1963). Late frosts, however, could have adverse effects, and these are perhaps more likely to occur if spring is unusually early. In 1918, hot summerlike weather in April induced an unusually early emergence of the larvae, accompanied by a flushing of the aspen (Criddle 1918). This was followed by cold weather that froze the foliage. Very few larvae survived.

Hot weather during May to July is detrimental (Table 4). This could be because the larvae feed in enclosures formed by rolling up or webbing together one or more leaves (Prentice 1955). Such an environment could become extremely hot during warm sunny weather, due to radiant heating. The high temperatures may also have an adverse effect on the eggs, which are laid mainly on the upper surface of what is left of the foliage (Criddle 1918), or on the newly-emerged larvae, many of which feed gregariously in the rolled-up leaves that formed the pupal cases of the previous generation (Beckwith 1968).

Chrysomela crotchi

In his paper describing this insect, Brown (1956) stated that "In the Ottawa district at least, the most important checks on *Chrysomela* are climatic. Larvae are beaten from the food plants by storms, and many adults die in winter quarters." Smereka (1965) believed that predation and overwintering mortality were the most important control factors in northwestern Ontario. He found that all overwintering adults in exposed locations above ground died, and 84% mortality occurred in the groups that were placed on the ground and beneath the duff layer.

The limited data available on related species tend to confirm that chrysomelids, as a group, are not particularly cold-hardy. Neel *et al.* (1976) found that only 5.5% of adult beetles of the closely related cottonwood leaf beetle, *Chrysomela scripta* Fabricius[42], survived the winter when confined in field cages. The Colorado potato beetle, a chrysomelid native to North America, also suffers severe winter mortality at times. Harcourt (1971) found that up to 70% of the hibernating adults suffered frost mortality in the Merrivale area of Ontario. Strickland (1928) noted that the potato beetle was destructive in the Edmonton, Alberta, area that year; this was apparently due to early snows in the fall of 1927, which served to insulate the soil and thus protect the insects (Mail 1930; Whitney 1976). Similar observations were made by Beirne (1971) regarding the Colorado potato beetle:

> Numerous records indicate that two factors are of primary importance in regulating whether or not infestations occur. The first is the number of adults that survive the winter. Early and heavy snowfalls protect the hibernating adults from killing by cold temperatures so that the survival rate is high. Low winter snow cover can result in heavy mortality from freezing with consequent low populations in the following spring. Severe winters intensify the effects of low snow cover and mild winters the effects of heavy snow cover. Moreover, in mild winters the species tends to survive further to the north than normally whereas severe ones push its northern limits southwards.

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[42] Coleoptera: Chrysomelidae.

Casagrande *et al.* (1977) found that overwintering adults of the cereal leaf beetle, an introduced chrysomelid species, could not survive the winter above ground and that overwintering survival of adults hibernating in the duff or soil ranged from 48% to 68%.

No unfavorable weather conditions were detected for *C. crotchi* in this study. Cool dry weather during August to October favored survival. This may indicate that fungus attacks the hibernating adults. Phillips (1977) found that chrysomelid beetles of all species (in Britain) became infected with a soil inhabiting fungus, *Verticillium* sp., which has been reported to be entomogeneous on caged insects. He felt that overwintering adults are probably attacked under field conditions, particularly since "groups of beetles (two to twelve) hibernate amongst damp leaf litter and plant debris where fungal infections could spread rapidly." *C. crotchi* overwinters under similar conditions, so that wet weather could favor the spread of the fungus. Heavy precipitation during the early winter favored population buildup. This probably indicates that the insect is not completely cold-hardy and requires the protection of an adequate snow cover for good survival. Why warm wet weather during May to July should favor survival is more difficult to understand; however, *C. crotchi* is a late insect (most defoliation occurring during July and August), so that the advantage may be indirect. It has already been shown that wet weather during May to July is unfavorable to *M. disstria* and that hot weather during the same period is detrimental to *Choristoneura conflictana* populations. Both of these insects occur much earlier in the season, as does *Gonioctena americana* (see below), and it is possible that *Chrysomela crotchi* populations can increase only in the absence of outbreaks of the other species, particularly *Choristoneura conflictana*. This conclusion is supported by the graphs showing outbreak history, particularly Figs. 6 and 8.

Gonioctena americana

No references to the population dynamics of *G. americana* could be found; however, most of the remarks about chrysomelids mentioned above probably apply to this insect as well. *G. americana* occurs earlier in the season than *Chrysomela crotchi* (Table 2) and is therefore not so dependent upon leftovers from *M. disstria* and *Choristoneura conflictana*. It seems to reach peak abundance mainly at different periods than either of these two insects, so perhaps it does not compete too well with them. This could explain why no favorable summer conditions were detected for this insect. Light precipitation during the early winter and mild conditions in the late winter appeared to favor survival. This can be interpreted as indicating that this insect is more cold-hardy than *Chrysomela crotchi*. It can also be interpreted to mean that small mammal predation of the hibernating adults, perhaps by the deer mouse, *Peromyscus maniculatus* (Wagner)[43], could be an important mortality factor, although this is pure speculation. It has been shown, however, that light snow cover coupled with cold weather increases overwintering mortality of both the white-footed mouse, *Peromyscus leucopus* (Rafinesque)[44], and the red-backed vole, *Clethrionomys gapperi* (Vigors)[45], (Beer 1961). In addition, *P. maniculatus* has been observed to enter torpor during cold weather (Fuller *et al.* 1969; Howard 1951; Stebbins 1971). This apparently has a survival advantage for the animal, but it also means that predation by this species is reduced during cold weather, particularly if there is light snow cover. Because *G. americana* adults start dropping to the ground in late July (Rose and Smereka 1959), they would be available to the deer mouse when its consumption of animal matter was highest (Jameson 1952). *Chrysomela crotchi*, on the other hand, does not hibernate as early (Table 2) so would be susceptible to summer predation for a shorter time. Predation that extended into the winter months would therefore be of less importance to population trends of *C. crotchi* than to population trends of *G. americana*. If predation of this species extended into the winter months it could easily be a coup de grace if it happened to follow heavy summer predation.

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[43] Rodentia: Muridae (Following nomenclature given by Banfield 1974).

[44, 45] Rodentia: Muridae.

Orthosia hibisci

No references to the population dynamics of this insect could be found. It feeds from May to July and overwinters as a pupa in the soil or duff. Beirne (1971), in a review of agricultural pests, referred to a field study of the bertha armyworm, another noctuid, which showed a mortality of 35% to 65% among overwintering pupae in an unworked stubble field in Saskatchewan.

Rings (1970) showed that *O. hibisci* has a very wide northern distribution. Nevertheless, it does not appear to be completely cold-hardy, since cold weather during the late winter was detrimental, while mild weather throughout the winter was favorable (Table 4). It also does not appear to be heat-tolerant, as hot weather during May to July was unfavorable. As with *C. crotchi*, the fact that cool dry weather in the fall favors survival can be construed to indicate that fungus or some other soil-borne disease could be an important source of mortality. Similarly, light precipitation during the early winter tends to limit small mammal activity, suggesting that their predation on the pupae may also be an important source of mortality. Krivda (1972) reported an instance in which Drummond's meadow voles, *Microtus pennsylvanicus drummondii* (Audubon and Bachman)[46], were responsible for decimating the overwintering pupal population of the butterfly *Erebia discoidalis* Kirby[47]. Although *M. pennsylvanicus* is normally thought of as a meadow-inhabiting species, it has been shown to move into forest habitats during the winter when the aggressive action of the red-backed vole, *Clethrionomys gapperi*, diminishes and snow cover affords protection (Turner *et al.* 1975). Campbell and Sloan (1976, 1977) found that vertebrate predators, especially the white-footed mouse, *Peromyscus leucopus*, were a major factor in controlling sparse populations of the gypsy moth. *O. hibisci* has never reached outbreak proportions in Manitoba and Saskatchewan, so it is conceivable that the deer mouse, *P. maniculatus*, or some of the other small mammalian predators might play a similar role in its population dynamics.

Campaea perlata

Very little information of any description could be found on the bionomics of this insect. It overwinters as a partly developed larva, but where it spends the winter could not be ascertained. The fact that heavy precipitation during the early winter was unfavorable suggests that it may be in the duff, since heavy snow cover would favor the small mammals and would tend to increase the amount of predation. The unfavorable effects of hot dry weather during May to July may indicate that the insect is not heat-tolerant, but it may also indicate that it simply cannot compete with *Malacosoma disstria.* Mild weather during the early winter was favorable, suggesting that the insect is not completely cold-hardy. Finally, the fact that cool weather (low heat units >4.5° C) in late winter favored population increase can be interpreted to mean that warm spells in late March or April induced premature emergence of the larvae from hibernation, with subsequent heavy mortality due to lack of food.

Pseudexentera oregonana

This is another insect about which there is very little information in the literature. According to Wong and Melvin (1967), the adults emerge in late March or early April, so development of the pupae must start as soon as the snow melts in the spring. Perhaps this is why heavy precipitation in late winter (Table 4) was favorable, as it would tend to limit premature development. Mild conditions throughout the winter were favorable, indicating a lack of complete cold hardiness. The fact that light snow cover in early winter was favorable suggests that mammal predation of overwintering pupae was a significant mortality factor. Warm dry weather from May to October was also favorable. Since this insect is a leaf roller this suggests that the feeding larvae are more heat-tolerant than *Choristoneura conflictana.* It also suggests that fungus diseases could be an important mortality factor affecting the hibernating pupae, since fungal development would be minimized during dry weather.

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[46] Rodentia: Muridae.

[47] Lepidoptera: Satyridae.

Sciaphila duplex

This insect has a life history that is similar in some respects to that of *C. conflictana.* The young larvae feed until the trees lose their leaves, and then they overwinter as second-instar larvae in hibernaculae (McGregor 1967). Consequently, the unfavorable effects of dry conditions from August to October (Table 4) may be due to a reduction in the palatability of the foliage. The apparently favorable overwintering conditions are difficult to interpret, since they appear to conflict. Perhaps the larvae are not completely cold-hardy in the early winter but by late winter have become conditioned to the cold, especially if protected by heavy snowfall. Hanec (1966) found such a progression in the cold hardiness of the pharate larvae of *M. disstria.* Pharate larvae collected on October 3, November 15, and January 11 had mean supercooling points of -26.4° C, -36.1° C, and -40.8° C, respectively. It is therefore quite conceivable that a similar increase in cold hardiness might occur in *S. duplex*. Heavy snowfall in late winter would also tend to limit premature emergence of the larvae from their hibernaculae, thus reducing mortality due to lack of food in the early spring. Apparently the larvae do not mine the buds (McGregor 1967): "With the onset of warm weather in May or June, 2nd instars emerge from their hibernacula and begin feeding. The small larvae skeletonize a portion of the leaves, then as they begin to grow they roll the leaf or tie several leaves together with silken threads and feed in seclusion". Warm weather during May to October was favorable, so the larvae must be heat-tolerant.

Enargia decolor

The full life cycle of this insect has not been adequately studied. In cage and insectary studies, Smereka (1970) and Wong and Melvin (1976) found that the eggs were laid in irregular masses in the soil and elsewhere. Cameron[48] found that the eggs were deposited in substantial clusters in fissures in aspen bark and were covered with a material that made them blend perfectly into the greyish mottled bark of the trees. Smereka (1970) found that the overwintering survival was better at 5° C than at 0° C, so the eggs are probably not completely cold-tolerant. This would explain why cold weather in late winter was unfavorable (Table 4). The fact that hot weather during May to July was unfavorable can probably be explained by a lack of heat tolerance on the part of the larvae, since they feed between two leaves fastened together around the edges with silk (Smereka 1970). The temperatures between those leaves could easily reach lethal levels on hot sunny days because of radiant heating.

It is easy to see why mild temperatures in late winter would favor survival, since it is indicative of the lack of complete cold hardiness already noted. It is more difficult to see how light winter precipitation could favor survival. It seems more likely that it benefits the insect indirectly by having an adverse effect on its competitors. The beneficial effect of cool weather during May to July is a corollary to the lack of heat tolerance already noted. Smereka (1970) noted that newly emerged larvae are small and extremely susceptible to factors such as low temperatures, rain, and condensation during the period between emergence and establishment of feeding sites. Because of the nature of these sites (between two leaves) it seems likely that wet conditions throughout the larval period would be unfavorable. This conclusion is borne out by the data, since dry conditions during May to July were favorable. Cool weather during August to October was also favorable, which seems to indicate that the eggs are either not heat-tolerant or are susceptible to desiccation during hot weather in the late summer or early fall.

Choristoneura fumiferana

The spruce budworm is a major forest pest and consequently has been studied intensively. McKnight (1968) cited 320 papers on the eastern, western, and 2-year cycle spruce budworms, and Jennings *et al.* (1979) listed over 1500 papers on spruce budworms. Only a fraction of these papers can be referred to here. The most comprehensive of these

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[48] Personal communication from E.A. Camerson, Pennsylvania State University, to H.R. Wong, Northern Forest Research Centre, dated 16 February, 1977.

studies was conducted by a group of workers in the Maritimes who studied the population dynamics of this insect for a number of years (Morris 1963b). Swaine (1928) recognized that favorable climatic conditions occurring for several years in succession in areas with large stands of overmature balsam probably explained the beginning of a major outbreak. Other workers have shown that dry sunny summers favor the buildup of outbreaks (Greenbank 1956; Ives 1974; Morris 1963b; Pilon and Blais 1961; and Wellington *et al.* 1950), while late spring frosts have often been associated with population decreases (Dowden *et al.* 1948; Fellin and Schmidt 1973; Johnson and Denton 1975; McDowall and Howse 1980; McKnight 1971; Prebble 1945; and Warren 1954). Most of these declines appeared to be due to starvation caused by freezing of the new foliage rather than to direct effects on the larvae. Morris (1949) found that a temperature of -5.6°C did not appear to cause direct mortality of larvae in mines, but a longer than normal period of needle mining (due to cool weather and consequent slow development of new foliage) reduced survival. Shepherd (1959) found that evaporation rates were consistently higher in outbreak areas (of the 2-year-cycle spruce budworm) than in nonoutbreak areas, agreeing with Wellington *et al.* (1950) that "Ideal physical conditions for spruce budworm development are sunlight and lack of rainfall."

Weather conditions at the time of hibernation may influence where the hibernaculae are spun (Wellington and Henson 1947). Larvae emerging on overcast days might spin their hibernaculae near the tips of the branches and then might be killed by desiccation during subsequent hot dry weather. Although overwintering mortality appears to be a factor in determining population trends of both the eastern (Dowden and Carolin 1950) and the western spruce budworm (McKnight 1971), the hibernating larvae seem to be cold-hardy, since temperatures of -42.8°C and -47.2°C appeared to have little effect on overwintering survival (McKnight 1968).

No unfavorable conditions for development of spruce budworm outbreaks could be detected in this study. Cold weather with heavy precipitation during early winter was favorable, indicating that the hibernating larvae are cold-hardy. Why heavy precipitation during this period should be favorable is difficult to explain. Perhaps the extra snow protects the larvae from bird predation. On young balsam fir most hibernaculae are spun near the tips of the branches (Jaynes and Speers 1949). On older trees many of the hibernating larvae are on the larger branches (Jaynes and Drooz 1952), although the highest percentage of larvae on older trees still emerged from the peripheral shoots on each branch (Miller 1958). Heavy snowfall could mean that these branch tips are snow-covered a good part of the time. Cool weather (low heat units >4.5°C) during late winter, accompanied by heavy precipitation, was also favorable. The heavy precipitation would continue to afford protection to the hibernating larvae and, with the cool weather, would tend to ensure that premature development of the larvae or the trees does not occur. Warm weather during May to July was favorable, which agrees with earlier findings, but the weather did not appear to be unusually dry. Warm dry weather during August to October was also favorable, indicating that the hibernating larvae are heat-tolerant and not unduly vulnerable to desiccation. The fact that dry weather during this period was favorable could be interpreted to mean that fungi were a more-important source of mortality than desiccation. Jaynes and Speers (1949) found in one of their experiments that over half of the hibernating larvae were killed by fungi.

Neodiprion abietis complex

There are a number of strains of this insect, each feeding on various groups of coniferous hosts (Knerer and Atwood 1972). No references to the population dynamics of the strain on spruce could be found.

Apparently the eggs are not completely cold-hardy, as mild weather throughout the winter favored population increases and cold weather during late winter was associated with population declines (Table 4). Cool dry weather during August to October was favorable. This may indicate that the eggs are not completely heat-resistant and that they may be susceptible to attack by fungus; however, there is no evidence to support this supposition. Struble (1957) studied this insect intensively on white fir in California and found that a polyhedral virus infecting late-instar larvae was very effective in controlling populations, but he made no reference to diseases of overwintering eggs.

Acleris variana

The eastern black-headed budworm is another insect that was at one time part of a complex. Originally, the specific name *variana* was used for both eastern and western forms, but the latter is now referred to as *Acleris gloverana* (Walsingham)[49] (Powell 1962). Several references to *variana* (Prebble and Graham 1945a, 1945b; Schmiege 1966a, 1966b; Silver 1960, 1963; Werner 1969) therefore actually refer to *gloverana*.

Prebble and Graham (1945b) observed that "The frequent prevalence of cold, wet weather during hatching of the eggs in late May and early June is distinctly unfavorable to the movement of the fragile larvae along the twigs to the new shoots, and their establishment therein. Frequently the newly hatched larvae become trapped and drown in drops of water persisting between adjacent needles and in newly opening buds". The authors go on to point out, however, that this did not appear to be of much importance in the outbreak at that time. Miller (1966) found that population release was associated with favorable weather (heat units above 5.6° C greater than 649 for the period June to August 20) and low parasitism, while population decline was largely determined by late larval parasitism. Silver (1960) found that populations of the western black-headed budworm in the Queen Charlotte Islands increased immediately following 1 or 2 years of below-average precipitation during July and August. Outbreaks decreased or collapsed during or immediately following periods of heavier than usual precipitation during the latter portion of the larval development stages (Silver 1960, 1963). Schmiege (1966a) could find no consistent weather patterns during years of population increase but found that population collapses in Alaska occurred in years with unusually warm dry weather in July. Hard (1974) found that all downward trends of budworm populations occurred when the mean temperature (during June, July, and August) was colder than normal, and most upward trends coincided with years warmer than normal. No relationship could be found between population trends and precipitation. Snow sliding off foliage may remove the eggs (Schmiege 1966b; Schmiege and Crosby 1970) and desiccation may be the cause of some overwintering mortality (Werner 1969).

The present study indicates that cold weather during the late winter was unfavorable, presumably because the eggs are not completely cold-hardy, while mild weather during the same period was favorable. Light precipitation throughout the winter was favorable, so perhaps the loss of eggs is an appreciable mortality factor, as Schmiege (1966a) and Schmiege and Crosby (1970) suggested. Warm wet weather during May to October was favorable, so presumably disease was not an important factor; Schmiege (1966a) found no evidence of disease in Alaska. The favorable effects of warm temperatures were also found by Hard (1974) and Miller (1966), although they found no relationship between population trends and precipitation. There seems to be no agreement with Schmiege's (1966a) or Silver's (1960, 1963) results, which also conflict with each other. Perhaps the explanation lies in the fact that the present study is dealing with a continental climate and the other two dealt with a maritime climate.

Choristoneura pinus pinus

This insect is closely related to *C. fumiferana* and has a similar life cycle, except that it tends to be a little later, in general. Graham (1935) recognized that the budworms on pine were different, biologically, from those on spruce and fir. This difference was confirmed, taxonomically, when Freeman (1967) described the insect on jack pine as a separate species.

Graham (1935) found that budworm outbreaks are correlated with the abundance of staminate flowers, which in turn is reduced

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[49] Lepidoptera: Tortricidae.

by budworm defoliation, with the result that an outbreak on pine ususally ends before defoliation has killed the trees. MacAloney (1944) referred to the fact that initial defoliation was particularly noticeable on trees that had produced a heavy crop of staminate flowers that year. He also showed that annual and growing season precipitation were both below normal for 7 out of 8 years preceding the first noticeable defoliation. Lejeune and Black (1950) and Kulman and Hodson (1961a) also found that high jack pine budworm populations were associated with a heavy crop of staminate flowers, but Foltz *et al.* (1972) could find no such relationship during an intensive study of the insect in Michigan. As the authors pointed out, however, most of their data were collected during and following the outbreak phases of the population cycle and do not necessarily prove the lack of such a relationship. They suggested that weather during the larval and adult dispersal periods is the key factor in permitting budworm outbreaks and that unfavorable weather and defoliation cause outbreaks to collapse.

Dixon and Benjamin (1963) conducted an intensive study of the parasites of jack pine budworm in Wisconsin and suggested that "factors other than entomophagous might have exercised a great influence in bringing about the collapse of the Wisconsin epiphytotic". Heron (1956) and Kulman *et al.* (1963) confirmed that budworm defoliation severely restricted staminate flower production. If this reduced flowering is a factor in reducing jack pine budworm populations, there could then be a self-regulating mechanism in the population dynamics of this insect, as Graham (1935) suggested.

No adverse weather conditions affecting the jack pine budworm were detected in this study. Mild weather in the early winter followed by cold weather in the late winter were both favorable. This may indicate that the hibernating larvae require a period of acclimation before becoming completely cold-hardy. Allen (1968) found that "Mortality within the hibernacula may be high (e.g. 68%) and variable, and it is not influenced by position within the crown or location on the branch". The fact that mortality is not affected by location suggests that temperature may be the cause. The cold weather in late winter, coupled with heavy precipitation, would tend to delay the onset of spring, thus preventing premature development of either the trees or the larvae. Hot weather during May to July followed by warm weather from August to October provided favorable conditions for the insect. Dispersal losses would probably be minimal under such conditions, and larval development would be rapid, provided the larvae are heat-tolerant (as they must be to survive in either the staminate flowers or webbed foliage).

Neodiprion nanulus nanulus

Low overwintering temperatures did not appear to have an adverse effect on this insect in Wisconsin (Kapler and Benjamin 1960), where temperatures often drop to -40° C. Feeding larvae apparently were unaffected by temperatures of 36° C, and these authors believed that storms had no adverse effects, since the larvae sought protection among the bases of the needles during the storms and resumed feeding afterwards. Schedl (1938) considered abiotic factors to be of minor importance; however, Philogène (1972) was able to show that simulated rainfall had an adverse effect on the survival of *N. swainei.* Larvae from two different areas suffered mortality of 84.9% and 70.4% when sprayed intermittently, compared to 33.33% and 30.5% for larvae from the same areas exposed to constant humidity. In Alaska, Hard (1976) found that most negative population trends of *N. tsugae* Middleton[50] between 1952 and 1974 occurred when there were two consecutive wet summers. It seems, therefore, that wet conditions are detrimental to the survival of *Neodiprion* spp., even though the larvae may appear to be unaffected.

The present study tends to support this conclusion, at least for *N. nanulus nanulus*, since wet weather from May to July had an adverse effect on populations (Table 4). Warm weather (high heat units >4.5° C)

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[50] Hymenoptera: Diprionidae.

during late winter was also unfavorable, presumably because this tends to encourage premature development of the embryos. Mild weather during the early winter was favorable, so the eggs may not be completely cold-hardy. It is hard to explain why heavy precipitation during the same period should be beneficial, unless it tends to shelter some of the eggs, either from extreme temperatures or from bird predation. The beneficial effects of cool weather (low heat units >4.5° C) during the late winter are a corollary to the adverse effects of warm weather during this period that have already been noted. Population buildup was also favored by warm dry weather during May to July, which agrees with Kapler and Benjamin's (1960) findings that the larvae are adapted to temperatures normally encountered.

N. virginianus complex

Wilkinson *et al.* (1966) studied this insect in Wisconsin and concluded that "Abiotic factors appear to cause little direct mortality on the egg and feeding-instar larvae stages. Feeding-instar larvae survived temperatures of 30°-98° F with no observable ill effects. Larvae dislodged from trees during violent storms were subject to starvation and predation on the ground."

Cold weather during the late winter was unfavorable (Table 4). A logical explanation of this is difficult, since cold weather in the early winter was apparently favorable. Perhaps small mammal predation of the overwintering cocoons was a major factor. Cold weather in the early winter would tend to reduce this predation, but if it continued into the late winter, the temperatures in the soil surrounding the cocoons might drop to lethal levels. If the late winter was mild, this temperature drop would not occur and the hibernating larvae could survive. Dry weather during May to July was favorable, agreeing with Philogène's (1972) results.

Semiothisa bicolorata

No references to the bionomics of this insect could be found. Cold weather during the late winter was unfavorable, probably indicating a lack of complete cold hardiness in the overwintering pupae, since mild late winters were favorable. The fact that light precipitation in the early winter was favorable seems to indicate that small mammal predation of the pupae was a significant mortality factor. The larvae seem to do best during cool wet weather, since this type of weather from May to October was favorable, while warm dry weather was not. From this it can be inferred that the larvae and possibly pupae are not heat-tolerant and that fungal diseases are probably unimportant.

Zale duplicata largera

No literature on the bionomics of this insect could be found. Mild weather during the early winter was favorable, so the overwintering pupae are probably not completely cold-hardy. They are also probably subject to small mammal predation, since light early winter precipitation, which restricts small mammal activity, apparently favors the insect. Lastly, cool weather during August to October was favorable. This may indicate a lack of heat tolerance on the part of the larvae or newly formed pupae. The ground surface in jack pine stands can become very hot during warm sunny weather, and this may affect the survival of larvae that have dropped to pupate. It could also affect pupae already in the duff, especially if they were near the surface.

Pristiphora erichsonii

This insect has been studied intensively in the United States and Canada for a number of years. Long-term studies were begun in Minnesota in 1920 and in Michigan in 1927 (Graham 1956). Records were kept until 1932. The larch sawfly was not abundant in this area for nearly 20 years, but in 1950 a few colonies were observed, and by 1955 the insect had reached outbreak proportions in Michigan, Minnesota, parts of Wisconsin, and central Canada. Canadian studies were conducted primarily in Manitoba. Early work concentrated on larch sawfly parasites (Lejeune and Hildahl 1954; Muldrew 1953) and on the effect of flooding on the survival of the insect while in the cocoon (Lejeune *et al.* 1955). Beginning in 1956, the first life tables for this insect were constructed, along the lines outlined by Morris and Miller (1954). This work gradually expanded and attempted to assess most factors in the population dynamics of the larch sawfly (Ives 1976a; Ives *et al.* 1968).

Weather, or some ramification of it, has long been recognized as being an important factor in determining larch sawfly survival and hence abundance. Nearly all stages of development are affected, but effects on adults are probably minimal because they can seek shelter in the moss during the heat of the day (Graham 1956). High temperatures have an adverse effect on eggs and newly hatched larvae (Ives 1961). Heat may also have an adverse effect on the feeding larvae. There is evidence suggesting that high temperatures may cause the larvae to drop prematurely (Drooz 1960; Graham 1956). Such larvae would tend to wander longer than normal, and Heron (1967) has shown that even acclimated larvae suffered appreciable mortality if exposed to temperatures of 40° C or more for relatively brief periods. These temperatures may be exceeded on dry ground in open sunshine, due to the effects of radiant heating. Graham (1931) reported nearly 100% mortality of cocoons in the litter beneath defoliated trees during a prolonged period of drought during July and August in Ontario in 1929.

