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CRAWFORD STANLEY HOLLING
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# THE ROLE OF SMALL MAMMALS AS PREDATORS UPON SAWFLY POPULATIONS. 


#### Abstract

The basic components and subsidiary factors comprising predation have been demonstrated in field and laboratory studies that analyzed the predation by small mammals of the European pine sawfly, Neodiprion sertifer (Geoff.). Predation was restricted to the cocoon stage of the insect and only three species of small mammals were important predators-Sorex cinereus cinereus Kerr, Blarina brevicauda talpoides Capper and Peromyscus maniculatus bairdii Hoy and Kennicott.


The characteristics of the prey and of the field conditions were so simple that prey and predator density were the only variables affecting predation. There were two basic responses to changes in prey density; the functional response, where the number of cocoons consumed per predator changed and the numerical response, where the density of predators changed. These responses differed for the three different predators. The relation between per cent predation and prey density resulted from a combination of the two basic responses, and this relation increased initially with prey density (concurrent density-dependence) and thereafter decreased (inverse density dependence). The forms of these peaked predation curves was different for each species of predator, for they reached different maxima and peaked at different prey densities.

The functional and numerical responses are the basic components of predation. Laboratory experiments, however, showed that subsidiary factors can exert an effect through these responses. Prey characteristics, by alternating the strength of stimulus from prey, can change both the functional and numerical responses. Similarly, increase in the number or palatability of alternate foods can decrease the functional response and increase the numerical response.

A hypothetical predator-prey model showed that under certain conditions the peaked type of predation can regulate the numbers of a prey and can damp oscillations of prey numbers.

The scheme of predation revealed in this study can explain all types of predation and types of parasitism as well. It seems, however, that there are four major types of predation conceivable, each type having different functional and numerical responses.

## PUBLICATIONS

1. Holling, C. S. 1955. The selection by certain small mammals of dead, parasitized, and healthy prepupae of the European pine sawfly, Neodiprion sertifer (Geoff.). Can. J. Zool. 33 : 404-419.
2. 
3. A radiographic technique to identify healthy, parasitized, and diseased sawfly prepupae within cocoons. Can. Ent., in press.

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THE COMPONENTS OF PREDATION AS REVEALED BY A STUDY OF PREDATION BY SMALL MAMMALS OF NEODIPRION SERTIFER (GEOFF.)
by

CRAWFORD STANLEY HOLLTNG
B.A., 1952, M.A., 1954, University of Toronto

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIRENENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY
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of
ZOOLOGY

We accept this thesis as conforming to the required standard


#### Abstract

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## INTRODUCTION

Predation is an important process affecting animal numbers. It is so complex, however, that it is difficult to understand its role in population dynamics unless we understand its characteristics as a behaviour. We must know the components into which this behaviour can be segregated. We must know the characteristics of the basis components and the way subsidiary ones affect them. These fractions can then be recombined to show how predation operates as a whole, and how predation, operating alone or together with other processes, can affect animal numbers. The main purpose of this thesis, therefore, is to analyze predation in this manner, to reveal the basic components and subsidiary factors underlying the behaviour, and to suggest the role predation plays in regulating the numbers of an animal, in the belief that predation is basically the same wherever it occurs - whether the predator is a wolf and the prey a deer or the predator a shrew and the prey an insect.

The data for this analysis were obtained from a study of predation by small mammals of the European pine sawfly, Neodiprion sertifer (Geoff.) in southwestern Ontario. This sawfly is a serious defoliator of pines and was first reported in North America in 1925 (Craighead, 1950). It spread rapidly, and in 1939 was observed in Ontario near Windsor (op. cit.). It later reached such high numbers in the pine plantations of southwestern ontario that by 1951 the insect caused 70 to $100 \%$ defoliation of Scots, jack, and red pines. This study, therefore, has an additional, more restricted purpose - i.e. to assess the role small mammals
play as predators of an economically important insect.
Similar studies conducted in the past have been concerned mainly with the role of small mammals as predators of various species of sawflies. Most of the reports, however, are cursory and give an indication of the amount of predation only in isolated cases and, as a result, the conclusions are conflicting. In 1912, Hewitt observed that small mammals destroyed cocooned larvae of the larch sawfly, Pristiphora erichsonii (Htg.), but considered that this predation was unimportant. In contrast, Graham (1928) found that $50 \%$ and occasionally 80 to $100 \%$ of cocooned larch sawfly were destroyed by small mammals. Buckner (1955), using a cocoon planting technique to measure predation, obtained results similar to Graham's. The effect of predation on another sawfly, Diprion similis (Htg.) has been reported by Hardy (1939). During 1936 in Poland, $46 \%$ of the cocoons were opened by small mammals. Since he assumed that parasitized and diseased cocoons were attacked as readily as healthy ones, Hardy felt that small mammal predation was not an efficient control factor. Morris (1949), however, showed that this assumption was incorrect for certain small mammals avoided opening cocoons containing dead larvae of the European spruce sawfly, Gilpinia heroyniae (Htg.). Subsequently Holling (1955) showed that this avoidance extended to parasitized and diseased cocooned larvae of the European pine sawfly, N. sertifer. Thus under certain conditions small mammals seem to exert considerable control of insect populations. The exact conditions, however, are not known.

STUIX AREA AND PLOT DESCRIPTIONS
The field work was conducted in southwestern Ontario in plantations near Strathroy and Bothwell. The plantations varied in size from $1 \frac{1}{2}$ acres to 200 acres and in age from one year to ever 20 years. Scots, jack, and red pines were the principal plantation trees and were uniformly spaced within the plantations.

Three plantations, Plots 1, 2 and 3, were selected for concentrated work. In each the mammal populations were estimated by live-trapping and the cocoon populations by quadrat sampling. A description of these plots is given in Tables I and II.

## FIELD TECHNIQUES

A study of the interation of predator and prey should be based upon accurate population measurements, and in order to avoid superficial interpretations, populations should be expressed as numbers per unit area. Three populations must be measured - those of the predators, prey and destroyed prey. Thus the aim of the field methods was to measure accurately each of the three populations in terms of their numbers per acre.

## Manmal Populations

## Methods

Trapping methods were devised to estimate the numbers of the four commonest species of small marmals found in the area:

Peromyscus maniculatus bairdii Hoy and Kennicott - The deer mouse,

Microtus pennsylvanicus pennsylvanicus ord. - The meadow mouse,

Table I
Tree Cover on Small Marmal Plots:


Table II
Per Cent Ground Gover on Small Manmal Plots

| Plot no. | Shrubs: | Herbaceous |  | Orass | Moss | Bare ground | Litter |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Ove inol | Under 8 <br> in.high |  |  |  | Needles | Logs; branches: |
| 1 | 0 | 0 | trace | 10 | trace | 10 | 70 | 10 |
| 2 | 0 | 0 | trace | trace | trace | trace | 90 | 10 |
| 3 | trace | 10 | 20 | 20 | trace | trace | 50 | trace |

Sorex cinereus cinereus Kerr - The masked shrew,
and Blarina brevicauda talpoides Gapper - The short-tailed shrew. Populations of these mamals were estimated using live-traps and snap-traps. Since animals caught in live-traps were marked and released after capture, it was hoped that the populations would be disturbed so little that the normal seasonal changes in mammal numbers could be followed. The live-trapping method, however, was so time-consuming that trapping had to be restricted to only three plantations each year. Such a restricted trapping could not give an adequate idea of the influence of different kinds of plantations upon small mammal populations, so the information from live-trapping was supplemented with additional estimates from snap traps. The disadvantage of snap-trapping, of course, was that captured animals were removed as they were trapped and the resulting population disturbance restricted its use in any plantation to one or two trappings each year.

Two types of live-traps were used, \$herman and bucket traps, each of which was provided with cotton nesting material and a one-to-one mixture of peanut butter and oatmeal. The Sherman traps, measuring $12 \times 3 \times 3$ in., were constructed of galvanized iron and trapped an animal when its weight depressed a treadle, closing a spring door. The bucket traps were 18 in. lengths of stovepipe, 10 in. in diameter, with wire screening on the bottom. These traps were buried with the openings flush with soil surface and, in addition to the peanut butter mixture and the cotton, were provided with fresh canned meat prepared as dog food.

Live-traps were arranged in plantations in a grid pattern similar
to that suggested by Burt (1940) and Blair (1941a). Traps were placed at permanently marked trap stations spaced at one chain ( 66 ft. ) intervals. Because of the marked uniformity of species, age and spacing of trees within plantations, no difficulty was encountered in selecting ecologically uniform areas in which to place the grids. In large plantations each grid measured seven by seven chains and thus enclosed 4.9 acres, while in smaller plantations the size of the grid was determined by the size of the plantation.

Each grid was trapped for six to 10 days during each month throughout the summer. At the beginning of each trapping period, traps were placed at the trap stations and were subsequently checked every 24 hours. Captured animals were marked, the mice by attaching numbered monometal finglerling tags to the ears, and the shrews by toe clipping, and then were released at the point of capture. The species, sex, breeding condition, age (inmature, sub-adult or adult), trap number and grid position of each animal were recorded.

Population estimates were calculated from capture-recapture data using the Peterson or Lincoln Index (Lincoln, 1930). This index estimates the population exposed to traps from the relationship $\frac{m n}{x}$, where $m$ is the number of marked animals in the population, and n is the number of animals captured in a sample of which x animals were marked. For reasons outlined in the following section, the Lincoln Index calculated on the last day of trapping was used as the population estimate.

When few animals are recaptured the Lincoln Index cannot be used. The shrew Sorex rarely survived capture in Sherman traps, and although there was little mortality when the shrews were trapped
in bucket traps, individuals were rarely recaptured. Of 132 shrews released after capture in bucket traps only nine were recaptured. This low incidence of recapture resulted from an initial low probability of capture together with an avoidance of the traps after one capture. In such cases population estimates were calculated using Hayne's method for estimating populations in removal trapping procedures (Hayne, 1949a). Assuming the number of animals captured during any 24 hour period is proportional to the number present, the number of new animals taken during this period may be represented by $y=p(P-x)$ or $\dot{y}=p P-p x$,

Where $P=$ original population
$\mathrm{p}=$ probability of capture $y=$ number of new animals captured during the period
and $\quad x=$ number previously captured before the beginning of the period in question.

When the data are fitted to this straight line formula, by plotting $y$ vs. $x$, the slope is numerically equal to the probability of capture and the $x$-intercept to the population, $P$.

Animals caught in Victor snap-traps provided additional population figures, as well as skins and skulls for identification. These traps were set in lines of 10 trapping stations separated by 30-foot intervals, with five traps set at each station one pace apart at right angles to the line's direction. The traps were baited with the peamut butter and oatmeal mixture and were set for three consecutive days. Since a three-day trapping period with snap-traps is considered sufficient by most workers to remove the resident population, the actual number trapped during this period was taken as the population estimate. The animals captured in snap-traps yielded additional information
that could not be obtained from live-trapping, since dissection revealed more precisely the breeding condition. In addition, measurements were taken of the total length, tail length, ear length and hind foot length of each animal. The stomach contents were examined and preserved in five per cent formalin.

## Analysis of Trapping Methods

Although the trapping methods outlined above, or variations of them, have been used extensively for over 15 years, there is little information in the literature as to their accuracy in estimating the numbers of small mammals. The absence of fundamental work necessary for the development of practical trapping methods has been emphasized by Morris (1955) in a succinct review of the literature since 1941. Some studies have pointed out various sources of error in existing methods, but have been insufficient to permit the evaluation of these errors. "Undoubtedly, any practical method will have sources of error, and the essential thing is to find their probable magnitude so that the insignificant ones can be disregarded and the more serious ones reduced by adjustments in field techniques or in analysis" (Morris, 1955, P.33). The lack of this information requires an analysis of the trapping methods to indicate their accuracy in estimating small mammal numbers.

## Estimates of numbers

Until Ricker (1948) reviewed the methods of sampling populations, manmalogists did not appreciate the conditions which must hold if the Lincoln Index is to be valid;
i.e. (1) The marked animals must not lose their marks, nor the unmarked animals gain marks.
(2) The marked animals must suffer the same natural mortality as the unmarked ones.
(3) There can be only a negligible amount of recruitment to the population being sampled during the sampling period.
(4) The marked animals must be as subject to sampling as the unmarked ones.
(5) The marked animals must become randomly mixed with the unmarked ones, or the distribution of sampling effort must be proportional to the number of animals in different parts of the habitat being studied.
(6) All marked animals must be recognized and reported on discovery.

Of the six assumptions only the first four conceivably: might not hold for the two species, Peromysus and Microtus, whose populations were estimated using the Iincoln Index. Failure of the first three would produce an error through a bias in the proportions of marked and unmarked animals in the population, failure of the fourth through a bias in the proportions of marked and unmarked in the sample. No bias is introduced by gain of tags, certainly, while the loss of tags is similargily unlikely (assumption 1). No tags were lost in a group of 139 tagged mice kept in cages for six to 24 months, and the incidence of torn right ears, upon which tags were clipped, was less than one per cent in the hundreds of mice trapped in the plantations. Mortality of tagged and untagged mice in cages, at least, was similar (assumption 2) and less than one per cent over a six month period.

Further information concerning the second assumption, as well as the third (negligible recruitment), was obtained from field data
for Peromyscus. In eight different trapping periods, trapping was continued for 10 days, and in Fig. 1 the data are pooled to show the daily changes in the cumulative numbers of new animals caught


Fig. 1 - Changes in the cumulative number of new animals caught and in the number of marked animals caught as trapping progressed. Data from eight separate trapping periods.
and in the numbers of marked animals caught. The curve for the former rises at a decreasing rate, approaching a constant at about nine days. If there were much recruitment to these populations in excess of losses, the curve should not level off. Thus recruitment is apparently negligible for the relatively short time comprising a trapping period (assumption 3). The curve for the number of marked animals caught also approaches a constant value when nearly all the animals had been captured. If the mortality of marked animals was very great the number caught should reach a maximum before nine days, and decline thereafter. Mortality among marked
animals was apparently negligible, and since that of unmarked ones would hardly exceed this, assumption 2 should hold.

The final condition that might not hold in the present study requires marked and unmarked animals to be equally subject to sampling. It is unlikely that the tags themselves could alter the susceptibility of marked animals to trapping, but the marking procedures or preliminaries might. Tanaka (1952,1953) has clearly shown that individuals of a number of species of field mice change their behaviour towards traps after the experience of being trapped and marked. In most cases, probabilities of capture of marked animals appeared to increase by a constant value. This permitted Tanaka to apply a simple formula to the relationship and obtain an estimate of the population unaffected by the bias in the susceptibility to trapping of marked and unmarked animals. Similar results were shown for populations of rats by Emlen et al. (1949) who showed that the response to traps after initial capture differed between individuals, some becoming very wary of traps and others becoming addicted to traps. The assumption of homogeneous probabilities of capture among marked and unmarked house mice is also unjustified, at least for the two populations studied by Young et al. (1952). In the present study the susceptibility of Sorex to trapping decreased after one capture to such an extent that less than seven per cent were ever recaptured.

There is little doubt then, that the experience of trapping causes individuals of some species to change their response to traps, some becoming more and some less susceptible to recapture. If the probability of capture of marked animals was greater than that of unmarked, $P$, the Lincoln Index estimate of population would
be too low, but would approach the true value as more animals were captured and marked. If animals avoided traps after one capture then $P$ would be in excess of the true population until all animals were marked. Thus changes in the daily population estimates as trapping progresses should reflect the reaction of marked and unmarked animals to traps. In Table III the data previously presented for Peromyscus (Fig. 1) are analyzed to show the changes in $P$ over a ten-day trapping period. The confidence limits for $P$ were obtained from tables presented by Hald (1952, P.67) showing the confidence limits for the binomial distribution at the 95 per cent level. There is a consistent rise in the population estimate as trapping progressed - a trend that was maintained in each of the eight trapping periods comprising the data. After the fifth day, when most of the animals were marked, the trend was obscured. The marked Peronyscus, therefore, must have been more subject to trapping than the unmarked ones. The results in the literature would at first suggest that the experience of being trapped made deer mice more suscepteble to subsequent capture. It this were true the probability of capture of the population as a whole would increase as progressively more animals received the experience of being trapped, and since less than $10 \%$ of the traps were ever occupied, the total number of animals caught each day ( $n$ ) would reflect this increase. From Table III, n apparently does not increase, but remains relatively constant between 38 and 46. We know that the marked animals, initially at least, are more susceptible to trapping, and yet the experience of being trapped apparently does not affect the probability of subsequent capture.
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Table III
Daily Lincoln Indices for $\underline{P}$. $\underline{m}_{\text {bairdii. }}$ Data Pooled from Eight Separate Trapping Periods.

| Day | No. marked previously <br> m | No. of captures |  | Lincoln Index estimates: |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { Marked } \\ & \mathbf{x} \end{aligned}$ | Total n | P | 95\% Conf. Limits |
| 1 | 0 | 0 | 46 |  |  |
| 2 | 46 | 25 | 38 | 70 | 57-95 |
| 3 | 59 | 28 | 41 | 86 | 72-174 |
| 4 | 72 | 32 | 47 | 92 | 81-115 |
| 5 | 81 | 33 | 43 | 105 | 92-132 |
| 6 | 91 | 35 | 42 | 109 | 98-133 |
| 7 | 98 | 37 | 41 | 109 | 101-128 |
| 8 | 102 | 38 | 40 | 107 | 103-123 |
| 9 | 104 | 39 | 40 | 107 | 104-120 |
| 10 | 105 | 39 | 39 | 105 | -m |



Fig. 2 - Daily changes in the probabilities of capture of all Peromyscus and of marked Peromyscus as trapping progressed. Data from eight separate trapping periods.
in the probabilities of capture of the total number of animals ( $\frac{n}{107}$ ) and of marked animals ( $\frac{x}{m}$ ). The probabilities of capture of the total number of animals do not change greatly throughout the trapping. Marked animals, however, initially have a higher probability of capture that declines as trapping progresses towards the relatively constant value observed for all animals. In Table IV the daily probabilities of capture of Peromyscus are grouped according to the day the animals were first marked. The mice marked early in trapping have consistently higher probabilities of capture than those marked later, and for any group the probabilities of capture remain relatively constant in the days following their initial capture. These results, therefore, cannot be explained by presuming that the experience of being trapped alters the probability

Table IV
Daily Probabilities of Capture of Peromyscus
Marked on Successive Days

| Day of trapping | $\begin{gathered} \text { Marked } \\ \text { day } 1 \\ \text { (46 animals) } \end{gathered}$ | $\begin{gathered} \text { Marked } \\ \text { day } 2 \\ \text { (13 animals) } \end{gathered}$ | $\begin{gathered} \text { Marked } \\ \text { day } 3 \\ \text { (13 animals) } \end{gathered}$ | $\begin{gathered} \text { Marked } \\ \text { day } 4 \\ \text { (9 animals) } \end{gathered}$ | $\begin{gathered} \text { Marked } \\ \text { day } 5 \\ \text { (10 animals) } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $\underline{2}$ | 0.543 |  |  |  |  |
| 3 | 0.565 | 0.154 |  |  |  |
| 4 | 0.521 | 0.308 | 0.308 |  |  |
| 5 | 0.500 | 0.384 | 0.232 | 0.222 |  |
| 6 | 0.478 | 0.154 | 0.232 | 0.445 | 0.400 |
| 7 | 0.500 | 0.232 | 0.232 | 0.111 | 0.100 |
| 8 | 0.543 | 0.308 | 0.254 | 0.222 | 0.200 |
| 9 | 0.521 | 0.308 | 0.154 | 0.000 | 0.200 |
| 10 | 0.500 | 0.308 | 0.232 | 0.111 | 0.000 |
| Av. | 0.520 | 0.269 | 0.220 | 0.186 | 0.220 |

of capture. A more realistic explanation must consider the probability of capture of a population as a characteristic, which, like practically all other characteristics, has a mean and a variability about the mean. On this basis the first trapping of a population would capture more animals whose probabilities of capture were above average than ones whose susceptibility to trapping was less than average. These animals, now marked, would be more susceptible to subsequent trapping than the whole population, and their higher probability of capture would not result from the experience of being trapped. As trapping continued the animals added daily to the marked group would be drawn from ones with lower probabilities of capture and the marked animals as a whole would become progressively less susceptible to trapping. This must occur Whenever traps function by attracting animals, for then probabilities of capture will surely follow a certain distribution among the animals. So long as the results are not complicated by a change in the behaviour to traps after initial capture, the first group of marked animals will have a high probability of capture, and as more animals are marked the probability of capture of the whole marked group will decline to the value of the whole population. This is what was observed for Peromyscus in this study. Although there were fewer data, captures of Microtus in Sherman traps were similarily biased.