Larvae about to spin cocoons tend to seek moist areas (Graham 1956; Graham and Satterland 1959; Ives 1955). During periods of drought, the cocoons will tend to be deep in the moss, although some cocoons will usually be spun near the surface, either because the larvae were unable to penetrate compact duff or because the surface layers had been moistened by showers. Cocoons spun in dry moss were poorly formed, and many of the larvae were soon desiccated (Ives 1955). Larvae in apparently normal cocoons spun near the surface may also suffer desiccation and death if the moss dries out during hot dry weather (Graham 1956; Graham and Satterland 1959). Larvae spinning cocoons in depressions or deep within the hummocks are usually flooded by a subsequent rise in the water table. If they were flooded in the fall, very few survived (Lejeune *et al.* 1955), and survival of larvae above the water table was also adversely affected (Ives and Nairn 1966a). If the cocoons were flooded in the early spring, the sawflies were less susceptible (Lejeune *et al.* 1955). Heron (1960) found that submergence for up to 30 days at 10° C caused very little sawfly mortality, but no *Bessa harveyi* (Townsend)[51] survived after 20 or more days of submergence at the same temperature.

The present study indicates that warm weather during August to October was unfavorable, agreeing with Graham's (1956) findings. Cool weather during the same period was favorable. Cool wet weather during May to July was favorable. This may have been due in part to a lack of heat tolerance among the larvae, but it may also have been due to indirect effects. One of the most prevalent parasites during the period under consideration, *B. harveyi*, was very susceptible to flooding (Buckner 1959; Heron 1960), which would tend to limit its effectiveness in wet years. Furthermore, the nesting of the masked shrew, one of the more-effective small mammal predators, appeared to be adversely affected by rainfall, while populations of the arctic shrew tended to be highest during dry summers (Buckner 1966a). Deer mice populations also tended to reach high numbers in bogs if a dry season and an abundance of larch sawfly happened to coincide (Buckner 1974). The end result of all these interactions, as Graham and Satterland (1959) suggested, is that cool wet weather is more favorable to the larch sawfly than is warm dry weather, even though a number of larvae may drown in wet years (Ives 1968, 1976a; Ruggles 1910). The fact that heavy precipitation during the early winter favored population buildup may indicate that the overwintering larvae are not completely cold-hardy. This possibility does not appear to have been examined by any of the workers studying the larch sawfly.

Semiothisa sexmaculata

Very little information on the population dynamics of this insect could be found in the literature. Bergeron (1973) presented graphs showing the abundance of larvae of this insect and of *P. erichsonii* and two other species of *Semiothisa* for six plots over a period of 8 years. There were some similarities in the population trends of *P. erichsonii*

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[51] Diptera: Tachinidae.

and *S. sexmaculata*, although only one plot showed any significant correlation; however, this was the same plot that Ives (1976a) discarded because of poor population estimates. The reason for this apparent lack of agreement can probably be found in the life histories of the two insects. *Semiothisa sexmaculata* spends about the same length of time in the moss as does *P. erichsonii* but tends to be about a month later in peak larval drop. Consequently, it probably has almost the same environmental pressures as the larch sawfly while in the moss, but the feeding larvae also have the competition of the larch sawfly to contend with. If larch sawfly defoliation is severe, there is very little food for most of the *S. sexmaculata* larvae.

In the present study, wet conditions during May to July were unfavorable, while dry conditions were favorable. As most of this time is spent in the moss it probably indicates that the pupae suffer mortality if flooded in the spring. Cool wet weather during August to October was favorable, and there are a number of possible interpretations of this fact. First, it may indicate a lack of heat tolerance on the part of the larvae; secondly, it probably also indicates that disease is of minor importance; and last, it may also mean that small mammal predation of the pupae and feeding larvae is an important mortality factor. The latter assumption is further substantiated by the fact that light precipitation during early winter favored population increase, since this is another indication that small mammal predation was important. This agrees with results of Ives (1976b), who showed that there was an inverse relationship between the numbers of *S. sexmaculata* caught in traps in generation $n + 1$ and the k-value (a measure of mortality) for larch sawfly mortality attributable to surface water and small mammal predation in generation n. Finally, mild weather with light precipitation in late winter was also favorable. This may indicate that the pupae are not completely cold-hardy. The light precipitation in late winter, coupled with the light precipitation in early winter, would minimize the amount of spring flooding which, as already noted, appears to be detrimental.

Anoplonyx canadensis

Little information on the ecology of this insect could be found in the literature. Ives (1977) showed that adult emergence almost coincides with that of *P. erichsonii*; however, development is slower, so the larvae do not drop until much later. The larval drop traps used in the larch sawfly studies were usually removed from the bogs in early September and thus missed many of the *A. canadensis* larvae.

Hot dry weather during May to July was unfavorable (Table 4). This coincides with the adult period (Table 2), indicating that one or more of the adult, egg, or early-instar larva stages are vulnerable to hot dry weather. Since the eggs are laid in slits cut into the needles (Wong 1955), it is conceivable that the injured needles dry out during hot dry weather, so that the eggs either desiccate or the young larvae become trapped. Cool wet weather during May to July was favorable, a corollary to the above. Cool wet weather during August to October was also favorable. This suggests that the larvae are not completely heat-tolerant and probably indicates that disease is not an important mortality factor. It could also mean that small mammal predation is a major factor, especially since cold weather in the early winter (which tends to curtail small mammal activity) was favorable to population increase. The overwintering larvae may not be completely cold-hardy, since heavy precipitation in the early winter followed by mild weather in the late winter appeared to be favorable. No explanation can be offered for the apparently favorable effects of light precipitation in late winter, except that it may be indicative of early springs, and these could be beneficial.

Anoplonyx luteipes

The only information on the ecology of this insect is in the papers referred to for *A. canadensis*. The life cycles are similar, except that adult emergence precedes that of *P. erichsonii*, while larval drop more or less coincides with that of the larch sawfly (Ives 1977).

Warm dry weather during May to July was favorable (Table 4). Probably most of the larvae have hatched before excessively hot weather occurs, so the eggs and young larvae would not be exposed to the adverse effects of needle desiccation hypothesized for *A. canadensis*. It also suggests that disease could be an important source of mortality as these would tend to spread faster in wet weather. It is perhaps significant that Wong (1955) recovered two fungal diseases from *A. luteipes* but made no mention of diseases from *A. canadensis*. Mild weather in early winter and heavy precipitation throughout the winter were both favorable, suggesting that the overwintering larvae are not completely cold-hardy and that small mammal predation is not an important mortality factor. The latter is hard to explain. The population trends of *A. luteipes* and *P. erichsonii* tend to be similar (Ives 1977), so perhaps the small mammals ignore the *A. luteipes* cocoons in favor of the more abundant larch sawfly cocoons.

SMALL MAMMALS

Some small mammals are considered to be pests from a forestry viewpoint because they destroy large quantities of coniferous seeds and girdle and kill seedlings and small trees. The destruction of seed is probably of minor importance in an established forest, where very few seedlings would become established anyway, but it can become a major concern if one is attempting reforestation by means of aerial seeding, since most spring-sown seeds can be destroyed by moderate populations of small mammals (Radvanyi 1970).

High populations, mostly of the meadow vole, *Microtus pennsylvanicus* (Ord)[52], have also caused excessive girdling of hardwood plantations in southern Ontario (Radvanyi 1975). Elton (1942) gave a thorough worldwide review of the ravages caused by mice and voles and of man's effort to combat the outbreaks. Some of these outbreaks have caused extensive damage to crops, pastures, orchards, and forests, very often over quite large areas. The Forest Insect and Disease Survey (Anonymous 1939-73) reported that 35% of the trees in a Norway spruce plantation in Quebec died in 1970 as a result of feeding by mice 2 years previously. Heavy mouse damage to Austrian and jack pine plantations in New Brunswick was reported in 1971. Moderate damage to Scots pine was also reported.

Girdling by rabbits (varying or snowshoe hares) is more serious and extensive. In 1961, damage was evident for about 200 km along the MacKenzie Highway in northern Alberta. Saplings up to 25 mm in diameter were chewed off, and larger trees were completely girdled. Jack pine suffered the most damage. In 1969, rabbits caused light to moderate damage to red, Scots, and jack pine plantations in Quebec. Similar damage to natural stands of balsam fir was also reported. Numerous leaders were eaten by rabbits in a Norway spruce plantation in Quebec in 1972. Extensive damage by varying hares was reported throughout the central and northern portions of the prairie provinces and in parts of the Yukon and the Northwest Territories during 1960-62 and in 1970-72 (Anonymous 1973).

The food preferences of the animal are important in determining whether or not it will have a detrimental effect on the forest. Williams (1959) found that most of the food of the deer mouse, *Peromyscus maniculatus*,in Wyoming and Colorado consisted of vegetable matter. He did not state when his trapping was done, but the fact that most of the food was conifer seeds suggests that it was done in the fall. Jameson (1952) studied the food habits of *P. maniculatus* for 2 years in the northern Sierra Nevada, California. He found that arthropods formed a fairly high percentage of its food during the summer months, but the percentage dropped during the remainder of the year. Batzli (1977) found that the white-footed mouse ate mainly seeds during the spring and autumn and that arthropods were more important in summer and winter. He found that beetles, lepidopterous larvae, and spiders were the main arthropods eaten. *Peromyscus maniculatus* is highly opportunistic (Flake 1973), eating the particular types of animal and plant material most available.

There is no evidence that snowshoe hares eat any forest insects, but mice and voles do, so they have a beneficial role as well. Although it is difficult to demonstrate quantitative relationships between small mammal predation and insect abundance, entomolo-

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[52] Rodentia: Muridae.

gists have long recognized that mice and voles destroy large numbers of forest insects. Hewitt (1912) reported that the meadow mouse, *Microtus agrestis* (Linnaeus)[53], had opened about 25% of larch sawfly cocoons from various localities in England in 1907-08. This increased to about 50% the following year. Graham (1928) showed that up to 83% of larch sawfly cocoons in Michigan and between 79% and 95% of those examined in Minnesota were destroyed by small mammals, principally *Microtus* sp. In another series of experiments, predation by mice ranged from 20% to 78%. Despite this early recognition of the role of small mammals in the population dynamics of a major forest pest, there has been relatively little emphasis placed on this aspect of the problem, although the masked shrew was introduced into Newfoundland to help reduce populations of the larch sawfly (Buckner 1966b). Most of the studies that have been conducted were concerned with the role of small mammals as predators of sawflies, probably because the teeth marks on the opened cocoons make evaluation of predation relatively easy. Examination of cocoons for these teeth marks shows that small mammals are capable of consuming large numbers of larvae in cocoons.

Perhaps one of the reasons why so little work has been done to evaluate the role of small mammals as insect predators is the cyclic behavior of many small mammal populations. There often appears to be little, if any, relationship between these cycles and the abundance of various insects, possibly because most insects constitute only part of any animal's diet. Mammalogists have been primarily concerned with trying to determine the underlying causes of fluctuations in small mammal populations. Elton (1924) examined population trends for a number of species of mammals and birds and was convinced that weather must be the underlying factor responsible for the fluctuations. He showed that lemmings had a periodic fluctuation in populations of about 3.5 years, while the varying hare had a period of 10 to 11 years. He also discussed the sunspot cycle, pointing out that it also had a period of about 11 years. He then attempted to relate varying hare cycles to sunspot cycles. Most rabbit peaks occurred during low spots in the sunspot cycle. The exception was the peak in 1905, which followed volcanic eruptions in 1902 and 1903. Watt (1973) also reviewed the literature on sunspot numbers and world temperature departures. Negative departures followed major volcanic eruptions, due to the shading effect of the large volumes of volcanic ash and dust ejected into the atmosphere. Elton (1924) showed this quite clearly when he plotted a combination of curves depicting sunspots and pyrheliometer readings and departures of the earth's temperatures from mean values. He thus attributed the fluctuations in rabbit populations to changes in temperatures.

Cole (1958) pointed out that Elton's (1924) paper on apparent relationships between population cycles and sunspot cycles "was the stimulus that set off a virtual explosion of papers on population cycles. The number published exceeds 2000, and I have not tried to make an accurate total count". He discussed a number of these papers and went on to say:

> Now, if one assumes the sunspot hypothesis to be correct he can deduce the logical consequences that the sunspot cycle and the population cycles should be of equal length, that populations in different regions should fluctuate simultaneously, and that the "cause and effect" should stay in phase, that is the population changes should not precede the sunspot changes .... these apparently necessary consequences are not actually realized. The population fluctuations differ in length from the sunspot cycle, the two wander in and out of phase with each other, and populations even in adjacent regions may fluctuate independently and be completely out of phase.

Elton (1942) admitted that the sunspot hypothesis was incorrect. Palmgren (1949) and Cole (1958) have both shown that apparently "cyclic" curves can be obtained by

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[53] Rodentia: Muridae.

mathematical manipulation of a series of random numbers.

Kalela (1962) examined population fluctuations of arctic and boreal small rodents and found that most peaks occurred when there were two consecutive warm summers. He contended that the fluctuations were most easily explained on the basis of what he termed "production biology". He considered that "The cyclic fluctuations found in the populations of small rodents living in arctic and adjacent areas are considered to be the interaction of two complex factors, viz: 1) random oscillation in summer temperature, which causes variation in flowering and, at the same time, in the nutritive value of the food plants as a whole, and 2) rhythms inherent in the food plants and/or in the rodent populations themselves." Chitty (1960) set up the hypothesis that "all species are capable of regulating their own population densities without destroying the renewable resources of their environment, or requiring enemies or bad weather to keep them from doing so .... under appropriate circumstances, indefinite increase in population density is prevented through a deterioration in the quality of the population." He also claimed that the effects of independent factors such as weather become more severe as the quality of the population falls; however, he offered no explanation for why increases in populations are often synchronous, or nearly so, over quite extensive areas.

Christian and Davis (1964) believed that this self-regulating mechanism operated through some endocrine system. "We believe that the evidence ... supports the existence of endocrine feedback mechanisms which can regulate and limit population growth in response to increases in overall 'social pressure' and which in turn are a function of increased numbers and aggressive behavior .... environmental factors in most instances probably act through these mechanisms by increasing competition."

Krebs and Myers (1974) reviewed the literature on population cycles and discussed the various hypotheses that have been advanced by way of explanation. They pointed out that "Reproductive rate is highest in the increase phase, owing to 1) longer breeding season, including winter breeding in some species, and 2) lower age at sexual maturity. In the peak and decline phases reproductive rate is reduced .... Mortality rates in all sex and age groups are lowest in the increase phase .... Aggressiveness of the male and female microtines increases, and home range size decreases with increasing population density." In conclusion, they suggested "that studies of the heritability of reproductive capabilities, growth potentials, and behavior of microtines will be the key to unlocking the mysteries of rodent cycles."

In a review of the population dynamics of the genus *Peromyscus*, Terman (1968) noted that "Some of the clearest and most direct evidence for growth control of populations of *Peromyscus* in nature is the rather consistent low density of these populations." His concluding remarks were similar to those of Krebs and Myers: "The data presently available on populations are suggestive of sensitive controlling mechanisms which are by no means fully understood. Prerequisite to understanding these mechanisms is the accumulation of additional information on the social and spatial dynamics of populations and the variables influencing reproduction, mortality and movement."

Watt (1968) reviewed the literature on population regulation for a large number of organisms. He believed that "many populations are regulated largely by climate. Even then, competition is the ultimate population regulator, in that if all other regulating factors fail, competition pressures will indeed come into operation, but this rarely happens." He later pointed out (Watt 1973) that "Density-dependent factors must be the ultimate controlling agent for any population. A more potent argument is quantitative: over the course of time, any population exhibits a mean reproductive rate. If this rate were strictly density-independent, then each population would either grow *infinitely* or become extinct. But one observes neither. Only density-dependent regulation can account for that."

Verification of the validity of these diverse opinions is extremely difficult, especially under field conditions, because so many interacting factors are involved and because there is probably an element of truth in all of the hypotheses. Which element is important in any given situation probably depends upon circumstances affecting the population under consideration. Buckner (1966a) reported some interesting observations during an unusually high peak in populations of the masked shrew, *Sorex cinereus* Kerr[54], and they tend to support aspects of several hypotheses:

> Evidence of the impending population eruption of *S. cinereus* in 1957 was first noticed in August of that year when an unusually high proportion of juveniles appeared. At the same time, a change in behavior was noticed. Animals in the traps were unusually excitable, although mortality in the traps was not excessive. Specimens that were brought in from the field lived only about 4 days; previously no difficulty was experienced in maintaining shrews alive in captivity. By September precocious breeding in subadults was occurring. Mortality in the traps increased, and additional precautions in trapping procedures, including a reduction in the interval between trap examinations and closure of the traps during the day, were required. At this stage, the average life expectancy in captivity was about 8 hr. In October the population had reached an unprecedented peak. Mortality in the traps was so excessive that over 25% of the captured animals died even though chlorpromazine was used in the bait and the traps were visited at 2-hr intervals during the night. Prior to this, trap mortality rarely exceeded 5%. Precocious breeding by this time had extended to the juvenile population, and when observations were terminated on 27 October, breeding was still in progress. Oxygen consumption measurements on members of this population were considerably above normal.

Elton (1942) encountered similar problems while studying meadow mouse, *Microtus agrestis*, populations in Britain:

> In January 1927, the mice began to appear in abnormal numbers in the traps, and by February an average of one trap in ten had a mouse in it every night. In December the figure had been only one in forty traps. Many of these mice were surplus to our needs and were kept alive in cages, where they lived quite well, as did those kept in later years. Some lived for more than twenty-eight weeks. But from the end of February until about the end of June the mice brought in died quickly, many after a day or two, and most of them within a week. The cause of death was never established . . . .

In addition, there have been numerous experimental attempts to determine the importance of various aspects of the environment and animal behavior upon population trends. The results have often been contradictory or inconclusive. For example, Kalela (1962) thought that variation in the quantity or quality of food in response to weather was responsible for the cyclic fluctuations in populations of arctic and boreal small rodents. Attempts to verify this experimentally have had varying results. Krebs and DeLong (1965) found that supplemental food did not cause an increase in populations of the California vole. Elton (1942) also found that excess "natural" food was not sufficient to maintain breeding of wild populations of *Microtus agrestis* established in outdoor pens set up in a grassfield. The voles stopped breeding about the end of July and beginning of August. "Thereafter it was inevitable that the populations would drop to lower and lower densities." On the other hand, Fordham (1971) found that

> There seems little doubt however, that provision of excess artificial food did affect *Peromyscus* populations. It apparently induced population growth in spring and summer to a level well above the control, and led to heavier individuals with a faster growth rate. Some of the changes in population can be attributed to breeding, but immigration possibly occurred . . . . Addition of food apparently did not improve the overall survival

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[54] Insectivora: Soricidae.

of young at experimental sites in summer, which suggests that aggression was not lowered from its normally high level at that time.

Andrzejewski (1975) cited two additional studies in which populations of other *Peromyscus* species increased when supplied with additional food. In his own studies he found that supplemental food did not increase winter survival of the bank vole, *Clethrionomys glareolus* (Schreber)[55]. It did, however, lead to "an increase in the population of voles during the winter due to the accumulation of a higher number of voles in the autumn, to winter reproduction, and also due to increased migration." He concluded that "Despite the fact that rodents utilize their food to a limited degree the data presented above are in agreement with the opinion of many authors suggesting that population numbers of rodents are in principle regulated by food abundance in the ecosystem, although in a more complicated way than would appear from the simple energy balance." Miller and Getz (1977) also agreed that differences in abundance of *Peromyscus* and *Clethrionomys* in Connecticut uplands were due to fluctuations in the food supply.

Weather is another aspect of the environment that one would expect to have an influence on small mammal survival and/or abundance. Smith *et al.* (1974) studied the annual fluctuations of small mammal populations in an eastern hardwood forest. They found that 73% of the significant correlations involved weather variables and that precipitation was more important than temperature. An analysis of variance revealed significant effects of summer, winter, and spring precipitation upon total numbers. Associated regression coefficients were positive for summer and spring but negative for winter precipitation. Buckner (1966a, 1974), however, found that dry summers tended to favor population increases of small mammals in tamarack bogs.

In cold climates, winter weather has a marked influence on small mammal activity. Formozov (1973) discussed the importance of snow in the evolution and distribution of mammals and birds in northern areas. He pointed out, for example, that shrews are common in snow-covered areas but not on steppes that lack snow cover in winter. He also pointed out that deep and/or crusted snow hampers predators that normally prey on voles under the snow. The effectiveness of snow cover in protecting small mammals is also due to the insulating property of the snow (Coulianos and Johnels 1962; Fuller *et al.* 1969). Studies on seasonal mortality show that it is highest in the summer and lowest in winter (Beer and MacLeod 1966; Golley 1961; Miller and Getz 1977; and Whitney 1976), even though subnivean temperatures may drop below -10°C for extended periods in northern areas (Stebbins 1971).

Early results of studies on small mammal survival in northern areas suggested that populations of the northern red-backed vole, *Clethrionomys rutilus* (Pallas)[56], declined following a prolonged cold period in the subnivean environment (Fuller *et al.* 1969). A later study by Fuller (1976) showed that there was no relationship between overwintering survival and subnivean temperatures: "Almost 70% of animals known to be alive at the end of August survived the winter before the major peak, and all ages survived well during the peak summer. Less than 5% of marked animals survived the postpeak winter. The prepeak winter was characterized by low and fluctuating temperatures beneath the snow, whereas the postpeak winter had high and uniform subnivean temperatures." Beer (1961), however, attributed a crash in populations of the white-footed mouse, *P. leucopus*, and the red-backed vole, *C. gapperi*, in Minnesota to a very cold winter with very little snow cover, coupled with food shortages. Howard (1951) also showed that small mammals were much more likely to die of cold exposure when they were short of food. Perhaps Fuller's apparently contradictory results can be attributed to availability of food, since this aspect was apparently not evaluated.

In most of Canada, small mammals do not breed during the winter, although some

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[55, 56] Rodentia: Muridae.

species do so in warmer climates. The length of the breeding season varies with location, species, and weather conditions. Beer and MacLeod (1966) found that it extended from approximately 1 April to 30 September for *P. maniculatus* in Quebec. Wrigley (1969) studied the ecology of a number of mammals in southern Quebec and made notes on their breeding conditions. The breeding seasons for some small mammals were as follows: masked shrew, *Sorex cinereus*—mid-April to late September; short-tailed shrew, *Blarina brevicauda* (Say)[57]—late April to early September; deer mouse, *P. maniculatus*, and white-footed mouse, *P. leucopus*—mid-April to mid-September; red-backed vole, *C. gapperi*—late April to early September; and meadow vole, *M. pennsylvanicus*—early April to late September. Similar breeding periods were recorded for *M. pennsylvanicus* in Manitoba (Turner and Iverson 1973) and for the northern red-backed vole, *C. rutilus*, and the tundra vole, *M. oeconomus* (Pallas)[58] in Alaska (Whitney 1976). Buckner (1966a) estimated that the breeding season for shrews in Manitoba tamarack bogs normally extended from early May to about mid-August, although it may occasionally extend into September or October.

A certain amount of variation in the length of the breeding season appears to occur with several species at least, but just what causes it is not too clear. In the case of *P. maniculatus* in a coastal forest, Sadleir (1974) found evidence that "Sudden increases in temperatures may have stimulated the onset of breeding but its cessation before the autumn equinox was always associated with a considerable decrease in temperature if this occurred after April." Presumably the converse is also true, so that breeding continues if weather conditions are favorable. Because there is no recruitment to populations during the nonbreeding season (except for immigration), changes in the number of individuals in the population are regulated by the length of such seasons (Petticrew and Sadleir 1974). In New England, Miller and Getz (1977) found that the length of the previous nonbreeding season appeared to be the primary factor influencing population densities reached in a given year by *C. gapperi* and *P. leucopus*. Declines in populations of *C. gapperi* and *P. maniculatus* in the Northwest Territories were attributed to an unusually late spring with subzero temperatures and snow cover through the first half of May (Fuller 1969).

Behavior of the males (and possibly of the females) influences the dynamics of small mammal populations. During the breeding season the males become aggressive toward other males of both their own species and other species. Intraspecific male aggressiveness has been demonstrated for *M. pennsylvanicus* (Turner and Iverson 1973) and for *P. maniculatus* (Sadleir 1965). Presumably it also occurs in other species. In the case of *P. maniculatus*, this antagonistic behavior was believed responsible for limiting the numbers of males and juveniles in the population (Petticrew and Sadleir 1974), but other factors appear to be responsible for regulating the number of females. The authors suggested that their number may be related to the length of the breeding season. Interspecific competition between *M. pennsylvanicus* and *C. gapperi* resulted in an almost complete habitat separation during the summer in aspen parkland (Morris 1969). There was a suggestion that this habitat separation breaks down during the winter and that the two species coexist in the same aspen stand when there is the protective cover of snow. Iverson and Turner (1972) demonstrated that the reverse also occurs and that *C. gapperi* invade grassland habitats during the winter. *Microtus pennsylvanicus* also moved into a spruce forest for the winter, even though it was occupied by *C. gapperi* (Turner *et al.* 1975). Thus, although each species may have its preferred habitat during the summer, this preference seems to disappear during the winter.

The type of habitat is the last aspect of the environment affecting small mammal abundance that will be discussed here. The amount of cover has a distinct bearing on the number of small mammals present. Morris

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[57] Insectivora: Soricidae.

[58] Rodentia: Muridae.

(1955) found that summer populations of small mammals in New Brunswick were nearly always highest in plots affording good cover in the form of slash, decaying logs, and fallen trees. In winter, small mammals also seem to be attracted to areas with good cover, presumably because this cover creates subnivean air spaces (Coulianos and Johnels 1962).

The type of vegetation also influences the species of mammals found in an area. Buckner (1958) gave a brief but excellent description of the habitat preferences of small mammals normally found in tamarack bogs. He also discussed the habitat preferences of shrews (Buckner 1971): "The most catholic in distribution is the cinereus shrew which ranges from the central water edge well up to the upland sites . . . . The saddle-backed shrew inhabits the deeper yet drier areas of the bogs . . . . The short-tailed shrew, principally an upland species, invades to some extent the drier areas of the bog." Morris (1955) trapped small mammals in 20 plots located in a number of different forest types and recorded the number of individuals of each species in each forest type. He found that the red-backed vole was the predominant species in all coniferous and mixed-wood stands in New Brunswick. The deer mouse, cinereus shrew, and short-tailed shrew were the other common species. The combined population of all species at the peak of the seasonal cycle varied from 1.5 to 37.1 per hectare. Grant (1976) conducted an 11-year study of the small mammal populations in Quebec. Most of his trapping was done in June, so that he missed the peak populations, but his results indicated that *P. maniculatus* was the most common species. Wrigley (1969) also found that *P. maniculatus* was usually the most abundant species present in southern Quebec. Wrigley (1974) conducted a study of mammals in the sandhills of southwestern Manitoba and once again found that *P. maniculatus* was the most abundant species. *Sorex cinereus*, *C. gapperi*, and *M. pennsylvanicus* were also common, although the latter was absent from forest sites.