The recognition of the error in the Lincoln Index is the first step towards the application of a correction. But such a correction would be impossible until the distribution of probabilities of capture within each population was known. However, if the last day
of trapping (the seventh in most cases) is used to calculate the population for Peronyscus, the error discussed above is negligible, since 91 per cent of the population has been marked. A correction is unnecessary. Microtus, on the other hand, has such a low probability of capture ( 0.170 ) that on the seventh day less than 47 per cent of the population is caught and a population estimate based on the Lincoln Index for that day would be mach too low. So few data were obtained for Microtus that a correction could not be calculated. The only compromise is to use the estimate obtained on the last day of trapping, realizing at all times that this is an underestimate.

Populations of Sorex could not be estimated using the Lincoln Index since their probability of capture dropped to nearly zero after initial capture. As discussed in the previous section, Hayne's method (1949a) of estimating populations in removal trapping procedures was used. A plot of the number of new animals caught per day ( $y$ ) against the number of animals caught previously ( $x$ ) should be a straight line whose slope is numerically equal to the probability of capture and whose X -intercept is an estimate of the population. But as with the Lincoln Index, this relation is based upon certain assumptions: (1) the amount of emigration, immigration, deaths and births must be negligible; (2) there must be no competition for animals between traps; and (3) the untrapped animals must be equally subject to capture throughout the trapping period.

Largely because the trapping periods were so short, the conditions requiring a negligible addition to and loss from the populations probably held. Competition between traps (assumption? ) would be a source of exror when the proportion of single-catch traps occupied
by animals: was high. Since this condition might not hold for Sherman traps, bucket traps, which pernit multiple captures, were used to provide estimates of the numbers of Sorex.

The final assumption, i.e. constant probability of capture throughtout trapping, is more suspect when we recall the way Peromyscus and Microtus reacted to trapping. If this condition did not hold, then the line obtained using Hayne's technique would be curved rather than straight. The slope would gradually decrease if the animals became progressively less subject to capture, and vice versa. In Fig. 3 typical data obtained from the highest populations of Sorex


Fig. 3 - Progressive decrease in the numbers of Sorez caught as trapping progressed.
trapped with buckets are plotted to show the progressive decrease in catch per day as trapping progressed. The points fall very closely about a straight line with a slope (the probability of capture) of -0.213 (standard error $\pm 0.011$ ) and an $x$-intercept ( the population
number) of 257. Data from other trapping periods were similar, with the probabilities of capture ranging from 0.147 to 0.220 . Since the graphs showed no obvious curve the probabilities of capture must remain relatively constant during trapping. Therefore all the assumptions necessary for an unbiased estimate of the numbers of Sorex seem to hold.

The trapping results for Blarina were very similar to those for Sorex. Few Blarina were ever recaptured, so Hayne's technique was again used. The three conditions necessary for an accurate estimate held for this species as well, at least when bucket traps were used. The graphs showing the decline in the numbers of new Blarina caught were very similar to those for Sorex, and the probabilities of capture ranged from 0.170 to 0.219 . It was concluded that the three conditions: necessary for accurate estimates also held for this species.

When insufficient numbers of Sorex or Blarina were captured Hayne's: technique could not be employed. In such cases the actual numbers caught were taken as the estimate of population number. Thus at the very low densities, the numbers of shrews are somewhat underestimated.

When the probabilities of capture for Peromyscus were analyzed, it seemed obvious that the susceptibility to trapping of marked and unmarked animals in populations of any species would change throughout the trapping period, a condition resulting from some individuals having innately high and others low probabilities of capture. The results for bucket trapping of Sorex and Blarina seem to deny this. The way Sherman and bucket traps operate in capturing animals may well differ, however. Sherman traps function by attracting animals, since different kinds of bait affect their probabilities of capture (Fowle and Edwards, 1954). Buckets, on the other hand, are more likely
to catch an animal by a chance encounter when a trap happens to lie in its path of movement. When this occurs animals would be trapped randomly, and probabilities of capture would not change as trapping progressed.

In summary, the Lincoln Index obtained on the last day of trapping provides an adequate estimate of the numbers of Peromyscus. The bias in the sampling of Microtus populations, on the other hand, is so great that no adequate estimates of their numbers can be obtained using the methods outlined. The best estimate available, based on the Lincoln Index for the last day of trapping, is still an underestimate. The assumptions upon which Hayne's (1947) method of estimation is based, hold for bucket-trapping of Sorex and Blarina, so that this method provides a reliable estimate of their populations.

## Estimates of density

One of the objects of this study requires a measure of the numbers of predator and prey per acre. To obtain per acre figures for small mammals the area sampled by traps must be known. Burt (1940) demonstrated from mark-and-release data that small mammals have definite home ranges. Traps on a quadrat therefore capture animals whose home ranges lie partially outside the quadrat, in addition to those whose home ranges lie wholly within the quadrat. The area actually sampled, or effective trapping area, is equal to the area covered by traps, plus a border on all sides of the quadrat equal in width to the mean radius of the home range (the cruising radius). In order to determine the effective trapping area, the home ranges of each species must be calculated.

Burt (1943) has defined home range as the area over which an animal travels in its normal activities of food gathering, mating and caring for young, but adds it must not be considered as having sharply
defined boundries. Hayne (1949b) has reviewed a variety of methods of calculating home ranges, and the principal ones based on capturerecapture data have been critically examined by Stickel (1954) using both artifical and natural populations. Since she showed that the exclusive boundiry strip method gave results closest to the true home range, this method was used in the present study. The measurement assumes that if an animal is caught in one trap, its range extends one-half the distance to the nearest trap. Thus the external points of capture are considered as centers of rectangles, the sides of which equal the distance between traps (in this instance 66 ft .). Since points of capture are often separated, adjacent corners of these rectangles are joined. The area thus enclosed by the rectangles and lines is taken as the home range of the individual.

Such home range calculations appear to be affected principally by trap spacing and number of captures. Hayne (1950) found that the trap-revealed home range of Microtus increased as the spacing between traps increased, a result that was duplicated by Stickel (1954) with a hypothetical population. She found, however, that if the "animals" in the hypothetical population were captured a sufficient number of times, similar home ranges were obtained with different trap spacings. She concluded that the traps should be set close enough together that all individuals can be caught in at least two traps and far enough apart that the traps do not prevent the animal from covering its whole home range during the trapping period. The 66 ft . spacing of traps fulfilled these requirements. With this spacing the trap-revealed home range increased up to about: four captures and then remained relatively constant. Thus, the data used in calculating home ranges included only animals caught four or more times and whose home ranges lay
within the grid.
Adequate home range data were obtained for two species Peromyscus and Microtus (Table V). Although the home range of males of both species seems to be larger than that of the females, a t-test revealed no significant differences. These home range values are similar to those quoted by Blair (1942) for P. m. bairdii and by Blair (1940a), Burt (1948) and Hayne (1950) for M. p. pennsylvanicus. Insufficient numbers of animals of other species were recaptured to obtain adequate home range data. The effective trapping areas for these species were calculated from home range data presented in the literature for animals in grids with a similar trap spacing and in areas with similar ecological characteristics. The effective trapping areas for grids and lines are listed in Table VI, and provide the figures necessary to calculate the number of mamals per acre.

## Population disturbance through trap-mortality

It is helpful in ecological studies of this type if the trapping procedures do not greatly disturb the populations. The data discussed thus far do not suggest any disturbance during trapping. Mortality in traps could, however, so lower the breeding population that subsequent seasonal changes in mammal numbers would not be typical. Table VII compares the mortality experienced by small manmals in Sherman and bucket traps. Only Peromyscus experienced negligible mortality in both traps, while Microtus, Sorex and Blarina were highly sensitive to capture in Sherman traps. The mortality of the latter three species was considerably less in bucket traps. Thus Sherman traps apparently deserve the name "live-trap" only with respect to Peromyscus. Although the least mortality of shrews occurred in buckets, it was
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> Table $V$
> Home Ranges of Adult P. m• bairdii
> and M• p. pennsylvanicus

| Species | Sex | No, of <br> indivi- <br> duals | Av, no, times <br> individuals <br> caught | Av, home <br> range <br> (acres) | Stand. <br> deviai <br> tion | Cruising <br> radius <br> (chains) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| male | 11 | 5.6 | 0.59 | 0.20 |  |  |
| Peromyscus female | 7 | 6.7 | 0.53 | 0.19 |  |  |
| moth | 18 | 6.1 | 0.57 | 0.20 | 1.34 |  |

$-24-$

Table VI
Effective Trapping Areas of Grids and Lines

| Species | Cruising radius | Source | Effective trapping area (acres) |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  |  | $\begin{aligned} & 7 \times 7 \text { chain } \\ & \text { grid } \end{aligned}$ | 270 ft. line |
| Peromyscus. | 1.34 | calculated | 9.22 | 1.66 |
| Microtus | 1.27 | calculated | 8.96 | 1.55 |
| Sorex | 2.11 | Buckner(1957) | 12.2 | 3.03 |
| Blarina | 2.02 | $\begin{array}{r} \text { Blair }(1940 \mathrm{~b}, \\ 194 \mathrm{bb}) \end{array}$ | 11.8 | 2.93 |

still high. When the data for shrews were re-analyzed to see if weather conditions accounted for some of the mortality, rain seemed to play an important part (Table VIII). The number of deaths in buckets when rain fell during the night was significantly higher than when no rain fell. Although this suggests that trap mortality could be greatly decreased by protecting the bucket traps in some way, no time was available to develop and adopt the necessary equipment.

Comparison of density estimates using different trapping methods
As a final test of the accuracy of the trapping methods, the estimates of numbers obtained using bucket, Shefman and snap traps were compared. In the first series of comparisons, Sherman and bucket traps were set simultaneously in different grids located in the same plantation. If the mammals were distributed uniformly throughout the plantations, traps on each grid would sample populations of the same density. Considering the rigid uniformity within plantations, such an assumption seems reasonable, at least until the populations are disturbed by trapping. Table IX compares estimates of the number of animals exposed to such grid pairs. The data are pooled from results obtained in three plantations, one in southern Ontario (Plot 4) and two in northern Ontario (Plots 5 and 6, near Thessalon, in the Kirkwood Forest Management Unit, Dept. of Lands and Forests). The two grids in each plantation were trapped simultaneously each month throughout the the summer, and the totals show that the bucket-trap estimates of the populations of every species differed significantly from the Shermantrap estimates. Estimates of the numbers of Blarina, Sorex, and Microtus from the bucket-trap grids were higher than from the Shermantrap grids, while the reverse was true for Peromyscus. Since the

Table VII
Comparison of Trap－Mortality in Sherman and Bucket Traps

| Species | Trap | Alive | Dead | Total | \％Dead | $\mathrm{x}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Blarina | Bucket | 95 | 20 | 115 | 17 | $27.5^{\text {n金 }}$ |
|  | Sherm． | 14 | 23 | 37 | 62 |  |
| Sorex | Bucket | 79 | 24 | 103 | 23 | $65.6{ }^{\text {堮 }}$ |
|  | Sherm． | 1 | 43 | 44 | 98 |  |
| Peromyscus： | Bucket | 47 | 1 | 48 | 2 | 2.12 |
|  | Sherm． | 837 | 9 | 846 | 1 |  |
| Microtus | Bucket | 36 | 0 | 36 | 0 | $4.75 *$ |
|  | Sherm． | 40 | 8 | 48 | 17 |  |

奴－difference significant at the $1 \%$ level
＊－difference significant at the $5 \%$ level

Table VIII
Effect of Rain on the Mortality of Shrews
in Bucket Traps


Table IX
Comparison of Estimates of the Number of Mammals
Exposed to $7 \times 7$ Chain Grids of Bucket and Sherman
Traps, Each Set in Different Parts of the Same Plantation. (Data from three plantations).

| Species |  | June | July | Aug. | Sept. | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Blarina | Bucket | 23 | 71 | 4 | 10 | 108 |
|  | Sherman | 1 | 7 | 4 | 8 | 20 |
|  | pooled $X^{2}$ <br> btwn. months |  |  | $22^{\text {ant }}$ |  |  |
|  | B/S | 23.0 | 10.0 | 1.0 | 1.2 | 5.4 |
| Sorex | Bucket | 35 | 46 | 36 | 20 | 137 |
|  | Sherman | 1 | 7 | 16 | 13 | 37 |
|  | pooled X ${ }^{2}$ btwn. months |  |  | $22^{\text {ata }}$ |  |  |
|  | B/S | 35.0 | 6.6 | 2.3 | 1.5 | 3.7 |
| Peromyscus | Bucket | 22 | 10 | 2 | 1 | 35 |
|  | Sherman | 21. | 23 | 47 | 24 | 109 |
|  | pooled $X^{2}$ btwn. months |  |  | $1{ }^{\text {at }}$ |  |  |
|  | B/S | 1.0 | 0.4 | 0.05 | 0.04 | 0.3 |
| Microtus | Bucket | 19 | 25 | 30 | 23 | 97 |
|  | Sherman | 1 | 2 | 9 | 8 | 19 |
|  | pooled $X^{2}$ <br> btwn. months | 6.42 |  |  |  |  |
|  | B/S | 19.0 | 12.5 | 3.3 | 2.9 | 5.1 |

results presented in the previous sections indicate that any error in these trapping methods tend to underestimate population numbers, Sherman traps are more accurate in measuring the numbers of only one of the four species, i.e. Beromyscus.

The same table shows the relative efficiency of the two traps for each month, measured by dividing the bucket-trap estimates by the Sherman-trap estimates ( $B / S$ ). There is a regular decline of this ratio from spring to fall, resulting either from bucket traps becoming less efficient or Sherman traps more efficient. As shown by the chi-squares in the table, the monthly differences in relative efficiency were highly significant for Blarina, Sorex and Peromyscus. Although the differences observed for Microtus could easily have occurred by chance ( $P=0.05$ to 0.10 ), the regular decrease in relative efficiency suggests they are real. While such differences could be explained by modified responses to traps related to seasonal changes in climatic and vegetative conditions, it seems possible that population disturbance resulting from mortality in traps accounts for the progressive change in relative efficiency. This possibility was tested in one of the plantations containing a pair of grids trapped throughout the summer (Plot 4, Strathroy), by placing Sherman traps in the buckettrap grid immediately after the last trapping period in September. Hence two comparisons of relative efficiency could be made; one when the two traps were set simultaneously on the pair of grids, and one when they were set consecutively on the same grid (Table X). When set on different grids, the relative efficiency ratio ( $B / S$ ) for Sorex was very low on the last trapping period. When set on the same grid, however, this ratio rose significantly $\left(X^{2}=8.69, P=0.01\right)$ to the original value observed for the first trapping period before populations

## Table X

Comparison of the Relative Efficiences of Bucket and
Sherman Traps in the Last Trapping Period When Both
Types of Trap Were in Different Grids in the Same
Plantation and When Both Were on the Same Grid.

| Species | Trap | Method of comparison of traps |  |
| :--- | :--- | :--- | :--- |

were disturbed by trapping. The apparent decline in the efficiency of bucket traps in estimating the numbers of Sorex apparently results: from the disturbance caused by trapping. If this disturbance was caused by mortality in traps, a greater proportion of the populations must die in bucket than in Sherman traps. Assuming for the moment that the highest estimate obtained in the first trapping period is accurate, the percentages of the populations of Sorex that died in bucket traps in the first trapping was 18\%. So few Sorex were captured in Sherman traps, however, that even though all died, the proportion of the population removed was negligible - only three percent. The decline in the accuracy of the estimates from bucket trapping throughout the season is not real, but results from removal of breeding stock, Very few Blarina were captured when the two kinds of traps were placed consecutively on the same grid so that the two types of comparison cannot be made. The population disturbance resulting from mortality in bucket traps can be calculated, however, since approximately $80 \%$ of the populations afe captured in one trapping period, and of these $17 \%$ die (see Table VII). Hence, $14 \%$ of the populations are removed by bucket traps in one trapping period, as compared to an estimated three percent by the less efficient Sherman traps. Therefore the seasonal decline in bucket-trap estimates of the numbers of Blarina probably results from population disturbance through trap mortality. Such an explanation does not hold for Peromyscus and Microtus, however, since trapping with bucket or Sherman traps removed less than two percent of the populations. In addition, placing the Sherman traps on the bucket grid after the last trapping did not significantly change the relative efficiency ratio (see Table $X$ ). The animals were present on the bucket-trap grid, but they were not being captured by
bucket traps. Since the buckets were pulled part-way out of the ground between trapping periods, the decline in efficiency may have resulted from the mice establishing runways around the traps, rather than from a change in the response to traps related to changes in climate or vegetation.

The data presented earlier (Table IX) comparing population estimates using bucket and Sherman traps included information collected from two different areas in Ontario. In Table XI these data are presented to show differences between the two areas. In order to reveal the actual efficiency of the estimates, the data for Blarina at Thessalon (two grid pairs) and for Sorex at Strathroy (one grid pair) and Thessalon (two grid pairs) include the first two trapping periods only, as well as data from the trapping period when buckets and Sherman traps were placed on the same grid (Plot 4, Strathroy). The remaining data include all trapping periods since the number of deaths in both types of traps happened to be similar. The relative efficiency of the two traps in estimating the numbers of Blarina differed significantly in the two areas. At Strathroy estimates obtained using the two traps were similar, while at Thessalon estimates using bucket traps were 13 times higher. Since these methods tend to underestimate numbers, bucket traps yield more accurate estimates of the numbers of Blarina at Thessalon. Although the data are scarce, both estimates for Blarina at Strathroy appear equally reliable. The results with Sorex and Microtus, on the other hand, were similar, with bucket traps approximately 13 times more accurate in estimating the numbers of Sorex and five times more accurate in estimating the numbers of Microtus. Since locality differences were observed in the population estimates for Blarina, it is dangerous to apply these conclusions to

## Table XI

Comparison of the Relative Efficiencies of
Bucket and Sherman Traps in Two Areas of Ontario.

other areas. Adequate measurements of small mammal populations in other areas should be preceded by an analysis and comparison of different trapping methods.

In the second series of comparisons a grid of Sherman traps was set at one end of a plantation and a line of snap traps at the other end. Grid and line were separated by at least five chains, to avoid interferences between them. Population estimates were obtained in eight plantations, four in southern Ontario and four in northern Ontario, and each plantation was trapped twice during the season, with the trapping periods separated by at least two months. Information therefore was obtained from 16 different trapping periods and these data were largely uninfluenced by disturbance arising from trapping. The results of the comparisons are shown in Table XII. The estimates of the densities of Blarina and Peromyscus obtained with snap and Sherman traps did not differ significantly. Estimates of the density of Peronyscus, in particular, were very similar in every trapping period. On the other hand, the estimates of the densities of Sorex and Microtus were significantly different, with snap-trap estimates approximately twice as high as the Sherman-trap estimates. These same data were tested for differences in relative trap efficiency between the two localities, but no significant difference was revealed ( $P=0.2$ to 0.7 ). The effect of season was also investigated, but again the differences observed were neither significant nor consistent. If the figures for the effective trapping areas are accurate, then any error in the trapping methods will tend to underestimate the numbers per acre. Thus for Peromyscus and probably Blarina, snap and Sherman traps provide equally reliable estimates, while for Sorex and Microtus snap traps provide more reliable estimates.

Table XII
Comparison of the Relative Efficiencies of Sherman and Snap Traps Set in Different Parts of the Same Plantation ( data from 16 trapping periods).

| Species: | Snaps |  | Shermans |  | $x^{2}$ <br> btwn. traps: | $\begin{aligned} & \text { Snaps }+0.01 / \\ & \text { Sherme }+0.01 \\ & \text { (range) } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. of anim. | Av. no. per acre | No, of anim. | Av. no. per acre |  |  |
| Blarina: | 13 | 0.28 | 32 | 0.17 | 2.22 | $\begin{gathered} 1.6 \\ (4.0-0.12) \end{gathered}$ |
| Sorex | 27 | 0.56 | 62 | 0.32 | $6.09{ }^{\text {a }}$ | $\begin{gathered} 1.7 \\ (2.1-0.84) \end{gathered}$ |
| Peromyscus | 37 | 1.39 | 188 | 1.27 | 0.31 | $(1.4 .1$ |
| Microtus | 59 | 2.39 | 207 | 1.40 | 12.06 $0^{\text {atim }}$ | $\begin{gathered} 1.7 \\ (10.0-0.60) \end{gathered}$ |

坆 - difference significant at the 1\% level。

As a third and final comparison of the accuracy of the population estimates using bucket, Sherman and snap traps, one seven by seven chain grid in southern Ontario was trapped with all three traps in September. The grid was first trapped with bucket traps for seven days, then by Sherman traps for the next six days, and finally by snap traps for the following three days. While the grid size remained constant throughout the 16 consecutive days of trapping, when snap traps were added the number of trap positions was increased to 225 by spacing the traps at half chain rather than chain intervals. This spacing, therefore, was similar to the spacing of snap traps in the traplines. This method of comparing traps consecutively on the same grid has certain advantages over the previous method of comparison. For example, since the area covered by traps was the same, errors in the effective trapping area figures could be ignored. In addition it could be reasonably assumed that all animals had been captured after trapping with three types of traps for 1,507 trap-nights.

The results of this comparison are shown in Table XIII and do not include data for Blarina since its numbers were too low. The number of animals exposed to each type of trap vary since some died and others were removed and caged for other studies. The numbers of Sorex and Microtus were accurately estimated using bucket traps. The estimates obtained for these animals using Sherman and snap traps, however, were very low, reflecting a low probability of capture in these traps as well as the error in the Lincoln Index estimates for Microtus. The numbers of Peromyscus, on the other hand, were inadequately estimated using bucket traps but only slightly under-estimated using Sherman and snap traps.

The results from the three sets of comparisons are consistent, and
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Table XIII
Comparison of Population Estimates of Small
Manmals Obtained Using Three Different Traps Consecutively on the Same Grid.

| Species | Buckets |  | Shermans |  | Snaps |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | No. anim. exposed to traps | Pop' $n$ estimate | No. anim. exposed to traps | Pop' $n$ estimate | No. anim. exposed to traps | Pop'n estimate |
| Sorex | 23 | 24(100\%) | 10 | 0 | 10 | 5(50\%) |
| Peromyscus | 18 | 1(5\%) | 18 | 17(95\%) | 17 | 15(88\%) |
| Microtus | 17 | 17(100\%) | 15 | 8(53\%) | 15 | 8(53\%) |

the accuracy of estimates can be summarized as follows:

| Blarina (s. Ont.) | : buckets $=(?)$ snaps $=$ Shermans, |
| :--- | :--- |
| Blarina (n. ont.) | : buckets $>$ snaps $=$ Shermans, |
| Sorex (s. and n. Ont.) | : buckets $>$ snaps $>$ Shermans, |
| Peromyscus (s. and n. ont.) | : Shermans $=$ snaps $>$ buckets, |
| Microtus (s. and n. Ont.) | : buckets $>$ snaps $>$ Shermans. |

Populations exposed to trapping with snap traps will, of course, have individuals removed and subsequent estimates will be affected by this disturbance. But as shown earlier, the same is true when Sorex and Blarina are captured with bucket traps. Until bucket traps can be designed to decrease the incidence of shrew mortality, reliable population estimates can only be obtained for those populations undisturbed by previous trapping.

For the purpose of the present study the foregoing analysis of trapping methods has been designed to show which method or methods provide accurate estimates of the density of the four cormon species of small mammals inhabiting the Scots pine plantations of southern Ontario. In this respect the analysis largely fulfills its purpose. An accurate estimate of the numbers of Sofex and Blarina can be obtained using Hayne's method of treating the data obtained from trapping with bucket traps. In addition, it seems that the numbers of Blarina can also be measured adequately in southern Ontario by using the actual number caught in snap traps or in Sherman traps. But these estimates are accurate only when the populations have not been disturbed by previous trapping. For Peromyscus, Iincoln Index estimates obtained from the results of trapping with Sherman traps provide an ideal way of estimating numbers that is both accurate and unaffected by previous trapping. The actual number of Peromyscus
caught in snap traps also is an adequate estimate, but of course such trapping will affect subsequent changes in the populations. Only with Microtus is it difficult to assess the accuracy of different estimates. The Lincoln Index applied to data collected from trapping with Sherman traps is certainly a gross underestimate because of a strong bias in the probabilities of capture of marked and unmarked animals. Similar estimates of Microtus populations trapped with buckets are higher and hence more accurate than those from Sherman and snap traps, but insufficient numbers of animals were captured to test the data adequately for the assumptions required in using the Lincoln Index. Since bucket traps appear to capture animals, or at least shrews, randomly, the important condition requiring homogeneous probabilities: of capture among marked and unmarked animals probably does hold for Microtus. Thus the bucket-trap estimates, particularily those obtained in the first trapping period, will be tentatively accepted as accurate.

## N. sertifer Populations


#### Abstract

Methods Since, as will be shown later, small mamal predation of $N$. sertifer was confined to cocoons, it was necessary to concentrate population measurements on this life-history stage. During the first two weeks of June, larvae drop from the trees and spin cocoons in the litter and duff of the forest floor. Most of the cocooned sawflies remain in the ground exposed to mammal predation until the latter part of September, when the adults emerge and lay eggs in the needles of pines. A certain proportion, however, have a prolonged diapause and overwinter in cocoons to emerge the following fall. Measurements of the numbers of cocoons exposed to predation by small mammals is considerably


simplified by this abmupt appearance and disappearance of life-history stages. A sampling technique was developed to estimate the number of cocoons containing living insects present imediately after larval drop in June.

Prebble (1943) investigated three methods designed to measure cocoon populations of the European spruce sawfly, Gilpinia hercyniae (Htg.), an insect with habits similar to those of N. sertifer. Estimates using two of these methods were so variable that the number of sample units required for moderate precision was beyond the capabilities of a. field crew. Adequate precision was obtained, however, in his third method, by distributing sub-samples within the restricted universe beneath the crowns of host trees. This method was specially designed to provide an index of population rather than an estimate of numbers per acre. But it is obvious from this work that any cocoon sampling technique designed to yield a direct estimate of the number of cocoons per acre would require an impractically large number of sample units. Anticipating the discussion in the next section, however, it proved feasible to apply a correction to the data collected using his third method in order to obtain a per-acre estimate. The method of sub-sample distribution within the restricted universe was adopted in sampling cocoons of N . sertifer. Briefly, at least 75 trees were selected and marked throughout a plantation, and one or usually two numbered square wooden stakes were placed directly beneath the crown of each tree, on opposite sides of the trunk. Stakes were never placed under overlapping tree crowns. The sides of each stake were lettered from $A$ to $1 T$ and the stake was placed so that the numbefed sides bore no relation to the position of the trunk. Samples were taken each year, two and one-half months after larval drop: by collecting
cocoons from the area delimited by one-square-foot frames placed at one corner of each stake. In the first year's sample the frames were placed at the $A B$ corner, in the second year's at the $B C$ corner, etc. In Prebble's: sampling, cocoons were manually separated from the extraneous material. Owing to the fine nature of the litter and duff beneath pines, in the present study cocoons could be mechanically separated using different sized screens, thus eliminating the chance of overlooking cocoons.

Cocoons were collected in early September before adult sawflies emerged and those from each quadrat were placed in separate salve tins for later analysis. These cocoons were analyzed by first segregating them into "new" and "old" categories. Cocoons of the former category were a bright golden colour and were assumed to have been spun in the year of sampling, while those of the latter were dull brown in colour and supposedly had been spun before the sampling year. The cocoons were then segregated into male and female of the following categories: healthy, emerged, parasitized, small holes (i.e. empty cocoons containing small holes), non-fungus-dead, fungus-dead, and opened by small mammals.

Sample data obtained from the two plots where repeated sampling was conducted are shown in Table XIV. One striking feature is the high variability of the estimates. Similar data shown by Prebble were considerably less variable, the coefficients of variability being approximately half of those shown in Table XIV. His means, however, were obtained by lumping the data from four one-square- foot quadrats set beneath each tree and therefore represent the average number of cocoons per four square feet. In the present study only one or at most two quadrats could be sampled under each tree so that

Table
Surmary of Cocoon Population Data: (The data for each sample were taken and are expressed as the
$\left.\begin{array}{lllllllll}\hline \begin{array}{l}\text { Plot } \\ \text { and } \\ \text { year }\end{array} & & & & \text { New cocoons plus old healthy }\end{array}\right]$

## XIV

Obtained in Plots 1 and 2, 1953 and 1954
from 150 one-square-foot quadrats
number of cocoons per quadrat).

| 01d cocoons |  |  |  |  | Totalnew plus old |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Emerg. | Small <br> holes | Dead | Opened <br> by sm . manmals | Total old |  |
| 49.28 | 52.89 | 13.09 | 30.49 | 145.58 | 202.70 |
| 35.69 | 28.98 | 11.31 | 28.59 | 80.63 | 93.42 |
| 72\% | 55\% | 86\% | 94\% | 55\% | 46\% |
| 2.93 | 2.38 | 0.93 | 2.35 | 6.63 | 7.68 |
| 53.13 | 113.14 | 5.56 | 34.29 | 206.12 | 226.00 |
| 39.77 | 64.17 | 8.95 | 28.64 | 109.66 | 118.11 |
| 75\% | $57 \%$ | 161\% | 83\% | 53\% | 52\% |
| 3.25 | 5.24 | 0.73 | 2.34 | 8.95 | 9.64 |
| 49.77 | 177.29 | 5.89 | 24.75 | 197.69 | 202.55 |
| 37.97 | 60.04 | 7.34 | 21.83 | 99.09 | 100.36 |
| 76\% | 51\% | 125\% | 88\% | 50\% | 49\% |
| 3.10 | 4.90 | 0.60 | 1.78 | 8.09 | 8.19 |
| 49.71 | 83.79 | 18.93 | 24.94 | 177.37 | 197.69 |
| 32.19 | 47.64 | 16.71 | 21.52 | 86.27 | 98.35 |
| 65\% | 57\% | 88\% | 86\% | 49\% | 49\% |
| 2.63 | 3.89 | 1.37 | 1.76 | 7.04 | 8.03 |

$$
-44=
$$

this method of combining data was not possible.

## Analysis of the Cocoon Sampling Method

Just as the trapping must satisfy certain requirements in view of the purpose of this study, so the cocoon sampling technique must meet certain objectives. If the numbers of predator and prey are to be related to predation, then the number of cocoons spun in the year of sampling must be known. Separating cocoons into new and old is an attempt to do this. It is essential, however, to find the magnitude of error in this separation and correct it if necessary. In addition, it is desirable to express populations of all animals in terms of a common unit. Hence, the cocoon population should be calculated on a per acre basis.

The basis for the segregation into new and old cocoons assumes first, that cocoons spun in the ground retain their golden colour for at least three months and, second, lose this colour after three to 14 months in the ground. If these assumptions are valid, then all "new" cocoons in the sample were spun in the year of sampling and all "old" cocoons were spun in previous years.

To test the validity of these assumptions the numbers of new and old cocoons collected in the regular sample in 1953 at Plot 2, were compared to the numbers collected from two check samples made before and after larval drop. The 100 quadrats of the check sample were arranged in the same manner as in the regular samples and were first sampled June 9 to 11, five days before the larvae began dropping from the trees. The material in the quadrats was removed in three separate layers - litter, duff, and soil. After the cocoons were screened and removed from each layer, that layer was returned to
the quadrat and the corners marked with small sticks. It was hoped that pre-spinning larvae would react to these disturbed, "sterile", quadrats in the same manner as to the undisturbed, regular quadratse. When the regular quadrats were examined August 24 to 26 , two and one-half months after larval drop, the previously sterile check quadrats were remexamined and the cocoons collected. Since the aim of the sampling was to estimate the number of living cocooned larvae (healthy cocoons) in the ground immediately after larval drop, the sawflies that remained in diapause overwinter (i.e. old, healthy cocoons in the regular sample, or healthy cocoons from the first check sample) therefore were added to the 1953 cocoon population. The comparison of the regular and check samples is presented in Table XV. Since the total number of male and female cocoons collected in the regular and check samples are almost identical ( $P$, males $=0.50-0.70 ; P$, females $=0.20$ ), the pre-spinning sawfly larvae could not have differentiated between disturbed and undisturbed quadrats. The number of cocoons collected in the second check sample plus the healthy cocoons collected in the first, therefore should be an accurate estimate of the number of healthy cocoons present after larval drop. That is, there were 21.63 healthy male and 17.34 healthy female cocoons per sq. ft. after larval drop in 1953. According to the estimate from the regular sample based upon the segregation of new and old cocoons by colour, these estimates were considerably higher - 30.91 and 24.83 respectively. Thus the second assumption (that cocoons lose their "new" appearance after 14 months in the ground) is erroneous; the number of cocoons in the new category is greater at the expense of those in the old. The first assumption, that cocoons retain their

$$
-46=
$$

Table XV
Comparison of Two Methods of Sampling Cocoons to Determine the Population of Healthy Cocoons Present After Larval Drop - 1953 Collections, Plot 2.

| Method of separating ' 53 pop'ns from earlier ones | No. of cocoons per sq. ft. |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Cocoons spun 153 plus healthy ones from prev. years |  | Cocoons spun before 153 less healthy ones |  | Total |  |
|  | Male | Female | Male | Female | Male | Female |
| by colour <br> (regular <br> samples) | 30.91 | 24.83 | 68.58 | 77.18 | 100.71 | 102.01 |
| by collecting cocoons before and after 153 larval drop (check samples) | 21.63 | 17.34 | 79.44 | 85.75 | 101.07 | 103.09 |

new appearance for approximately three months, however is valid, since all cocoons collected in the second check sample were a gold colour.

These results can only be explained in terms of the factor that determines the colour change. This factor apparently is the amount of soil moisture. When new cocoons are immersed in water the colour changes in approximately one month. On the other hand, when new cocoons are in a dry environment the new appearance is retained for over a year. A sample of 500 new cocoons still appeared new after one and one-half years in a clean bottle open to room atmosphere. In the natural cocoon environment, the amount of soil moisture is determined in part by the quality of the soil and in part by the amount of precipitation. In the area where this project was studied, N. sertifer spins cocoons in the well drained, sandy soils of the Caradoc and Bothwell Sand Plains (Chapman and Putnam, 1951). Such soil conditions, together with a moderate rainfall (mean anmual precipitation 32 to 38 in., Putnam and Chapman, 1938) cause a dry soil, particularly in the top two inches where cocoons are spun. Owing to the dry conditions of this environment, all cocoons retain their golden colour for at least three months, and some retain the colour for at least 14 months. The resulting error in the estimation of the number of healthy cocoons present in the year of sampling immediately after larval drop requires more than passing acknowledgement.

Before attempting to corfect the data collected from the regular fall samples, it is convenient to divide the cocoons into three categories - "sound" cocoons containing healthy and parasitized prepupae (ㅇ), "emerged" cocoons from which sawfly adults have emerged $(\underline{E})$, and the remaining cocoons (opened by small mammals, containing
small holes, etc. - R ). The sound cocoons collected in the fall must have been sound after larval drop, so that these represent part of the desired estimate. None of the emerged cocoons, on the other hand, could have been sound during the summer, since Griffiths (unpublished MS.) observed that no sawflies emerged from 12,000 cocoons before regular cocoon samples were taken (Aug. 25 to Sept. 3). All adult sawflies emerged after Sept. 5. The remaining categories of cocoons, however, contain coccons that were sound in June, after cocoons were formed, their contents having been destroyed before the fall samples were taken. The numbers of these cocoons must be determined so that they can be added to the known number of sound cocoons (s) in order to provide an estimate of the number that were sound immediately after larval drop in June. A clue to the value of this unknown can be obtained from the composition of emerged cocoons (E) and the remaining cocoons (승 in any fall sample. These are shown below:

| Category | Vintage | Colour | Symbol |
| :---: | :---: | :---: | :---: |
| emerged cocoons | previous year's | old colour | $\mathrm{E}_{0}$ |
|  |  | new colour | En |
| remaining cocoons | previous year's | old colour | $\mathrm{R}_{0}$ |
|  |  | new colour | $\mathrm{R}^{1}$ |
|  | current year's | new colour | $R_{n}$ |

The sample data provides the numbers, $E_{0}, E_{n}^{\prime}, R_{0}$, and $\left(R_{n}^{\prime}+R_{n}\right)$. All the remaining cocoons spun in the year of sampling ( $R_{n}$ ) would be sound immediately after larvae dropped from the trees to spin cocoons. On the other hand, very few of those remaining cocoons spun in
previous year's ( $R_{0}$ and $R_{n}^{\prime}$ ) would be sound at that time, since only a small proportion of sawflies overwinter in cocoons. Furthermore, it will be shown later that the ones that do overwinter are rarely attacked by small mammals. Hence $R_{0}$ and $R_{n}^{\prime}$ are not part of the desired estimate, while $R_{n}$ is. If the colour change in emerged cocoons is the same as in the remaining cocoons then $E_{0}: E_{n}^{\prime}:: R_{0}: R_{n}^{\prime}$ or $R_{n}^{\prime}=R_{0} E_{n}^{\prime} / E_{0}(I)$ of which $R_{0}, E_{n}^{1}$, and $E_{0}$ are known, and hence $R_{n}^{\prime}$, the number of unsound cocoons that retained their new appearance, can be calculated. The value of ( $R_{n}^{\prime}+R_{n}$ ) is known from the sample analysis so that $R_{n}$ can be calculated by subtracting $R_{n}^{\prime}$ obtained from (1). Thus the number of cocoons that were sound immediately after larval drop equals $S+\left(R_{n}+R_{n}\right)-R_{n}^{1}$.