The foregoing discussion indicates that it is impossible to determine if there is a relationship between small mammal predation and insect abundance unless population figures for the small mammals are available, since prediction of probable abundance based on weather records is out of the question. The only small mammal records that I could find for the period and area in question are those collected during a study of the larch sawfly in southwestern Manitoba (Buckner 1957 and unpublished[59]). The effects of small mammals on insect populations are therefore presented primarily as a review of the available literature. The order of presentation is the same as in Figs. 2-8; however, in the interest of brevity, the insect species is not listed if pertinent literature could not be found.

Choristoneura fumiferana

As Morris *et al.* (1958) pointed out, "the spruce budworm is available to small terrestrial mammals only under special circumstances, and even then only for a small portion of their breeding season." They concluded that the populations of rodents and insectivores did not respond to budworm density, but fluctuated independently. There was some evidence, however, that decreased peak heights in the cycles of the red-backed vole and the deer mouse may have been associated with a shortage of seed, which resulted from budworm damage.

Choristoneura pinus pinus

Mattson *et al.* (1968) studied the vertebrate predation of jack pine budworm in Michigan. They placed snap-back traps in the trees and found that *P. maniculatus* was seldom caught. (The traps were nailed to the trunks of the trees, but perhaps a better location might have been the upper surface of the lower branches.) The least chipmunk, *Eutamias minimas* Backman[60], was commonly caught, but examination of the contents of 10 stomachs indicated that the jack pine budworm was not an important component of their diet.

Neodiprion nanulus nanulus

Kapler and Benjamin (1960) found that small mammals were the most effective cocoon predators of this insect in Wisconsin. Mammalian predation began as soon as the

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[59] Unpublished field data on file at the Northern Forest Research Centre, Edmonton, Alberta.

[60] Rodentia: Sciuridae.

larvae dropped to spin cocoons in the litter and continued until adult emergence in the fall. The only small mammal collected was the white-footed mouse, *P. leucopus*, which ate up to 100 cocoons per day in cage studies. Estimates of predation in the field ranged from 21% to 78% during a 3-year period.

Neodiprion virginianus complex

Wilkinson *et al.* (1966) studied the biology of this insect in Wisconsin; however, they do not appear to have assessed the amount of small mammal predation on the cocoons. This is unfortunate, as the cocoons are spun in the litter to a depth of about 8 cm, a location which should make them very vulnerable to small mammal attack. In Europe, Mallach (1974) found that shrews, mice, and voles were the most important predators on cocoons of the pine-feeding sawfly *Diprion pallipes* (Fallen)[61]. About 70% of the hibernating insects in the cocoons were destroyed by small mammals. Similarly, Holling (1959) showed that small mammals were important predators of cocooned *Neodiprion sertifer* (Geoffroy)[62], another pine sawfly that remains in the duff from early June until late September. McLeod (1966) studied the distribution of cocoons of another jack pine sawfly, *N. swainei* (Middleton)[63], in Quebec. This insect overwinters in the cocoon, so is very similar in this respect to the *N. virginianus* complex. McLeod found that small mammal predation, probably mostly by the masked shrew, *S. cinereus*, ranged from 45% to 65%. This animal is a particularly effective predator because it is capable of a large intake of prey relative to its body size (Buckner 1964; Platt and Blakely 1973). It therefore seems almost certain that small mammal predation must be an important factor in the population dynamics of *N. virginianus* complex.

Pristiphora erichsonii

Hewitt's (1912) and Graham's (1928) studies on small mammal predation of the larch sawfly have already been mentioned. Graham (1956) referred to these early studies and gave additional information on the role of small mammals as predators. Graham and Satterlund (1959) found that predation of cocoons in hummocks was higher than predation of those spun in depressions. This was confirmed by Buckner (1959), who further showed that small mammal predation of larch sawfly cocoons decreased rapidly as the distance from small mammal tunnels increased. Buckner (1974) also found that there were significant but variable numerical responses of cinereus shrew populations to numbers of sawflies, beginning at low and moderate sawfly densities. There was no relationship at high sawfly densities. The red-backed vole also showed a weak numerical response to varying densities of larch sawfly cocoons. In addition to numerical response, there is also a functional response (Buckner 1974). The percentage of cocoons eaten increases rapidly as the cocoon population increases, but it tends to drop off again at high cocoon densities. The net effect of the interaction of these two responses is that there is no overall relationship between the number of cocoons and the amount of small mammal predation (Ives 1976a). Although small mammal predation on larch sawfly cocoons may, on occasion, be as high as 98% (Buckner 1958), it nevertheless appears to occur largely in a density-independent manner and could not be shown to be a key factor in the dynamics of larch sawfly populations (Buckner 1967).

This density independence is reflected in the populations of voles and shrews when sorted according to increases or decreases in larch sawfly populations (Table 5). There were more of both voles and shrews in three of the four plots when sawfly populations were increasing rather than decreasing. It may perhaps be significant that the Pine Falls plot was one of the plots in which surface water or adverse moisture was not a factor causing sawfly mortality (Ives 1976a).

Semiothisa sexmaculata

Ives (1976b) showed that there was a marked similarity in the shapes of the curves for *S. sexmaculata* abundance and the inversely-plotted **k**-values for larch sawfly mortality attributable to surface water and small mammal predation during the preceding gen-

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[61, 62, 63] Hymenoptera: Diprionidae.

Table 5. **Mean bird and small mammal populations in relation to changes in insect populations between generations n and n + 1 in tamarack bogs containing larch sawfly plots during the years 1952 to 1969. Populations are expressed as number of territorial male birds and number of small mammals per 40 hectares in generation n. Underlined numbers indicate when bird or small mammal populations are greater by 10 or more during decreasing insect populations than during increasing insect populations.**

		Bird populations				Small mammal populations			
		Warblers		Sparrows		Voles		Shrews	
Insect species	Plot	Insects increasing	Insects decreasing	Insects increasing	Insects decreasing	Insects increasing	Insects decreasing	Insects increasing	Insects decreasing
Pristiphora erichsonii	Telford	154	175	115	152	142	118	275	63
	Seddon's Corner	69	131	29	49	283	106	62	34
	Rennie	190	154	94	98	400	254	277	189
	Pine Falls	119	85	59	64	289	668	64	74
	Average	133	136	74	91	278	286	170	90
Semiothisa sexmaculata	Telford	151	174	134	136	85	140	68	206
	Seddon's Corner	71	91	34	38	394	96	22	45
	Rennie	144	177	82	102	303	675	297	255
	Pine Falls	109	83	66	70	380	601	46	88
	Average	119	131	79	86	290	378	108	148
Anoplonyx canadensis	Telford	135	191	122	134	145	56	47	25
	Seddon's Corner	108	92	35	43	320	92	84	21
	Rennie	240	163	94	89	517	447	84	246
	Pine Falls	91	122	62	60	450	564	54	61
	Average	144	142	78	82	358	290	67	88
Anoplonyx luteipes	Telford	107	145	85	113	40	148	99	51
	Seddon's Corner	74	126	28	50	230	113	45	47
	Rennie	-	169	-	92	223	483	472	227
	Pine Falls	97	110	67	57	377	545	72	66
	Average	93	138	60	78	218	322	172	98

eration. It was concluded that these two factors combined were probably acting as a key factor in the dynamics of *S. sexmaculata* populations.

The results in Table 5 tend to confirm this conclusion, as populations of both voles and shrews were higher in three of the four plots during declining *S. sexmaculata* populations.

Anoplonyx canadensis

No pertinent literature on small mammal predation could be found. Although vole populations in the Pine Falls plot (and shrew populations in the Rennie plot) were higher during declining sawfly populations, there does not seem to be any consistent relationship (Table 5).

Anoplonyx luteipes

No literature on small mammal predation could be found. Data in Table 5 seem to indicate that vole (but not shrew) populations were higher when *A. luteipes* populations were declining than when they were increasing. Consequently, voles could be a factor in the population dynamics of *A. luteipes*.

BIRDS

The role of birds in the dynamics of forest insects has been reviewed by Otvos (1979) and is even more difficult to assess than is that of small mammals. The vast majority of northern birds are migratory and consequently feed on forest insects only during the warmer months of the year. Even those species that do not migrate are much more mobile than small mammals, so that studying their food requirements, especially during the winter, is a difficult and time-consuming undertaking.

Generalized discussions of the feeding habits of birds are based on stomach and gizzard analyses without considering populations. From accounts of insectivorous birds (Bent 1948, 1964a, 1964b; Lawrence 1973a, 1973b; McAtee 1926; Nero 1973; Pearson 1936; Salt and Salt 1976; and Scott and Patton 1975) one gets the impression that birds are a major factor limiting the abundance of forest insects. Perhaps this is true for the vast majority of insect species, since relatively few species become abundant enough to become serious pests; however, obtaining conclusive or convincing evidence that such is the case is another matter (Bruns 1960). It is difficult enough to study the complex interrelationships between birds and insects when both are relatively abundant. It is even more difficult when the insects being studied are at endemic levels.

One approach is to exclude birds from one or more areas and compare the numbers of insects in the protected areas to those in the areas exposed to bird predation. Holmes *et al.* (1979) excluded birds from patches of striped maple by enclosing areas measuring 6 X 6 X 2 m high in crop protection netting. Foliage sampling throughout the season showed that the numbers of lepidopterous larvae were consistently higher within the enclosures than outside. The species of birds primarily responsible for this predation were two warblers, two thrushes, and two vireos. Solomon *et al.* (1976) allowed codling moth larvae to spin cocoons on apple logs in the laboratory. These logs were then placed in apple orchards, in as natural a position as possible, and some were protected from birds by wire netting. The experiments were conducted during three winters and resulted in codling moth larval mortalities of 94.7%, 94.9%, and 95.6% on exposed logs, all of which was attributed to bird predation. The only bark-hunting birds seen frequently in the orchards were blue tits, with smaller numbers of great tits. Askenmo *et al.* (1977) studied the overwintering spider populations on protected and exposed spruce branches and found that the density of spiders at the end of the winter was more than 50% higher on the protected branches. As only the larger spiders were affected to any degree, an even higher proportion in this size group must have been taken. Goldcrests were believed to be the main predators.

A second approach is to study the feeding habits of particular birds in one or more environments over a period of time to obtain an idea of their requirements at different times of the year. Betts (1955) conducted this type of study with titmice in an oak woodland in England. She found that the size of food eaten by the various species of birds was relative to the size of the bird. Her analyses on size of food did not include larvae, but even so, 58.7% of the insects eaten by the blue tit were 2 mm or less. The percentage would have been higher if larvae had been included, since the blue tit takes a very large number of small larvae (mostly of species measuring up to 4 mm) during the autumn and winter. The food of the coal tit, the smallest species (Lack 1971), consisted 73.6% of insects measuring 2 mm or less in size. Betts also found that aphids formed the greatest proportion of the food of adult blue tits during June 1949 and 1950; however, when she studied the food brought to nestlings in June 1951, she found that aphids were not included, although they were present on leaves at the time. This points out that the food eaten by the adults is not necessarily the same as that offered to the young. Presumably the small size of the aphids in Betts' study made them less attractive as food for the nestlings.

Dahlsten and Herman (1965) noticed similar feeding behavior in nesting mountain chickadees. The adult birds continued to feed on lodgepole needle miner larvae and pupae, but fed their young on the larger, more succulent larvae gathered from aspens near the margins of the lodgepole pine stands.

This selective and differential feeding behavior is a factor that must be kept in mind when studying feeding patterns of young birds. Gibb and Betts (1963) conducted extensive foliage sampling to determine the lengths of caterpillars present on the foliage. The frequency distribution of these sizes, when compared to the sizes of larvae that coal tits and great tits fed to their nestlings, clearly indicated that the birds were selecting the larger larvae: "*Panolis* caterpillars taken by the great tits in early July 1955, for instance, were on the average 83% longer and 600% heavier than the average of those in the foliage compared with a more modest 58% longer and 330% heavier for those taken by coal tits, about half the weight of a great tit. Likewise, in May 1955 coal tits selected geometers some 14% longer and 43% heavier than those in the foliage, and in May 1956 about 24% longer and 62% heavier." Lack (1966) reported similar data.

Tinbergen (1960) conducted extensive studies of the food of tits, particularly the great tit, in Holland. He advanced the theory of "specific searching images" to account for the fact that the birds tended to feed on a limited number of species at any one time, even though other species were present. Royama (1966, 1970) was critical of this idea. Using photographic equipment to record the size and species of larvae brought to nestlings, Royama (1970) also found that the birds would stop taking abundant species of prey if bigger but less abundant species became available. He advanced the hypothesis of profitability to explain this response.

The size of food offered to the nestlings is not necessarily a reliable indicator of the size of winter prey either. As Lack (1966) pointed out, "Nearly all the prey taken in winter are extremely small compared with the caterpillars taken in summer . . . ." Gibb (1960) conducted an extensive sampling of the stock of invertebrates available to birds in pine plantations in England during the winter. He found that most of the invertebrates were less than 2 mm long. He also found that "In winter, tits spend most of their time feeding; each bird examines some 1100 trees daily, and must find about 5 mg. dry weight of food, or 24 average-sized insects, every minute of the day to maintain itself . . . . In the crucial mid-winter period of November to February, about two-thirds of the foraging activity of all birds present in the pine plantations is concentrated in the living foliage . . . ."

The above studies, while conducted mainly in England with different species of birds and insects from those found in Canada, have been emphasized to point out that the size of food utilized by birds may be markedly different between adults and nestlings and between winter and summer. One should not be too hasty in deciding that insects are unattractive to birds, especially in winter, simply because they are small in size. Availability may well be more important.

Studies of bird predation in North America during the summer are much more

> dees .... Both species descended with lower temperatures and higher wind until at -9.0 [to] 0.0°C and 2.1-3.0 m/sec they were concentrated in a narrow band low in the woods, attending shrubs heavily .... At low temperatures, I watched chickadees and titmice plunge vertically into the depths of the shrub layer with each wind gust, only to rebound upward several meters onto the more exposed small branches of trees during calm intervals.

He repeated a similar series of observations on downy woodpeckers, Carolina chickadees, tufted titmice, and white-breasted nuthatches in a more severe environment in Ohio (Grubb 1977) and obtained similar results. In addition, he noted:

> My findings ... indicate that in only slightly more severe weather conditions the woodlot as a whole would have become an unacceptable foraging area for any of the birds. Indeed, it was vacated by Carolina Chickadees under the most inhospitable conditions recorded (sun occluded, wind velocity 0.1-1.0 m/sec, temperature -20.0 to -29.9°C). I could not penetrate with the necessary stealth the blackberry-hawthorne tangle to the east of the woodlot, but I heard the four species calling there when the woodlot was essentially empty. I suspect that the dense old-field thicket served as a thermal refuge during the most stressful conditions by offering shelter from the wind.

These two studies clearly show that weather changes affect the foraging behavior of overwintering birds. The effects may be even greater in the more severe climate of the boreal forest. Lawrence (1958) studied overwintering populations of black-capped chickadees at Pimisi Bay in central Ontario. She found that the weights of the chickadees gradually increased as the weather turned colder, provided that the birds had an adequate supply of food. There was also a daily cycle in fat accumulation and utilization:

> Increases in weight and fat were brought about chiefly by accelerated feeding. Feeding was markedly intensified during the colder season and on colder days. Two peaks occurred in the feeding activity during the day, one in the morning or forenoon which halted the weight loss incurred during the night and the other in late afternoon when maximum weight and accumulation of fat were achieved before roosting time. When the early morning temperature dropped far below zero (Fahrenheit) the chickadees temporarily lost their ability to adjust to the energy drain of excessively cold weather by an adequate feeding response, but this condition of maladjustment was never known to become so critical as to cause death, except in the case of sick or otherwise impaired birds.

On very cold mornings

> the chickadees ... were conspicuously absent from the feeding-station. Instead they sought sheltered places exposed to the rising sun. Perched on a twig with all feathers fluffed, they sat facing the sun even on days when its rays did not penetrate the clouds. As protection against the north winds they kept behind them rocks, or the rising ground, or the voluminous branches of dense evergreens. On clear days they perched high up in a tree bathing in sunshine. It seemed as if the acquisition of some warmth from this external source of heat was essential before the chickadees could throw all their effort into feeding on these extremely cold mornings. As the sun rose into the sky, they began moving again and the steady acceleration of their feeding activities, imperative for survival, maintained the rise in weight until roosting time.

Perhaps these birds were suffering from hypothermia. Steen (1958) found that the body temperatures of a number of newly captured birds dropped to between 30°C and 38°C (compared to a normal 40°C). "The degree of hypothermia was independent of how low the external temperature was. It should be pointed out that these birds seemed to be in a torpor-like sleep during the cold nights, but that they nevertheless woke up by themselves in the morning." Birds acclimated at -10° C, with plenty of food, were able to maintain normal body temperatures. These experiments were conducted in Oslo, where the mean minimum for January, February, and March was -2° C. Tests were conducted at temperatures ranging from -25° C to +25° C. Since newly caught birds were unable to maintain normal body temperature, while acclimated ones were, Steen believed that "many free living birds are not normally exposed to cold during the night, but rather seek some sort of protective shelter. The nocturnal hypothermia may be regarded as a sort of 'second defence' against abnormally cold weather." Our winter temperatures are often much lower than those in Oslo, and only a limited amount of thermal protection is available in a forest environment. Consequently, the birds observed by Lawrence may have been exposed to temperatures low enough to cause hypothermia, since there is probably a limit to the amount of acclimation possible.

Studying the effect of food on overwintering populations of birds is a major undertaking; however, Gibb (1960) conducted such an experiment and was able to show that "In winter, the birds' density was closely related to their stock of food. Coal tits' survival . . . from October to March was extremely variable and was closely correlated with the stock of food. This confirms that the population of tits was controlled by food shortage; nevertheless their territorial behaviour in autumn was probably also important."

Birds such as chickadees may have some control over the amount of winter food available because they store food if it is abundant. "When food is plentiful, particularly in late summer and fall, the chickadee becomes a food hoarder. Leaving the flock, it carefully tucks a morsel away under a buckled piece of bark, or in a patch of lichens—often only to pull the morsel out again and repeat the tucking-away ceremony in another place." (Lawrence 1973a). Butts (1931) noted hoarding by black-capped chickadees of sunflower seeds collected at a feeder on a warm sunny day in March. The birds would shell the seeds and hide the kernels. Between 10:10 a.m. and 5:00 p.m. it was estimated that one bird had taken between 250 and 300 seeds.

Haftorn (1974) studied the storage of food by boreal chickadees in Alaska:

> On average, the chickadees stored their food at a lower level to that at which they foraged, in fact at a fairly constant height above the ground independent of tree height . . . . All parts of the spruce, in a horizontal plane, were utilized for foraging and storage purposes . . . . A very high proportion of the store points (44%) was located on dead main branches . . . . On live main branches, foraging as well as storage were concentrated on the outer parts; only 12% of all store points recorded were situated on the inner parts and the trunks . . . . Only seeds were observed to be hidden on the trunk itself, whilst insects were always placed on the branches.

Most of the storage, even on live branches, was under dead bark, presumably because this provided numerous crevices suitable for storage of food items, which were surprisingly well anchored. One clump of eight aphids, stored in 1959, was still in place 15 years later, but

> The extent to which the Boreal Chickadee may be dependent on stored food during the winter is an open question. It is noteworthy, however, that all the food stored was hidden at various heights in trees, but very seldom in actual tree tops. This distribution of stored food, combined with the birds' manner of hiding the food in such a way on the branches that it can best be seen from below, or is most accessible from below, increases the birds' chances of finding the food in winter when snow covers the tree tops, the upper parts of the branches (especially their extremities), and the forest floor.

Bock and Lepthien (1972) noted that there was perfect agreement between years in which there was a cone crop failure in Maine and years in which a fall migration of black-capped chickadees was noted in southern Ontario. Svärdson (1957) suggested that just the opposite may also occur: unusually abundant food supplies in an area may result in an invasion type of bird migration. Birds that would normally migrate through an area do not do so, because the abundant food supply brings the flight to a stop.

White spruce seeds are not available in the cones during the winter. Waldron (1965) showed that for white spruce in Riding Mountain National Park "Seed fall generally began in early August with peak seedfall occurring in late August or early September. However, in several years below average air temperatures and sunshine and above average precipitation delayed peak seedfall until late September. Early- and late-falling seed was not as sound as that which fell during the period of peak seedfall." If chickadees are dependent upon seeds for winter survival, it must mean that they have stored enough of them to meet their needs, since very few seeds would remain in the cones during the winter. Gibb (1960) referred to Haftorn's work in Norway, which estimated "that up to about 60% of the food of Crested Tits *Parus cristatus* in midwinter consisted of spruce seeds that the birds must have stored the previous autumn." If one adds to this the insect material that has also been stored, it is readily apparent that hoarding could be an important element in winter survival of chickadees.

In the summer, food usually appears to be at least reasonably abundant for insectivorous birds, so that it is difficult to demonstrate that it is a factor in limiting the size of bird populations. MacArthur (1958) believed that such was the case, however, for bay-breasted and Cape May warblers. Both of these species become very abundant during outbreaks of the spruce budworm in Maine but are not common between outbreaks. MacArthur interpreted this to mean that food was a limiting factor in determining the size of population for these two species. Kendeigh (1947) also noted that birds were found less frequently in stands of black spruce than in stands of balsam fir or white spruce. He suggested that "There is no reason to believe that differences in abundance of birds on the plots were determined by available nest-sites, cover, song posts or other less tangible features. It is likely, however, that they are to be explained by differences in the abundance of the insect food supply." As an example, he cited budworm population figures of 9.5, 6.1, and 3.4 larvae per sample from unsprayed balsam fir, white spruce, and black spruce, respectively.

Competition between birds is mainly for territory and food. Many species of birds have territories during the breeding season that are of a more or less typical size for each species. Kendeigh (1947) noted that "many species do not have territories of a rigid invariable size; on the contrary, when populations are high the territories may be compressed at least down to a certain minimum. An irreducible minimum compatible with successful reproduction would seem necessary for each species, and there can be little question but that wherever attained it will limit the breeding population." Territories are usually maintained during the breeding season only and are defended only against others of the same species. During the winter some resident birds, such as black-capped chickadees, maintain a territory in which the flock does most of its feeding (Glaze 1973; Hartzler 1970). It was noted that excursions into the territories of other flocks frequently occurred, but the resident birds were dominant only while in their own territory.

Intraspecific competition for food has been demonstrated by MacLellan (1959) in his studies of winter predation of the codling moth in Nova Scotia. Watt's (1959) attack model gave a straight-line relationship when plotted against the natural logarithms of the numbers of woodpeckers, which never exceeded four per location. If MacLellan's estimate of 50 larvae per 1.8 m of trunk is a valid maximum for the number of prey that one woodpecker can take per season, then this relationship shows that competition can be a major factor, even when the numbers of birds are not large.

Competition between species may not be as great as one might imagine, because of the different requirements for each species. Willson (1970) studied the foraging behavior of some winter birds in deciduous woods: "In winter the White-breasted Nuthatch and Red-bellied Woodpeckers used large live branches especially; Brown Creepers and female Downy Woodpeckers selected primarily trunks; Red-headed Woodpeckers . . . concentrated on large dead branches; and male downies used a diversity of sites almost equally .... Vertical distribution of foraging in winter found both male and female downies in the low ranges, Brown Creepers and nuthatches in the low and middle heights, and red-bellies and red-heads in the upper story of the woods."

MacArthur (1958) found that, even for closely related species such as different warblers, "There are differences of feeding position, behavior, and nesting date which reduce competition. These, combined with slight differences in habitat preference and perhaps a tendency for territoriality to have a stronger regulating effect upon the same species than upon others, permits the coexistence of the species." Similarly, the preferred habitat of the black-capped chickadee is open deciduous woods, while that of the boreal chickadee is moist coniferous forest (Lack 1971; Smith 1967). This not only reduces competition, but helps to maintain ecological isolation in closely related species.

Several workers have also shown that there are differences in the feeding sites utilized by different sexes of the same species. Jackson (1970) and Willson (1970) found that male downy woodpeckers tended to forage on small branches, while the females tended to forage on the trunk and larger limbs. Jackson also found that mean foraging heights of males was significantly lower on live trees than on dead trees, while the females showed no such difference. Travis (1977) found that downy woodpeckers moved at random from tree to tree. He also observed that the birds preferred rough-barked trees in winter but not in summer and that the birds tended to forage on larger trees during the winter.

Black-capped chickadees band together in small flocks for the winter. Glaze (1973) found that most flocks consisted of six or seven birds, although flock sizes ranged from four to nine. "For birds whose sex had been determined on the basis of breeding behavior, males always dominated females .... Of the birds classified as males, adults always dominate juveniles." Adult females usually dominated juvenile females. Also, "The adult males that had bred within the flock's winter range were always the most dominant birds in the flock. The previous mates of these males were always the most dominant females. If more than two pairs had bred within the flock's winter range . . . the pair with the largest and most centrally located breeding territory, relative to the winter range, became the most dominant individuals within their sex class in the flock." Hartzler (1970) termed within-flock relationships as peck-right dominance, but he felt that inter-flock relationships were better characterized as peck-dominant.

These dominance relationships affect foraging sites for different sexes and age classes (Glaze 1973):

> In summary, juvenile males differ from adult males only in their greater use of trunks as foraging sites. Adult females, although they forage at about the same height as males, differ from them in all other parameters considered, feeding in significantly shorter trees, on fewer trunks, and more frequently on smaller branches in the outer canopy. Juvenile females differ most: they differ significantly in all five foraging parameters compared to adult and juvenile males, and in four parameters compared to females. Thus, juvenile females forage in smaller trees, feed lower within these trees, forage infrequently on trunks, and spend more time foraging on smaller branches in the outer canopy of the tree.

Glaze concluded that

> Inter-sexual foraging differences, I believe, result from the passive exclusion of the subordinate birds from the better foraging sites by the more dominant individuals. This system should allow adults of both sexes, particularly in the previous breeding pairs, the greatest chance of surviving periods of low food availability.

This somewhat lengthy review should suffice as background on the potential influence of bird predation on the dynamics of forest defoliators. Before discussing individual insect species, two more aspects of bird populations need consideration: 1) populations in different forest types; and 2) variability of populations between years.

Estimates of breeding-bird populations in the boreal forests of central Canada are very limited. Kendeigh (1947) conducted a breeding-bird census in a spruce-fir forest near Black Sturgeon Lake in Ontario in 1945 during a spruce budworm outbreak. Sanders (1970) conducted surveys in spruce-fir forests in the same general area in 1966, 1967, and 1968 during the endemic phase of the budworm cycle. Kendeigh found a density of 319 pairs per 40 hectares, compared to the 123 that Sanders found. Kendeigh attributed the high populations to increases in the numbers of bay-breasted, Cape May, and Tennessee warblers; these species were virtually absent when Sanders conducted his survey.