This correction will hold only when the proportion of sawflies that emerge from cocoons is constant from year to year. While this would probably be true in a stable population, the densities of cocoons observed in this study declined from year to year. With concurrent and inverse density-dependent factors operating upon cocoons, the percentage of emergence from cocoons would similarily change and introduce an error into the correction factor. The decline in sawfly numbers, however, could be directly attributed to a highly virulent, introduced virus disease (Bird, 1950,1952,1953) that attacked the larvae. Since the density-dependent factor causing the greatest mortality affected the larval and not the cocoon stage, the change in the percentage of emergence from cocoons with change in density, and hence the error, was not as great as might be expected. Although no data on the actual emergence were obtained, the percentages of cocoons remaining healthy after two and one-half months in the ground ranged from 65\% at the highest density to $88 \%$ at the lowest
(Plots 1 and 2 between 1952 and 1954). If the percentages of emergence from cocoons were similar the correction would not be greatly in error. The error would certainly be less than if no correction was applied.

In Table XVI this correction is applied to the cocoons collected in the regular sample, Plot 2, 1953. When the corrected number of sound cocoons per square foot present after larval drop is compared to the actual number (final column) as determined from the check samples, the estimates are similar. In this sample, at least, the correction permits a more accurate estimate of the number of cocooned sawflies exposed to predation by small mammals.

The corrected yearly samples provide the best approximation of the number of sound cocoons per square foot. But before these estimates can be expressed as number per acre, the distribution of cocoons in reference to the sampling area under tree crowns must be determined. This sampling afea included a circle around the base of the trees with ai radius of approximately two feet. The problem now is to determine the relation between the cocoon population within these circular areas and that outside these areas. This relation was measured by sampling cocoons obtained in one-square-foot samples along radii starting at the tree trunk. Data were collected along radii from eight trees located within a plantation similar in age and ground cover to those in which cocoons were regularily sampled. The numbers of cocoons collected from these successive quadrats are shown in Fig. 4. The density of cocoons within two feet of the trunk is quite different from that beyond two feet. For purposes of calculating the number of cocoons per acre the forest floor must be stratified. Three strata: were recognized;

Table XVI
Calculations Correcting the 1953 Cocoon Sample Data from
Plot 2 (148 square-foot quadrats) for the Number of
Sound Cocoons After Larval Drop

| Sex | $\mathrm{R}_{0}{ }^{\mathbf{2}}$ | $\mathrm{E}_{\mathrm{n}}^{\prime}$ | $\mathrm{E}_{0}^{\text {t }}$ | $S+\left(R_{\underline{n}}^{\prime}+R_{n}\right)^{\text {n }}$ | $\underset{\underline{n}}{R^{\prime}}=\frac{R_{0} E_{n}^{n}}{E_{0}}$ | $S+\left(R_{n}^{\prime}+R_{n}\right)-R_{n}^{\prime}$ | No. of sound cocoons/ sq. ft. after larval drop |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  | Corrected | Actual (check sample |
| Male | 6484 | 667 | 3683 | 4087 | 1174 | 2913 | 19.68 | 21.63 |
| Female | 7794 | 371 | 3610 | 3304 | 801 | 2503 | 16.91 | 17.34 |
| Total | $\underline{4278}$ | 1038 | 7293 | 7391 | 2032 | 5359 | 36.21 | 38.97 |

$\mathrm{L}_{\mathrm{R}_{\rho}}=$ number of cocoons with "old" colour less emerged and sound cocoons.
$\mathrm{F}_{\mathrm{h}}^{\mathrm{\rho}}=$ number of energed cocoons with "new" colour.
$\mathrm{E}_{\mathrm{o}}=$ number of emerged cocoons with "old" colour.
$S^{\circ}$ number of sound cocoons.
$R_{n}^{\prime}=$ number of cocoons from previous years that retained their $n_{n e w n}$ colour less emerged and sound cocoons.
$R_{n}=$ number of cocoons spun in 1953 less sound cocoons.


Fig. 4 - Number of cocoons collected in successive one-squarefoot quadrats radiating from the trunks of eight trees growing within a plantation.
(1) circles around the tree trunks with two foot radii,
(2) intermediate rings with inner radii two feet and outer radii three feet,
and (3) outer strata comprising the remaining area (three to five feet from the trees).

The number of cocoons in the first strata can be determined directly from the square foot figures obtained in the regular samples, since this is the area actually sampled by quadrats. The density of the cocoons in the remaining areas is some fraction of this. From Fig. 4, the densities in the remaining two strata are, respectively, 0.607 and 0.357 of that in the first strata. Although the number of cocoons collected along each radius ranged from 105 to 649, these fractions were much less variable, i.e. from 0.333 to 0.761 and from
0.202 to 0.404 respectively. This suggests, as does observation of the movements of pre-spinning larvae, that the fractions are not related to density but simply to the extent of larval wandering. These fractions permit an estimate of the number of cocoons per acre, by using the following formula:

$$
P=A_{1} d x+0.607 d x\left(A_{2}-A_{1}\right)+0.357 d\left(A-A_{2} x\right)
$$

where $P=$ number of cocoons per acre,
$\mathrm{d}=$ number of cocoons per square foot as determined from regular quadrat samples,
$x=$ number of trees per acre,
$A=$ number of square feet in an acre $=43,560$,
$A_{1}=$ number of square feet in a circle with two-foot radius $=$ 12.57,
$A_{2}=$ number of square feet in a circle with three-foot radius $=$ 28.27.

Substituting the constants

$$
P=12.57 \mathrm{dx}+0.607 \mathrm{dx}(28.27-12.57)+0.357 \mathrm{~d}(43,560-28.27 x),
$$

which reduces to

$$
P=(12.0 x+15,500) \mathrm{d}
$$

The populations calculated in this manner ranged from 39,000 (Plot 1, 1954) to 1,080,000 (Plot 2, 1952) cocoons per acre.

## Predation

Methods
Small mammal predation has a direct and indirect effect on N. sertifer populations. The direct effect of predation is studied in detail in this thesis. The indirect effect, resulting from the mutual interaction of various control factors (parasites, disease,
and predators) has been discussed in a previous paper (Holling, 1955).

The direct effect of predation was measured in a variety of ways. General information concerning predation was obtained from studies of the consumption of insects by caged animals and from the analysis of stomach contents obtained from animals trapped in sawfly-infested plantations. More particular information was obtained from the analysis of cocoons collected in the regular quadrat samples and from laboratory experiments which studied the effect of cocoon density upon predation.

Animals from which stomachs were removed for analysis were trapped with snap traps. Shortly after capture the stomachs were removed and the volume of the various food items was estimated to the nearest 10\%. Since the food items were mainly vegetable or insect, three categories were recorded: plant, N. sertifer, and other insects. Familiarity with the appearance of the food was acquired by examining stomach contents of caged animals fed one particular item. In this manner a reference collection of stomach contents was obtained with the following food items represented: Scots and jack pine seeds, grasses, N. Sertifer larvae and prepupae, Carabids, ants, and miscellaneous Coleoptera, Hymenoptera, and Diptera. N. sertifer could be easily separated from other insects even when the larvae were well masticated.

The actual numbers of $N$. sertifer cocoons destroyed were calculated from cocoons collected in the regular quadrat samples described previously. Cocoons opened by small mammals were easily recognized. To determine the appearance of these cocoons, caged animals were provided with healthy cocoons. The openings made in
approximately 4,000 cocoons opened by five caged Sorex, 2,000 cocoons opened by five caged Blarina, and 5,000 cocoons opened by 10 caged Peromyscus, were examined and compared with those from which sawflies and parasites had emerged. The jagged, asymmetrical holes chewed in cocoons by small mammals can be distinguished readily from the smooth uniform holes made by emerging sawflies and parasites and from the small holes made by predatory insects such as elaterid larvae. It is also possible to classify the chewed cocoons as to species of predator (Fig. 5). The chewed category of cocoons was


Fig. 5 - N. sertifer cocoons showing, from left to right, cocoons opened by S. c. cinereus, B. b. talpoides and $\underline{P}$. m. bairdii.
therefore subdivided into cocoons chewed by Sorex and those chewed by other small mammals, principally Peronyscus and Blarina.

The problem remains to estimate the number of cocoons opened in
a given time, over a given area; that is, the number opened per acre from the time of larval drop to the time when cocoon samples were taken. Per acre figures were obtained in the manner previously described. Similarly, the estimation of the number of cocoons opened in the time designated depended on the new-old cocoon segregation described previously. In an earlier section the error involved in this segregation was corrected so that a reliable estimate of the number of cocoons present immediately after larval drop could be obtained. To estimate the numbers of these cocoons that were opened by small mammals, the percentage of the new cocoons (uncorrected) that were opened was calculated. The corrected number of healthy cocoons present immediately after larval drop was multiplied by this percentage to give the number of cocoons opened from the time of larval drop to the time samples were taken. This percentage certainly appears to reflect the degree of predation in the year of sampling. In the first year samples were taken (1952) from Plot 2, $11 \%$ of the uncorrected new cocoons and $29 \%$ of the old cocoons were chewed. The following year, 1953, the percentage of the old cocoons that were opened dropped to $21 \%$ as a result of the dilution of the 11\% predation of the previous year. In 1953, $10 \%$ of the uncorrected new cocoons were chewed and again this low predation lowered the percentage of old chewied cocoons to $13 \%$ in 1954. This relationship also held in the yearly samples collected from Plot 1. The percentage of new cocoons chewed therefore appears to be quite separate from that of old cocoons, and provides the best estimate of predation from the time of larval drop to the time when cocoon samples were taken.

An attermpt was made to measure predation more conveniently by using cocoon "plants". Both Graham (1928) and Morris (1949) used
this technique by burying small cheese-cloth bags, each containing five cocoons, throughout various plots. Buckner (1955) later used a variation of this technique and wired two cocoons to a small tree tag "in order to simulate natural conditions more closely". This latter technique was used in this study with one male and one female cocoon wired to each tag. The plants were buried about two inches in the litter and duff so that the top inch of the tag projected above the litter. The tags were distributed throughout the plots at one chain intervals in a grid pattern. Seven days after planting, they were removed and the cocoons recorded as untouched, opened by Sorex, or opened by other small mammals. The predation was calculated as the percentage of the planted cocoons destroyed in the seven-day period. Multiplying the number of cocoons per acre (calculated from the quadrat samples) by this pefcentage should give the number of cocoons destroyed per acre over the seven-day period. The reliability of this estimate will be examined in the following section.

Comparison of Quadrat Sampling and Cocoon Planting for Measuring Predation
As a preliminafy to a comparison of the two principal methods of measuring predation, cocoon planting experiments were conducted in az 10 to 15 year old plantation. Plants were buried three times in 1953. The cocoon density was roughly estimated by collecting cocoons from 10 one-square-foot quadrats, at the time each group of plants were buried; mammal populations were estimated with a grid of Sherman traps. The results are presented in Table XVII. According to these results, from 1,000 to 7,000 cocoons were opened per mouse-day. Since Peromyscus is nocturnal, the animals would be active for approximately eight hours per day, and from two to 14 cocoons would have to be opened per minute. This is obviously implausible and is certainly

Table XVII
Preliminary Analysis of the Accuracy of
Measuring Predation Using Cocoon Plants.

| $\begin{aligned} & \text { Date } \\ & 1953 \end{aligned}$ | No. of plants | No, of cocoons per acre | \% Plants chewed by Peromyscus | No. chewed per acre | No. of mousedays/ acre | No. chewed/nouse/ day |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\begin{aligned} & \text { May } 16 \\ & -23 \end{aligned}$ | 122 | 300,000 | 23.8 | 71,000 | 23.1 | 3,000 |
| $\begin{aligned} & \text { June } 29 . \\ & \text {-July } 6 \end{aligned}$ | 122 | 600,000 | 27.1 | 160,000 | 23.8 | 7,000 |
| $\begin{aligned} & \text { Aug. } 12 \\ & -19 \end{aligned}$ | 122 | 300,000 | 10.6 | 32,000 | 29.4 | 1,000 |

Table XVIII
Comparison of the Number of Cocoons Opened per MamnalDay, Calculated from Cocoon Plants and Quadrat Samples.

| Source of predation data | No. cocoons per acre | \% cocoons opened by Peromyscus | No. opened per acre | No. of mousedays | No. opened/ mouse/day |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 112 coc. plants set for 7 days | 139,000 | 69.6 | 96,700 | 24 | 4;030 |
| $\begin{aligned} & 150 \text { one- } \\ & \text { sq.-ft. } \\ & \text { quadrats } \end{aligned}$ | 139,000 | 1.94 | 2,690 | 382 | 7.04 |

not supported by data obtained from caged animals. The error must result from over-estimates of the cocoon density, or predation, or an underestimate of the mammal density. Buckner (1955) observed the same high values using cocoon plants, and, on presumptive evidence, felt that the cocoon density was overestimated. Since in the present study at least, the method of measuring predation is most suspect, experiments were conducted comparing the effectiveness of cocoon plants and quadrat samples in measuring predation.

In Plot 1 in 1953, 112 cocoons were buried from June 30 to July 7, one week after larval drop had stopped. The quadrat sample was taken August 26. Cocoons were collected from 150 one-square-foot quadrats and were analyzed in the manner previously described. From both methods the number of cocoons opened per mouse-day was calculated. With each method, cocoon density was derived from the quadrat samples, and mammal density from Sherman grid trapping conducted throughout the summer. Thus any difference must result from differences in measuring the amount of predation. The results of the comparison are presented in Table XVIII. The number of cocoons opened per mouse-day calculated from quadrat samples is reasonable in view of data to be presented later, while that from cocoon plants is again implausibly large. The cocoon planting technique as used in the study does not accurately measure predation, for the animals react to the tags plus the cocoons and not to the cocoons alone. In a previous paper (Holling, 1954) it was shown that small mammals locate buried cocoons by olfactory stimuli. In locating cocoons tied to tags, the normal response directed by olfactory stimuli apparently becomes directed. additionally by more obvious stimuli, perhaps visual, from the tag. It is understandable, therefore, that predation on cocoon plants
would not reflect predation on naturally distributed cocoons in the ground.

In view of the error involved in measuring predation with cocoon plants, these data afe not included here. It is possible, however, that some cocoon planting technique can be developed in the future to provide reliable data.

It has proved difficult to obtain a predation and cocoon population estimate of the desired precision and accuracy. Although the corrections and calculations applied to the raw sampling data provide the best available approximation of the number of cocoons, and the number opened per acre, the results and conclusions derived from field data are suspect. Their validity has been completely supported, however, by controlled laboratory experiments.

## LABORATORY TECHNIQUES

Several experiments were conducted with caged animals in order to support and expand results obtained in the field. The most important of these measured the number of cocoons consumed by Peronyscus at different cocoon densities. These experiments were conducted at room temperature (ca. $20^{\circ} \mathrm{C}$ ) in a screen-topped cage, $10^{\prime} \times 4^{1 / \times 611 . ~ A t ~}$ the beginning of an experiment, cocoons were first buried in sand where the lines of a removable grid intersected, the grid was then removed, the sand was pressed flat and a metal-edged leveling jig was finally scraped across the sand so that an even 12 mm . covered the cocoons. A single deer mouse was then placed in the cage together with nesting material, water, and an alternate food - dog biscuits. In each experiment the amount of this alternate food was kept approximately
the same (i.e. 13 to 17 gms. dry weight). After the animal had been left undisturbed for 24 hours, the removable grid was replaced, and the number of holes dug over cocoons, the number of cocoons opened, and the dry weight of dog biscuits eaten were recorded. Removed cocoons were replaced by fresh ones, and if the density was to remain the same the sand was scraped down to the cocoons, redistributed around the cage, pressed flat, and levelled as before, in preparation for the next 24 hr . experiment. Consumption of every animal was measured at either four or five different densities ranging from 2.25 to 36.00 cocoons per sq. ft. The specific densities were provided at random until all were used, and once chosen the consumption at each density was measured for three to six consecutive days. Ideally the size of the cage should remain constant at all densities but since this would require over 1,400 cocoons at the highest density, practical considerations required a compromise. The full sized cage was used at the lowest densities, but it was shortened at the higher so that there would be sufficient time available to check one experiment and set up the next. In this arrangement the total number of cocoons provided ranged from 88 at the lowest densities to 504 at the highest. At all densities, however, these numbers represented a surplus of which no more than $40 \%$ were ever consumed. Hence consumption was not limited by shortage of cocoons, even though the size of the cage changed.

The sources and characteristics of the cocoons and Peromyscus used in these experiments require some comment. Supplies of the prey were obtained by collecting cocoons in sawfly-infested plantations or by collecting late-instar larvae and allowing them to spin cocoons in boxes provided with foliage and litter. The sound cocoons were then
segregated into healthy, parasitized, and diseased using a method of X-ray analysis described in another paper (Holling, 1.957). The small male cocoons were separated from the larger female cocoons by size, since this criterion had previously proved adequate (Holling, 1954). To simplify the experiments, only male and female cocoons containing healthy, living prepupae were used and in each experiment equal. numbers of cocoons of each sex were provided, alternately, in the grid pattern already described.

Three mature non-breeding male deer mice were used in the experiments. Each animal had been born and raised in small rearing cages $12 \times 8 \times 6$ in. and had been isolated from cocoons since birth. They therefore required a period to become familiar with the experimental cage and with cocoons. This experience was acquired during a preliminary three-week period. For the first two weeks the animal was placed in the experimental cage together with nesting material, water, dog biscuits and sand, and each day was disturbed just as it would be if an experiment was in progress. For the final week cocoons were buried in the sand at the first density chosen so that the animal could learn to find and consume the cocoon contents. It will be shown that a seven-day period is more than ample to permit complete learning.

This experimental design is based on the assumption that the animals did not learn to locate cocoons by the position where they were buried. The extent of position learning was tested by counting the total number of holes dug, and the number dug over grid positions before, during and after cocoons were buried at a density of 36 per sq. ft. The behaviour of two inexperienced animals was examined. Counts of the holes dug were recorded after each animal had been
familiarized with the experimental cage for two weeks. As shown in Fig. 6, which represents the data for one animal, only one hole was


Fig. 6 - Number of holes dug over grid positions before, during, and after cocoons were buried at the positions. The expected number of holes dug were calculated assuming the holes were dug at random, with no orientation to the grid positions.
dug when no cocoons were present. As soon as cocoons were added, however, the animal dug 132 holes the first day, of which 131 were located over cocoon positions. Thus this foreign stimulus, suddenly appearing in familiar surroundings, immediately elicited a positive response. As experience was acquired and as a probable association was formed between the stimulus detected from buried cocoons and the gustatory sensations derived from consuming their contents, the subsequent number of holes dug each day increased
until learning was complete. At all times nearly $100 \%$ of the holes were dug over cocoon positions, showing that there was a definite orientation to some stimulus emanating from cocoons. In another paper (Holling, 1954) this stimulus was shown to be an odour. When cocoons were removed, the total number of holes dug each day declined slowly and the number dug over grid positions, were cocoons were once buried, approached the number to be expected if digging was at random. That is, the removal of cocoons destroyed the previous orientation to grid positions, indicating the absence of position learning, and validating the experimental design. Even in the absence of cocoons, digging was maintained for some time as a result of the rewards the animal previously received from this behaviour. The rate of digging declined, however, since the behaviour no longer was being reinforced. On days 26 to 28 digging spontaneously recovered, a characteristic of mary conditioned behaviours (Mun, 1951).

## PRELIMINARY RESULTS

The following twelve species of small mamals were either trapped or observed in the plantations infested with N. sertifer:

Sorex cinereus cinereus Kerr - masked shrew Blarina brevicauda talpoides Gapper - short-tailed shrew Peronyscus maniculatus bairdii Hoy and Kennicott - deer mouse Microtus pennsylvanicus pennsylvanicus Ord. - meadow mouse Sylvilagus floridanus Allen - cottontail

Zapus hudsonius Zimm. - meadow jumping mouse
Synaptomys cooperi cooperi Baird - bog lemming

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Mus musculus Linnaeus - house mouse
Tamiasciurus hudsonicus Errleben - red squirrel
Tamias striatus Linnaeus - eastern chipmunk
Mephitis mephitis Schreber - striped skunk
Mustela erminea Linnaeus - short-tailed weasel
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The latter seven species were so uncommon that their food consumption would have to be impossibly large before they could destroy a detectable number of N. sertifer. In addition the cottontail can be eliminated from the present discussion because of its well known herbivorus habits. Thus only four species, Sorex; Blarina, Peromyscus, and Microtus need be considered as possible predators.

General information concerning the food preferences of these four species was obtained by analyzing the stomach contents of animals trapped in sawfly-infested plantations. Results of these analyses are presented in Table XIX. Insect material occurred in the stomach contents of individuals of every species. Microtus, however, was essentially a complete vegetarian, with only traces of insect material in $24 \%$ of the stomachs. Zapus and Peromyscus were omnivorous, while Blarina and Sorex were almost completely insectivorous. Hence the gradation in increasing insectivorous habits was as follows: Microtus, Zapus, Peronyscus, Blarina, and Sorex. Since Microtus was almost an obligate vegetarian and since Zapus was uncommon, the important predators can be limited to Sorex, Blarina, and Peronyscus.

The foregoing table shows that these three species consume $N$. sertifer in nature. But if their caloric requirements are low enough, insufficient numbers of N. sertifer will be destroyed to exert any effect on sawfly populations. Experiments therefore were conducted to measure the maximum number of $N$. sertifer consumed by caged animals.
-66-

Table XIX
Per Cent Occurrence and Per Cent Volume of Insect and Plant Material in the Stomachs of Small Mammals.

| Species | No. of stom. | Analysis | Plants | N. Sertifer | Other <br> insects | A그․ <br> insects |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Microtus | 54 | no.of stom. | 54 | 10 | 3 | 13 |
|  |  | \%occurrence | 100\% | 18\% | 6\% | $24 \%$ |
|  |  | \% volume | 100\% | trace | trace | trace |
| Zapus | 10 | no.of stom. | 10 | 7 | 0 | 7 |
|  |  | \%occurrence | 100\% | 70\% | 0\% | 70\% |
|  |  | \% volume | $50 \%$ | 50\% | $0 \%$ | $50 \%$ |
| Peromyscus | 33 | no. of stom. | 18 | 25 | 19 | 31. |
|  |  | \%occurrence | 54\% | 76\% | 58\% | 94\% |
|  |  | \% volume | 20\% | 50\% | 30\% | 80\% |
| Blarina | 5 | no. of stom. | 1 | 5 | 5 | 5 |
|  |  | \%occurrence | 20\% | 100\% | 100\% | 100\% |
|  |  | \% volume | trace | 30\% | 70\% | 100\% |
| Sorex | 16 | no. of stom. | 0 | 16 | 12 | 16 |
|  |  | Qoccurrence | 0\% | 100\% | 75\% | 100\% |
|  |  | \% volume | 0\% | 60\% | 40\% | 100\% |

Experiments were conducted with individual animals in screen cages measuring $30 \times 24 \times 6$ in. During the preliminary conditioning period of three days and the final testing period of six days, the only source of food was a surplus of cocoons containing healthy sawfly prepupae. The testing period was divided into two halves, one when only male cocoons were provided and the other when only female cocoons were provided. Hence, the consumption of the two sexes was measured separately. When both sexes are present in nature, small mammals open more female than male cocoons (Holling, 1954), and this must be taken into account if the maximum consumption of male and female cocoons together is to be calculated. Given equal numbers of both sexes the number of female cocoons open by Blarina, Peronyscus, and Sorex is respectively $67.0 \%, 57.3 \%$ and $54.3 \%$ of the total number opened (op. cit.). These figures permit us to calculate the maximum number of male and female cocoons that will be opened when both are present (see Table XX).

The maximum cocoon consumption decreases from Blarina to Peronyscus to Sorex. These values should be related to the metabolic rate of the animals. Pearson (1947) observed that the oxygen consumptions of Blarina, Peromyscus, and Sorex were $4.0,2.5$ and 10.6 c.c./gmo/hr., respectively, giving a calculated consumption per animal of 84,52 and $39 \mathrm{ccs} / \mathrm{hr}$. This corresponds roughly to the gradation in the maximum number of cocoons consumed by the three species. The numbers of cocoons consumed are sufficiently great that all three species must be considered in order to adequately describe predation in this study.

Since there is a direct relationship between the density of predators
-68-

Table XX
Maximum Number of Cocoons Opened by Caged
Small Mammals per Day; No alternate Foods
Available

and the degree of predation, the regular seasonal fluctuations in small mammal numbers will be followed by similar changes in the degree of predation. Typical seasonal changes in small marmal populations are shown in Fig. 7. No significant deviation from the


Fig. 7 - Typical example of the seasonal changes in the numbers of Peromyscus, Blarina, and Sorex.
form of these graphs was observed in the three years of trapping. The seasonal rise and decline of density can be correlated with changes in breeding activity. This correlation was most clearly shown for Peromyscus. During the winter when breeding stops, the density of small mammals drops to a low value. In 1952, the first pregnant Peromyscus was captured May 20, and in 1953, April 28. Since the gestation period is approximately 20 days, breeding must have started April 8 or earlier. Many authors have related various reproductive changes in animals to the length of day, and the
experiments of Whitaker (1940) suggest that increasing day-length instigates breeding in Peronyscus leucopus noveboracensis Fisher. This possibility was investigated for $\underline{P}$. m. bairdii during the winter of 1954-55. In November 1954, 20 pairs of non-breeding over-wintering Peronyscus were placed in separate cages in a constant temperature $\left(72^{\circ} \mathrm{F}\right)$, constant humidity ( $65 \%$ R.H.) room. Two 100 -watt bulbs placed approximately three feet from the cages provided illumination for a fixed period - 16 hours for 10 pairs and 10 hours for the remainder. During the six months these conditions were maintained, litters were borne to six of the 10 pairs of deer mice exposed to the longer period of illumination. No breeding activity was evidenced by the mice exposed to the shorter period. Thus, with the advent of longer days and perhaps warmer temperatures in the spring, breeding recommences and populations begin to increase in numbers. Breeding activity gradually increases until the early part of July and declines thereafter. In a sample of 20 female Peromyscus captured July 21, 1953, 14 were pregnant. This represented the pregnancy peak. By inference the breeding peak occurred in early July. Breeding declines after mid-summer until, with the advent of lower temperatures and shorter days, breeding stops. As a result, losses exceed births and populations decline after mid-summer.

These seasonal population fluctuations to some extent determine the stage of N. sertifer that will experience the greatest predation. The peak in mammal numbers occurs after sawfly larvae drop from the trees and before the adults emerge (see Fig. 7). Thus as far as predator density is concerned, the cocoon stage is the one most susceptible to predation.

This does not completely preclude, however, predation of sawfly
adults, eggs, or larvae. No adult sawflies were observed in the stomach contents of seven Peromyscus and two Sorex captured while adults were emerging from cocoons. Their ability to fly and their short life apparently frees them from small mammal predation. Similarly the examination of over 1000 egg colonies did not reveal any damage that could possible be construed as being the result of small mammal attack.

Larvae, on the other hand, are larger and more accessible, at least to Peromyscus, the one arboreal species present. Although no direct data were obtained to indicate the extent of predation of larvae, the maximum possible predation by Peronyscus can be estimated. The maximum number of N. sertifer prepupae the average deer mouse can consume in 24 hrs. is about 200 (Table XX). The number of late instar larvae consumed would hardly exceed this value. Thus the maximum theoretical predation can be calculated for the two plots where Peronyscus was most abundant (Table XXI). The number of mouse-days from egg hatch to larval drop was estimated from Shermangrid trapping and the number of larvae was calculated from the cocoon population estimates by assuming a $10 \%$ larval mortality (Griffiths, 1955). Even assuming that the number of larvae consumed does not decrease with decrease in prey density, the predation could not exceed $8 \%$. Anticipating results presented later, it is very likely that it is considerably less, for the consumption of sawfly prepupae by individual deer mice decreases below densities of about 820,000 per acre. Thus, if larvae are no more palatable than prepupae, predation of larvae would hardly exceed $2 \%$.

The relative palatability of sawfly larvae and prepupae was tested in experiments using three caged Peromyscus. Separate experiments were
-72-

Table XXI
Maximum Possible Predation of N. sertifer
Larvae by Peronyscus

| Plot no. | Year | No. of mouse-days per acre | Theoretical max. no. of larvae eaten per acre | Larval <br> density <br> - per <br> acre | Theoretical maximum \% predation |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 2 | 1952 | 77.6 | 16,000 | 1,200,000 | 1.3 |
| 2 | 1953 | 75.9 | 15,000 | 910,000 | 1.6 |
| 1 | 1952 | 46.6 | 9,000 | 280,000 | 3.2 |
| 1 | 1953 | 62.6 | 13,000 | 160,000 | 8.1 |

conducted with each animal in wire screen cages $30 \times 24 \times 6 \mathrm{in}$. provided with nesting cotton, dog biscuits, and water. Each afternoon 76 IV-and V-instar larvae and 76 prepupae removed from their cocoons ( 38 male and 38 females) were distributed equally among five Scots pine needle clusters. Each cluster was stapled to a board $25 \times 12 \times 2$ in. with a trough 2 in. wide and oneand one half inches deep cut along the sides and ends and lined with tanglefoot to prevent occassional wandering of larvae. The animals were familiarized with the experimental conditions and with larvae and prepupae for 14 days before the experiments. Twenty-six consecutive experiments were conducted. At the end of each 24 hr . period, the uneaten larvae and prepupae were removed and fresh foliage and another set of sawflies were provided for the next experiment. Table XXII presents the results of these selection experiments.

Selection is given a numerical value by an index of selection, $I$, adopted from Dice (1949):

$$
I=\frac{a-b}{a+b}
$$

where $a=$ number of prepupae eaten
and $\quad \mathrm{b}=$ number of larvae eaten.
The index ranges from 1.0 when $b=0$, through 0.0 when $a=b$, to -1.0 when $a=0$. The significance of any selection is tested using the chi-square test for $2 \times 2$ contingency tables. Each deer mouse ate significantly more prepupae than larvae and, as shown by the ranges in the indices of selection, this selection was consistent in every experiment. Feeding larvae are avoided, possibly: because of their habit of exuding a drop of sticky substance when disturbed. Prepupae do not show this reaction and are much less active. Whatever the explanation may be, the avoidance of larvae is strong enough to reduce

$$
-74-
$$

Table XXII
Seliection of N．sertifer Prepupae Vs．IV and V Instar Larvae by Peromyscus

| $\begin{aligned} & \text { Anim. } \\ & \text { no. } \end{aligned}$ | No．provided |  | No．eaten |  | $\mathrm{x}^{2}$ | Index of Sel－ ection（range） |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Prepupae | Larvae | Prepupae | Larvae |  |  |
| 322 | 608 | 608 | 582 | 269 | $69.3 \begin{aligned} & \text { 效 }\end{aligned}$ | $\begin{gathered} 0.386 \\ (0.101 \text { to } 0.949) \end{gathered}$ |
| 324 | 684 | 684 | 649 | 278 | 90．9 ${ }^{\text {㿾 }}$ | $\begin{gathered} 0.422 \\ (0.128 \text { to } 0.807) \end{gathered}$ |
| 326 | 684 | 684 | 653 | 259 | $105^{\text {辛 }}$ | $\begin{gathered} 0.450 \\ (0.281 \text { to } 0.819) \end{gathered}$ |

－difference significant at the $0.1 \%$ level．
predation of this stage to a very negligible amount.
The only stage of N . sertifer that could experience significant predation is the cocoon stage. Mammal populations are highest between the time of larval drop and adult emergence, and since all cocoons are spun in the ground, the insects are accessible to all species of small mammal predators. In addition, when larvae drop from the trees, their three-dimensional environment becomes replaced by the essentially two-dimensional cocooning environment of the duff-soil interface. The resulting concentration of the sawflies increases their density, and hence their susceptibility to predation.

In summary, the present study of predation is considerably: simplified since only a few species of predators are important, and the effect of their activity is confined to only one life-history stage of their insect prey. A complete description of the role small mammals play as predators of $\mathbb{N}$. sertifer need consider only three species, Sorex, Blarina, and Peromyscus, and one life-history stage of their prey, the cocoon.

THE COMPONENTS OF PREDATION

Leopold (1933), in a treatise on game management, considered that mortality from predators in a given species of prey depends on five variables:
(1) density of the prey population
(2) density of the predator population
(3) characteristics of the prey, e.g. reactions to predators
(4) number and variety of alternate foods available for the predator
(5) predilections, primarily food preferences, of the predators.

Each one of these variables could exert a considerable influence, and the effect of any one may depend upon changes in another. For example, Errington (1934, 1946, 1954, 1956) has shown that the characteristics of many vertebrate prey species change when their density exceeds the number that the available cover can support. This change causes a sudden increase in predation. When such complex interactions are involved, it is difficult to understand clearly the principles involved in predation. To do so we must find a simplified situation where some of the variables are constant or are not operating. The problem studied here presents such a situation. Firstly, the characteristics of cocoons do not change as the other factors vary and there are no reactions to the predators. We therefore can ignore, temporarily, the effect of the third variable, prey characteristics. Secondly, since the work was conducted in plantations noted for their uniformity as to species, age and distribution of trees, there was a constant and small variety of possible alternate foods. In such a simple and somewhat sterile environment, the fourth factor, the number and variety of alternate foods and the related fifth factor, food preferences of the predators, can be initially ignored. There are thus only two basic variables affecting predation in this instance, i.e. prey density and predator density. It is in such a simple situation that the basic principles governing predation in general can best be revealed.

## The Basic Components

Few authors clearly appreciate that the response of predators or parasites to changes in prey density may be twofold. There is certainly abundant evidence that the numbers of natural enemies may increase as the density of their prey or hosts increase. Solomon (1949) has termed
this response the numerical response. But this effect of prey density is caused by an increased rate of reproduction or of survival, or both, resulting from an increase in the number of prey or hosts attacked by individuäl predators or parasites. Such an increase in the number of prey consumed by individual predators as prey density rises, has been termed the functional response (Solomon, 1949). In the present study the functional response is measured by the change in the consumption of cocoons by individual small mammals as cocoon density increases and the numericalresponse by the change in the density of small mammals as cocoon density increases.

In analyzing the functional response the first problem is to separate predation by species of predator i.e. Sorex, Blarina or Peromyscus. This was not difficult with Peromyscus since it was the only animal residing in two plantations, Plots 1 and 2, where regular trapping and cocoon quadrat sampling was conducted. Data with respect to predation by Sorex and Blarina were obtained in Plot 3, a plantation where Sorex, Blarina, and Microtus were the common residents. Since Microtus is almost a complete vegetarian, the problem was to separate cocoons opened by Sorex from those opened by Blarina. As indicated earlier (see Fig. 5) cocoons chewed by Sorex invariably have small openings of elliptical shape and with few abrupt serrations. The openings in cocoons chewed by Blarina, on the other hand, are larger and much more irregular, thus permitting a separation of the opened cocoons into those opened by Sorex and by Blarina.

The second problem is the difficulty in obtaining predation values at a sufficient number of prey densities to reveal a trend. Normally one host density value would be obtained per plot per year. Thus the mammal and cocoon populations would have to be sampled in at least two
plots over three years in order to obtain, for each species, predation values at six host densities. The work involved would be prohibitively great. A sufficient number of values, however, was obtained more simply. Predation values of Sorex and Blarina were obtained in one plantation, Plot 3, in one year, 1952. In the spring of 1952, Dr. F. T. Bird of the Laboratory of Insect Pathology, Sault Ste. Marie, Ont., sprayed this plantation with a virus disease that attacked N. sertifer larvae (Bird, 1953). The virus, sprayed from an aircraft flying along parallel lines 300 feet apart, was applied in three concentrations, with the lowest at one end of the plantation and the highest near the other. An area at one end, not sprayed, served as a control. When cocoon populations were sampled in the fall, a line of 302 trees was selected at right angles to the lines of spray and the duff under each was sampled with one one-square-foot quadrat. The line, approximately 27 chains long, ran the complete length of the plantation. When the number of new cocoons per square foot was plotted against distance, discrete areas could be selected which had fairly constant populations that ranged from 44;000 to 571,000 cocoons per acre. The areas of low population corresponded to the areas sprayed with the highest concentration of virus. In effect, the plantation could be divided into rectangular strips each with a particular density of cocoons. The width of these strips varied from 126 to 300 feet with an average of 193 feet. In addition to the 302 quadrats examined, the cocoons from another 100 quadrats were collected from the areas of lowest cocoon densj.ties. Thus, in this one plantation in 1952, there was a sufficient number of different cocoon densities to show the functional response of Sorex and Blarina. The data for Peromyscus were obtained from the yearly cocoon quadrat samples in Plots 1 and 2.

Each of these plots which had been sprayed with a low concentration of virus in 1951, showed population declines from 248,000 and 1,080,000 cocoons per acre, respectively, in 1952 to 39,000 and 256,000 cocoons per acre in 1954. Thus predation values at six different cocoon densities were obtained. The Plot 2 check quadrats, described previously, yielded an additional value since the healthy cocoons from previous years had been removed.

The third problem is to estimate predator densities. In Plots 1 and 2 this was done with grids of Sherman traps run throughout the summer. In Plot 3 both a grid of Sherman traps and a line of snap traps were used. This grid, measuring 18 chains by 4 chains, was placed so that approximately the same area sampled for cocoons was sampled for small mamnals. The populations determined from these trapping procedures were plotted against time, and the number of "mammal-days" per acre, from the time of larval drop (June 14) to the time cocoon samples were made (Aug. 20-30), was determined for each plot each year. This could be done with Peromyscus and Blarina since the trapping technique was shown in a previous section to provide an accurate estimate of their populations. But this was not true for Sorex. Instead, the number of Sorex-days per acre was approximated by dividing the number of cocoons opened at the highest density by the known number consumed by Sorex per day, i.e. 101 (see Table XX). Since the number of cocoons opened at the highest cocoon density was 151,000 per acre, then the number of Sorex-days per acre should be $151,000 / 101=1,490$. This is approximately 10 times the estimate that was obtained from trapping with Sherman traps. When the various trapping methods were compared earlier, estimates from Sherman trapping were shown to underestimate the numbers of Sorex by about
the same amount, i.e. $1 / 10$ th (see Table XI).
With estimates of the numbers of predators, prey and destroyed prey available, the functional responses can be calculated. These are expressed as the number of cocoons opened per predator per day at various cocoon densities, and are shown in Fig. 8.


Fig. 8 - Functional responses of Blarina, Sorex, and Peromyscus in Plots 1, 2, and 3.

The number of cocoons opened by each species increases until a maximum daily consumption is reached which corresponds approximately to the maximum number that can be consumed in any one day (see Table XX ). For Sorex this of course follows from the method of calculation. The rates at which these curves rise differ for the different species being greatest for Blarina and least for Peromyscus. Even if the plateaus are equated by multiplying points on each curve by a constant, the rates still decrease in the same order, reflecting a real difference in species behaviour.
-81-

The existence of a functional response was also shown by data from the analysis of stomach contents. The per cent occurrence and per cent volume of the various food items in stomachs of Peromyscus captured immediately after larval drop and two months later is shown in Table XXIII. When cocoon densities were high immediately after larval drop, the per cent occurrence and per cent volume of N. sertifer material was high. Two months later when various cocoon mortality factors had taken their toll, cocoon densities were lower and $N$. sertifer was a less important food item. The decrease in consumption of N. sertifer was accompanied by a considerable increase in the consumption of plant material and a slight increase in the consumption of other insect material. Plants and other insects act as buffer or alternate foods. Microtus, even though it ate few non-plant foods in nature, also showed an increase in the per cent occurrence of N. sertifer material in stomachs as cocoon density increased (Table XXIV). Before larval drop, when cocoon densities were low, the incidence of N. sertifer in Microtus stomachs was low. After larval drop, when cocoon densities were higher, the incidence increased by 3.5 times. Even at the higher cocoon densities, however, N. sertifer comprised less than one per cent of the volume of stomach contents so that the functional response of Microtus is extremely low.