Although generalized accounts have been written on birds in forested areas of Saskatchewan (Houston and Street 1959; Nero and Lein 1971), there were no breeding-bird censuses for the forested areas of Manitoba and Saskatchewan until Erskine (and others) published a series of reports on bird populations in a number of forest habitats (Table 6). While very few of these surveys were conducted in the same stands in consecutive years, they nevertheless give an excellent cross section of bird populations in the different habitats. Open bog habitats had very few bird species and low populations, as did jack pine stands and the one white spruce bottomland that was surveyed. Black spruce and tamarack stands had a fair number of species and slightly higher populations. The two highest populations, with good species representation, were in an aspen stand and in a disturbed fir-spruce stand. These results tend to indicate that bird populations are potential control agents for insect populations in all but open bogs and jack pine stands. There were probably very few insects in these habitats, and this may have been the reason for the low bird populations.

The potential effectiveness of birds as predators of forest insects will be seriously affected if bird populations fluctuate wildly from year to year. Kendeigh (1944) showed that there was a relatively constant bird population on an estate in Ohio for a 15-year period. The number of nests per year on the 15-acre estate ranged from a low of 94 to a high of 181. Kendeigh also studied the number of breeding pairs in a 55-acre wood area in Illinois. Bird populations in this area showed a gradual increase from 60 to 150 pairs over a 15-year period. Part of this increase could have been due to an improvement in the nesting habitat, since the area had been protected from grazing for a number of years. Goodwin and Jarvis (1964) presented data that showed that both the number of species and number of territorial males in a tamarack swamp in Ontario remained relatively stable during a 6-year period. Wiens (1975), however, reviewed over 130 breeding censuses in various coniferous forest habitats in North America and concluded that there were substantial annual variations in avian density and biomass in most regions. It may be significant that these variations were smallest in the northern region, which includes the area under study here.

The only continuous breeding-bird records for the period and area dealt with in this study were those obtained by Ives *et al.* (1968) in tamarack bogs in southeastern Manitoba during the larch sawfly population dynamics study (Table 7). The quality of these data varies and does not always meet the standards required by the Audubon breeding-bird census (Hall 1964), but the data should be adequate to show general trends. The average number of species is very similar to that observed by Goodwin and Jarvis (1964), but the mean number of males is slightly higher. There does, however, appear to be greater variation in the present data. On average, there were large numbers of species and high populations in all plots in 1962 and 1968, while both values were much lower in all bogs in 1966. There were also differences between plots in the mean numbers of species and in the mean numbers of territorial males. Part of these differences in bird populations was probably due to stand differences, but the largest variations in both species composition and population levels occurred between years within the same plots.

The only additional bird data that could be found that had any relevance to the present study were the Saskatchewan Christ-

Table 6. Breeding bird censuses in various forest types

Type of forest	Location	No. species	No. males[1]	Reference
Shrubby marsh	South of Dawson Bay, Manitoba	13	211	Erskine 1972e
Willow-alluvial deposit	Near Clayhurst, B.C.	9	59	Erskine 1974c
Tamarack bog (wet and open)	Near Lac Larder, Quebec	8	15	Erskine 1970e
Tamarack swamp	York County, Ontario	20	190	Goodwin and Jarvis 1964
Black spruce bog (wet and open)	Near Senneterre, Quebec	9	26	Erskine 1970f
Stunted black spruce (raised bog)	Near Mile 339, Alaska Highway, B.C.	7	14	Erskine 1974f
Black spruce	Near Val D'Or, Quebec	14	82	Erskine 1970d
Black spruce	Cochrane District, Ontario	15	94	Erskine 1971b
Black spruce	Near Mafeking, Manitoba	16	71	Erskine 1972b
Black spruce with alder	Near Doré Lake, Saskatchewan	19	86	Erskine 1973d
Black spruce on mountain side	Near Mile 346, Alaska Highway, B.C.	12	52	Erskine 1974d
Balsam fir	South of Dawson Bay, Manitoba	20	112	Erskine 1972d
Balsam fir	Near Doré Lake, Saskatchewan	19	145	Erskine 1973c
Disturbed fir-spruce	Near Duparquet, Quebec	27	177	Erskine 1970c
Disturbed fir-spruce	Near Duparquet, Quebec	26	226	Erskine 1971d
White spruce bottomland	Near Mile 336, Alaska Highway, B.C.	10	43	Erskine 1974e
Mixed jack pine	Near Senneferre, Quebec	13	34	Erskine 1970b
Mature jack pine	Cochrane District, Ontario	11	35	Erskine 1971c
Jack pine	Near Mafeking, Manitoba	12	41	Erskine 1972c
Young aspen	Near Doré Lake, Saskatchewan	10	91	Erskine 1973b
Aspen	Rainy River District, Ontario	26	366	Price and Speirs 1971
Mature poplar	Cochrane District, Ontario	20	138	Erskine 1970a
Mature poplar	Cochrane District, Ontario	23	145	Erskine 1971a
Mature poplar	Near Mafeking, Manitoba	15	211	Erskine 1972a
Mature birch and poplar	Near Doré Lake, Saskatchewan	12	157	Erskine 1973a
Mature aspen	Near Mile 320, Alaska Highway, B.C.	13	63	Erskine 1974b
Balsam poplar bottomland	Near Mile 335, Alaska Highway, B.C.	24	86	Erskine 1974a

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[1] Number of territorial males per 40 hectares.

Table 7. Number of species and number of territorial male birds per 40 hectares in four tamarack bogs containing larch sawfly plots. Summarized from Appendixes 5-8.

	Telford		Rennie		Seddon's Corner		Pine Falls		Average for year	
Year	No. species	No. males	No. species	No. males	No. species	No. males	No. species	No. males	No. species	No. males
1954	-[1]	447	-	-	-	-	-	-	-	-
1956	-	340	-	-	-	-	-	-	-	-
1957	-	315	36	497	-	-	-	-	-	-
1958	-	324	19	277	-	-	-	-	-	-
1959	-	290	21	279	-	-	-	-	-	-
1960	-	325	21	207	-	-	-	-	-	-
1961	17	347	19	376	13	162	15	130	16.0	253.8
1962	30	337	25	362	20	265	38	279	28.2	310.8
1963	19	196	19	193	20	139	23	191	20.2	179.8
1964	16	161	28	274	12	78	31	234	21.8	186.8
1965	-	-	-	-	14	100	-	-	-	-
1966	14	99	17	222	15	113	22	142	17.0	144.0
1967	20	277	26	309	12	82	19	129	19.2	199.2
1968	26	228	32	342	22	280	26	231	26.5	270.2
Averages[2]	20.3	235.0	23.7	296.9	16.3	159.9	24.9	190.9	21.3	220.7

[1] Data not collected or averages not calculated.

[2] Plot averages for 1961 to 1968, excluding 1965.

mas Bird Counts (Anonymous 1943-1977). Renaud and Wapple (1977) have already reviewed these data and have clearly shown that the only insectivorous forest-inhabiting birds of any consequence are the hairy woodpecker, downy woodpecker, black-capped chickadee, and boreal chickadee. The brown creeper, red-breasted nuthatch, and white-breasted nuthatch occur but are rather uncommon. In another paper, Renaud (1979) discussed the effect of vegetation on early-winter bird distribution. He concluded that the black-capped chickadee is a very common species except in the shortgrass prairie and northern coniferous forest. The boreal chickadee was much less common, even in the northern coniferous forest. Hairy and downy woodpeckers are quite common in all forested areas. This agrees with the general results given for the United States by Bock and Lepthien (1975). Both of these species were primarily northern birds, although the downy woodpecker's winter range extended further south than the hairy woodpecker's.

Christmas bird counts have a number of weaknesses that have been discussed by Preston (1958). They are only pseudoquantitative, as the numbers observed are usually based on varying periods of observation by differing numbers of people. Part of this variability can be removed by expressing the counts as numbers per party-hour (Bock and Lepthien 1975; Bock and Smith 1971). This still leaves the nagging question of whether 10 observers in one party will record more birds than one or two, but there seems to be little that can be done in this regard.

Only a relatively small number of the observations were applicable to the present study. These were the ones that were made in (or adjacent to) the Hudson Bay area or the Prince Albert area, as delineated in Fig. 1. Counts for black-capped and boreal chickadees and for downy and hairy woodpeckers are summarized in Table 8. The black-capped chickadee is by far the most common species, particularly in the Hudson Bay area, although there are large variations from year to year in the numbers observed. Whether those variations are related to changes in insect populations will be discussed in the following paragraphs.

Because information regarding bird predation on the insect species discussed here is very limited for most species, the species will only be listed if relevant data or references are available.

Malacosoma disstria

Witter and Kulman (1972b) in their review of the parasites and predators of the genus *Malacosoma* listed 60 species of birds that have been recorded as predators of tent caterpillars. McAtee (1926) reported that birds were responsible for local extirpation of the eastern tent caterpillar, *Malacosoma americanum* (Fabricius)[65], and cited an instance when birds were believed responsible for removal of most of the surviving larvae of *M. disstria* following a cold spell. Generally speaking, however, birds do not seem to be a major factor in the dynamics of *M. disstria* populations. Probably the limited bird populations would have little impact on the vast number of larvae present during an outbreak, even if they were a favorite food. Most birds apparently dislike the large hairy larvae (Root 1966) and eat mainly the smaller ones (Witter and Kulman 1972b), probably even actively seeking them out later in the season (Fashingbauer *et al.* 1957). A few species, such as Baltimore orioles, will eat larvae readily, and yellow-billed and black-billed cuckoos are apparently very fond of tent caterpillar larvae (McAtee 1926). The yellow-billed cuckoo is rare in Manitoba and Saskatchewan, and the breeding range of the black-billed cuckoo is restricted to the southern parts of the two provinces (Salt and Salt 1976). Consequently, both of these species are probably of minor importance as larval predators of *M. disstria* in the forested areas of those provinces.

Several species of birds have been reported eating *M. disstria* pupae (Fashingbauer *et al.* 1957; Hodson 1941), but there is no evidence that this predation is important. Adults and their eggs have been reported eaten by chickadees (Pearson 1936) but the

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[65] Lepidoptera: Lasiocampidae.

Table 8. Christmas bird counts for four species of birds in the Hudson Bay and Prince Albert areas of Saskatchewan, expressed as number of birds per 100 party hours

	Hudson Bay area				Prince Albert area			
Year[1]	Black-capped chickadee	Boreal chickadee	Downy woodpecker	Hairy woodpecker	Black-capped chickadee	Boreal chickadee	Downy woodpecker	Hairy woodpecker
1945	133	36	30	30	86	38	32	11
1946	108	4	27	23	23	23	11	57
1947	50	0	29	8	36	23	4	9
1948	91	0	42	30	122	17	13	9
1949	152	0	32	23	92	0	0	15
1950	110	0	32	19	40	0	0	20
1951	67	10	15	22	128	72	14	43
1952	198	27	18	19	87	9	23	28
1953	453	2	32	17	162	23	46	15
1954	180	9	19	21	136	5	39	34
1955	185	0	34	32	76	0	5	5
1956	188	8	18	15	54	4	10	11
1957	160	0	21	22	130	10	4	12
1958	206	8	24	20	150	13	11	13
1959	223	4	19	16	165	22	0	0
1960	406	0	50	33	87	43	11	2
1961	476	0	38	48	61	0	7	0
1962	320	4	52	68	62	0	14	10
1963	600	20	90	60	126	0	18	8
1964	379	0	76	76	91	4	15	11
1965	550	0	83	50	58	10	10	13
1966	314	0	49	45	132	2	18	11
1967	238	0	52	62	110	9	10	12
1968	116	4	24	12	108	3	16	21
1969	177	0	35	27	77	0	10	16

[1] The data for 1945 to 1950 are tenuous, as some rather broad assumptions had to be made to obtain the number of party-hours in some cases.

wording implies that the eggs were ingested with the moths.

Christmas counts of woodpeckers and chickadees during increasing and decreasing phases of *M. disstria* infestations in the Hudson Bay and Prince Albert areas showed no differences in chickadee populations (Table 9). It may be significant, however, that woodpecker populations were higher in both areas during the declining phase of *M. disstria.* No reference to woodpeckers eating tent caterpillar eggs could be found in the literature, but the small size of the downy woodpecker (the more abundant species) would probably enable it to forage on the smaller twigs where the tent caterpillar eggs are laid.

Choristoneura conflictana

Very little information on bird predation of this insect could be found in the literature. Criddle (1918) observed several species of birds feeding on *C. conflictana* during an outbreak in southwestern Manitoba. No assessment of the amount of predation was made, but probably only a small fraction of the large number of insects present could have been eaten by the birds.

During the winter, the hibernating larvae of *C. conflictana* may be vulnerable to predation by overwintering birds. How many larvae can be found by the birds, especially chickadees, is difficult to say; however, the numbers of chickadees were higher in both areas during the declining phase of *C. conflictana* than they were during its increase (Table 9). There is therefore at least the possibility that chickadees are a factor in the population dynamics of *C. conflictana.*

Choristoneura fumiferana

Tothill (1923) recognized that birds can be an important factor in controlling spruce budworm where the host trees occur in patches. He also recognized that birds are incapable of controlling populations that have reached outbreak proportions over wide areas. Graham and Orr (1940) referred to two decimations of insectivorous birds, one in 1907 and the other in 1910. In the spring of each of these years unseasonably warm weather was followed by a freezing period with ice and snow. These cold periods came during the warbler migration, and populations of blackburnian and chestnut-sided warblers were severely decimated. "We know that these birds are among the more important species . . . . This circumstantial evidence indicates the possibility that the 1912 outbreak was precipitated by a scarcity of small insectivorous birds." Graham and Orr recognized that birds cannot control budworm once it reaches outbreak proportions, but they pointed out that birds have the potential for controlling populations between outbreaks.

Several workers have attempted to estimate the amount of avian predation upon spruce budworm. Dowden *et al.* (1953) believed that bird predation contributed to the decline of a budworm infestation in Maine. Morris (1949) estimated that larval and pupal mortality attributable to predation by birds, insects and spiders, plus other factors amounted to 76%. Although a large number of birds eat spruce budworm larvae and pupae (Hope 1949; Mitchell 1952), the amount of bird predation during the spring and early summer is usually much lower than this. George and Mitchell (1948) estimated predation to be between 3.5% and 7%, Kendeigh (1947) gave a figure of 4.3%, and Morris *et al.* (1958) and Miller (1975) estimated bird predation during an outbreak to be less than 1%. Morris (1963b) indicated that functional response (implicitly recognized by Tothill (1923)) can be important when considering bird predation. This was probably most dramatically illustrated by the response of evening grosbeaks to budworm populations (Blais and Parks 1964; Blais and Price 1965). It appeared that large numbers of the birds were attracted to outbreak areas during their spring migration.

Winter predation of spruce budworm by birds is difficult to assess because the larvae are so small. Dowden and Carolin (1950) found that overwintering mortality due to unknown factors, including birds, ranged from 55% to 86% in 1947 and from 6% to 85% in 1948. Miller (1958) obtained estimates of mortality due to bird predation and sloughing of hibernaculae ranging from 11% to 22%. Jaynes and Drooz (1952) conducted some exclusion cage studies and obtained estimates of bird predation of

Table 9. **Christmas bird count mean number of chickadees and woodpeckers in the Hudson Bay and Prince Albert areas of Saskatchewan during increasing and decreasing phases of our forest insects between 1945 and 1968**

Insect species	Insect phase	Hudson Bay area Chickadees	Hudson Bay area Woodpeckers	Prince Albert area Chickadees	Prince Albert area Woodpeckers
Malacosoma disstria	Increasing	373	79	142	20
	Decreasing	350	136	110	40
Choristoneura conflictana	Increasing	176	65	131	31
	Decreasing	287	47	143	21
Choristoneura pinus pinus	Increasing	-	-	110	26
	Decreasing	-	-	115	25
Choristoneura fumiferana	Increasing	319	75	-	-
	Decreasing	254	69	-	-

Table 10. **Mean percentage total parasitism for nine host species in generation n in relation to changes in these host populations between generations n and n + 1 between 1945 and 1968**

Host species	Increasing host populations Percentage parasitism	Increasing host populations Number of observations	Decreasing host populations Percentage parasitism	Decreasing host populations Number of observations
Malacosoma disstria	39.8	8	49.7	14
Choristoneura conflictana	50.0	11	60.5	11
Choristoneura fumiferana	23.3	6	26.6	11
Neodiprion abietis complex	9.4	13	14.6	16
Acleris variana	23.9	8	33.0	4
Choristoneura pinus pinus	19.0	9	31.3	13
Neodiprion nanulus nanulus	9.0	7	10.1	11
Neodiprion virginianus complex	16.7	7	23.0	9
Pristiphora erichsonii	44.2	16	44.5	30

11.6% and 3.9% for the winters of 1949-50 and 1950-51, respectively.

In the present study, there was no relationship between chickadee populations and population trends for *C. fumiferana* in the Hudson Bay area (Table 9). This may be due to the foraging preference of black-capped chickadees, the principal species, for deciduous trees in their search for food.

Acleris variana

Morris (1959) recognized that bird predation was a factor in the dynamics of *A. variana* populations, but he treated it as a constant. Gage *et al.* (1970) found it to vary from 3% to 14% over a 3-year period and found evidence to strongly suggest that the birds acted in a density-dependent manner. McNamee (1979) carried analyses a step further and constructed a process model that predicts that

> At low population densities, bird predation acts to keep the defoliator at endemic levels and removal of bird predation causes budworm populations to move toward the upper stable equilibrium .... Therefore, an experiment in a chronically endemic area in which the birds were taken out and kept out of a stand of balsam fir for a number of consecutive years should result in a localized population increase of the budworm.

This is an interesting idea but would probably be impractical. Birds from the surrounding area likely would continue to move into the stand.

Choristoneura pinus pinus

Mattson *et al.* (1968) studied vertebrate predation of the jack pine budworm in Michigan. They found that jack pine stands were rather sparsely populated by birds, which agrees with results of surveys conducted in Canada (Erskine 1970b, 1971c, 1972c). They also found that icterids were the most voracious predators, followed by fringillids. One of the study areas contained only about 240 hectares of jack pine and was easily accessible to birds in adjacent and nearby communities. The center of the stand was no further than 1.6 km from at least five marsh communities and was even closer to other kinds of environments. Consequently, there was a large influx of bird predators from these places.

> We estimated that in 1965, resident and about 150 nonresident birds killed approximately 40-45% of the late-instar larvae and pupae. In 1966, with the same jack-pine budworm population level, the resident birds and about 700 nonresidents killed approximately 60-65% of the late-instar larvae and pupae .... Gizzard analyses of the nonresident species ... indicated that there were no significant differences among their budworm consumption rates from 1965 to 1966 .... The difference in mortality, then, was definitely the result of a larger influx of nonresident predators in 1966 than in 1965 .... In summary, bird predation will not likely be a variable mortality factor in large forests where budworm populations are above the endemic level. In small forests, on the other hand, bird predation has greater potential to be variable even when budworm populations are moderately high, because nonresident birds can move into the jack pine communities to feed and thereby add to the mortality caused by residents. Hence, there is a greater possibility that bird predation will be a key mortality factor in a small jack pine forest than in a large one.

In the present study, there was no indication that overwintering populations of either chickadees or woodpeckers had any relationship to population changes of *C. pinus pinus* in the Prince Albert area (Table 9).

Neodiprion nanulus nanulus and *Neodiprion virginianus* complex

Schedl (1938) considered that predation by birds was the most important larval mortality factor affecting these sawflies in Ontario. Total predation of *Neodiprion nanulus nanulus* larvae (mostly by birds) amounted to 95%, expressed as a percentage of the original number of eggs. The corresponding value for *N. virginianus* complex was 67%.

Pristiphora erichsonii

Buckner and Turnock (1965) studied avian predation of the larch sawfly. They found that

> Forty-three of the 54 species of birds collected in or near tamarack bogs were predators of the larch sawfly .... Some species popularly regarded as vegetarian (viz. sparrows) proved to prey heavily upon sawflies. The warblers, popularly regarded as important insect predators, were clearly of less importance as predators of the larch sawfly than the fringillids. A preference was indicated by many bird species for adult sawflies, even when they were relatively rarer than larvae. Larger then smaller larvae followed in order of preference .... Positive functional responses were indicated at low to high prey densities for 22 predators .... Numerical responses were suggested for all except those of sporadic occurrence. Nonresident species were prominent in the plot with a high prey density. Birds are likely to influence sawfly population trends at low insect densities, and perhaps at higher densities as well.

In the present study, populations of both warblers and sparrows in the two wet plots (Telford and Seddon's Corner) were higher in the declining phase of the larch sawfly than in the increasing phase (Table 5). These two plots also tended to have the lowest sawfly populations and, according to the results of Buckner and Turnock (1965), should be the areas in which bird predation could be important.

Semiothisa sexmaculata

Warblers may have been a factor in the dynamics of this species, since populations were higher in the declining phase in three of the four plots (Table 5). Sparrows could have been a factor in the Rennie plot. The development of this insect species is midway between the following two, so some of the larvae would be available during the nesting period. In addition, it is a lepidopterous insect in an environment dominated by sawflies, so it could be a preferred food for many of the birds.

Anoplonyx canadensis

Warblers and sparrows may have been a factor in the dynamics of this insect in the Telford plot, while warblers could have been a factor in the Pine Falls plot (Table 5). Perhaps this insect develops too late in the season to be attractive to nesting birds.

Anoplonyx luteipes

This insect develops earlier than the preceding two species and appears to be influenced by bird predation, since the highest warbler populations occurred during the declining phase of the insect populations in three of the four plots, and sparrow populations were highest during this phase in two of the four plots (Table 5).

PARASITES AND INVERTEBRATE PREDATORS

Parasites (or more correctly, parasitoids) and invertebrate predators will be discussed together, since there is very little detailed information on the effects of invertebrate predators upon the insect species dealt with in this report. Furthermore, the distinction between the two groups is rather subtle. Parasite adults usually deposit one or more eggs (or sometimes larvae) in, on, or near the host species eggs, larvae, or pupae, one of which provides enough food for the development of the parasite larva (or larvae, in the case of multiple parasitism). The parasite larvae usually do not kill the host until their own larval development is complete, but some do and feed upon the putrefying remains of the host. Invertebrate predators, on the other hand, require a series of hosts in order to complete their development, since they kill their host at each meal.

Because parasites and invertebrate predators are among the density-dependent factors in classical population dynamics theory, the controversy in this field extends into most discussions on the effects of parasites. In addition, there is the added problem of demonstrating density dependence between hosts and parasites under field conditions. Varley and Gradwell (1971) favored Nicholson's theories on population dynamics, yet after extensive field experience stated:

> We know of no field measurements of host density and percentage parasitism for a reasonably long series of successive generations which shows parasitism to act as a density-dependent factor. The

> **undoubted ability of parasites to regulate or control the density of the host arises in other ways.**

There are a number of reasons why this occurs. Some parasites are exposed to different mortality factors than are the host species, at least during part of the life cycle. For example, *Sarcophaga aldrichi*, a parasite of *Malacosoma disstria*, overwinters as a puparium in the duff on the forest floor, whereas its host overwinters as a pharate larva in the egg bands surrounding the aspen twigs. Other parasites, although they may overwinter in the same area as the host, may be more (or less) vulnerable to mortality factors. An example of this is *Bessa harveyi*, an internal dipterous parasite of *Pristiphora erichsonii.* Sawfly larvae parasitized by this insect are more susceptible to the adverse effects of excess moisture than are unparasitized larvae, presumably because of the greater oxygen requirement of the parasitized larvae. Alternatively, the parasite may be partially or totally multivoltine, and its host may be univoltine. In this case, the second generation of the parasites must find alternate hosts in order to survive, and the numbers of these hosts will partly or totally determine the size of the overwintering parasite population. *B. harveyi* has a partial second generation, and most of these die without leaving progeny. Alternate hosts are usually not abundant, and the few *P. erichsonii* larvae remaining on the trees late in the season become so heavily parasitized by *B. harveyi* that few, if any, of the parasites develop to maturity. Finally, yet another factor affecting the relationship between host and parasite is the mutual interference between the parasites, which decreases their relative effectiveness as the parasite density increases (Hassell and Varley 1969).

Demonstration of density relationships under field conditions requires special effort and suitable techniques (DeBach and Huffaker 1971; DeBach *et al.* 1976). Many biological control studies lacked any detailed follow-up. Nevertheless, there can be no argument that parasites and invertebrate predators have a bearing on host insect numbers, as the numbers of successes and partial successes in biological control will attest. Worldwide biological control attempts have been thoroughly reviewed by DeBach (1964, 1971, 1974) and Canadian attempts have been discussed elsewhere (Anonymous 1962, 1971), so there is no need to go into detail here. Huffaker *et al.* (1976) considered that 102 biological control attempts for insects were completely successful and that another 144 attempts gave substantial success.

Many of the successes in biological control have been in warm climates. DeBach (1971) showed that the percentages of complete success among biological control attempts in tropical, subtropical, temperate-subtropical, and temperate climates were 60, 45, 33, and 24, respectively. Among pests of coniferous trees, Turnock *et al.* (1976) considered 3 of 10 major biological control attempts to be completely successful, while several others gave at least partial control. Waters *et al.* (1976) believed introductions against 10 species attacking broad-leaved trees to be at least partially successful.

Embree (1971) studied winter moth, *Operophtera brumata* Linnaeus[66], populations in Nova Scotia before and after the introduction of a tachinid and an ichneumonid. The two parasites appeared to complement one another: the number of ichneumonid attacks increased with increasing numbers of host larvae per cluster for small clusters and then levelled off, while the number of tachinid attacks increased when the cluster size became larger. It appeared that the joint action of the two parasites should control the winter moth in Nova Scotia, although the appearance of a virus disease has made interpretation of the roles of the parasites more difficult.

A further indication of the usefulness of parasites and invertebrate predators (if one is needed) is provided by the fact that many insects and mites that were formerly innocuous have become serious pests following the extensive use of insecticides. DeBach (1974)

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[66] Lepidoptera: Geometridae.

cited a number of examples that clearly show the buildup of pest populations on insecticide-treated plots.

Limited data on total parasitism for each of a number of host species have been collected during this study and are shown graphically in Figs. 2-8. (Numerical values are listed in Appendix 1). Some data are too fragmentary to be useful, but enough data were available for nine host species to indicate trends, and these are shown in Table 10 for increasing and decreasing host populations. Discussion will be limited to the species listed in the table and to a few species for which pertinent references were found.

Malacosoma disstria

Papers dealing with the parasites and predators of the genus *Malacosoma* have been thoroughly reviewed by Witter and Kulman (1972b) and will not be considered in detail here. Witter and Kulman (1979) reported rearing 41 species of insects from the eggs, larvae, and pupae of *M. disstria*; however, six species of Diptera were scavengers and six species of Hymenoptera were hyperparasites, reducing the total number of primary parasites to 29 species. In addition, Witter and Kulman (1972b) listed 66 species of invertebrate predators. In most cases their relative importance does not appear to have been evaluated, although Green and Sullivan (1950) and Ayre and Hitchon (1968) have shown that various species of ants are capable of destroying large numbers of small tent caterpillar larvae. In New Brunswick, Tothill (1918) estimated that ants destroyed 75% of the second- to fourth-instar larvae during an outbreak of the forest tent caterpillar in 1913.