The graphs presented in Fig. 8 and the results of the analysis of stomach contents, leave little doubt that the consumption of cocooned sawflies by animals in the field increases with increase in cocoon density. If the same functional responses could be shown in laboratory experiments, not only would the field data be substantiated but also interpretations and explanations would be facilitated. Such laboratory experiments were conducted with three Peromyscus using the

$$
\begin{gathered}
\text { Table XXIII } \\
\text { Stomach Contents of Peromyscus Trapped Immed- } \\
\text { iately after Larval Drop and Two Months Later. }
\end{gathered}
$$

| Time <br> trapped | Approx. no. <br> cocoons per <br> acre | No. of <br> stom. | Plant | N. sert. | Other <br> insects | All <br> insects |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| June 16 <br> -21 | 600,000 | 19 | $37 \%$ | $95 \%$ | $53 \%$ | $100 \%$ |
| Aug. 17 <br> -19 | 300,000 | 14 | $79 \%$ | $50 \%$ | $64 \%$ | $86 \%$ |

Table XXIV
Occurrence of Food Items in Stomachs of Microtus
Trapped Before and After Larval Drop.

| Time trapped | Plant | N. sertifer | All insects |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |

methods already described and results are presented in Fig. 9. The number of cocoons consumed daily by each animal increased with increase in cocoon density, again reaching a plateau as did the previous functional responses. Whenever the number of prepupae consumed did


Fig. 9 - Functional responses of three caged Peromyscus (means and ranges shown).
not meet the caloric requirements, these were met by consumption of the dog biscuits, the alternate food provided. Only one of the animals (A) at the highest density fulfilled its caloric requirements by consuming prepupae; the remaining animals ( $B$ and $C$ ) consumed less than one-half the number of sawflies they could consume if no alternate foods were present. The cocoons used in experiments involving animals $B$ and $C$, however, had been spun 12 months earlier than those involving animal A. When the characteristics of the functional response are examined in a later section, it will be shown that the strength of stimulus from older cocoons is less than that from younger cocoons, and
that these differences are sufficient to explain the low consumption of cocoons by animals $B$ and $C$. The shape of the curves and the density at which they level is very similar for all animals, so similar that multiplying points along any one curve by the proper constant will equate all three.

For the moment, we are interested in showing the basic responses comprising predation. One of these is the functional response and its forms have been shown for three species of predator :by data collected in the field and in experiments with caged animals. Later, when all the basic responses have been revealed, their characteristics and the subsidiary factors affecting them will be examined.

The numbers of predators, as well as their individual consumption, may also respond to changes in prey density. The characteristics of these numerical responses were determined by relating the number of predators per acre to the number of cocoons per acre. Conclusions can be derived from these relations but they are tentative. The data were collected over a relatively short period of time (four summers) and thus any relationship between predator numbers and prey density may have been fortuitous. Only those data obtained in plantations over 12 years old are included, since small mammal populations were most stable in these areas. The numerical responses for the three most important species of predators are shown in Fig. 10. For any one curve each point represents the highest summer population observed either in different plantations or in the same plantation in different years. The data for Peromyscus were obtained from Plots 1 and 2, from 1952 to 1955 incl. During this time, sawfly populations declined following the introduction of a virus disease in 1951. The densities of Peronyscus were estimated from trapping with Sherman traps on grids.


Fig. 10 - Numerical responses of Blarina, Sorex, and Peromyscus.

The data for Sorex and Blarina were obtained from Plot 3 from 1952 to 1954, as well as from two similar plantations in 1952 and 1953. In the graphs for these two species, the first to third points inclusive, as well as the fifth and last point, were obtained by trapping with buckets once in the summer. In order to coincide this trapping with the peak in shrew numbers, monthly trapping of a line of snap traps at one end of the plantations revealed the seasonal changes in numbers. The remaining points were obtained from trapping with Sherman traps set on grids. Although these grids were trapped throughout the summer, results from a previous section showed that such trapping does not greatly disturb the populations. Since results from the same section showed that estimates of the numbers of Sorex obtained from trapping with Sherman traps were one-tenth of the actual populations, these estimates were increased ten times. Such a correction was unnecessary for Blarina.

The densities of Blarina were lowest while those of Sorex were highest. In this situation, Blarina apparently does not show a numerical response, for its numbers did not noticeably increase with increase in cocoon density. Some agent or agents other than food must limit their numbers. Initially populations of Peromyscus and Sorex, on the other hand, apparently do increase with increase in cocoon density, ultimately ceasing to increase as some agents other than food became limiting. The response of Sorex was most marked. There was no evidence that the numbers of any species of small mamnals were lower at higher cocoon densities. Such inverse numerical responses have been shown by the magnolia warbler (Kendeigh, 1947), apparently as a result of competition with high populations of the bay-breasted, Tennessee and Cape May warblers during an outbreak of the spruce budworm in northern Ontario. A similar decrease in populations has been observed for the same species by Morris (personal communication) during an outbreak of the spruce budworm in New Brunswick.

These two responses, the functional and numerical, are the basic components of predation. Consequently, when the three remaining factors listed by Leopold (op. cit.) are constant or not operating, as in this study, the proportion of prey destroyed will be determined by the combined effects of the two responses. In Fig. 11, the functional and numerical responses are combined to reveal the relation between per cent predation and prey density during the 100-day period between cocoon formation and adult emergence. Since the data obtained for the numerical responses are tentative, some reservations must be applied to the more particular conclusions derived from this figure, The general conclusion, that per cent predation by each


Fig. 11 - Functional and numerical responses combined to show the relation between per cent predation and cocoon density.
species shows an initial rise and subsequent decline as cocoon density increases, however, is valid. The numerical responses would have to change radically before this was disproved. This from zero to some finite cocoon density, predation by small mammals shows a concurrent density-dependent action and thereafter shows an inverse density-dependent action. The initial rise in the proportion of prey destroyed can be attributed to both the functional and numerical responses. The functional response is presumed to have a roughly sigmoid shape and hence the proportion of prey destroyed by an individual predator will increase with increase in cocoon density up to and beyond the point of inflection. Now the data for any one functional response curve are not complete enough to establish a sigmoid relation, but the six curves presented thus far and several curves to be presented in the following section all suggest a point
of inflection. The positive numerical responses shown by Sorex and and Peromyscus also promote a concurrent density-dependent action up to the point at which predator densities remain constant. Thereafter, with individual consumption also constant, the per cent predation will decline as: cocoon density increases. The late Dr. L. Tinbergen apparently postulated the same type of curves for the proportion of insects destroyed by birds. His data were only partly published (1949, 1955) before his death but Klomp (1956) and Voute (1956a) have commented upon the existence of these "optimal curves". This term, however, is unsatisfactory and anthropocentric. From the viewpoint of the forest entomologist, the highest proportion of noxious insects destroyed may certainly be the optimum, but the term is meaningless for an animal that consumes individuals and not percentages. Progress can best be made by considering predation first as a behaviour before translating this behaviour in terms of the proportion of prey destroyed. The term "peaked curve" is perhaps more accurate.

Returning to Fig. 11, we see that the form of the peaked curve for Blarina is determined solely by the functional response. There was no numerical response. The abrupt peak occurs because the maximum consumption of prepupae was reached at a very low prey density before the predation was "diluted" by large numbers of cocoons. With Sorex both the numerical and functional responses are important. Predation by Sorex is greatest principally because of the marked numerical response. The two responses again determine the form of the peaked curve for Peronyscus, but unlike Sorex, the numerical response was not marked, and the maximum consumption of cocoons was reached at a relatively high density. The result is a low per cent predation
with a peak occurring at a high cocoon density.
Predation of all species destroyed a considerable number of cocooned sawflies over a wide range of cocoon densities. The presence of more than one species of predator not only increased predation but also extended the range of prey densities over which predation was high. This latter effect is particularily important, for if the predation by several species of predators peaked at the same prey density the range of densities over which predation was high would be slight. If the prey had a sufficiently high reproductive capacity they might jump this vulnerable range of densities and hence escape a large measure of the potential control that could be exerted by predators. Before we can proceed further in the discussion of the effect of predation upon prey numbers, the additional components that make up the behaviour of predation must be revealed.

## The Subsidiary Components

In the foregoing discussion I have attempted to show that the functional and numerical responses are the basic components of predation. But additional factors, prey characteristics, the number and variety of alternate foods, and predilections of the predators can also be important. It is necessary now to demonstrate the effect of these factors and how they operate. This can best be done experimentally.

There are four classes of prey characteristics, those that influence the caloric value of the prey and the length of time prey are exposed, those that affect the "attractiveness" of the prey to the predator (e.g. palatability, defense mechanisms), and those that affect the strength of stimulus used by predators in locating prey (e.g. size, habits, and colours). Only those characteristics that
affect the strength of stimulus were studied experimentally. Changes in the strength of stimuli from cocoons can be induced experimentally and the effect on predation determined. Since it has been shown that small mammals detect cocoons by the odour emanating from them (Holling, 1954), the strength of this odour perceived by a mammal can be easily changed by varying the depth of sand covering the cocoons. One Peronyscus was used in these experiments and its daily consumption of cocoons was measured at different cocoon densities and different depths of sand. These data are plotted in Fig. 12.


Fig. 12 - Effect of strength of stimulus from cocoons (i.e. depth under sand) upon the functional response of one caged Peronyscus. (Each point represents the mean of three to six separate measurements.)
be an inverse one, the depths of sand are reversed on the axis so that values of the strength of stimulus increase away from the origin. Each point represents the mean of three to six separate measurements. Increasing the depth of sand, i.e. decreasing the strength of the perceived stimulus, causes a marked decrease in the functional response. A 27 mm . increase in depth (from 9 to 36 mm .) causes the peak consumption to drop from 196 to four cocoons per day. The daily number of calories consumed in all these experiments was constant since dog biscuits were always present as alternate food. The densities at which each functional response curve levels appear to increase somewhat as the strength of stimulus perceived by the animal decreases. We might expect that the increase in consumption is directly related to the increase in the proportion of cocoons in the amount of food available, at least up to the point where the caloric requirements are met solely by sawflies. The ascending portions of the curves, however are S-shaped and the level portions are below the maximum consumption, approximately 220 cocoons for this animal. Therefore, the functional response cannot be explained by random searching for cocoons. When more data are presented, the functional response will be analyzed in greater detail. For the moment the important conclusion is that changes in prey characteristics can have a marked effect on predation but this effect is exerted through the functional response.

The numerical response is closely related to the functional response since an increase in predator density depends upon the amount of food consumed. Hence such prey characteristics as strength of stimulus will also affect the numerical response. For example, if the functional response is lowered by a lower strength of stimulus
from the prey, as shown above, then the numerical response will similarly be less. Predation will be low as the result of decreased functional and numerical responses.

In the field, cocoons are not covered by sand. Nearly all the cocoons afe spun in the duff-soil interface where they are covered by litter and duff formed from pine needles. Such loose material will not have as great an effect upon the strength of stimulus emanating from the ground surface as will a dense compacted material like sand. The effect of litter and duff of needles was tested in the 1953 and 1954 cocoon samples from Plots 1 and 2. The depth of litter and duff in each quadrat was measured at two points- one nearest to the tree trunk and one furthest from the trunk - and these two figures were averaged. The number of new cocoons and the number of new cocoons opened in each quadrat were related to the depth in that quadrat and these figures are grouped in Table XXV so that each depth range includes approximately 1,000 cocoons. There is a suggestion in this table that the number of cocoons per quadrat increases with the depth of litter and duff. The effect of these changes in density upon predation can be partially eliminated by calculating the proportion of cocoons opened. It will be show shortly that the search for cocoons in a plantation is not random since the animals concentrate their attention upon the areas where cocoons are most dense. Although the values for the per cent cocoons opened therefore are still influenced by density, this influence is not great enough to mask an obvious relation between depth and number of cocoons opened. As shown in the table, the precentages of cocoons opened do not show a trend with increasing depth. The litter and duff must be so loose as to scarcely impede the passage of odour from

## Table XXV

Effect of Depth on Number of Cocoons Opened

| Depth <br> range - mm. | AV. <br> depth | No. of <br> quadrats | AV. no <br> new <br> cocoons <br> per quad. | Av. no. <br> new <br> opened <br> per quad. | \% new <br> cocoons <br> opened |
| :--- | :--- | :--- | :--- | :--- | :--- |
| $15.5-22.0$ | 19.4 | 64 | 15.8 | 0.95 | 6.04 |
| $22.5-25.5$. | 24.1 | 43 | 25.6 | 2.00 | 7.81 |
| $26.0-29.0$ | 27.4 | 43 | 23.3 | 2.07 | 8.86 |
| $29.5-32.5$ | 31.1 | 54 | 19.6 | 1.87 | 9.51 |
| $33.0-34.5$ | 33.7 | 39 | 22.9 | 1.79 | 7.81 |
| $35.0-37.0$ | 35.8 | 40 | 30.6 | 2.38 | 7.78 |
| $37.5-40.0$ | 38.6 | 41 | 23.7 | 0.93 | 3.91 |
| $40.5-43.0$ | 41.7 | 42 | 27.8 | 1.50 | 5.38 |
| $43.5-46.5$ | 44.8 | 33 | 33.3 | 2.76 | 8.27 |
| $47.0-50.0$ | 48.7 | 28 | 36.8 | 2.57 | 6.99 |
| $50.5-52.5$ | 51.5 | 26 | 37.4 | 1.81 | 4.83 |
| $53.0-58.0$ | 55.0 | 35 | 31.7 | 2.94 | 9.27 |
| $58.5-62.0$ | 60.4 | 18 | 61.2 | 5.22 | 8.54 |

cocoons. In nature then, differences in the depth of litter and duff between plantations will have little influence upon predation.

Changes in strength of odour from cocoons could occur in nature, however, if age had any effect. If this was true more new cocoons should be dug for than old, since small mammals react only to odour in the digging phase of the search for cocoons (Holling, 1954). Two caged Peronyscus were used to test this possibility. The animals were tested separately after being conditioned to the experimental cage for two weeks. Old ( 15 months) and new ( 3 months) healthy cocoons were buried alternately in a grid pattern and dog biscuits, water, and nesting cotton were always present in excess. Each day the number of holes dug over cocoons of each category was recorded and fresh cocoons were added for another 24 -hour experiment. Selection is again given a numerical value by the Index of selection: $I=\frac{a-b}{a+b}$, where $a=$ number of holes dug over new cocoons
and $b=$ number of holes dug over old cocoons.
Table XXVI shows that less than one-third of the holes were dug over old cocoons. This difference is highly significant and the selection was consistent in every experiment as shown by the range in the indices of selection. This selection must be caused by a difference in the kind or degree of odour emanating from new and old cocoons. In previous experiments (Holling, 1954, 1955) when differences in kind of odour were involved, selection was the same in the digging and opening phase of the search for cocoons. But When differences in the degree of odour were involved (e.g. male vs. female cocoons), selection in the opening phases was quite independent of that in the digging phase. The results from the present experiments were similar to this latter situation (Table XXVII).

Table XXVI
Effect of Age of Cocoon upon the Number of Cocoons Dug for by Two Caged Peronyscus

| Age of cocoons <br> provided | No. cocoons <br> provided | No. holes dug <br> over cocoons | $\mathbf{P}$ | Index of Selec- <br> tion (range) |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 15 months | 5306 | 680 | $<0.01$ | 0.381 <br> $(0.180-0.650)$ |
| 3 months | 5306 | 1518 |  |  |

Table XXVII
Effect of Age of Cocoon upon the Number Opened by Two Caged Peromyscus

Treatment No. of No. cocoons No. cocoons $\quad \mathbf{F}$ Index of Selecof cocoons exp'ts provided opened tion (range)

15 mo. 3 mo. 15 mo .3 mo . old old old old


When cocoons were buried in sand, more young than old cocoons were opened as a result of selection in the digging phase. When the digging phase was bypassed by providing cocoons uncovered on the cage floor, the selection disappeared and approximately equal numbers of both categories of cocoons were opened. It seems reasonable, therefore, that selection in the digging phase is forced upon the animals by a greater strength of odour from new cocoons. As soon as the mice are in visual or tactile contact with cocoons, however, the prey are not located by odour and selection disappears.

As age of cocoons increases, the function response will decrease. This decrease is probably unimportant during the three months between larval drop and adult emergence, but it might be more important for those cocoons that remain in a prolonged diapause overwinter. An estimate of the overwintering predation was obtained in Plot 2, where Peroryscus was the only species present. Two cocoon samples were taken, 144 quadrats on Sept. 14, 1952, and 100 quadrats on June 3, 1953, just before larval drop. The analysis of the two samples indicated 43.70 healthy cocoons per square foot ( $1,080,000$ per acre) were present after the 1952 larval drop and of these, 17.23 per sq. ft. (427,000 per acre) or $39 \%$ overwintered. During the period between the two samples, the number of chewed cocoons increased by 0.82 per sq. ft. (from 15.85 to 16.67).

This negligible winter predation can be attributed to three main causes. The first two concern the densities of predator and prey. With cessation of breeding in the fall, small mammal populations decline and remain low throughout the winter. This decrease in number of predators would be accompanied by a decrease in the total number of cocooned sawflies consumed. Similarly, owing principally to adult
sawfly emergence in the fall, there was a decrease in the density of healthy cocoons from 1,080,000 per aere to 427,000 per acre. According to the functional responses shown in Fig. 8, individual Peromyscus open 240 cocoons each day at the former density and 73 at the latter density. Thus a decrease in the consumption of cocooned sawflies resulting from a decrease in their density, is another factor accounting for the slight winter predation. Finally, there is a suggestion that the consumption of sawflies during the summer, as shown in Fig. 8, is greater than that during the winter. It was mentioned that the number of opened cocoons increased by 0.82 per sq. ft. during the winter. That is, 20,000 cocoons per acre were opened. The number of mammal-days during this period was estimated by extrapolating the 1952 summer's graph for Peronyscus populations to meet the 1953 graph. Thus in the 262 days from Sept. 14, 1952 to June 3, 1953, there were approximately 793 mouse-days per acre. The number of cocoons opened per mouse per day during the winter was therefore $\frac{20,000}{793}=25$. At this same cocoon density, the individual consumption of cocoons during the summer was almost three times as great, i.e. 73 per day. This decrease in consumption probably reflects a decrease in the strength of the odour from cocoons with increasing age. The presence of sawflies with prolonged diapause therefore takes added significance, for the longer they are in the ground, the less susceptible they become to predation. They provide a secure residue of sawflies that can reinfest an area in the event of a catastrophic larval mortality.

Data from laboratory experiments and from the field indicate that such prey characteristics as strength of stimulus can have a profound effect upon predation. This effect, however, is exerted through the basic functional and numerical responses.

The remaining subsidiary factors, the number and variety of alternate foods and predilections of the predators, can also affect predation. The effect of alternate foods could not be studied in the undisturbed plantations because the amount of these "buffers" was constant and very low. The effect on the functional response, however, was demonstrated experimentally using one Peronyscus. The experiments were identical to those already described except that at one series of densities an alternate food of low palatability (dog biscuits) was provided, and at the second series one of high palatability (sunflower seeds) was provided. When both foods are available, deer mice select sunflower seeds over dog biscuits. In every experiment a constant amount of alternate food was available - 13 to 17 gms . dry weight of dog biscuits and 200 sunflower seeds.

Fig. 13 shows the changes in the number of cocoons opened per day and in the amount of alternate foods consumed. The functional response decreases with an increase in the palatability of the alternate food (Fig. 13A). Again the functional response curves show an initial, roughly sigmoid rise to a constant level.

As cocoon consumption rose, the consumption of alternate foods decreased (Fig. 13B) and this decrease was at a greater rate with dog biscuits, the low palatability alternate food. Each line indicating the change in the consumption of alternate food was drawn as a mirror image of the respective functional response and these lines closely follow the mean of the observed points. The variability in the consumption of sunflower seeds at any one cocoon density was considerable, probably as a result of the extreme variability in the size of seeds.



Fig. 13 - Effect of different alternate foods upon the functional response of one Peromyscus. A (upper) shows the functional responses when either a low (dog biscuits) or a high (sunflower seeds) palatability alternate food was present in excess. $B$ (lower) shows the amount of these alternate foods consumed.

Again we see that there is not a simple relation between the number of cocoons consumed and the proportion of cocoons in the total amount of food available. This is most obvious when the functional response curves level, for further increase in density is not followed by an increase in the consumption of sawflies. The plateaus persist because the animal continued consuming a certain fixed quantity of alternate foods. I. Tinbergen (1949) observed a similar phenomenon in a study of predation by tits of pine-aating larvae in Holland. He presented data for the consumption of larvae of the pine beauty moth (Panolis griseovariegata) and of the webb-spinning sawfly (Acantholyda pinivora), each at two different densities. In each case more larvae were eaten per nestling tit per day at the higher prey density. This, then, was part of a functional response, but it was that part above the point of inflection, since the proportion of prey eaten dropped at the higher density. It is not sufficient to explain these results, as well as the ones presented in this paper by claiming, with Tinbergen, that the predators "have the tendency to make their menu as varied as possible and therefore guard against one particular species being strongly dominant in it". This is less an explanation than an anthropomorphic description. The occurrence of this phenomenon depends upon the strength of stimulus from the prey, and the amount and quality of the alternate foods. Its explanation must await the collection of further data.

We now know that the palatability of alternate foods affects the functional response. Since the number of different kinds of alternate food could also have an important effect, the consumption of cocoons by a caged Peromyscus was measured when no alternate foods, or one or two alternate foods, were present. Only female cocoons were
used and these were provided at a density of 75 per sq. ft. to ensure that the level portion of the functional response would be measured. As in the previous experiments, the animal was familiarized with the experimental conditions and with cocoons for a preliminary two-week period. The average numbers of cocoons consumed each day with different numbers and kinds of alternate foods present are shown in Table XXVIII. This table again shows that fewer cocoons are consumed when sunflower seeds (high palatability) are present than when dog biscuits (low palatability) are present. In both cases, however, the consumption is lower than when no alternate foods are available. When two alternate foods are available, i.e. both sunflower seeds and dog biscuits, the consumption drops even further. Thus increase in both the palatability and in the number of different kinds of alternate foods decreases the functional response.

The number and variety of alternate foods could also affect the numerical response. Returning to the numerical responses shown in Fig. 10, if increase in alternate foods involved solely increase in food "per se", then the number of mammals would reach a maximun at a lower cocoon density, but the maximun itself would not change. If increase in alternate foods also involved changes in the agents limiting the numerical responses (e.g. increase cover and depth of humus), then the maximum density the small mammals could attain would increase. Thus increase in the amount of alternate foods could increase the density of predators.

Increase in alternate foods decreases predation by dilution of the functional response but increases predation by promoting a favourable numerical response. The relative importance of each of these effects will depend upon the particular problem. Voute (1946)
has remarked that insect populations in cultivated woods show violent fluctuations; whereas in virgin forests or mixed woods where the number of alternate foods is great, the populations are more stable. This stability might result from alternate foods promoting such a favourable numerical response that the decrease in the functional response is not great enough to lower predation.

The importance of alternate foods will depend upon the food preferences of the predators. Thus an increase in plants or animals 'other than N. sertifer will most likely affect the responses of those predators, like the omnivore Peromyscus, that are not extreme food specialists. Predation by the more stenophagus shrews, would only be affected by some alternate, animal food.

Food preferences are only one of the aspects of predilections of the predators. Other aspects involve their ability to detect, capture, and kill prey. But as with the other subsidiary factors, the effect of these predator characteristics will be exerted through the two basic responses, the functional and numerical. The differences observed between the functional responses of the three species shown earlier in Fig. 8 undoubtedly reflect differences in their abilities to detect, capture and kill. The amount of predation will similarily be affected by the kind of sensory receptor, whether visual, olfactory, auditory or tactile, that the predator uses in locating prey. An efficient nose, for example, is probably a less precise organ than an efficient eye. The source of an undisturbed olfactory stimulus can only be located by detecting a gradient in space, whereas a visual stimulus can be localized by an efficient eye from a single point in space - the telotaxis of Fraenkel and Gunn (19L0). As N. Tinbergen (1950) remarks, localization of direction is developed to the highest degree in the eye. Thus the

Table XXVIII
The Effect of Different Numbers and Kinds of Alternate Foods upon the Number of Cocoons Consumed per Day by One Peromyscus

| Alternate <br> food | No. of <br> exp'ts | No. of Cocoons opened |  |
| :--- | :---: | :---: | :---: |
|  |  | S.E. $\overline{\mathrm{x}}$ |  |
| none | 7 | 165.9 | 011.4 |
| dog biscuits | 5 | 143.0 | 8.3 |
| sunflower seeds | 8 | 60.0 | 6.2 |
| sunflower seeds <br> and dog biscuits | 8 | 21.5 | 4.2 |

functional response of a predator which locates prey by sight, will probably reach a maximum at a much lower prey density than the response of a small manmal when it locates prey by odour. In the data presented by Tothill (1922) and L. Tinbergen (1949), the per cent predation of insects by birds was highest at very low densities, suggesting that the functional responses of these "visual predators" indeed reached a maximum at a low density.

The basic components and the subsidiary factors that affect them are sufficient to explain even the most complex forms of predation. We do not know, however, why the functional and numerical responses take the forms they do nor what effect predation has upon prey numbers. Each question is a study in itself. The first is a causal analysis of feeding behaviour as well as a study of the population dynamics of small mammals; the second is a study of a part of the population dynamics of the sawfly. Since information has been obtained to give partial answers to some of these problems, the functional and numerical responses will be further analyzed and the effect of predation discussed.

ANALYSIS OF THE BASIC COMPONENTS OF PREDATION

## Functional Response

Every animal has a particular technique of searching for food. Many cold-blooded animals, for example, have very simple responses to food, simply reacting to any moving object of a certain size. Small mammals, on the other hand, have a number of more specific techniques to recognize and locate different prey. When the prey is a buried cocoon, as in this case, it is detected by its odour. Once the mammals are in visual and tactile contact with the cocoons, however, the prey
are accepted or rejected on the basi.s of a number of different stimuli which are associated with a particular gustatory sensation (Holling, 1954). The role of these stimuli in selection have been described in the paper cited. The techniques of searching for cocoons, where odour is the only stimulus detected, was analyzed for all three species of predators in laboratory experiments. Only animals that had been isolated from cocoons for at least four months or that had been raised from birth upon artificial food were used. The number of cocoons opened by each of these inexperienced animals was measured for 12 consecutive 24-hour experiments. After each animal was familiarized with its experimental cage for two weeks, it was provided with 100 healthy cocoons buried in two cm. of sand together with an alternate food and water. After 24 hours the number of cocoons operied was recorded and fresh cocoons added for another experiment. The number of cocoons opened each day was expressed as a percentage of the average number opened during the last six days. Thus the degree of learning of animals with different levels of consumption could be directly compared.

In Fig. 14 the ability of individuals of each species to locate and open cocoons is shown to change with successive experiments, reaching a constant in three to four days. The cumulative number of cocoons opened during this initial learning period differs for the different species, being highest for Peronyscus and least for Sorex. There are thus two different criteria for rate of learning. When the criterion is the number of days, the rate of learning is similar for the three species. When the criterion is number of cocoons opened, this rate is apparently different. In any case, the appearance of a strange odour in a familiar environment immediately elicits a response. It was shown earlier in Fig. 6 that this is indeed a new


Fig. 14 - Effect of experience on the opening of cocoons by inexperienced animals - twelve Peroryscus, seven Sorex and three Blarina.
response for no holes are dug in sand before cocoons are added. As the response is reinforced, through association of the odour from cocoons with the reward in them, more and more cocoons are located and opened, until learning is complete. Now the original reaction, which is a generalized response to any foreign odour, becomes more specific. If the odour added is not associated with a reward, the course of events is quite different. For example, when empty cocoons, cocoons containing fungus-attacked prepupae, or merely bits of cotton batten are buried in sand, all are dug for initially (Holling; 1955) but as learning progresses, the number of these objects dug for becomes less, until finally their odour is ignored. Although a small mammal in nature must be surrounded by a bewildering display of stimuli, their energies are channeled towards
those that possess "valence" (Russel, 1936) as a result of past experience. But since the appearance of a new stimulus immediately elicits a responste, the complex of valent stimuli can change, and new foods can appear in the diet.

This, then, is the searching technique that leads to the functional response. The characteristics of the response itself are determined by two separate components - the pattern of searching and the rate of searching. For example, if we wished to construct the functional response of a hypothetical animal, we would first have to assume a specific pattern of searching, e.g. random, and would then have to specify a certain rate of searching at each density. In nature, each density is really an average figure, for very few prey are distributed so uniformly that the variability is negligible. Hence each individual predator is exposed to a certain range of prey densities within its own range of movement. If the numbers of prey and the numbers of prey destroyed are measured with small quadrats, as in this study, then the relation between these two should indicate both the pattern and rate of searching at the particular range of densities. For example, if the relation was linear with the line passing through the origin, the pattern of searching would be random, and the rate of searching would equal the slope of the line. Since it is likely that the pattern of searching will remain the same at all densities, the form of the functional response will be determined by the changes in the rates of searching at each density.

The pattern of searching for cocoons by small mammals can be revealed from an analysis of the regular cocoon samples by relating the number of new cocoons opened in each quadrat to the total number of new cocoons present in that quadrat. Quadrats were grouped, in each
sample, into convenient density ranges, and the average number of cocoons opened in each group was corrected for the number of mammals present. When plotted on arithmetic paper, each set of data showed a curvilinear relation between the number of cocoons opened and the number present per quadrat. Square root transformations, such as the typical ones show in Fig. 15, converted these curves into straight line's. Small manmals therefore do not search for cocoons at random,


Fig. 15 - Effect of number of cocoons per quadrat upon the number opened per quadrat - Each line represents the data obtained in one plot in one year and the means $\pm 1$ S.E. are plotted.
but concentrate their activity in those areas where the cocoons are most dense.

The different rates of searching can hardly be compared fron these data since it was impractical to correct each quadrat for the cocoons erroneously called new. The rates can be inferred, however, from the form of the functional responses already presented. Each of these
appeared to show an initial S-shaped rise followed by plateau. Thus the rates of searching must increase up to the point of inflection and decrease thereafter. It is the change in the rates that largely determine the form of each functional response.

Differences in the time taken by small mammals to learn to open cocoons at various densities might account for the different rates of searching. The rates of learning of two groups of inexperienced Peromyscus (two animals in each group) were measured at two cocoon densities - 36.00 per sq. ft. (Group 1) and 2.25 per sq. ft. (Group 2). In Fig. 16 the time taken to complete learning is shown to be similar


Fig. 16 - Effect of cocoon density upon the rate at which Peromyscus learns to open cocoons. Data from four animals, two in each group.
for the two groups (four to five days), even though the number of cocoons opened before learning was complete was quite different - 447 cocoons per animal of Group 1 and 31 per animal of Group 2. After 12
days, the densities were reversed so that animals of Group 1 were exposed to the lower density and those of Group 2 to the higher. Since this change did not alter the degree of learning, the experience received at the original densities must have been sufficient to permit complete learning. Differences in the rate of learning therefore cannot explain the form of the functional response.

A clue to the explanation of the response might be found if we knew the effect of density upon other activities involved in the search for cocoons. The opening of cocoons is just one of these and is preceded by specific movements and by digging. Some of this information is available since the numbers of holes dug over cocoons was recorded when the functional responses of caged Peromyscus were studied. The number of cocoons opened and dug for by three Peromyscus at different cocoon densities are shown in Table XXIX. Although more coccons were dug for than opened, the ratio of holes dug to cocoons opened is not significantly different at the different densities. The digging response to a change in cocoon density therefore follows the same form as the opening response. The two differ in degree only. All we can say is that the process that determines the form of the functional response occurs before the digging phase of the search for cocoons. More data are required, particularily during earlier phases in the search for cocoons.

The functional response remains unexplained. We have learned its form and its two components - the pattern and rate of searching. We have learned it cannot be explained by a simple relation between consumption and the proportion of prey in the total food available, nor do different rates of learning at different densities seem important. We have learned, further, that its characteristics are determined before cocoons are dug for. Since we cannot explain the response by external

Table XXIX
Effect of Cocoon Density upon the Ratio of the Number of Holes Dug to the Number of

Cocoons Opened by Peronyscus

| No. cocoons per sq. ft. | $\begin{aligned} & \text { Animal } \\ & \text { no. } \end{aligned}$ | No. holes dug - H | No. cocoons opened - 0 | H/O | P |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 2.25 |  | 115 | 72 | 1.60 |  |
| 7.11 |  | 547 | 413 | 1.33 |  |
| 11.75 | A | 1604 | 1153 | 1.39 | $>0.30$ |
| 16.00 |  | 1751 | 1157 | 1.51 |  |
| 25.00 |  | 1064 | 734 | 1.44 |  |
| 36.00 |  | 3997 | 2694 | 1.49 |  |
| Total |  | 9078 | 6223 | 1.46 |  |
| 2.25 |  | 78 | 64 | 1.22 |  |
| 9.00 | B | 299 | 248 | 1.21 | $>0.70$ |
| 16.00 |  | 348 | 314 | 1.11 |  |
| 32.00 |  | 420 | 336 | 1.25 |  |
| Total |  | 1145 | 962 | 1.19 |  |
| 2.25 |  | 140 | 103 | 1.36 |  |
| 9.00 | C | 328 | 202 | 1.62 | $>0.30$ |
| 16.00 |  | 354 | 250 | 1.41 |  |
| 32.00 |  | 360 | 268 | 1.34 |  |
| Total |  | 1182 | 823 | 1.43 |  |

variables, the final explanation probably involves changes in the neural circuits mediating the feeding behaviour; changes that operate together with changes in the strength and number of repetitons of stimuli from prey and so determine the form of the observed functional responses.

## Numerical Response

While the characteristics of the functional response can be studied in laboratory experiments, the numerical response does not lend itself to laboratory study. Thus experiments were begun in 1956 to study the numerical response of Peronyscus in red pine plantations of the Kirkwood Forest Management Unit, near Thessalon, Ontario. These experiments were designed to indicate (1) if the density of small mammals increased with the addition of artificial food, (2) if there was any critical time at which food had to be present and (3) whether changes in births or deaths accounted for any increase in mammal density. These experiments are part of a more complete study of the population dynamics of small mamals, and will be continued for some time. The following discussion is therefore incomplete and preliminary and will only include the data obtained during the summer of 1956.

Five red pine plantations were selected for study. In each plantation the trees are from 20 to 25 yrs. in age and are planted uniformly in rows. The plantations are small (six to 15 acres) and are isolated by fields, so that immigration is slight. One (Plot 15) serves as a control, while food has been added at different times to the remaining four. Once food is added, it is replenished monthly. The food, poultry scratch-feed, was added to Plot 3B on May 27, to Plot 13 on June 20, to Plot 12 on July 5, and to Plot $14_{4}$ on Aug. 5. The grain has been provided on $2 \times 2$ foot metal trays protected by a flat metal roof placed about two inches above them.

Twelve trays are placed in a grid pattern in each plot at 1.5 chain intervals, so that the grid measures $3 \times 4.5$ chains and covers 1.35 acres. Since mammals have ranges over which they wander, the trays are exposed to animals residing on about four acres. Each plantation was trapped with a $3 \times 5$ chain grid of Sherman live traps for six days every three weeks from May 24 to Sept. 7.

The number of Peronyscus caught in the plots is shown in Table XXX. The numbers under "control" include data from the control plot and from the food plots before food was added. During the first three trapping periods, the average numbers per plot were similar in both control and food plots. Thereafter the numbers declined in the controls and continued increasing in the food plots. Thus addition of food has apparently resulted in a displacement of the time when the peak occurred, and in an increase in the populations. Most of this increase resulted from increased breeding as shown in Table XXXI. There were proportionately more immature and breeding animals and fewer non-breeding ones in food plots. Since the rate of disappearance of animals was slightly higher in the food plots than in the control plots ( $56 \%$ and $53 \%$ resp., after nine weeks) these numerical responses seem to result mainly from increased breeding.

As shown in Table XXXII the mamals reacted immediately to the presence of food, whether it was supplied early or late in the summer. The populations in all four food plots were almost identical once food was present in all of them.
$\rightarrow$ Mammal populations are essentially an annual crop. It was argued earlier that breeding stops during the winter and begins in the spring with the onset of warmer temperatures and longer days. As a result, populations begin to increase until breeding stops in the fall when the

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Table XXX
Number of Peromyscus Trapped in Control
and Food Plots

| Treatment of plots: | Plot | No. captured |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | May 24 | June 14 | July 5 | July 26 | Aug. 16 | Sept. 6 |
| $C$ control: no axtifical food present | 3B | 3 |  |  |  |  |  |
|  | 13 | 0 | 2 |  |  |  |  |
|  | 12 | 1 | 5 | 4 |  |  |  |
|  | 14 | 0 | 2 | 4 | 1 |  |  |
|  | 15 | 0 | 1 | 1 | 3 | 2 | 1 |
|  | Total | 4 | 10 | 9 | 4 | 2 | 1 |
|  | Av. | 0.8 | 2.5 | 3.0 | 2.0 | 2.0 | 1.0 |
| Artifical <br> food <br> present | 3B |  | 3 | 2 | 5 | 4 | 4 |
|  | 13 |  |  | 4 | 4 | 6 | 4 |
|  | 12 |  |  |  | 4 | 6 | 2 |
|  | 14 |  |  |  |  | 6 | 2 |
|  | Total |  | 3 | 6 | 13 | 22 | 12 |
|  | Av. |  | 3.0 | 3.0 | 4.3 | 5.5 | 3.0 |

Table XXXI
Number of Immature, Non-breeding and Breeding
Peronyscus per Plot (actual number caught in
brackets)

| Treatment | Breeding cond' n | June 14 | $\begin{gathered} \text { July } \\ 5 \end{gathered}$ | $\begin{gathered} \text { July } \\ 26 \end{gathered}$ | $\begin{gathered} \text { Aug. } \\ 16 \end{gathered}$ | $\underset{6}{\text { Sept. }}$ | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Control | Imm. | $0.5(2)$ | $1.0(3)$ | 0.0(0) | 0.0(0) | 0.0(0) | $1.5(5)$ |
|  | Non-br. | $0.0(0)$ | 0.3(1) | 1.0(2) | 1.0 (1) | 1.0(1) | 3.3 (5) |
|  | Br 。 | 2.0(8) | 1.3(4) | $0.5(1)$ | 1.0(1) | 0.0(0) | 4.8 (14) |
| Food | Imm. | 2.0(2) | 0.5 (1) | 0.0(0) | $1.0(4)$ | 1.0(4) | 4.5(11) |
|  | Non-br. | 0.0(0) | 0.0(0) | $0.7(2)$ | 0.7 (3) | 0.5(2) | 1.9(7) |
|  | Br . | 1.0(1) | 2.5 (5) | 2.7(8) | 3.2(13) | 1.3(5) | 10.7(32) |

Table XXXII

Comparison of Peromyscus Populations, Aug. 17 to
Sept. 10, in Control and Food Plots

| Plot | Date food <br> added | Highest no. trapped <br> in period | No. marmal- <br> days in period |
| :---: | :---: | :---: | :---: |
| control | $-\cdots$ | 2 | 30 |
| $3 B$ | May 27 | 4 | 84 |
| 13 | June 20 | 6 | 105 |
| 12 | July 5 | 6 | 84 |
| 14 | Aug. 5 | 6 | 84 |

temperature drops and day length shortens. It seems, then, that the extreme limits to the breeding season are set by the physical conditions of temperature and day length. But within these extremes the amount of food present sets further limits. When artificial food was added to plantations, breeding was maintained for a longer period. Presence of an abundance of food permits a greater realization of the potential breeding capacity.