Sarcophaga aldrichi is the most common pupal parasite of *M. disstria* and is especially prevalent in older infestations. Early entomologists considered this insect to be a saprophyte that attacked only dead or diseased larvae; however, Hodson (1939) showed that it was a true parasite. It kills the host larva or pupa in the cocoon and feeds in the putrefying remains, which creates the impression of being a saprophyte. Because it kills the host early in its own development, it also kills any other parasites that may be present, thus decreasing their numbers. Hodson (1939) referred to the extreme abundance of the adult flies under certain conditions. Witter *et al.* (1972) attributed low generation survival of *M. disstria* to high pharate larval mortality and parasitism by *S. aldrichi*. Hodson (1977) estimated pupal parasitism to be about 98% following severe starvation among the larvae. Similarly, Witter and Kulman (1979) found that parasitism of late cocoon collections by *S. aldrichi* and tachinids usually exceeded 98%.

Most estimates of parasitism in the present study (Figs. 2-8) were somewhat lower than this, although there appeared to be an increase in percentage parasitism as the age of the outbreak increased. When the samples were sorted on the basis of being collected from increasing or decreasing host populations, it was found that parasitism was about 10% higher for the decreasing populations (Table 10).

Choristoneura conflictana

The large aspen tortrix is attacked by a large number of parasites. Prentice (1955) listed 20 species of parasites and two hyperparasites recovered from rearings of *C. conflictana* collected in Manitoba and Saskatchewan and another 13 species reared from collections made elsewhere. Torgersen and Beckwith (1974) listed 24 species recovered from *C. conflictana* in interior Alaska and produced a key to aid in their identification. Wong (1979) listed three additional species not given by Prentice (1955), although two of the species had been recovered by Torgersen and Beckwith (1974) in Alaska. None of the above papers give an evaluation of the parasite's effectiveness.

Beckwith (1968) studied the parasitism of *C. conflictana* in interior Alaska and found that several species of parasites caused reductions in host populations. Egg parasites killed about 15% of the eggs, tachinids destroyed about 50% of the larvae, and hymenopterous parasites caused up to 22% pupal mortality.

In the present study there was about a 10% difference in the rate of parasitism in samples collected from increasing populations and from decreasing populations (Table 10).

Chrysomela crotchi

Very little information could be found on the parasites or invertebrate predators attacking this species. Elliot and Wong (1966) thought that the main cause of the collapse of a 187 000-km^2 outbreak of *C. crotchi* in Manitoba and Saskatchewan was syrphid predation on the eggs and larvae of the beetle. They found that 963 out of a total of 1000 egg masses had been totally or partially destroyed by the syrphid.

Neel *et al.* (1976) found that a pteromalid wasp and a tachinid parasitized the closely related *C. scripta*. They also found coccinellids and pentatomids to be common predators but believed a species of coccinellid to be the most important.

Orthosia hibisci

Raizenne (1952) reared four species of hymenopterous parasites from *O. hibisci* larvae collected in southern Ontario. Rings (1970) reared two additional species of hymenopterous parasites from larvae collected in Ohio and referred to another paper listing two species of tachinids parasitic on *O. hibisci*. No data on the impact of these parasites could be found.

Sciaphila duplex

Raizenne (1952) reared eight species of hymenopterous parasites from *S. duplex* collected in southern Ontario. McGregor (1967) reared 12 species of hymenopterous parasites and three species of dipterous parasites from larvae collected during an outbreak of *S. duplex* in Utah, western Wyoming, and southeastern Idaho. In addition, ants were observed feeding on egg masses in the field. No assessment was made of the effectiveness of parasites or predators.

Enargia decolor

Wong and Melvin (1976) reared 15 species of primary parasites and one hyperparasite from larvae of *E. decolor* collected in northern Alberta during an infestation of this insect. Five of the parasites are known to attack other aspen-feeding Lepidoptera. No assessment of parasite effectiveness was made.

Choristoneura fumiferana

Numerous studies have been made of the parasites of *C. fumiferana*. Hewitt (1913) reported 77% and 75% parasitism of eggs collected in the Ottawa and Maniwaki areas and considered the high rate of parasitism to be a factor in the decline of the outbreak. Graham and Orr (1940) recognized that parasites and predators could not control budworm outbreaks, but that they could become very effective toward the end of an outbreak, when budworm numbers have been reduced by starvation. Prebble (1945) noted that larval parasites were quite effective in attacking the relatively few budworm larvae that had survived late spring frosts in Ontario.

Dowden and Carolin (1950) conducted extensive studies of budworm parasites in the Adirondacks. At that time there were at least 60 known species of parasites attacking the various stages of *C. fumiferana*. Their studies showed that aggregate parasitism of eggs, larvae, and pupae ranged from 46% to 93% in various locations over a 3-year period, and this parasitism was believed to be one of the major factors (along with overwintering mortality and predation by insectivorous birds) in reducing the severity of the infestation before serious tree mortality occurred.

Jaynes and Drooz (1952) conducted similar studies in New York and Maine. They found that aggregate parasitism in New York increased from 62% to 75% over a 3-year period, while in Maine it increased from 42% to 76% over a 4-year period. They also believed parasitism to be a factor in the decline of budworm populations in both states.

Following intensive investigations in New Brunswick, Miller (1963) concluded that the only egg parasite of the budworm, *Trichogramma minutum* Riley[67], is not likely to be an important control factor for *C. fumiferana* because it is dependent upon one or more alternate hosts. Pupal parasites tend to attack a variety of hosts and show no strong preference for the budworm, while some overwinter

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[67] Hymenoptera: Pteromalidae.

in alternate hosts; hence this group is probably ineffective except at low budworm densities. Similarly, many of the larval parasites are known or suspected to overwinter in alternate hosts and consequently do not exert control during an outbreak, nor can they prevent an outbreak from developing. Miller (1963) believed, as did Graham and Orr (1940) and Prebble (1945), that larval parasites are only effective during the final phase of an outbreak, when (in combination with other factors) they bring about its collapse.

Relatively little information was found on the effects of invertebrate predators upon the spruce budworm. Warren (1954) found that *Dioryctria reniculelloides* Mutuura and Munroe[68] larvae ate an appreciable number of budworm pupae under field conditions, and he conducted experiments that indicated that the amount of predation would probably increase if defoliation was severe and the larvae were forced to feed on old foliage. Morris (1963a) considered invertebrate predation of spruce budworm eggs to be an important factor. Invertebrate predators, principally spiders, may have an effect on large larval survival at low budworm densities, although (as with parasites) they are incapable of controlling budworm populations because they are dependent upon alternate hosts for survival during the periods when budworm larvae are absent. Morris did not consider that ants were important in New Brunswick; however, Finnegan (1978) reported that the introduced ant, ***Formica lugubris*** Zetterstedt[69], consumed up to 11 500 late-instar larvae per colony per day. Further study showed that defoliation in 1975 reached about 63% in areas where the ants were absent but amounted to only 43% near the nests. He concluded that the ants can be an important factor in controlling endemic spruce budworm populations. Sanders and van Frankenhuyzen (1979) noted large numbers of carabid beetles in spruce plantations in Ontario, and these were observed feeding on late-instar larvae. No actual assessment of the amount of predation by the beetles was made, but differences in the numbers of budworm larvae in samples taken about one month apart suggested that it could have been appreciable.

Parasites did not appear to have had a significant effect on spruce budworm populations in the present study, as the rates of parasitism for increasing and decreasing budworm populations were very similar (Table 10).

Neodiprion abietis complex

Raizenne (1957) reared two species of tachinid parasites and nine species of hymenopterous parasites (including one hyperparasite species) from *N. abietis* collected from balsam fir and white spruce in southern Ontario. Struble (1957) listed five identified and five unidentified invertebrate predators and 11 species of hymenopterous parasites of *N. abietis* on white fir in California. Neither paper assessed the importance of these enemies in the dynamics of *N. abietis* populations.

Parasites do not appear to have been a major factor in the present study, as rates of parasitism were very similar for increasing and decreasing populations (Table 10).

Acleris variana

Schmiege and Crosby (1970) reported that more than 70 species of parasites have been recovered from the closely related *A. gloverana* in western North America. Morris (1959) found that total larval parasitism of *A. variana* was a key factor in determining population trends of this insect in New Brunswick. Miller (1966) extended this analysis of *A. variana* populations in eastern Canada and showed that low rates of parasitism (plus favorable weather) were associated with population release, while high rates of late larval parasitism were associated with population decline.

In the present study, the rate of parasitism was nearly 10% higher in the decreasing phase of *A. variana* in Manitoba and Saskatchewan (Table 10), so that parasitism was probably a factor in the dynamics of this insect in this area as well.

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[68] Lepidoptera: Pyralidae.

[69] Hymenoptera: Formicidae.

Choristoneura pinus pinus

A number of workers have studied the parasites of the jack pine budworm. Early studies in Michigan (Benjamin and Drooz 1954; Drooz and Benjamin 1956) listed a number of parasites attacking the jack pine budworm and showed that several species also attacked *C. fumiferana*. Kulman and Hodson (1961b) conducted similar studies in Minnesota. They listed a total of 30 parasite species that had been recovered from *C. pinus pinus* by various workers: 22 of these had also been reported as parasites of *C. fumiferana*. Twenty-six species of primary parasites and four species of hyperparasites were reared from *C. pinus pinus* collected in Michigan (Allen 1968; Allen *et al.* 1969). Maximum rates of parasitism for the early larval, late larval, and pupal stages were 51.3%, 17.9%, and 24.5%,respectively. When expressed as real mortality, the maximum total parasitism amounted to only 8.5%. Eight species of insects were observed preying on the jack pine budworm, and three species of spiders were also probably predacious on the budworm. Foltz *et al.* (1972) constructed a series of life tables for jack pine budworm populations in Michigan. On the basis of this analysis, they concluded that parasites and predators display very limited numerical response to budworm density, because most are dependent upon alternate hosts for survival during part of the year. Consequently, their abundance is largely independent of budworm density. Brandt and Melvin (1970) listed 15 dipterous and 24 hymenopterous species of parasites that had been recovered from extensive rearings of jack pine budworm collected in Manitoba, Saskatchewan, and northwestern Ontario between 1941 and 1966.

In the present study, the difference between the rates of parasitism for increasing and decreasing *C. pinus pinus* populations amounted to slightly more than 12% (Table 10), suggesting that parasitism could be a factor in the population dynamics of this insect in Manitoba and Saskatchewan.

Neodiprion nanulus nanulus

Raizenne (1957) recovered five species of hymenopterous parasites from *N. nanulus nanulus* but only one dipterous parasite, a tachinid. Coppel (1954) reared nine hymenopterous parasites and one species of tachinid from *N. nanulus nanulus* collected in a pine plantation near Belleville, Ontario. Kapler and Benjamin (1960) also reared nine hymenopterous species and one tachinid from larvae collected in Wisconsin, but the species complex differed slightly from that reported by Coppel (1954). An introduced parasite, *Dahlbominus fuscipennis* (Zetterstedt)[70], was the most effective cocoon parasite, attacking from 39.0% to 74.2% of the larvae in cocoons. Expressed as real mortality, however, total parasitism ranged from 6.9% to 52.2%. Kapler and Benjamin (1960) also observed lynx spiders preying on all five larval instars of the sawfly and considered that they could be important control factors affecting endemic populations, since complete sawfly colonies were destroyed by the spiders on several occasions.

Parasitism of *N. nanulus nanulus* did not appear to be an important factor in the present study, as total parasitism for increasing populations averaged 9.0%, compared to 10.1% for decreasing populations.

Neodiprion virginianus complex

Raizenne (1957) reared two species of hymenopterous parasites and four tachinid species from *N. rugifrons* Midd. collected in southern Ontario. Wilkinson *et al.* (1966) reared 10 species of Hymenoptera and three species of Diptera from eggs and prepupal larvae of *N. rugifrons* collected in Wisconsin. They considered the two species of egg parasites to be unimportant; however, larval parasitism, mainly by dipterous forms, appeared to have a major influence on *N. rugifrons* populations. In addition, mirids and pentatomids were observed feeding on eggs, and about one-third of a sample of nearly 400 eggs showed evidence of hemipteran feeding. Pentatomid predation of larvae, mainly by *Podisus maculiventris* (Say)[71], was believed to have a significant influence on sawfly populations, particularly so in a stand that supported a population of an alternate host to sustain the stinkbugs during periods when sawflies were not available. In Ontario, Schedl

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[70] Hymenoptera: Eulophidae.

[71] Hemiptera: Pentatomidae.

(1938) reported egg parasitism by *Closterocerus cinctipennis* Ashmead[72] to be 14.5% in 1930 and 20.4% in 1931. Another egg parasite, *Tetrastichus* sp., attacked 8.0% and 14.9% of the eggs in 1930 and 1931, respectively, while hemipterous egg predators (mainly *Eremocoris ferus* (Say)[73], *Adelphocoris rapidus* (Say)[74], and *Pilophorus uhleri* Knight[75]) accounted for a further 19.9% and 17.2% mortality in 1930 and 1931.

Underwood (1970) studied an infestation of *N. virginianus* complex in northeastern New Brunswick. He recovered no parasites from 2000 eggs, and larval parasites were rare. He did, however, rear 14 species of parasites (11 Hymenoptera and 3 Diptera) from cocoons of *N. virginianus* complex and found that parasitism ranged from 30.9% to 38.7% over a 3-year period. Examination of cocoons collected in the field provided an estimate of parasitism of 45.3%. This rate of parasitism, coupled with mammalian predation of 13.1% and wireworm predation of 14.0%, appeared to be a major factor contributing to the collapse of the infestation. Schedl (1938) examined cocoons collected in the spring of 1931, prior to adult emergence. He found that 1.4% had been parasitized by ichneumonids, 15.7% had been killed by tachinids, and 50.0% had been destroyed by elaterid larvae, which were very abundant in the area.

The difference of only 6.3% in rates of parasitism for increasing versus decreasing *N. virginianus* complex populations (Table 10) seems to indicate that parasitism was not an important factor in the dynamics of this insect in Manitoba and Saskatchewan.

Pristiphora erichsonii

The larch sawfly has a relatively poor parasite complex in North America. Because of this, an ichneumonid parasite, *Mesoleius tenthredinis* Morley, was introduced into Manitoba in 1912 and 1913 (Hewitt 1917). It initially seemed that this parasite might control the larch sawfly, as parasitism increased from 19% in 1916 to nearly 90% in 1927 (Graham 1931); however, when the larch sawfly started to increase in numbers in the early 1940s, it became apparent that the parasite had decreased in effectiveness. Muldrew (1953) found that encapsulation by phagocytic cells prevented the parasite eggs from hatching and reduced the effective parasitism to less than 5% in most areas. Attempts to achieve biological control of *P. erichsonii* were again made in the early 1960s, when a number of parasite species were released in Manitoba (Turnock and Muldrew 1971). One of those, an ichneumonid named *Olesicampe benefactor* Hinz[76], appears to be effectively controlling the larch sawfly. It has been redistributed into several locations in North America (Anonymous 1973a; Embree and Underwood 1972; Kulman *et al.* 1974), but the appearance of the hyperparasite *Mesochorus dimidiatus* Holmgren[77] has caused some apprehension concerning the ultimate effectiveness of *O. benefactor* in regulating larch sawfly populations.

The present study was conducted during the period when *Mesoleius tenthredinis* was ineffective and was terminated before *O. benefactor* had become widespread. During this period, the tachinid *Bessa harveyi* was the only parasite exerting any influence on larch sawfly populations, although a number of other species were present (Lejeune and Hildahl 1954). *B. harveyi* is not well adapted to the larch sawfly (Turnock and Muldrew 1973) and was a minor component in the population dynamics of this insect in southeastern Manitoba (Ives 1976a). The k-values for *B. harveyi* attack were completely independent of the densities of fifth-instar larvae.

The ineffectiveness of parasites in regulating larch sawfly populations is indicated in the present study as well. The mean

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[72] Hymenoptera: Eulophidae.

[73] Hemiptera: Lygaeidae.

[74, 75] Hemiptera: Miridae.

[76, 77] Hymenoptera: Ichneumonidae.

rates of parasitism, although fairly high, were almost identical for increasing and decreasing *P. erichsonii* populations (Table 10).

DISEASES

Diseases of insects are caused by various viruses, bacteria, rickettsia, fungi, protozoa, and nematodes. Because of the diversity of the organisms involved, the literature on the topic is voluminous (Angus 1973) and much is of a highly technical nature. A thorough review of this literature is beyond the scope of this report, partly because of its technical nature, but primarily because there appears to be relatively little information on the impact of diseases (with the exception of viruses) upon forest insect populations. For the sake of completeness, however, brief reference will be made to some of the more pertinent papers.

Some excellent reviews, all of a technical nature, have been published in recent years, and readers interested in details should refer to them. Franz (1961), MacBain Caeron (1963), and Weiser (1970) presented overviews of the current trends in insect pathology, while Stairs (1972) discussed the use of pathogens in the control of forest insect pests. In addition, there have been a number of reviews dealing with specific groups of organisms and their use or potential use in insect control. David (1975), Falcon (1976), and Tinsley (1979) reviewed various aspects affecting the use of viruses. Heimpel (1967) and Heimpel and Angus (1963) discussed spore-forming bacteria, the group primarily responsible for causing insect diseases. Ferron (1978) and Madelin (1966) reviewed the use of fungal parasites to control insects, while Poinar (1972) and Welch (1965) discussed the nematodes. No one appears to have reviewed the use of protozoa to control insects, probably because there is currently little research in this field (MacBain Cameron 1963).

Steinhaus (1964) discussed the development of insect pathology and presented a general discussion of the different types of organisms involved in causing insect diseases. Weiser *et al.* (1976) considered the role of pathogens in biological control and pointed out that there are very few examples of pathogens being used successfully. They cited the European spruce sawfly and the European pine sawfly in Canada and the Japanese beetle in the United States as examples. Maddox (1975) also cited these examples and gave a brief general discussion of the different types of pathogens, their methods of infection, and symptoms.

A more detailed discussion of the effects of a virus upon populations of the European spruce sawfly in the Maritime Provinces is given by Bird and Elgee (1957) and Neilson and Morris (1964). Both of these papers concluded that the virus was very effective in controlling the sawflies at relatively high densities, while parasites regulated the populations at lower densities. These results were confirmed by introducing the virus into European sawfly populations in Ontario in areas where parasitism was extremely low (Bird and Burk 1961). The virus spread rapidly and apparently controlled the sawfly populations, but at a level considerably higher than in the Maritimes, where parasites were also effective.

A detailed discussion of the efforts to control the European pine sawfly by parasite introductions and a virus introduction is given by Griffiths *et al.* (1971). Although the virus is very virulent, it is not effective in controlling the sawfly or in preventing its spread. If applied as an insecticide when the eggs are hatching, however, it will kill the larvae when they are in the second or third instar, thus preventing any appreciable damage to the foliage. Aerial application of this virus has also given complete control. Cunningham *et al.* (1975) studied a 125-ha area that was sprayed from an aircraft. Coverage was adequate, although not exceptional, but because of the virulence of the virus, the sawflies were virtually eliminated from the area.

Some of the native viruses and other diseases also appear to exert an influence upon population trends. In a recent paper, Anderson and May (1980) examined available data on the effects of infections by viruses, bacteria, protozoa, and helminths upon natural populations of invertebrates and concluded, by means of mathematical models, that disease may explain the cyclic population curves of the larch bud moth, *Zeiraphera griseana* (= *diniana* Gn.), in the European Alps. They also suggested that various diseases may be responsible for the cyclic population trends of several forest insects. A nuclear polyhedrosis virus of *Neodiprion lecontei* (Fitch)[78] was discovered in Ontario in 1950 and has given effective control of the sawfly in both ground and aerial spray trials (de Groot *et al.* 1979; Kaupp *et al.* 1978). In the Maritime Provinces and in Quebec, a virus has been credited with terminating or shortening outbreaks of the Bruce spanworm (Forbes *et al.* 1964, 1965; Martineau 1964, 1965). Small-scale field tests of this virus against Bruce spanworm in Alberta indicated that it is also virulent (Ives and Cunningham 1980). A nuclear polyhedrosis virus has also shown promise in large-scale tests for control of the Douglas-fir tussock moth and has been registered in the United States for control of this pest (Martignoni 1978). Because viruses must be propagated in living tissues, which at the moment means whole insects if virus propagation is on a production basis, the cost of production remains high, and neither of these preparations is truly competitive with insecticides if evaluated on a cost basis.

Bacillus thuringiensis Berliner[79], a spore-forming bacteria that kills larvae of a large number of insect species (predominantly lepidopterans) is economical to produce and is therefore competitive cost-wise. Commercial preparations contain a mixture of spores and toxic crystals and may kill larvae in one of three ways (Weiser *et al.* 1976): 1) the insects may be poisoned by the crystals; 2) the insects may die from a combination of poisoning and septicemia caused by the bacteria; and 3) the insects may not be affected by the toxin but are killed by the septicemia caused by the bacteria. Although *B. thuringiensis* has been used effectively to control a number of insects, including forest pests, it does not propagate itself and must be used as a biological insecticide. It therefore does not constitute a factor in the natural environment and will not be further discussed in this report.

Apart from these recent developments, the current status of insect pathology is perhaps best reflected in a statement by Maddox (1975): "Virus and fungi are the two groups of insect pathogens most often credited with causing epizootics. Bacteria, protozoans and nematodes are thought to cause epizootics less frequently than viruses and fungi, but this is no doubt influenced by the fact that viral and fungal infections are more easily recognized than are protozoan, nematode, and bacterial infections."

The present study did not evaluate the prevalence of diseases. There are, however, references in the literature to diseases affecting a number of the species discussed in this paper, and the more significant of these will be cited briefly.

Malacosoma disstria

The diseases of *M. disstria* are reviewed briefly by Witter and Kulman (1972b) and are thoroughly discussed by Bird (1971) and Stairs (1972). This insect is affected by several bacteria and fungi, but the more important diseases are caused by a microsporidian (protozoan), a nuclear polyhedrosis virus (NPV), and a cytoplasmic polyhedrosis virus (CPV). The incidence of infection by the microsporidian is often high, but it is difficult to assess. Although infection of young larvae will kill them, the main effect of the disease is to cause a reduction in the size of the insect and a possible reduction of vigor in the offspring. CPV is lethal to young larvae, but infected older larvae may not die. All larval instars are susceptible. NPV is highly infectious to young larvae, but late-instar larvae require massive doses to infect them. Infected larvae always die, unless the infection occurred late in the larval stage.

Although an NPV occurs naturally in *M. disstria* populations, is usually quite widespread in older infestations, and sometimes reaches epizootic proportions (Stairs 1972), it

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[78] Hymenoptera: Diprionidae.

[79] Family Bacilliaceae.

does not appear to be capable of controlling or preventing outbreaks under natural conditions. Hodson (1941) noted that the virus was not important during the 1933-38 outbreak in Minnesota. Similarly, Witter *et al.* (1972) did not consider viruses to be an important mortality factor in their Minnesota studies during 1967 to 1969. One must therefore assume that the viruses are not particularly virulent. Nevertheless, Ives and Muldrew (1978) obtained almost complete mortality of eggs and young larvae when heavy doses of NPV were applied as an aqueous spray. Perhaps this is another virus that is only effective when used as a biological insecticide.

Choristoneura fumiferana

The diseases of *C. fumiferana* were thoroughly discussed by Neilson (1963). Viruses, bacteria, fungi, and microsporidia all cause diseases, but none of them appeared to be particularly lethal or important during a 5-year study of natural populations in New Brunswick. The microsporidia were the most prevalent, and the main effect of infection was to reduce fecundity and fertility.

Although neither the microsporidia nor the virus appeared to have much influence on natural populations of *C. fumiferana*, they both gave promising results when applied experimentally in the field. Preliminary field tests, in which an aqueous suspension of spores was sprayed onto a number of small white spruce trees, indicated that the incidence of microsporidia in the larvae was increased appreciably in relation to that in larvae from unsprayed trees (Wilson and Kaupp 1975). Furthermore, the subsequent incidence of the disease in the adults and in their offspring was also appreciably higher.

Large-scale aerial applications of a nuclear polyhedrosis virus to fourth-instar larval populations gave encouraging results (Cunningham *et al.* 1975a, 1975b). In 1974, budworm populations on balsam fir in a 520-ha area were reduced by about 60% during the year of application. The following year, virus carry-over reduced populations on balsam fir by 44%, but the reduction on white spruce (which had been only 5% the previous year) increased to 77%. In 1975, population reduction on white spruce exceeded 90% on two of the five plots sprayed. None of the areas showed any noticeable reduction in defoliation. In 1976, virus applications were made when the larvae were in the second instar and are susceptible to virus infection (Kaupp *et al.* 1978). The levels of virus infection were lower than in previous years. In 1977, a number of formulations, dosages, and virus strains were tested (Cunningham *et al.* 1978), mainly against fourth-instar larvae. A dosage of 750 billion polyhedra per hectare gave a population reduction of 92%. In 1978, the same dosage applied when the larvae were in the fifth and sixth instars gave population reductions of 33% to 92% on white spruce and 37% to 76% on balsam fir (Cunningham *et al.* 1979).

Neodiprion abietis complex

A virus disease of *N. abietis* larvae has been reported from Manitoba and Alberta (Cumming 1954) and from Quebec (Martineau and Lavallee 1972), but no indication was given of its impact on sawfly populations. Brown (1951) believed that populations of *N. abietis* near Archerville in Saskatchewan had been reduced by a virus. Struble (1957) reported virus infections for 3 consecutive years during an outbreak of *N. abietis* on white fir in California. He considered that the natural virus infections, which showed up in the last two larval instars, were a major factor in reducing sawfly infestation levels and in preventing major damage to the host trees. Experimental application of the virus to small balsam fir trees in Ontario, while the larvae were in the first instar, showed that concentrations of 1×10^6 and 1×10^7 polyhedral inclusion bodies per millilitre caused complete mortality and gave good foliage protection (Olofsson 1973). The higher concentration, applied when the larvae were in the third instar, also caused complete mortality, but some defoliation occurred.

Acleris variana

This insect has been studied extensively in New Brunswick during a 15-year period, and annual examination of small samples of larvae showed no evidence of disease (Miller 1966). Prebble and Graham (1945b), however, considered a wilt disease of the larvae and pupae to be a major natural control factor in populations of the closely related *Acleris gloverana* in British Columbia. The pattern of seasonal larval mortality for this insect given by Silver (1960) is consistent with what might be expected during a virus epizootic, although he noted that "There was no record or indication of a disease in the field populations." Because of the contradictory evidence, the role of disease in the dynamics of *A. variana* populations must be considered to be undetermined.

Pristiphora erichsonii

The larvae of *P. erichsonii* are attacked by a number of disease-producing organisms. Drooz (1960) recovered three genera of fungi and two species of bacteria from larch sawfly in Minnesota, and he reported that nematodes are capable of killing all larval instars. The importance of disease in regulating field populations is minimal, however. MacLeod and Heimpel (1955) examined 16 000 larvae collected in the field over a 5-year period and found that infection by *Beauvaria* species ranged from 0.2% to 1.5%. Mortality of 11 000 cocoons over the same period ranged from 2.8% to 23.5%, but it was not clear if all of this mortality was due to *Beauvaria.* Similarly, bacteria caused little mortality among feeding larvae. Close observation of 5200 larvae over a 4-year period showed that death due to bacterial infection ranged from 0.6% to 2.0%. The absence of any reference to disease in papers describing long-term population studies of the larch sawfly in the Lake States (Graham 1956) and in southeastern Manitoba (Ives 1976a) is further confirmation of the relative unimportance of disease in the population dynamics of this insect.

COMPETITION FROM OTHER DEFOLIATORS

Competition between animals of the same species for some limited resource, usually food, is one of the main tenets underlying most theories on population dynamics. Interactions between animals of different species have also been discussed extensively from a theoretical standpoint, especially as they pertain to predator-prey relationships. Andrewartha and Birch (1954) discussed the interrelationships between populations of a number of nonpredatory organisms under experimental conditions. In most of these experiments one species eventually dominated and the other died out; however, if there are slight differences in the species' requirements, it is possible for two or more species to coexist indefinitely. In forest entomology there is relatively little information of a comprehensive nature on the interaction among the various forest insect pest species (Baltensweiler 1976). This holds true even in Europe, where forest entomologists have been compiling data for a much longer period than in North America.

While the present data may not be comprehensive, they are certainly extensive, and an examination of them to determine possible interrelationships may provide insights into factors affecting insect abundance in a boreal forest community. The present study cannot examine intraspecific competition, nor can it measure interspecific competition directly. By calculating simple correlation coefficients, however, it is possible to assess the degree of association between numbers of the various species. It must be pointed out that these correlations do not in any way imply a cause and effect relationship. This is fully discussed in many elementary statistical texts: a clear concise presentation is given by Hoel (1947, p. 88). This does not mean that there cannot be a cause and effect relationship. In the case of insects, such a relationship is probably most likely if the correlation coefficient is negative. The variables can also be responding to a third, perhaps unmeasured, variable, and detailed examination of ancillary data may reveal a plausible explanation for the observed correlation.

The degree of association between annual estimates of the mean numbers of insects per positive sample for each of the seven areas (Fig. 1) was assessed by calculating the simple correlations between all possible pairs of species for each area. The overall correlations, disregarding areas, were also calculated from the area means. For the sake of simplicity, discussion will be limited to those interrelationships in which the absolute value for the overall correlation was $\geqslant 0.30$ (Table 11). Many of the other correlations may have statistical and/or biological mean-

Table 11. Correlations ⩾0.30 for paired comparisons of the annual mean number per positive sample for 17 insect species collected in seven areas from 1952 to 1969

Insect species	r values
Malacosoma disstria and *Neodiprion nanulus nanulus*	+0.47
Chrysomela crotchi and *Anoplonyx luteipes*	+0.41
Orthosia hibisci and *Acleris variana*	+0.50
Choristoneura pinus pinus and *Choristoneura fumiferana*	+0.40
Orthosia hibisci and *Pseudexentera oregonana*	+0.38
Campaea perlata and *Enargia decolor*	+0.31
Choristoneura pinus pinus and *Sciaphila duplex*	+0.30
Semiothisa bicolorata and *Semiothisa sexmaculata*	+0.39
Anoplonyx canadensis and *Anoplonyx luteipes*	+0.39
Choristoneura conflictana and *Chrysomela crotchi*	−0.33
Choristoneura pinus pinus and *Orthosia hibisci*	−0.30
Orthosia hibisci and *Anoplonyx luteipes*	−0.31
Pristiphora erichsonii and *Anoplonyx luteipes*	−0.35

ing, but trying to interpret all of the possible interrelationships on a purely speculative basis is completely impractical. Some may argue that trying to interpret the 13 correlations in Table 11 is stretching the imagination; however, an attempt will be made, in the order listed in the table. In the following discussions, the life histories and weather conditions referred to are as in Tables 2 and 4. They are repeated here for the sake of clarity.

Malacosoma disstria and *Neodiprion nanulus nanulus*

The larval periods are somewhat similar for both species, 19 May to 12 July for *M. disstria* and 13 June to 24 July for *N. nanulus nanulus*, although *M. disstria* is probably about 2 to 3 weeks earlier than *N. nanulus nanulus*. *Malacosoma disstria* overwinters as pharate larvae in the egg bands on twigs, and *N. nanulus nanulus* overwinters as eggs on the foliage. Both insects are favored by warm dry weather during May to July, and wet weather at this time is unfavorable. Mild weather during November to January is favorable to both species. Cold weather during November to April is unfavorable to *M. disstria*, while warm weather in February to April is unfavorable to *N. nanulus nanulus* (Ives (1973) noted a similar trend for *M. disstria*). Weather conditions therefore appear to be responsible for the positive correlation coefficient.

Chrysomela crotchi and *Anoplonyx luteipes*

The larval periods are similar, 7 July to 6 September for *C. crotchi* and 25 June to 24 August for *A. luteipes* although *C. crotchi* occurs about 2 weeks later than *A. luteipes*. *Chrysomela crotchi* overwinters as sexually immature adults in the duff, while *A. luteipes* overwinters in cocoons in the moss. Both species are favored by heavy precipitation during November to January and by warm weather from May to July. Although *C. crotchi* is favored by wet weather during May to July, *A. luteipes* does better if the weather is dry during this period. Since at least half of this period is spent in the duff or moss, it can be postulated that the wet weather prevents desiccation of *C. crotchi*, while the dry weather minimizes the flooding of *A. luteipes* cocoons. Populations of *C. crotchi* therefore probably tend to be higher during the wetter years, while those of *A. luteipes* peak during the drier years. Nevertheless, weather conditions are probably primarily responsible for the observed positive correlation coefficient.

Orthosia hibisci and *Acleris variana*

The larval periods are somewhat similar for the two species, 19 May to 6 July for *O. hibisci* and 1 June to 31 July for *A. variana. Orthosia hibisci* overwinters as pupae in the soil, and *A. variana* overwinters as eggs on the foliage. Light precipitation from November to April favors both insects, as does mild weather during February to April. Similarly, cold weather during February to April is unfavorable to both insects. Warm wet weather during May to July favors *A. variana*, while hot weather during this period is unfavorable to *O. hibisci*. Also, cool dry weather during August to October is favorable to *O. hibisci*, but warm wet weather during the same period favors *A. variana*. Weather does not therefore seem to be the principal factor underlying the correlation in the abundance of these two species, unless the effects of weather during the winter are of overwhelming importance.

Choristoneura pinus pinus and *Choristoneura fumiferana*

These closely related insects have similar life histories. The larval period for *C. pinus pinus* is 1 June to 24 July and for *C. fumiferana* it is 25 May to 18 July. Adults of both species are present from early July to early August, and both insects overwinter as second-instar larvae in hibernaculae spun on the host trees. Cold or cool weather with heavy precipitation during February to April is favorable to both species. Similarly, warm or hot weather during May to July and warm weather from August to October favor both insects. Weather therefore appears to be the main factor responsible for the positive correlation between the abundance of the two budworms.

Orthosia hibisci and *Pseudexentera oregonana*

Both species overwinter as pupae in the soil, and the adults emerge in the spring. The larval period for *O. hibisci* is 19 May to 6 July, and for *P. oregonana* it extends from 19 May to 24 June. Mild weather from November to April favors both species, as does light precipitation from November to January and dry weather from August to October. Warm weather from May to July is favorable to *P. oregonana*, while hot weather during this period is unfavorable to *O. hibisci*. Also, warm weather during August to October favors *P. oregonana*, while cool weather during this period favors *O. hibisci*. It is therefore difficult to see how weather can be the factor responsible for the observed correlation, unless overwintering conditions are of paramount importance.

Campaea perlata and *Enargia decolor*

The larval periods are somewhat similar for both insects, 19 May to 24 June for *C. perlata* and 25 May to 6 July for *E. decolor*, and adults of both species are active from late July to late August. *Campaea perlata* overwinters as partly grown larvae, and *E. decolor* overwinters as eggs on the tree trunks. The only weather element that the two species have in common is that hot weather during May to July is unfavorable. Unless this fact is of overriding importance, it is difficult to see how weather can be the factor directly responsible for the correlation between the numbers of the two species.

Choristoneura pinus pinus and *Sciaphila duplex*

The larval period for *S. duplex*, 19 May to 30 June, is considerably earlier than for *C. pinus pinus*, which extends from 1 June to 24 July. The adults of *S. duplex* are also active about a month earlier than are those of *C. pinus pinus* (early June to early July, compared to early July to early August). Both species overwinter as second-instar larvae in hibernaculae in bark crevices and other such places. Mild weather from November to January followed by cold weather with heavy precipitation from February to April favors both species, as does hot or warm weather from May to July and warm weather from August to October. Dry weather from August to October is unfavorable to *S. duplex*, probably because it makes the foliage unpalatable to the first-instar larvae, which feed until fall. Since this is the only major difference in weather conditions affecting the two species, it seems likely that weather is responsible for the observed correlation.

Semiothisa bicolorata and *Semiothisa sexmaculata*

These two insects are on different hosts, but their life cycles are very similar. The larval period for *S. bicolorata* extends from 13 July to 12 September and that of *S. sexmaculata* from 19 July to 6 September. The adult flight periods are similar, and both overwinter as pupae in the duff or moss. Both insects are favored by light precipitation from November to January followed by mild weather from February to April. Cool wet weather during August to October favors both species. Warm dry weather during May to July is unfavorable to *S. bicolorata*, while wet weather during this period is unfavorable to *S. sexmaculata.* Since both species spend most of this time as pupae in the forest floor, it probably means that *S. bicolorata* pupae are prone to desiccation in the spring, while those of *S. sexmaculata* are probably vulnerable to flooding. Since this is the only major difference in weather factors affecting the two species, it probably means that weather is once again the most likely factor responsible for the observed correlation.

Anoplonyx canadensis and *Anoplonyx luteipes*

These closely related species feed on the same host and are exposed to similar environmental conditions, but *A. luteipes* occurs about a month earlier than *A. canadensis.* The larval period for *A. luteipes* is from 25 June to 24 August, while that of *A. canadensis* extends from 1 August to 18 September. Both species overwinter as cocoons in the moss. The only weather condition favorable to both species is heavy precipitation from November to January. Warm dry weather during May to July favors *A. luteipes*, but hot dry weather during the same period is unfavorable for *A. canadensis.* Weather conditions therefore do not seem to be directly responsible for the observed correlation.

Choristoneura conflictana and *Chrysomela crotchi*

These two insects, although occurring on the same host, have considerably different life cycles. The larval period for *C. conflictana* is 19 May to 30 June, while that for *C. crotchi* is 7 July to 6 September. Adults of *C. conflictana* are active from early June to early July, and those of *C. crotchi* are active in the fall and spring. Finally, *C. conflictana* overwinters as second-instar larvae in hibernaculae in bark crevices and elsewhere, whereas *C. crotchi* overwinters as adults in the duff. The only weather condition that is favorable to both species is heavy precipitation from November to January. Hot weather during May to July is unfavorable to *C. conflictana*, while warm wet weather during this period favors *C. crotchi.* Because of the differences in the life cycles, it is impossible to say what influence weather has on the interrelationship between the two species. It seems probable, however, that the negative correlation may be due to competition, since the amount of food for *C. crotchi* would be reduced whenever *C. conflictana* populations were high.

Choristoneura pinus pinus and *Orthosia hibisci*

The larval period for *O. hibisci* is somewhat earlier than for *C. pinus pinus*: 19 May to 6 July versus 1 June to 24 July. Also, the adults of *O. hibisci* are active in the spring, while those of *C. pinus pinus* occur from early July to early August. Finally, *O. hibisci* overwinters as pupae in the soil, while *C. pinus pinus* overwinters as second-instar larvae in hibernaculae. Mild weather from November to January favors both species. Light precipitation during November favors *O. hibisci*, while heavy precipitation during this period favors *C. pinus pinus.* Cool dry weather from August to October is favorable to *O. hibisci*, while warm weather at this time favors *C. pinus pinus.* Cold weather from February to April is unfavorable to *O. hibisci* but is favorable to *C. pinus pinus.* In spite of the differences in life cycles, the difference in the effect of weather upon the two insects is probably responsible for the observed negative correlation.

Orthosia hibisci and *Anoplonyx luteipes*

The larval period for *O. hibisci* extends from 19 May to 6 July, while that of *A. luteipes* is from 25 June to 24 August. Adults of both species are probably active about the same time, and both overwinter in the forest floor. Both species are favored by mild weather from November to January; however, *O. hibisci* is favored by light precipitation during this period, while heavy precipitation favors *A. luteipes.* Similarly, hot weather during May to July is unfavorable to *O. hibisci*, although warm weather at this time favors *A. luteipes.* There is therefore at least a suggestion that weather may be the factor responsible for the observed negative correlation.

Pristiphora erichsonii and *Anoplonyx luteipes*

The life cycles of these two insects are very similar, and they feed on the same hosts. The larval period for *P. erichsonii* is from 25 May to 24 August, while that for *A. luteipes* extends from 25 June to 24 August. Adults of *P. erichsonii* are active from late May to late July, while those of *A. luteipes* are active in May and June. Both species overwinter in cocoons in the moss. Heavy precipitation from November to January favors both species; however, cold weather during this period favors *P. erichsonii*, while *A. luteipes* is favored by mild weather. Also, *P. erichsonii* is favored by cool wet weather from May to July, whereas *A. luteipes* is favored by warm dry weather during the same period. Weather is therefore a possible factor contributing to the observed negative correlation. Because both species are feeding on the same host, and because *P. erichsonii* is the more abundant species, there is also a strong possibility that competition between the two insects may be a contributing factor. *Anoplonyx luteipes* is unlikely to limit *P. erichsonii* population increase, but defoliation by *P. erichsonii* could certainly have an adverse effect on the survival of *A. luteipes* larvae.

SUMMARY AND CONCLUSIONS

This report has reviewed the outbreak histories for 21 North American defoliating insects and summarized their infestations for seven forested areas in Manitoba and Saskatchewan between 1945 and 1969, grouped according to main host-tree species. On trembling aspen *Malacosoma disstria* Hübner, *Choristoneura conflictana* Walker, *Chrysomela crotchi* Brown, and *Gonioctena americana* Schaeffer all reached outbreak levels in one or more of the areas during the period under study, but *Orthosia hibisci* (Guenée), *Campaea perlata* Guenée, *Pseudexentera oregonana* Walsingham, *Sciaphila duplex* Walsingham, and *Enargia decolor* Walker were of minor importance. On white spruce *Choristoneura fumiferana* (Clemens) was the principal insect pest, and *Neodiprion abietis* complex and *Acleris variana* (Fernald) were both relatively unimportant. *Choristoneura pinus pinus* Freeman was the major defoliator of jack pine, and *Neodiprion nanulus nanulus* Schedl and *Neodiprion virginianus* complex caused damage in localized areas. *Semiothisa bicolorata* Fabricius and *Zale duplicata largera* Smith were both unimportant. *Pristiphora erichsonii* (Hartig) was the only important defoliator of tamarack. *Semiothisa sexmaculata* Packard, *Anoplonyx canadensis* Harrington, and *Anoplonyx luteipes* (Cresson) were all relatively common on tamarack but caused very little damage.

Seasonal weather data (expressed as total precipitation, heat units below -18°C and above 4.5°C, and water deficits) were accumulated for each of the seven areas by 3-month periods: August to October; November to January; February to April; and May to July. Each variable was then expressed as a percentage of the range in order to simplify presentation and to eliminate area differences. The insect sampling data for each species were then used to group the appropriate weather data into four categories on the basis of population trends. The categories were: 1) insect absent; 2) insect present but no obvious trend or trend unknown; 3) insect populations increasing; and 4) insect populations decreasing. The effect of each weather variable was assessed by comparing differences between the last two categories.

The report also reviewed the literature on population dynamics, particularly in relation to insects, and on the effects of environmental factors (seasonal weather, small mammals, birds, parasites, invertebrate predators, and diseases) upon insect population trends. The available data for Manitoba and Saskatchewan were examined, and particular emphasis was placed upon the effects of seasonal weather, which was shown to influence population trends for each of the 21 species of insects. Temperature and precipitation in each of the four 3-month periods seemed to play approximately equal roles in influencing population trends, and conditions favoring one species of insect were often unfavorable to another. Most of the results agreed with those reported by other workers. Although seasonal weather was shown to be related to population trends, the predictive value of these relationships seems to be limited. This may be due, in part, to interactions between seasonal weather and other environmental factors such as small mammals, birds, parasites, invertebrate predators, and diseases. The limited amount of data available in the literature and in the present study indicate that all of these factors can be important at one time or another for certain of the insects. Although I do not wish to become embroiled in the controversy concerning the relative importance of density-dependent versus density-independent factors in regulating insect populations, an evaluation of the present findings makes this unavoidable.

As has already been pointed out, records from meteorological stations provide only an index of the microclimatic conditions surrounding each insect species or individual. Nevertheless, the conclusion seems inescapable that weather is the overriding factor in determining the abundance of forest insects in Manitoba and Saskatchewan. Other factors (such as small mammals, birds, invertebrate predators, parasites, diseases, and competition from other insects) all play important roles but do not, in themselves, appear to be the most important factors determining insect abundance. One or more may assume importance in any given situation.

The limited data makes impossible a full assessment of the importance of these factors, although their actions, jointly or singly, are probably responsible for the poor predictive value of weather conditions for forecasting insect population trends. Because the effects of these factors are often density independent, though one might expect them to be otherwise, it is impossible to judge when or if they are going to act. Consequently, although there appear to be good relationships between certain seasonal weather conditions and insect population trends, these relationships are not consistent enough to make useful predictions. They do, however, suggest a number of relationships that should be fairly simple to verify experimentally. It is hoped that this report may stimulate such investigations and thus ultimately lead toward better understanding of the complex factors determining the abundance of forest insect defoliators.

ACKNOWLEDGMENTS

The data upon which this report is based were collected by the staff of the former Manitoba and Saskatchewan region, which had its headquarters in Winnipeg. There are too many people involved to mention individually, but without their joint efforts this study would not have been possible.

It is a pleasure to acknowledge the financial and moral support given during the rather long gestation period by R.M. Prentice, then Forest Insect and Disease Survey Coordinator, Canadian Forestry Service, Ottawa. Sincere thanks are also extended to Dr. D.M. Brown, Director General, Computing and Applied Statistics Directorate, Environment Canada, Ottawa, and to members of his staff, especially J.M. Valenzuela, R.J. McManus, W. McMahon, and R. Webster, all at one time or another with the directorate, who jointly were responsible for reducing the tremendous volume of data to manageable levels. Thanks must also be sincerely extended to W. Chow, Northern Forest Research Centre (NFRC), Edmonton, who further reduced these data into the format used in preparing this report.

I am also grateful to Dr. C.H. Buckner, now Program Leader (Canada), Canadian/United States Spruce Budworms Program, Canadian Forestry Service, Ottawa, for permission to use previously unpublished data on bird and small mammal populations in southeastern Manitoba. Although these data were collected under Dr. Buckner's supervision, I assume responsibility for any shortcomings they may contain, as it was my decision to reproduce them in this report.

Further, I would like to thank K. Froning (NFRC) for translating a German paper into English. Dr. W.G. Evans, Department of Entomology, University of Alberta, Edmonton, kindly agreed to act as an outside reviewer and contributed greatly to improvements in the manuscript. Finally, I would like to thank my colleagues at NFRC, Dr. H.F. Cerezke, Dr. J.M. Powell, and Dr. H.R. Wong, for their many helpful suggestions and comments.

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APPENDIXES

The following eight appendixes are tables containing data summaries upon which this report has been based. The data are not essential in the presentation of the results, and it was felt that inclusion of these tables in the body of the report would have made it unnecessarily unwieldly. The tables have been included as appendixes for the benefit of those who may be interested in greater detail than is presented in the body of the report.

1. Insect species data from seven geographical areas for 1951 to 1969, showing number of insects per positive sample, percentage positive samples, number of samples, and percentage parasitism.
2. Weather data from seven meteorological stations for 1944 to 1969.
3. Mean 3-month period values of weather data for years when various insect populations were present, absent, increasing, or decreasing.
4. Populations of the four most common species of small mammals in larch sawfly plots in tamarack bogs.
5. Number of territorial male birds per 40 hectares in the tamarack bog containing the Rennie larch sawfly plot.
6. Number of territorial male birds per 40 hectares in the tamarack bog containing the Telford larch sawfly plot.
7. Number of territorial male birds per 40 hectares in the tamarack bog containing the Seddon's Corner larch sawfly plot.
8. Number of territorial male birds per 40 hectares in the tamarack bog containing the Pine Falls larch sawfly plot.

APPENDIX 1

INSECT SPECIES DATA FROM SEVEN GEOGRAPHICAL AREAS FOR 1951 TO 1969, SHOWING MEAN NUMBER OF INSECTS PER POSITIVE SAMPLE ($\bar{x}$), PERCENTAGE POSITIVE SAMPLES (p), NUMBER OF SAMPLES (n), AND PERCENTAGE PARASITISM (P)

Areas and years	*Malacosoma disstria*				*Choristoneura conflictana*				*Chrysomela crotchi*			*Gonioctena americana*			*Choristoneura pinus pinus*				*Choristoneura fumiferana*				*Pristiphora erichsonii*			
	$\bar{x}$	p	n	P	$\bar{x}$	p	n	P	$\bar{x}$	p	n	$\bar{x}$	p	n	$\bar{x}$	p	n	P	$\bar{x}$	p	n	P	$\bar{x}$	p	n	P
Southeastern Manitoba (Area 1)																										
1951	5	10	50	9	1	11	37	-	0	0	17	67	3	37	33	2	83	17	2	29	42	11	91	88	41	35
1952	13	46	50	27	0	0	39	-	0	0	28	11	13	39	30	3	35	32	2	12	34	9	134	87	77	27
1953	9	54	71	30	1	1	67	-	0	0	19	14	15	67	0	0	42	22	2	18	33	-	24	93	59	23
1954	6	17	35	-	2	6	34	-	0	0	23	9	29	34	0	0	47	22	42	27	30	8	33	90	30	53
1955	0	0	8	-	0	0	2	-	0	0	16	0	0	2	12	56	37	45	24	35	20	3	20	88	8	34
1956	1	20	5	-	0	0	5	-	10	4	25	0	0	5	16	85	36	-	24	65	17	44	49	100	6	32
1957	0	0	2	-	0	0	2	-	0	0	10	8	50	2	29	73	33	-	56	83	12	28	25	100	7	49
1958	0	0	22	-	2	30	20	-	0	0	6	11	45	20	5	83	19	11	6	47	15	6	51	80	5	-
1959	0	0	11	-	3	9	11	-	0	0	6	13	27	11	16	80	25	-	4	21	24	-	33	100	4	51
1960	2	8	48	-	1	13	45	-	0	0	12	16	20	45	13	43	30	-	15	7	59	-	181	75	20	49
1961	6	58	40	23	0	0	37	-	0	0	6	18	30	37	9	57	14	-	1	3	35	-	18	65	34	60
1962	14	34	71	20	1	2	65	-	5	50	10	5	6	65	0	0	20	-	0	0	24	-	7	35	17	57
1963	5	25	44	60	0	0	32	-	23	73	22	10	13	32	4	31	29	-	0	0	25	-	31	57	7	41
1964	3	33	81	41	0	0	63	-	9	46	35	13	14	63	11	23	46	14	2	10	48	-	206	48	21	33
1965	1	7	27	82	0	0	18	-	9	38	8	17	28	18	60	52	35	16	1	12	26	-	18	56	16	18
1966	0	0	22	-	0	0	17	-	7	45	11	23	12	17	31	42	22	41	0	0	16	-	34	60	10	45
1967	0	0	10	-	0	0	8	-	0	0	3	0	0	8	11	33	21	30	8	20	10	-	91	50	11	68
1968	2	8	12	-	0	0	5	-	14	57	7	23	20	5	4	27	12	40	2	20	10	-	40	70	10	31
1969	0	0	16	-	2	25	12	-	6	17	23	21	75	12	3	5	19	-	0	0	15	-	33	40	10	56
Interlake and Westlake area, Manitoba (Area 2)																										
1951	0	0	11	-	3	22	9	-	0	0	3	8	11	9	0	0	1	8	3	71	7	16	55	96	26	39
1952	0	0	16	-	7	27	15	19	0	0	5	0	0	15	0	0	9	8	2	5	37	-	36	94	31	32
1953	0	0	2	-	0	0	2	-	-	-	-	0	0	2	0	0	12	20	-	-	-	-	18	100	10	10
1954	0	0	6	-	0	0	5	-	0	0	4	0	0	5	0	0	6	20	0	0	4	13	5	75	4	43
1955	0	0	3	-	0	0	1	-	0	0	7	0	0	1	0	0	1	-	0	0	3	9	8	100	1	-
1956	0	0	7	-	6	40	5	100	0	0	1	0	0	5	0	0	1	-	3	43	7	35	-	-	-	-
1957	0	0	9	-	11	89	9	-	-	-	-	0	0	9	21	50	6	-	89	86	7	26	18	100	2	-
1958	1	3	29	-	6	93	29	100	0	0	16	17	14	29	5	75	12	0	17	69	26	17	39	88	8	-
1959	0	0	28	-	5	20	25	-	8	17	12	9	8	25	37	100	13	-	114	78	23	21	51	100	5	35
1960	0	0	23	-	3	32	19	40	30	50	2	2	11	19	9	75	4	-	4	57	53	36	13	96	24	25

1961	2	12	51	-	1	6	33	-	0	0	8	0	0	33	0	0	2	-	5	24	45	-	9	94	16	68
1962	0	0	11	-	0	0	9	-	15	33	3	0	0	9	6	67	3	-	0	0	9	-	14	86	7	47
1963	1	9	33	32	0	0	27	-	12	81	16	3	4	27	8	9	11	-	2	22	18	-	8	82	11	54
1964	4	7	67	49	2	4	48	-	5	47	36	17	8	48	21	40	10	7	0	0	23	-	7	50	20	46
1965	0	0	12	95	0	0	12	-	12	35	23	12	17	12	30	58	18	13	6	12	17	-	35	93	15	26
1966	0	0	17	-	0	0	15	-	8	15	13	0	0	15	2	40	5	42	0	0	9	-	20	44	9	31
1967	0	0	10	-	2	20	5	-	0	0	4	24	40	5	2	25	5	31	1	20	5	-	185	64	17	31
1968	0	0	5	-	0	0	3	28	1	50	2	26	33	3	5	20	5	-	0	0	7	22	20	92	12	65
1969	0	0	11	-	6	50	6	-	0	0	4	15	43	7	4	33	6	-	0	0	13	-	11	75	16	45

Riding Mountain and Duck Mountain area, Manitoba (Area 3)

1951	0	0	71	-	3	2	55	-	0	0	10	24	27	55	0	0	10	-	1	5	65	-	138	89	38	21
1952	0	0	43	-	2	18	22	60	0	0	19	18	32	22	0	0	9	-	1	1	97	-	25	100	35	26
1953	0	0	6	-	-	-	-	-	-	-	-	-	-	-	0	0	4	-	1	3	32	-	19	75	8	26
1954	0	0	26	-	0	0	9	-	0	0	25	5	22	9	0	0	3	-	3	16	31	14	17	67	9	40
1955	3	5	22	-	2	25	20	-	0	0	9	3	20	20	0	0	7	-	3	11	37	0	15	63	24	57
1956	0	0	8	-	3	43	7	22	0	0	8	0	0	7	2	43	7	-	3	21	29	-	10	47	15	-
1957	1	7	15	-	6	57	14	-	0	0	5	3	21	14	0	0	1	-	4	22	36	-	12	76	17	-
1958	1	39	54	0	5	65	51	100	0	0	4	10	16	51	0	0	2	-	3	74	31	4	10	90	30	-
1959	2	30	44	-	4	84	37	-	43	13	8	11	19	37	1	20	5	-	5	28	25	-	13	71	24	40
1960	1	3	35	-	4	50	30	40	8	29	17	11	30	30	0	0	3	-	0	0	23	-	20	81	16	32
1961	3	48	31	66	2	26	27	-	0	0	8	9	11	27	0	0	5	-	4	28	25	-	14	61	18	57
1962	2	35	23	44	3	16	19	-	53	80	5	10	47	19	-	-	-	-	0	0	10	-	141	67	6	54
1963	1	8	12	57	0	0	8	-	20	55	11	8	25	8	0	0	3	-	0	0	5	-	85	83	6	66
1964	8	30	20	-	1	7	15	-	11	55	11	31	47	15	0	0	2	-	0	0	12	-	46	77	9	62
1965	0	0	18	-	0	0	17	-	17	29	17	16	65	17	0	0	2	-	1	4	28	-	23	81	11	40
1966	0	0	13	-	0	0	7	-	0	0	12	70	43	7	3	50	2	-	1	9	11	-	17	80	5	47
1967	0	0	16	-	3	14	7	-	0	0	19	14	14	7	0	0	4	-	4	23	13	-	80	22	9	47
1968	0	0	16	-	2	30	10	10	0	0	3	5	30	10	1	29	7	-	2	22	9	-	15	50	6	15
1969	0	0	21	-	4	33	12	-	0	0	9	28	14	14	0	0	2	-	2	23	22	-	27	57	23	5

Northwestern Manitoba (Area 4)

1951	0	0	91	-	5	65	51	40	0	0	45	8	4	51	3	2	64	19	1	6	16	0	47	91	65	25
1952	3	1	67	-	1	9	34	-	0	0	29	24	15	34	0	0	15	-	3	5	21	0	51	92	38	40
1953	17	15	13	-	0	0	10	-	0	0	19	3	10	10	0	0	3	-	3	14	7	-	12	100	15	35
1954	1	2	54	-	1	6	48	-	0	0	15	15	19	48	0	0	8	-	0	0	10	-	51	75	28	41
1955	0	0	28	-	2	8	26	-	0	0	19	11	19	26	4	20	20	23	11	35	26	6	20	70	37	55
1956	0	0	23	-	0	0	18	-	0	0	9	11	17	18	3	30	10	-	32	25	28	100	8	75	20	-
1957	0	0	17	-	0	0	15	-	3	5	21	7	27	15	0	0	10	-	6	20	15	-	13	74	27	-
1958	0	0	24	-	3	29	21	-	0	0	2	11	33	21	0	0	8	-	5	46	26	0	10	91	32	62
1959	0	0	9	-	2	50	6	-	0	0	10	45	50	6	0	0	8	-	6	31	16	-	17	100	10	50
1960	0	0	8	-	1	25	4	-	8	23	13	0	0	4	0	0	9	-	5	30	10	-	30	73	11	45
1961	3	41	17	20	3	7	14	-	3	13	8	18	21	14	1	40	5	-	9	17	24	-	25	78	9	69
1962	3	52	31	39	0	0	24	-	1016	13	8	0	0	24	0	0	9	-	34	56	32	19	28	69	13	67
1963	4	50	28	52	1	9	23	-	30	85	13	14	22	23	0	0	10	-	29	60	25	9	24	90	10	34
1964	6	36	44	55	0	0	32	-	9	39	18	9	19	32	3	8	12	-	58	45	40	12	9	75	20	34
1965	1	3	39	-	0	0	30	-	12	50	16	23	27	30	0	0	11	0	8	41	17	22	23	76	21	71

Continued on next page

APPENDIX 1 continued

Areas and years	*Malacosoma disstria*				*Choristoneura conflictana*				*Chrysomela crotchi*			*Gonioctena americana*			*Choristoneura pinus pinus*				*Choristoneura fumiferana*				*Pristiphora erichsonii*			
	$\bar{x}$	*p*	*n*	*P*	$\bar{x}$	*p*	*n*	*P*	$\bar{x}$	*p*	*n*	$\bar{x}$	*p*	*n*	$\bar{x}$	*p*	*n*	*P*	$\bar{x}$	*p*	*n*	*P*	$\bar{x}$	*p*	*n*	*P*
1966	0	0	25	-	0	0	16	-	5	30	10	37	25	16	6	27	11	-	10	32	25	22	81	46	15	49
1967	0	0	22	-	0	0	9	-	2	8	13	0	0	9	11	27	11	43	11	46	28	24	12	80	15	79
1968	0	0	31	-	0	0	17	-	0	0	7	16	6	17	1	21	14	-	7	53	32	30	16	74	35	46
1969	0	0	30	-	1	6	16	-	0	0	8	12	6	16	0	0	12	-	5	22	32	-	25	59	59	29
Hudson Bay area, Saskatchewan (Area 5)																										
1951	0	0	91	-	4	38	63	67	0	0	11	18	37	63	0	0	9	-	2	8	39	-	53	85	40	21
1952	0	0	72	-	15	2	51	-	0	0	23	23	37	51	0	0	4	-	0	0	44	-	56	95	44	22
1953	1	3	78	-	1	3	58	-	0	0	23	9	22	58	0	0	5	-	0	0	22	-	22	81	21	18
1954	0	0	87	-	2	15	61	-	8	4	24	25	16	61	0	0	6	-	3	2	48	-	24	80	40	32
1955	1	2	102	2	1	13	88	50	0	0	41	25	50	88	6	58	15	15	1	5	78	-	9	78	41	-
1956	0	0	60	-	3	19	52	40	0	0	22	16	29	52	2	22	18	-	3	5	61	-	16	74	31	-
1957	0	0	58	-	4	32	53	35	0	0	24	19	56	54	2	25	8	-	4	13	39	-	24	90	31	-
1958	3	7	58	-	6	54	54	33	0	0	4	17	33	55	0	0	5	-	3	9	11	-	16	91	35	-
1959	2	9	34	-	4	66	35	-	-	-	-	7	31	35	0	0	1	-	1	15	13	-	16	97	33	73
1960	3	10	41	-	4	34	32	-	17	28	39	8	3	32	0	0	2	-	0	0	13	-	27	79	29	67
1961	2	21	58	-	3	7	55	-	5	20	15	14	13	55	0	0	3	-	1	7	14	-	16	54	26	67
1962	3	2	50	62	0	0	45	-	13	57	7	15	2	45	0	0	4	-	2	9	23	-	21	80	20	81
1963	3	6	32	58	0	0	21	-	7	60	10	8	10	21	0	0	4	-	3	5	22	-	12	53	15	44
1964	4	10	59	46	0	0	42	-	9	43	14	6	19	42	3	33	3	-	0	0	27	-	5	64	22	58
1965	3	5	42	-	3	4	25	-	5	18	17	9	32	25	3	14	7	-	0	0	25	-	23	75	29	61
1966	0	0	13	-	0	0	7	-	2	22	18	9	29	7	0	0	5	-	0	0	14	-	63	75	4	63
1967	0	0	19	-	0	0	11	-	1	6	17	0	0	11	0	0	2	50	0	0	11	-	2	45	11	61
1968	0	0	34	-	0	0	17	-	2	4	23	0	0	17	0	0	2	-	0	0	15	-	2	40	10	74
1969	0	0	41	-	2	4	26	-	0	0	16	3	12	26	0	0	6	-	2	3	32	-	9	41	29	21
Prince Albert area, Saskatchewan (Area 6)																										
1951	5	6	68	0	5	55	55	39	0	0	21	9	29	55	0	0	85	8	1	1	70	-	43	82	64	7
1952	9	25	64	36	7	26	50	70	0	0	24	12	32	50	0	0	48	7	27	3	62	32	9	91	79	13
1953	15	42	36	46	3	28	18	89	0	0	18	21	22	18	0	0	20	45	32	26	35	8	20	100	23	17
1954	5	4	68	-	4	52	54	71	3	3	37	20	28	54	0	0	34	19	26	9	33	36	48	85	53	29
1955	0	0	78	-	3	34	50	64	0	0	22	14	38	50	12	44	32	43	25	25	17	50	78	70	66	39
1956	0	0	45	-	3	27	37	85	3	11	9	21	51	37	23	42	19	-	89	17	30	-	30	84	32	30
1957	2	5	39	-	6	58	33	-	0	0	18	10	55	33	2	44	16	-	135	17	24	-	48	82	34	-
1958	1	42	100	2	25	72	90	100	0	0	13	10	23	90	20	56	18	80	31	33	27	8	79	92	36	48
1959	2	33	73	-	13	56	70	-	0	0	14	15	36	70	0	0	5	-	5	10	21	-	42	95	24	54
1960	1	11	95	-	9	54	79	29	3	3	30	19	32	79	3	8	12	-	70	26	47	-	29	95	42	45

1961	2	18	56	37	2	17	46	-	33	14	22	16	24	46	3	18	11	-	108	28	50	-	21	85	47	51
1962	2	31	29	24	0	0	27	-	15	17	6	46	11	27	3	35	40	34	11	22	23	24	34	89	27	53
1963	2	22	60	64	0	0	35	-	31	27	22	6	23	35	5	44	52	17	34	13	45	6	11	81	43	34
1964	2	16	45	55	0	0	42	-	11	68	31	10	14	42	6	51	41	10	46	10	62	5	13	81	43	47
1965	1	7	45	-	0	0	26	-	10	36	11	26	15	26	11	50	26	25	9	27	56	27	37	64	37	39
1966	0	0	53	-	3	3	32	-	7	21	28	21	19	32	35	42	48	28	12	21	48	16	144	63	49	54
1967	0	0	49	-	2	4	27	-	0	0	23	7	11	27	21	31	16	54	8	27	37	18	58	53	54	23
1968	0	0	56	-	2	6	32	-	0	0	26	10	9	32	4	6	18	-	6	22	36	28	41	57	54	62
1969	0	0	76	-	2	7	30	-	7	9	47	0	0	30	0	0	31	-	1	5	32	-	8	43	37	49

Meadow Lake area, Saskatchewan (Area 7)

1951	10	16	43	13	8	50	40	41	0	0	5	17	18	40	0	0	10	-	0	0	31	-	35	87	38	7
1952	10	24	25	55	10	50	18	33	0	0	6	0	0	18	0	0	4	0	0	0	17	-	49	67	15	5
1953	18	88	24	48	33	43	23	79	0	0	13	16	57	23	0	0	2	-	0	0	3	-	30	67	6	8
1954	19	15	52	78	8	58	41	84	0	0	6	6	24	42	0	0	5	0	0	0	7	-	54	92	13	17
1955	0	0	81	-	6	52	61	43	0	0	1	9	16	61	3	20	5	0	0	0	12	-	44	56	18	18
1956	0	0	14	-	3	8	12	50	-	-	-	9	33	12	3	20	5	-	0	0	1	-	5	100	1	37
1957	0	0	19	-	4	35	17	-	0	0	2	13	18	17	-	-	-	-	0	0	2	-	17	100	2	-
1958	1	7	46	-	5	33	36	100	0	0	8	9	25	36	3	17	6	-	0	0	9	-	13	78	9	-
1959	2	6	50	-	2	18	39	-	0	0	6	2	10	39	0	0	8	-	0	0	16	-	17	87	23	38
1960	2	17	77	-	3	14	69	-	1	4	25	16	13	69	0	0	15	-	0	0	21	-	21	83	23	44
1961	3	52	60	54	2	10	52	-	8	13	15	28	17	52	3	6	17	-	0	0	30	-	20	90	39	64
1962	2	61	36	41	1	3	34	-	0	0	8	20	21	34	0	0	19	-	1	5	22	-	18	97	32	69
1963	5	67	36	49	0	0	30	-	0	0	9	15	10	30	3	4	23	-	0	0	33	-	25	76	34	70
1964	1	43	28	70	2	13	24	-	5	20	10	20	13	24	1	5	20	-	0	0	35	-	15	70	27	26
1965	3	11	19	36	0	0	11	-	17	25	8	15	9	11	8	10	10	30	0	0	8	-	68	63	11	50
1966	0	0	19	-	0	0	10	-	7	27	11	3	20	10	34	38	13	16	0	0	12	-	21	72	11	31
1977	0	0	9	-	0	0	7	-	0	0	14	30	14	7	2	25	8	-	0	0	8	-	11	60	15	34
1968	0	0	14	-	0	0	9	-	0	0	10	0	0	9	0	0	6	-	2	7	14	-	8	40	15	36
1969	0	0	59	-	2	7	29	-	6	3	30	0	0	29	0	0	12	-	1	3	32	-	9	3	29	-

APPENDIX 2 continued

Stations and years	November - January		February - April			May - July			August - October		
	Heat units <-18°C	Precipitation (mm)	Heat units >4.5°C	Heat units <-18°C	Precipitation (mm)	Heat units >4.5°C	Soil moisture deficits (mm)	Precipitation (mm)	Heat units >4.5°C	Soil moisture deficits (mm)	Precipitation (mm)
1964-65	336	78	44	156	66	931	28	258	617	41	188
1965-66	346	65	28	126	58	980	81	147	725	70	124
1966-67	216	87	6	188	115	945	104	120	821	125	127
1967-68	218	71	87	58	42	871	88	139	633	69	117
1968-69	307	65	108	95	37	820	26	208	703	53	140
The Pas A, Manitoba (Area 4)											
1944-45	213	73	11	80	53	713	38	155	608	31	173
1945-46	336	86	56	145	55	809	21	205	562	25	219
1946-47	295	109	11	130	64	869	91	125	651	13	209
1947-48	222	92	6	205	107	950	81	158	796	145	69
1948-49	244	55	70	194	69	826	59	154	650	0	219
1949-50	558	54	2	167	56	805	68	143	535	30	161
1950-51	359	70	32	167	49	823	15	233	554	15	201
1951-52	417	42	120	84	17	855	12	270	600	80	73
1952-53	183	67	19	53	84	787	13	219	681	67	151
1953-54	384	97	2	69	66	798	24	200	546	28	149
1954-55	138	66	49	387	81	990	54	194	654	78	104
1955-56	356	129	3	159	92	884	91	125	554	84	98
1956-57	373	71	37	104	80	832	114	87	615	40	145
1957-58	191	79	39	107	91	793	121	79	556	51	153
1958-59	385	100	18	121	45	846	37	187	513	35	168
1959-60	187	66	8	105	100	942	90	147	678	119	78
1960-61	244	49	10	60	75	943	110	113	608	106	101
1961-62	420	97	13	221	82	912	141	77	633	27	187
1962-63	393	69	40	189	47	914	7	264	816	23	174
1963-64	228	43	35	113	56	921	25	226	497	20	197
1964-65	480	47	34	253	44	820	58	177	500	28	178
1965-66	437	79	10	168	54	847	18	243	690	53	133
1966-67	313	68	2	226	65	803	76	123	713	77	171
1967-68	343	87	37	113	55	788	50	157	532	29	141
1968-69	441	84	70	98	34	709	88	97	579	45	173

Hudson Bay, Saskatchewan (Area 5)

1944-45	180	38	18	81	89	695	25	165	581	49	128
1945-46	263	52	96	110	26	820	58	156	571	60	121
1946-47	247	86	24	142	47	891	61	174	637	16	180
1947-48	209	107	12	180	103	938	112	121	715	150	54
1948-49	238	98	108	161	59	834	23	232	656	79	87
1949-50	560	68	11	128	39	808	30	187	542	61	121
1950-51	300	93	52	140	82	837	21	221	524	25	185
1951-52	357	35	154	67	31	856	24	219	617	113	43
1952-53	140	57	35	58	94	824	1	280	702	21	155
1953-54	329	98	4	59	66	794	0	290	559	2	165
1954-55	88	55	71	159	102	965	101	134	640	60	125
1955-56	319	112	13	165	114	908	11	258	536	39	116
1956-57	307	87	51	88	102	863	106	107	623	113	75
1957-58	125	73	62	90	92	802	63	149	596	56	128
1958-59	328	79	41	87	37	881	60	166	504	0	253
1959-60	146	62	22	101	91	915	42	199	702	98	93
1960-61	205	52	30	50	70	964	132	97	644	129	76
1961-62	365	76	37	188	79	921	134	96	638	23	171
1962-63	309	52	59	138	47	920	64	159	821	113	98
1963-64	224	61	55	107	62	944	30	230	495	17	162
1964-65	451	49	46	204	46	862	1	300	531	13	163
1965-66	424	72	18	157	67	869	21	236	643	32	151
1966-67	267	102	6	185	68	849	105	97	714	102	111
1967-68	324	79	67	91	40	790	15	242	532	34	127
1968-69	422	74	98	92	36	751	79	118	616	44	215

Prince Albert A, Saskatchewan (Area 6)

1944-45	213	37	20	85	65	768	41	170	638	68	112
1945-46	251	54	114	116	53	868	69	141	597	59	135
1946-47	304	66	31	186	33	942	193	42	647	26	176
1947-48	159	75	8	219	87	995	81	158	749	90	113
1948-49	302	71	118	201	64	902	37	207	672	71	108
1949-50	623	76	14	138	59	886	51	177	580	88	108
1950-51	312	96	43	196	68	851	62	161	576	69	115
1951-52	432	38	156	78	17	897	29	230	633	57	118
1952-53	159	66	37	78	87	838	72	138	709	106	85
1953-54	351	91	4	97	79	791	1	256	556	1	218
1954-55	91	56	42	203	115	951	89	148	633	94	93
1955-56	359	106	9	180	69	963	87	150	588	100	62
1956-57	298	50	59	90	76	934	104	119	634	61	117
1957-58	107	53	49	100	102	851	94	120	630	88	106
1958-59	327	74	58	113	34	865	121	89	489	41	201

Continued on next page

APPENDIX 2 continued

Stations and years	November - January		February - April			May - July			August - October		
	Heat units <-18°C	Precipitation (mm)	Heat units >4.5°C	Heat units <-18°C	Precipitation (mm)	Heat units >4.5°C	Soil moisture deficits (mm)	Precipitation (mm)	Heat units >4.5°C	Soil moisture deficits (mm)	Precipitation (mm)
1959-60	140	39	26	100	43	916	58	178	695	123	65
1960-61	168	56	31	59	115	1012	142	96	636	114	69
1961-62	364	72	48	225	47	931	128	103	660	145	50
1962-63	309	43	62	112	61	933	19	233	827	88	103
1963-64	250	40	58	77	33	1000	178	58	527	28	163
1964-65	495	36	46	230	54	903	78	162	531	59	105
1965-66	463	45	20	175	49	882	36	203	646	77	95
1966-67	282	54	8	169	34	874	113	99	744	140	70
1967-68	311	69	72	64	36	839	24	230	526	6	174
1968-69	500	69	100	102	31	787	57	147	604	82	159
St. Walburg, Saskatchewan (Area 7)											
1944-45	274	31	27	125	36	763	97	97	567	89	75
1945-46	196	38	90	120	52	781	93	101	523	93	110
1946-47	251	33	47	214	18	847	122	88	536	34	140
1947-48	77	55	17	213	50	985	143	85	682	153	44
1948-49	334	51	111	200	64	778	55	140	641	92	87
1949-50	613	33	27	104	27	863	95	120	566	97	88
1950-51	297	57	51	219	57	745	42	158	487	47	86
1951-52	428	25	143	51	22	808	15	216	603	66	88
1952-53	119	28	45	34	78	816	60	142	652	55	130
1953-54	324	45	13	73	25	746	19	199	537	3	217
1954-55	53	37	40	162	75	850	69	152	555	92	74
1955-56	311	72	16	159	69	946	29	231	571	12	148
1956-57	253	36	75	83	26	912	109	93	542	6	205
1957-58	49	69	54	85	71	825	64	149	651	94	78
1958-59	269	28	64	85	24	780	36	182	411	0	279
1959-60	102	31	36	79	64	825	28	207	594	58	101
1960-61	92	25	21	32	70	943	76	153	607	116	58
1961-62	289	71	58	198	52	870	10	249	629	28	75
1962-63	257	84	69	73	47	885	70	150	768	128	67
1963-64	170	66	42	55	45	930	82	156	491	2	219
1964-65	520	79	49	195	41	860	33	286	534	43	114
1965-66	390	113	23	102	73	845	78	129	598	92	77
1966-67	244	96	12	132	63	814	40	173	707	122	71
1967-68	291	119	60	52	41	802	56	161	475	27	139
1968-69	498	92	94	83	29	760	76	123	545	60	124

APPENDIX 3

MEAN 3-MONTH PERIOD VALUES (EXPRESSED AS PERCENTAGES OF RANGE) OF WEATHER DATA FOR YEARS WHEN VARIOUS INSECT POPULATIONS WERE PRESENT, ABSENT, INCREASING, OR DECREASING. MEAN VALUES ARE UNDERLINED IF THERE IS A DIFFERENCE ≥5 BETWEEN THE PRESENT VS. ABSENT OR INCREASING VS. DECREASING CATEGORIES.

	November - January		February - April			May - July			August - October			
Insect species and status	Heat units <-18°C	Precipitation	Heat units >4.5°C	Heat units <-18°C	Precipitation	Heat units >4.5°C	Soil moisture deficits	Precipitation	Heat units >4.5°C	Soil moisture deficits	Precipitation	No. of readings
Malacosoma disstria												
Present	35.4	28.9	32.8	46.4	49.7	60.7	42.0	46.8	46.3	52.5	34.5	30
Absent	48.1	44.2	29.7	42.5	41.4	47.4	39.0	42.2	35.1	42.6	44.2	52
Increasing	26.7	27.7	33.4	21.7	55.1	61.0	45.4	40.4	40.8	45.9	38.8	24
Decreasing	45.5	30.3	24.4	56.8	51.9	53.5	28.5	57.6	27.2	34.4	53.4	26
Choristoneura conflictana												
Present	38.8	31.0	34.9	39.0	43.2	49.2	36.2	46.8	31.7	41.1	42.9	45
Absent	48.5	37.1	26.0	51.6	49.2	56.1	34.0	50.6	41.8	45.7	44.2	36
Increasing	43.9	45.5	34.0	35.6	43.8	45.0	39.4	41.5	35.8	42.3	39.5	24
Decreasing	32.8	31.6	23.3	40.4	57.6	67.4	48.7	42.1	41.7	47.1	42.9	27
Chrysomela crotchi												
Present	47.6	46.4	20.8	52.1	44.3	57.4	34.9	53.4	36.1	42.6	46.4	24
Absent	35.0	34.7	36.8	35.8	49.3	47.5	38.2	43.1	33.4	38.2	43.9	58
Increasing	42.0	33.0	27.3	44.4	50.4	61.6	42.1	48.0	40.0	56.8	39.4	20
Decreasing	44.6	26.5	22.6	48.6	48.1	59.3	44.3	40.3	47.6	47.0	41.3	24
Gonioctena americana												
Present	40.9	34.9	29.0	44.5	46.7	50.1	37.2	46.5	31.4	43.2	44.3	60
Absent	47.9	39.3	37.4	32.5	37.8	51.6	31.6	50.1	41.2	37.0	47.0	10
Increasing	41.8	28.5	33.5	37.4	48.2	59.0	41.5	45.8	41.9	43.9	42.5	33
Decreasing	38.6	42.9	25.2	45.8	53.4	57.4	41.2	43.3	42.8	46.9	38.0	29

Continued on next page

APPENDIX 3 continued

	November - January		February - April			May - July			August - October			
Insect species and status	Heat units <-18°C	Precip-itation	Heat units >4.5°C	Heat units <-18°C	Precip-itation	Heat units >4.5°C	Soil moisture deficits	Precip-itation	Heat units >4.5°C	Soil moisture deficits	Precip-itation	No. of readings
Orthosia hibisci												
Present	40.7	33.1	26.3	44.2	52.4	54.3	40.6	45.5	37.9	45.3	40.5	56
Absent	45.0	38.1	32.9	40.3	42.3	49.5	37.5	46.6	35.2	43.9	43.0	53
Increasing	29.8	22.7	43.2	26.5	41.4	54.9	34.2	48.9	33.3	43.3	44.5	12
Decreasing	34.8	45.6	19.2	55.1	57.4	71.1	37.5	46.6	47.8	35.4	52.4	12
Campaea perlata												
Present	34.2	33.4	29.1	37.3	51.5	52.9	37.6	48.1	37.9	45.6	41.6	54
Absent	46.9	31.1	32.1	44.8	44.7	53.2	37.5	46.1	37.7	41.8	45.0	59
Increasing	28.2	42.0	22.2	44.0	52.6	53.2	33.4	50.6	31.1	44.0	42.0	8
Decreasing	53.2	63.8	31.3	52.4	43.1	64.3	55.2	30.4	33.7	44.9	36.5	10
Pseudexentera oregonana												
Present	33.0	24.3	34.0	34.5	53.9	64.0	44.2	43.5	45.4	53.7	34.7	30
Absent	44.8	40.2	29.4	45.9	46.0	49.4	37.0	46.9	35.2	41.5	44.1	93
Increasing	-	-	-	-	-	-	-	-	-	-	-	4
Decreasing	-	-	-	-	-	-	-	-	-	-	-	4
Sciaphila duplex												
Present	42.5	40.4	29.6	44.6	53.4	53.0	42.6	41.9	28.8	39.8	42.7	44
Absent	42.4	32.7	27.8	38.0	46.0	56.8	36.4	50.0	44.0	47.0	40.0	60
Increasing	34.3	32.4	36.9	51.0	47.5	51.4	38.8	43.9	38.7	38.3	54.1	20
Decreasing	41.2	35.2	30.7	36.4	32.8	45.5	35.3	42.9	30.0	55.2	33.3	8
Enargia decolor												
Present	38.0	34.1	32.2	38.1	47.1	53.5	37.8	50.4	36.9	48.7	43.0	54
Absent	45.3	39.5	26.0	46.5	47.8	54.1	39.0	44.6	36.4	41.2	42.4	55
Increasing	35.7	19.0	43.7	30.5	43.8	48.2	43.0	36.3	30.9	35.6	44.6	12
Decreasing	38.6	38.0	22.6	50.9	55.6	61.1	34.8	46.1	49.5	39.4	43.0	12

Choristoneura fumiferana												
Present	38.9	35.1	28.4	46.4	49.3	57.7	38.1	49.2	33.6	41.8	46.6	53
Absent	50.1	32.0	34.8	42.8	44.0	58.6	26.2	53.5	41.6	43.9	44.8	17
Increasing	44.6	41.6	24.1	38.9	51.3	58.7	49.9	38.8	39.4	52.0	37.9	23
Decreasing	39.0	29.6	36.9	39.0	37.7	48.3	45.9	40.7	32.3	46.6	45.3	20
Neodiprion abietis complex												
Present	39.4	33.4	33.4	39.4	46.8	61.4	47.4	40.8	36.5	45.6	38.6	39
Absent	43.5	40.2	29.0	46.5	47.8	42.4	31.6	46.5	39.1	40.7	43.3	37
Increasing	38.0	33.3	32.7	33.0	48.1	54.8	36.5	49.0	34.1	43.1	41.9	29
Decreasing	44.0	34.9	23.0	50.5	50.1	58.0	38.6	49.2	39.7	46.8	48.5	27
Acleris variana												
Present	39.3	33.0	28.0	43.9	53.9	57.6	37.9	48.0	38.8	44.1	39.2	51
Absent	44.1	39.3	33.1	44.5	38.6	44.4	45.4	35.8	34.3	45.8	42.3	25
Increasing	39.3	26.8	37.9	29.4	40.7	58.8	33.2	55.1	42.5	41.2	50.3	26
Decreasing	43.4	45.0	23.7	48.4	52.9	51.8	40.8	41.4	33.6	45.2	41.6	29
Choristoneura pinus pinus												
Present	43.9	30.0	31.4	39.9	50.3	56.8	43.5	44.4	37.3	46.8	37.5	29
Absent	43.0	41.7	28.4	35.5	48.5	46.0	32.3	51.2	37.7	40.6	41.8	33
Increasing	32.3	35.7	28.1	54.5	61.8	66.6	39.0	52.2	41.0	42.6	45.1	20
Decreasing	42.6	40.6	28.9	42.5	49.3	45.1	39.5	45.8	34.0	45.9	41.2	25
Neodiprion nanulus nanulus												
Present	44.2	44.9	26.0	61.8	58.0	52.4	37.0	47.7	30.2	28.7	56.3	10
Absent	42.5	42.4	27.7	38.9	51.1	48.1	36.1	48.4	33.3	39.2	42.6	51
Increasing	32.0	37.8	27.3	44.7	57.4	61.0	50.8	41.3	41.9	47.1	39.4	16
Decreasing	40.4	19.9	39.0	43.1	43.6	50.1	27.8	63.0	40.4	53.7	33.2	15
Neodiprion virginianus complex												
Present	47.5	34.0	35.8	44.1	46.7	56.5	44.2	45.7	37.7	50.9	33.6	18
Absent	36.2	46.6	26.6	39.6	55.5	50.7	33.6	51.2	37.2	38.6	42.7	47
Increasing	44.8	25.6	30.2	41.4	49.5	48.0	44.8	44.8	34.2	42.4	45.5	14
Decreasing	36.6	25.5	22.9	53.2	51.0	46.8	34.8	53.6	34.7	46.8	45.4	11
Semiothisa bicolorata												
Present	37.5	30.5	28.1	47.8	51.2	51.6	33.2	53.8	40.4	42.5	47.4	31
Absent	41.4	36.2	29.2	39.2	46.0	48.0	37.9	43.0	38.5	50.2	39.4	47
Increasing	41.1	31.4	29.6	34.6	48.9	53.6	36.6	48.6	24.1	31.2	47.1	27
Decreasing	45.7	47.3	31.9	54.8	46.3	62.8	44.5	46.9	46.4	49.9	41.6	19

Continued on next page

APPENDIX 3 continued

	November - January		February - April			May - July			August - October			
Insect species and status	Heat units <-18°C	Precip-itation	Heat units >4.5°C	Heat units <-18°C	Precip-itation	Heat units >4.5°C	Soil moisture deficits	Precip-itation	Heat units >4.5°C	Soil moisture deficits	Precip-itation	No. of Readings
Zale duplicata largera												
Present	41.4	40.2	22.2	46.1	60.3	57.7	36.5	51.5	39.5	43.6	40.2	27
Absent	40.7	36.4	30.4	37.5	42.4	47.6	38.6	42.0	35.8	41.7	45.6	64
Increasing	36.2	26.0	35.2	48.0	49.0	63.9	39.1	49.8	32.3	49.3	40.0	19
Decreasing	46.0	35.6	33.7	48.7	46.5	59.5	37.9	53.4	41.4	46.0	42.6	20
Pristiphora erichsonii												
Present	43.0	34.6	33.3	40.7	46.7	50.4	35.1	49.2	32.6	42.7	43.5	80
Absent	-	-	-	-	-	-	-	-	-	-	-	0
Increasing	45.8	40.8	25.0	58.1	47.7	55.1	40.5	44.8	34.6	47.6	41.3	21
Decreasing	31.4	32.6	25.2	33.7	51.0	62.1	45.5	40.5	50.5	43.0	43.0	31
Semiothisa sexmaculata												
Present	42.8	32.5	30.2	46.1	46.8	54.5	42.6	42.5	34.6	46.4	40.4	58
Absent	-	-	-	-	-	-	-	-	-	-	-	6
Increasing	36.6	32.4	30.7	35.3	45.0	54.9	40.3	44.1	36.4	37.7	50.7	35
Decreasing	40.2	39.6	26.8	44.0	52.8	53.1	29.7	57.6	42.2	45.7	40.6	32
Anoplonyx canadensis												
Present	42.9	29.2	28.9	41.9	38.0	51.1	27.6	59.6	40.6	47.1	41.6	23
Absent	40.7	38.1	30.7	43.7	51.2	53.2	39.1	43.2	33.8	44.3	39.9	71
Increasing	43.2	36.5	30.7	38.6	40.1	42.6	35.1	48.9	36.0	39.1	53.3	17
Decreasing	36.8	27.8	24.7	39.9	53.9	68.5	52.5	41.1	48.3	44.3	45.0	17
Anoplonyx luteipes												
Present	36.3	28.1	34.8	47.0	47.4	64.3	39.3	48.9	45.2	49.3	42.3	43
Absent	42.3	42.7	31.3	33.0	46.7	45.9	29.3	55.6	36.4	40.0	42.1	41
Increasing	38.3	37.4	23.3	43.7	56.3	54.6	52.0	31.5	30.9	42.4	46.6	26
Decreasing	49.4	32.1	26.3	47.8	41.1	47.5	37.6	42.1	30.8	40.3	41.9	22

APPENDIX 4

POPULATIONS OF THE FOUR MOST COMMON SPECIES OF SMALL MAMMALS (EXPRESSED AS NUMBER PER 0.4 HECTARES) IN LARCH SAWFLY PLOTS IN TAMARACK BOGS

Species and plot	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Clethrionomys gapperi loringi																		
Rennie	0.70	0.90	0.70	1.70	1.60	1.81	0.43	2.23	2.02	2.98	0.53	1.38	10.53	2.23	5.74	6.06	3.19	1.70
Telford	6.20	1.20	0.00	0.50	-	0.10	0.10	0.10	0.40	0.64	0.00	0.11	1.81	0.00	0.00	0.21	1.06	0.21
Seddon's Corner	-	-	-	-	-	-	-	0.39	0.39	1.45	0.39	0.19	9.45	0.09	1.28	2.39	0.00	0.09
Pine Falls	-	-	-	-	-	-	-	-	-	1.92	4.04	3.08	10.74	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
Microtus pennsylvanicus																		
Rennie	0.50	0.00	0.70	0.00	0.47	0.35	0.12	0.12	0.00	0.71	0.00	0.00	0.95	0.00	0.00	0.59	0.12	0.00
Telford	1.00	1.30	1.10	4.20	-	0.10	0.00	0.00	0.00	0.47	0.12	0.35	2.35	0.35	0.00	0.47	2.00	0.00
Seddon's Corner	-	-	-	-	-	-	-	0.00	0.54	0.32	0.00	0.11	0.20	0.00	0.00	1.33	0.10	0.00
Pine Falls	-	-	-	-	-	-	-	-	-	0.59	0.12	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
Sorex cinereus cinereus																		
Rennie	2.10	4.70	2.30	0.50	0.88	5.00	1.12	2.72	0.08	0.24	0.32	0.80	1.28	4.56	6.80	1.04	1.36	1.52
Telford	0.30	3.00	0.10	1.00	0.20	9.30	0.40	0.20	0.20	0.32	0.24	0.64	0.80	1.68	1.36	0.16	0.96	0.56
Seddon's Corner	-	-	-	-	-	-	-	0.29	0.07	0.29	0.15	0.58	0.07	0.00	1.57	0.00	0.16	0.34
Pine Falls	-	-	-	-	-	-	-	-	-	0.08	0.16	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
Sorex arcticus																		
Rennie	0.10	0.50	2.90	4.60	0.39	1.14	0.39	0.31	0.37	0.08	0.00	0.00	0.31	0.16	1.33	0.31	0.08	0.00
Telford	0.00	0.00	0.00	0.00	-	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.31	0.00	0.08	0.00
Seddon's Corner	-	-	-	-	-	-	-	0.00	0.07	0.00	0.00	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	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

APPENDIX 5

NUMBER OF TERRITORIAL MALE BIRDS PER 40 HECTARES IN THE TAMARACK BOG CONTAINING THE RENNIE LARCH SAWFLY PLOT. COMMON NAMES FOLLOW SALT AND SALT (1976).

Bird species	1957	1958	1959	1960	1961	1962	1963	1964	1966	1967	1968
Spruce Grouse	0	0	0	0	0	0	0	0	0	T[1]	0
Ruffed Grouse	T	0	0	0	0	0	0	+[2]	0	T	T
Belted Kingfisher	0	0	0	0	0	+	0	0	0	T	0
Common Flicker	7	0	0	0	T	+	0	+	0	0	0
Yellow-bellied Sapsucker	14	0	7	7	0	7	7	3	T	0	T
Black-backed Three-toed Woodpecker	0	0	0	0	0	0	0	T	0	0	0
Northern Three-toed Woodpecker	T	0	0	0	0	0	0	0	0	0	0
Eastern Kingbird	0	0	0	0	0	+	0	0	+	4	5
Eastern Phoebe	13	9	4	5	9	5	+	5	+	0	0
Yellow-bellied Flycatcher	4	0	0	0	0	8	4	0	0	0	0
Least Flycatcher	14	9	9	10	5	14	5	14	14	0	13
Eastern Wood Pewee	14	0	0	0	0	+	0	+	+	0	0
Olive-sided Flycatcher	13	4	4	5	0	0	0	0	0	0	0
Gray Jay	28	14	4	T	0	+	7	T	0	0	T
Blue Jay	T	T	0	0	T	T	0	T	0	T	T
Black-capped Chickadee	9	4	0	5	0	T	0	0	T	0	17
Red-breasted Nuthatch	T	0	0	0	0	0	0	0	0	0	0
House Wren	T	0	0	0	0	0	0	0	0	0	0
Winter Wren	0	0	0	0	0	0	+	0	0	0	3
Catbird	0	0	0	0	0	0	0	0	0	0	4
Brown Thrasher	0	0	0	0	0	0	0	T	T	0	0
American Robin	4	0	0	0	T	7	0	5	8	4	7
Hermit Thrush	4	0	0	0	0	0	0	0	4	0	8
Swainson's Thrush	5	0	0	0	0	+	0	0	0	5	0
Veery	0	0	0	0	0	+	11	22	17	19	27
Golden-crowned Kinglet	21	0	9	4	0	8	4	0	0	0	0
Ruby-crowned Kinglet	0	0	0	0	8	0	0	0	0	0	0
Cedar Waxwing	P[3]	P	P	P	P	P	P	P	P	P	P
Solitary Vireo	0	0	0	0	0	+	0	0	0	0	4
Red-eyed Vireo	19	8	8	9	16	36	13	10	17	21	24

Black and White Warbler	0	0	0	0	0	20	0	9	20	19	0
Tennessee Warbler	55	27	32	35	42	25	26	16	31	17	21
Orange-crowned Warbler	0	0	0	0	0	0	0	0	0	+	0
Nashville Warbler	51	45	34	37	127	60	35	45	64	81	49
Magnolia Warbler	5	9	14	9	0	9	10	10	0	0	19
Yellow-rumped Warbler	5	0	0	0	40	8	4	9	+	5	9
Blackburnian Warbler	5	0	0	5	14	15	16	21	0	16	9
Chestnut-sided Warbler	11	0	0	5	0	10	+	4	5	5	4
Bay-breasted Warbler	9	0	0	0	0	0	0	5	0	0	0
Blackpoll Warbler	5	0	0	0	0	0	+	0	0	0	0
Palm Warbler	0	0	0	0	9	0	0	0	0	0	0
Ovenbird	0	0	0	0	0	0	T	T	+	T	T
Connecticut Warbler	0	0	0	0	0	5	0	0	0	0	0
Mourning Warbler	5	0	0	0	0	0	0	0	+	6	6
Common Yellowthroat	29	46	32	24	23	33	10	25	13	30	18
Canada Warbler	5	0	0	0	0	0	0	0	0	0	0
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	T	T
Brown-headed Cowbird	0	0	0	0	0	0	0	0	0	T	0
Scarlet Tanager	0	4	4	0	0	0	0	0	0	0	0
Rose-breasted Grosbeak	+	11	9	4	8	4	0	T	0	11	25
Evening Grosbeak	0	0	25	0	0	0	0	0	0	0	0
Pine Grosbeak	0	39	21	0	0	0	0	0	0	0	0
Purple Finch	53	13	8	4	11	15	+	14	0	0	0
American Goldfinch	0	0	0	0	0	0	0	T	+	+	+
Dark-eyed Junco	14	0	14	11	8	13	8	5	5	0	0
Chipping Sparrow	36	12	11	4	13	18	4	9	0	0	8
Clay-colored Sparrow	0	0	0	0	0	0	5	0	0	0	0
White-crowned Sparrow	0	0	0	0	0	0	0	0	0	0	4
White-throated Sparrow	27	15	21	13	43	37	24	37	20	46	42
Lincoln's Sparrow	0	0	0	0	0	0	0	6	0	0	6
Swamp Sparrow	0	0	0	0	0	0	0	0	0	5	5
Song Sparrow	13	8	9	11	0	5	+	0	4	15	5

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[1] T = Populations too low to measure.

[2] + = Birds in area but not on plot.

[3] P = Birds present in plot as roving flocks.

APPENDIX 6

NUMBER OF TERRITORIAL MALE BIRDS PER 40 HECTARES IN THE TAMARACK BOG CONTAINING THE TELFORD LARCH SAWFLY PLOT. COMMON NAMES FOLLOW SALT AND SALT (1976).

Bird species	1954	1956	1957	1958	1959	1960	1961	1962	1963	1964	1966	1967	1968
Spruce Grouse	–	–	–	–	–	–	0	0	0	0	0	+[1]	0
Common Flicker	–	–	–	–	–	–	0	0	0	0	0	0	T[2]
Yellow-bellied Sapsucker	0	0	0	0	0	0	0	0	T	0	0	0	0
Eastern Kingbird	–	–	–	–	–	–	0	0	0	4	0	0	0
Eastern Phoebe	3	0	0	0	0	0	0	+	0	0	0	0	0
Yellow-bellied Flycatcher	0	0	0	0	0	0	0	5	0	0	6	0	0
Least Flycatcher	0	0	0	0	0	0	0	3	5	+	0	14	4
Olive-sided Flycatcher	0	0	0	0	0	0	0	+	0	0	0	0	0
Tree Swallow	–	–	–	–	–	–	0	0	0	0	0	+	0
Gray Jay	0	0	0	0	0	0	0	T	0	T	T	+	T
Blue Jay	0	0	0	0	0	0	0	T	0	+	T	+	0
Black-capped Chickadee	0	0	0	0	0	0	9	0	0	0	0	0	0
White-breasted Nuthatch	–	–	–	–	–	–	0	5	0	0	+	0	0
Red-breasted Nuthatch	–	–	–	–	–	–	T	0	0	0	0	+	0
Winter Wren	–	–	–	–	–	–	0	0	0	0	0	0	T
Short-billed Marsh Wren	–	–	–	–	–	–	T	11	T	0	0	5	0
Brown Thrasher	–	–	–	–	–	–	0	0	T	0	0	0	0
American Robin	3	0	0	T	0	0	T	0	0	0	0	0	0
Hermit Thrush	0	0	0	0	0	0	0	5	0	0	0	5	10
Swainson's Thrush	0	0	0	0	0	0	0	T	0	0	0	0	0
Veery	0	0	0	0	0	0	0	0	0	0	0	0	5
Golden-crowned Kinglet	0	0	0	0	0	0	0	+	0	0	0	0	0
Ruby-crowned Kinglet	–	–	–	–	–	–	0	10	0	5	0	0	0
Cedar Waxwing	0	0	0	0	0	0	0	P[3]	0	P	P	P	P
Solitary Vireo	0	0	0	0	0	0	0	5	0	0	0	4	11
Red-eyed Vireo	17	10	10	10	10	12	7	5	11	6	0	5	5
Black and White Warbler	0	0	0	0	0	T	0	5	0	0	4	4	6
Tennessee Warbler	60	45	38	45	35	50	58	33	19	0	+	0	5
Nashville Warbler	35	20	15	20	15	15	16	60	7	24	25	61	18
Magnolia Warbler	25	15	17	17	15	15	0	10	16	+	0	0	4

Yellow-rumped Warbler	17	15	17	15	10	10	11	10	7	20	5	14	5
Blackburnian Warbler	0	0	0	0	0	0	11	5	0	0	0	0	0
Chestnut-sided Warbler	-	-	-	-	-	-	0	5	0	0	0	0	0
Bay-breasted Warbler	-	-	-	-	-	-	0	5	0	0	0	0	0
Blackpoll Warbler	52	40	35	40	45	45	48	10	11	6	0	0	0
Palm Warbler	-	-	-	-	-	-	0	5	7	10	5	18	14
Ovenbird	-	-	-	-	-	-	0	0	0	+	+	+	0
Connecticut Warbler	-	-	-	-	-	-	0	11	6	0	4	4	14
Common Yellowthroat	45	25	22	25	20	28	19	44	29	11	20	32	20
Canada Warbler	0	0	0	0	0	0	0	5	0	0	0	0	0
Red-winged Blackbird	-	-	-	-	-	-	0	0	0	0	0	+	+
Brown-headed Cowbird	-	-	-	-	-	-	0	0	T	0	0	0	0
Rose-breasted Grosbeak	0	0	0	0	0	0	14	0	0	0	0	0	T
Evening Grosbeak	0	0	0	0	0	0	3	0	0	0	0	0	0
Purple Finch	0	0	0	0	0	0	7	+	0	0	0	0	0
Dark-eyed Junco	-	-	-	-	-	-	0	7	0	4	0	9	4
Grasshopper Sparrow	-	-	-	-	-	-	0	6	0	0	0	5	10
Chipping Sparrow	80	72	58	62	55	55	57	12	7	14	6	21	14
Clay-colored Sparrow	-	-	-	-	-	-	0	34	28	5	0	9	10
White-throated Sparrow	58	50	48	50	40	50	52	+	22	6	6	17	19
Lincoln's Sparrow	-	-	-	-	-	-	0	12	5	37	9	18	19
Swamp Sparrow	-	-	-	-	-	-	0	0	0	0	0	5	27
Song Sparrow	52	48	55	40	45	45	35	9	16	9	9	27	4

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[1] + = Birds in area but not on plot.

[2] T = Populations too low to measure.

[3] P = Birds present in plot as roving flocks.

APPENDIX 7

NUMBER OF TERRITORIAL MALE BIRDS PER 40 HECTARES IN THE TAMARACK BOG CONTAINING THE SEDDON'S CORNER LARCH SAWFLY PLOT. COMMON NAMES FOLLOW SALT AND SALT (1976).

Bird species	1961	1962	1963	1964	1965	1966	1967	1968
Ruffed Grouse	0	0	0	0	T[1]	0	0	0
Eastern Kingbird	0	0	0	0	0	T	0	5
Eastern Phoebe	5	5	3	0	0	0	0	0
Yellow-bellied Flycatcher	0	5	0	5	3	0	0	0
Least Flycatcher	0	8	T	0	4	11	0	7
Gray Jay	0	5	8	0	T	T	0	T
Blue Jay	0	0	0	0	0	T	T	10
Black-capped Chickadee	21	0	0	T	0	0	0	0
American Robin	11	0	0	0	0	0	6	5
Swainson's Thrush	0	0	4	0	5	0	0	5
Gray-checked Thrush	0	7	0	5	0	0	0	0
Veery	0	0	11	0	0	0	0	9
Golden-crowned Kinglet	0	5	0	0	0	5	0	0
Ruby-crowned Kinglet	0	14	0	0	0	+[2]	0	0
Cedar Waxwing	P[3]	P	P	P	P	P	P	P
Solitary Vireo	14	0	0	0	0	4	0	0
Red-eyed Vireo	5	12	0	0	0	9	0	20
Black and White Warbler	0	0	0	0	0	0	0	14
Tennessee Warbler	15	14	5	0	5	0	0	11
Nashville Warbler	25	74	28	28	32	38	30	66
Magnolia Warbler	0	6	0	5	0	0	9	5
Yellow-rumped Warbler	0	12	8	4	4	10	0	14
Blackburnian Warbler	0	6	0	0	0	0	0	9
Chestnut-sided Warbler	0	10	5	0	0	0	0	0
Blackpoll Warbler	0	0	5	0	0	0	0	9
Palm Warbler	13	0	0	0	0	0	0	0
Ovenbird	0	0	+	0	0	0	0	0
Connecticut Warbler	0	13	7	13	13	11	0	19
Mourning Warbler	0	0	+	0	0	0	0	0
Common Yellowthroat	15	19	12	5	12	9	9	36
Red-winged Blackbird	0	0	0	0	0	0	T	T
Brown-headed Cowbird	0	+	4	0	+	+	T	0
Rose-breasted Grosbeak	0	0	0	0	0	0	7	0
Indigo Bunting	0	0	5	0	0	0	0	0
Purple Finch	0	0	0	4	0	4	0	0
White-winged Crossbill	0	0	0	0	0	0	0	T
Dark-eyed Junco	0	22	12	+	4	0	4	0
Chipping Sparrow	9	17	9	+	13	7	4	8
White-throated Sparrow	23	11	5	9	5	5	13	28
Lincoln's Sparrow	0	0	4	0	0	0	0	0
Song Sparrow	6	0	4	+	0	0	0	0

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[1] T = Populations too low to measure.

[2] + = Birds in area but not on plot.

[3] P = Birds present in plot as roving flocks.

APPENDIX 8

NUMBER OF TERRITORIAL MALE BIRDS PER 40 HECTARES IN THE TAMARACK BOG CONTAINING THE PINE FALLS LARCH SAWFLY PLOT. COMMON NAMES FOLLOW SALT AND SALT (1976).

Bird species	1961	1962	1963	1964	1966	1967	1968
Spruce Grouse	0	T[1]	0	0	0	0	T
Ruffed Grouse	T	0	0	0	0	0	0
Belted Kingfisher	0	+[2]	+	0	T	0	T
Common Flicker	0	0	0	7	T	T	T
Yellow-bellied Sapsucker	0	T	7	T	0	0	0
Hairy Woodpecker	0	0	0	T	T	0	0
Black-backed Three-toed Woodpecker	0	0	0	T	0	0	0
Northern Three-toed Woodpecker	0	T	0	0	T	0	0
Eastern Kingbird	0	T	0	0	0	0	T
Eastern Phoebe	4	8	10	+	0	0	+
Yellow-bellied Flycatcher	0	9	0	5	0	0	0
Least Flycatcher	9	9	13	9	+	5	18
Gray Jay	0	5	7	7	T	T	T
Blue Jay	0	0	T	7	0	0	0
Black-capped Chickadee	0	10	0	10	T	0	T
White-breasted Nuthatch	0	0	+	T	0	0	0
Red-breasted Nuthatch	0	0	0	0	0	0	T
Winter Wren	0	3	3	3	3	3	3
Short-billed Marsh Wren	0	T	0	0	0	0	0
American Robin	T	0	0	0	0	0	0
Hermit Thrush	0	0	0	5	0	11	14
Swainson's Thrush	0	5	0	21	13	0	4
Gray-cheeked Thrush	0	T	0	0	0	0	0
Veery	0	0	0	0	0	0	8
Golden-crowned Kinglet	0	T	4	0	0	0	0
Ruby-crowned Kinglet	0	T	0	8	5	11	9
Cedar Waxwing	0	P[3]	P	P	P	P	P
Solitary Vireo	8	0	0	0	9	0	22
Red-eyed Vireo	0	17	14	10	0	8	23
Warbling Vireo	0	T	0	0	0	0	0
Black and White Warbler	0	13	13	0	11	4	12
Tennessee Warbler	4	42	40	0	0	5	0
Nashville Warbler	17	22	5	38	24	9	32
Yellow Warbler	0	T	0	0	0	0	0
Magnolia Warbler	0	4	14	9	0	9	4
Yellow-rumped Warbler	0	15	11	6	21	15	11
Blackburnian Warbler	0	T	0	0	0	0	9
Chestnut-sided Warbler	0	T	0	4	0	0	0
Bay-breasted Warbler	0	14	5	0	10	0	0
Blackpoll Warbler	0	5	0	0	0	0	0

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APPENDIX 8 continued

Bird Species	1961	1962	1963	1964	1966	1967	1968
Pine Warbler	0	5	0	0	0	0	0
Palm Warbler	0	0	5	0	0	0	0
Ovenbird	0	0	0	0	+	0	0
Connecticut Warbler	0	12	4	7	4	0	11
Mourning Warbler	0	4	14	4	+	0	0
Common Yellowthroat	5	14	0	5	5	14	14
Canada Warbler	0	0	0	0	+	0	0
Rose-breasted Grosbeak	0	9	0	5	5	5	0
Purple Finch	4	4	T	0	0	0	0
Pine Siskin	5	0	0	T	0	0	0
American Goldfinch	4	0	0	0	0	T	T
White-winged Crossbill	0	0	0	11	0	0	0
Dark-eyed Junco	42	8	4	4	8	0	0
Chipping Sparrow	4	12	3	8	4	8	0
White-throated Sparrow	19	18	12	28	16	18	28
Lincoln's Sparrow	0	0	0	9	0	0	0
Song Sparrow	5	12	3	4	4	4	9

[1] T = Populations too low to measure.

[2] + = Birds present in area but not on plot.

[3] P = Birds present in plot as roving flocks.