As long as food becomes plentiful before mid-August, the mammals respond by an increase in populations. There is apparently no critical time during the summer before which food must be added. This fact increases the range of cases where small mammal predation might be important. If it happened that there was some critical period during the summer, then effective predation by small mammals would be restricted to those insects whose susceptible life history stage appeared at this critical time.

When an animal shows a numerical response, food must limit its numbers. It has been argued that such limitation is rare since animals seldom becone so numerous that their food is noticeably exhausted. But the amount of food available is not as important as the amount of food that can be consumed, i.e. the numerical response depends upon the functional response. An animal, limited by food, might have such a low functional response that there is an apparent surplus of food available. This produces a paradox of "scarcity amid plenty" (Andrewartha and Birch, 1954). On the other hand, the importance of food in limiting the numbers of animals cannot be determined merely from the study of a few species. Its importance will depend on the characteristics of each species and of the area where each lives: Numerical responses were shown by some species of small mammals in the
pine plantations investigated in this study but in less sterile environments (e.g. natural woodlands) the same species might not show increases in numbers. Morris (1955), for example, studied the populations of small mammals in 21 mixed spruce stands in New Brunswick. The populations showed definite increases with increase in cover so that food could not have been limiting. In a normal spruce stand we would not expect that small mammals would become much more abundant when their prey were abundant. A positive numerical response would be prevented by cover limitations.

We can hardly examine all the agents that affect the numbers of animals here, for this requires a complete knowledge of their population dynamics. There are many cases, however, where food limits the density of vertebrates. Lack (1954) presents many examples of food affecting the numbers of birds. The evidence is largely indirect and he extends this conclusion, often on very tenuous grounds, to other classes of animals. Perhaps the best examples amongst mammals concerns ungulates. Since large scale predator control measures have been established, the numbers of deer in some localities in North America seem to be limited by food shortage, which affects both their fecundity and death rate (Leopold, 1943; Cheatum and Severinghaus, 1950). Similarly, Cowan (1950) has associated the high mortality and decreased fecundity of elk in the Canadian Rockies with food shortage.

The evidence of numerical responses among predators is more numerous, for many show regular changes in abundance following changes in the numbers of their prey. Such correlations have been shown for snowy owls (Chitty, 1950), for the rough-legged hawk (Shelford, 1943), and for arctic fox, red fox, marten, and lynx (Elton, 1942) in North America and Europe. Craighead and Craighead (1950) presented an

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interesting analysis of the ecology of raptor predation based upon two year's data. Predation by raptors was density-dependent largely as a result of numerical responses produced by increased immigration and reproduction.

Little information is available to show the effect of food upon small mamal numbers. Allen (1943) has observed that fox squirrels in Michigan were very numerous in years with a good acorn crop, whereas in poor-crop years breeding almost ceased and many animals died. The resulting decrease in numbers could be directly attributed to food shortage since few animals died and breeding continued in farmlands where additional food was available. Muskrat populations can also be affected by food. Not only did twice as many breeding females occupy areas along central Iowa streams well supplied with corn, but also for similar densities of females the spring to fall increases were about twice as great in food-rich as in food-poor environments (Errington, 1941). Extensive increases in the numbers of Microtus arvalis populations were observed by Frank (1954) in grain mounds during the winter. Normally breeding stops in the fall but abundance of food permitted the maintenance of breeding activity so that higher populations occurred in the spring.

Numerical responses therefore seem widespread, but with the evidence available we cannot ascribe to food the all-pervasive influence that Lack (1954) does. When they occur, numerical responses seem to result from an increased reproductive rate as well as from a decreased mortality rate. Immigration of animals into areas where prey are abundant is an additional extrinsic process that promotes a numerical response, and is most important for those predators, like birds, that are highly mobile. The numerical responses of less mobile
animals like small mammals could also be affected by movements. Strecker and Emlen (1950) have shown that in a population of house mice living wild in a room the amount of egress from the room increased markedly as food consumption feached the point where all available food was consumed each day. In a population that was denied egress when this point was reached breeding stopped.

The characteristics of a numerical response can be conveniently divided into two parts, the initial rising phase and the upper, stable phase that marks the highest density attainable. The powers of movement and the rate of reproduction of a predator will determine the rate at which the initial phase will rise. For example, the response $X$ of a small mammal would hardly be as rapid as that of a more vagile predator like a bird for it would lack the great mobility to concentrate quickly into areas where prey was particularily abundant. This low vagility would hardly be offset by high fecundity: The upper, stable phase of the numerical response must occur with all predators since there must be a certain maximum beyond which the effective reproductive rate cannot rise no matter how abundant the food. This maximum level is determined by a variety of agents other than food and the predator that normally operates well below these limits will achieve the highest numerical response. Thus while the great mobility of birds endows them with the potential for a rapid increase in numbers, their rigid space requirements, the importance of territory, puts a low ceiling to the numerical response.

It has already been shown in an earlier section that a number of factors can change the intensity and form of the numerical response. Increase in the number and variety of alternate foods will produce an increase in numbers. Decrease in the strength of stimulus from prey,
and presumably from alternate foods as well, will decrease the numerical response. Although in the present study there appeared to be no critical time during which food had to appear before the density of small mamals would respond, the length of time the prey were exposed might be important. With predators, like small marmals, that have a high reproductive capacity, even a short exposure to food during the latter part of the breeding period will cause a response. But even here the perisitence of the prey during the winter might enhance survival and hence the numerical response.

From this discussion we can predict three major types of numerical response. There might be a positive response as shown by Sorex and Peromyscus in this study, there might be no response as shown by Blarina, or there might be an inverse response as shown by the magnolia warbler (Kendeigh, 1947; Morris, personal communication).

## DISCUSSION

## The Effect of Predation on Prey Populations

One of the most important characteristics of a mortality factor concerns its ability to regulate the numbers of an animal - to promote a "steady density" (Nicholson, 1953; Nicholson and Bailey, r 1935) such that a continued increase or decrease of numbers from this steady state becomes progressively unlikely the greater the departure from it. Regulation in this sense therefore requires that the mortality factor change with change in the density of the animal attacked. It requires a density-dependent mortality (Smith, 1935, 1939). Densityindependent factors can affect the numbers of an animal but they cannot regulate the numbers. There is abundant evidence that changes in
climate, some of whose aspects are presumed to have a densityindependent action, can lower or raise the numbers of an animal. But this need not be regulation. This effect will only fesult from an interaction with a density-dependent factor, an interaction that might be the simplest, i.e. merely additive. Recently, the densitydependent concept has been severely criticized by Andrewarthria and Birch (1954). They call it a dogma but such a comment is only a criticism of an author's use of the concept. Its misuse as a dogma does not militate against its value as a hypothesis.

We have seen from this study that predation by small mammals does change with change in prey density. As a result of the functional and numerical responses the proportion of prey destroyed increases from zero to some finite prey density and thereafter decreases. Thus predation over some ranges of prey density shows a concurrent densitydependent action. This is all that is required for a factor to regulate.

The way in which predation, of the type shown in this study, can regulate the numbers of a prey species can best be showm by a hypothetical example. To simplify this example we will assume that the prey has a constant rate of reproduction over all ranges of its density, and that only predators are affecting its numbers. Such a situation is, of course, unrealistic. The rate of reproduction of real animals probably is low at low densities when there is slight possibility for contact between individuals (e.g. between male and female). It would rise as contacts became more frequent and would decline again at higher densities when the environment became contaminated, when intraspecific stress symptoms appeared, or when $\mathcal{K}$ cannabilism became common. Such changes in the rate of reproduction
have been shown for experimental populations of Tribolium confusum * (MacLagén, 1932) and Drosophila (Robertson and Sang, 1944). Introducing more complex assumptions, however, confuses interpretations without greatly changing the conclusions.

This hypothetical model is shown in Fig. 17. The curve that


Fig. 17 - Theoretical model showing regulation of prey by predators (see text for explanation).
describes the changes in predation with changes in prey density is taken from the actual data shown earlier in Fig. 11. It is assumed that the birth-rate of the prey at ary density is balanced by $x$ per cent predation, and that the variation in the environment causes a variation in the predation at any one density. The per cent predation necessary to balance the birth-rate is represented by the horizontal line in the diagram and variation in predation is represented by the thickness of the mortality curve. The death-rate will equal the birth-rate at two density ranges, between $A$ and $B$ and
between $C$ and $\mathbb{D}$. When the densities of the prey are below $A$, the mortality will be lower than that necessary to balance reproduction and the population will increase. When the densities of the animal are between (AB) and (CD), death-rate will exceed birth-rate and the populations will decrease. Thus, the density of the prey will tend to fluctuate between densities $A$ and $B$. If the density happens to exceed $\mathbb{D}$, death-rate will be lower than birth-rate and the prey will increase in numbers, having "escaped" the control exerted by predators. This would occur when the prey had such a high rate of reproduction that its density could jump, in one generation, from a density lower than $A$ to a density higher than $\mathbb{D}$. If densities $A$ and $\mathbb{D}$ were far apart, there would be less chance of this occurring. This spread is determined by the number of different species of predators that are present. Predation by each species peaks at a different density (see Fig. 11), so that increase in the number of species of predator will increase the spread of the total predation. This will produce a more stable situation where the prey will have less chance to escape control by predators.

Predation of the type shown will regulate the numbers of an animal whenever the predation rises high enough to just equal the effective birth-rate. When the prey is an insect and predators are small manmals, as in this case, the reproductive rate of the prey will be too high for predation alone to regulate. But if other mortality occurs, density-independent or density-dependent, the total mortality could rise to the point where small mammals were contributing, completely or partially, to the regulation of the insect.

Predation of the type shown will produce stability if there are large numbers of different species of predators operating. Large
numbers of such species would most likely occur in a varied environment, such as mixed woods. Perhaps this explains, in part, Voute's (1946) observation that insect populations in mixed woods are less liable to show violent fluctuations.

We cannot agree with Voute (1956a and b) that factors causing a peaked mortality curve are not sufficient for regulation. He states (1956b) that "this is due to the fact that mortality only at low densities incfeases with the increase of the population. At higher densities, mortality decreases again. The growth of the population is at the utmost slowed down, never stopped!". He believes that such predation can only cause regulation when mortality among prey rises to $100 \%$. This would not cause regulation however; it would cause extinction. All that is necessary for regulation is a rise in per cent predation over some range of prey densities and an effective birth-rate that can be matched at some density by mortality from predators.

Neither can we agree with Thompson (1930) when he ascribes a minor role to vertebrate predators of insects and states that "the number of individuals of any given species (i.e. of vertebrate predators) is ......... relatively small in comparison with those of insects and there is no reason to suppose that it varies primarily in function of the supply of insect food, which fluctuates so rapidly that it is impossible for vertebrates to profit by a temporary abundance of it excepting to a very limited extent". We know that they do respond by an increase in numbers and even if this is not great in comparison with the numerical response of parasitic flies, the number of prey killed per predator is so great, and the increase in the number killed with increase in prey density is so marked as to fesult
in a heavy proportion of prey destroyed, a proportion that, furthermore, increases between zero and some finite density. Thompson depreciates the importance of the numerical response and ignores the functional response.

In entomological literature there are two contrasting mathematical theories of regulation. Each theory is based on different assumptions and the predicted results are quite different. Both theories were developed to predict the interaction between parasitic flies and their insect hosts but they can be applied equally to predator-prey relations. Thompson (1939) assumed that a predator has a limited appetite and that it has no difficulty in finding its prey. Nicholson (1933) assumed that predators had insatiable appetites and that they had a specific capacity to find their prey. This limited searching capacity was assumed to remain constant at all prey densities and it was also assumed that the searching was random.

The validity of these mathematical models depends upon how closely their assumptions fit natural conditions. We have seen that the appetites of small mammal predators in this study are not insatiable. This fits one of Thompson's assumptions but not Nicholson's. When the functional response was described and analyzed, it was obvious that predators did have difficulty in finding their hosts and that their searching ability did not remain constant at all prey densities. Searching by small marmals was not random for they concentrated their attention upon those localities where prey was most dense. Hence in the present study of predator-prey relations, the remaining assumptions of both Thompson and Nicholson do not hold. Thompson's and Nicholson's theories, therefore, must be used with caution and in this situation, at least, neither applies. In other situations, however, the theories
might be accurate as a first approximation and will certainly broaden our understanding of regulation.

Klomp (1956) considers the damping of oscillations of animal numbers as important as regulation. If the oscillations of the numbers of an animal affected by a delayed density-dependent factor (Varley, 1947) like a parasite, do increase in amplitude, as Nicholson's theory predicts (Nicholson and Bailey, 1935), then damping is certainly important. It is not at all certain, however, that this prediction is true. We have already seen that the assumptions underlying Nicholson's theory do not hold in at least some cases. He ignores the possibility of a functional response. If the parasites did show. a functional response that reacted immediately to change in host density, the amplitude of the oscillations would not increase as rapidly, and might not increase at all.

Oscillations undoubtedly do occur however, and whether they increase in amplitude or not, any damping is important. The factor that damps oscillations most effectively will be a concurrent densitydependent factor that reacts immediately to changes in the numbers of an animal. Predation by small mammals fulfills these requirements when the density of their prey is low. The consumption of prey by individual predators responds immediately to increase in prey density (functional response). Similarly, at least part of the numerical response is not greatly delayed, probably because of the high reproductive capacity of small mammals. Thus if the density of a prey is low, chance increases in its numbers will imediately increase the per cent mortality caused by small mammal predation. When the numbers of the prey decrease the effect of predation will be immediately relaxed. Thus, incipient oscillations can be damped by small mammal predation.

We have seen that small mammals theoretically can regulate the numbers of prey and can damp their oscillations under certain conditions. Insufficient information was obtained to precisely assess the role of small mammals as predators of $N$. sertifer in the pine plantations of southwestern Ontario, however. Before the general introduction of a virus disease in 1952 (Bird, 1952, 1953), the sawfly was exhausting its food supplies: 70 to $100 \%$ defoliation of Scots, jack and red pines was observed in this area. Predators were obviously not regulating the numbers of the sawfly. After the virus was introduced, however, sawfly populations declined rapidly. In Plot l, for example, their numbers declined from 248,000 cocoons per acre in 1952 to 39,000 per acre in 1954. The area was revisited in 1955 and larval and cocoon populations had obviously increased in this plot, before the virus disease could cause much mortality. It will be recalled that Peroryscus was the only species of small mamal residing in Plot 1 and it is interesting that similar increases were not observed in other plantations where sawfly numbers had either not decreased so greatly, or where shrews, the most efficient predators, were present. These observations suggest that predation by small mammals was damping the oscillations resulting from the interaction of the virus disease with its host.

## Types of Predation

Many types of predation have been reported in the literature. Ricker (1954) believed that there were three major types of predatorprey relations, Leopold (1933) four, and Errington (1946, 1956) two. Many of these types are merely minor deviations, but the two types of predation Errington discusses are quite different from each other. He distinguishes between "compensatory" and "non-compensatory" predation.

In the former type, predators take a heavy toll of individuals of the prey species when the density of prey exceeds a certain threshold. This "threshold of security" is determined largely by the number of secure habitable niches in the environment. When prey densities become too high some individuals are forced into exposed areas where they are readily captured by predators. In this type of predation, predators merely remove surplus animals, ones that would succumb even in the absence of enemies. Errington feels, however, that some predator-prey relations depart from this scheme, so that predation occurs not only above a specific threshold density of prey. These departures are ascribed largely to behaviour characteristics of the predators. For example, predation of ungulates by canids is not compensatory and Errington feels that this results from intelligent, selective searching by the predators.

If the scheme of predation presented here is to fulfill its purpose it must be able to explain these different types of predation. Noncompensatory predation is easily described by the normal functional and numerical responses, for predation of N. sertifer by small mammals was of this type. Compensatory predation can also be described using the basic responses and subsidiary factors previously revealed. The main characteristic of this type of predation is the "threshold of security". Prey are more vulnerable above and less vulnerable below this threshold. That is, the strength of stimulus perceived from prey increases markedly when the prey density exceeds the threshold. We have seen from the present study that an increase in the strength of stimulus from prey increases both the functional and numerical responses. Therefore, below the "threshold of security" the functional responses of predators will be very low and as a result there will probably be no numerical response.

Above the threshold, the functional response will become marked and a positive numerical response could easily occur. The net effect will result from a combination of these functional and numerical responses so that per cent predation will remain low so long as there is sufficient cover and food available for the prey. As soon as these supply factors are approaching exhaustion the per cent predation will suddenly increase.

This type of predation will occur (1) when the prey has a specific and rigid threshold density near which it normally operates, and (2) when the strength of stimulus perceived by predators is so low below this threshold and so high above it that there is a marked change in the functional response. Most insect populations tolerate considerable crowding and the only threshold would be set by food limitations. In addition, their strength of stimulus is often high at all densities. For N. sertifer at least, the strength of stimulus from cocoons is great and the threshold occurs at such high densities that the functional responses of small mammals are at their maximum. Compensatory predation is probably uncommon among insects.

Entomologists studying the biological control in insects have largely concentrated their attention on a special type of predator parasitic flies. A true predator is distinguished from an insect parasite by the stage of the predator that attacks, by the stage that feeds, and by the number of prey consumed per predator. The true predator searches actively for prey and each individual requires a number of prey to sustain it. The searching behaviour of the parasite, on the other hand, is largely restricted to the adult fly which usually lays one or more eggs on or in a host. Feeding on hosts is largely confined to the larvae which require only one host per individual.

If parasitism is really a type of predation, the two basic responses
to prey (or host) density and the subsidiary factors affecting these responses should describe parasitism. The functional response of a true predator is measured by the number of prey it destroys; of a parasite by the number of hosts in which eggs are laid. The differences observed between the functional responses of predators and parasites will depend upon the differences between the behaviour of eating and the behaviour of egg laying. The securing of food by an individual predator serves to maintain that individual's existence. The laying of eggs by a parasite serves to maintain its progenies' existence. It seems likely that the more a behaviour concerns the maintenance of an individual, the more demanding it is. Thus the restraints on egg laying could exert a greater and more prolonged effect than the restraints on eating. This must produce differences between the functional responses of predators and parasites. But the functional response of both are similar in that there is an upper limit marked by the point at which the predator becomes satiated and the parasite has laid all its eggs. This maximum is reached at some prey or host density above zero. The form of the rising phase of the functional response would depend upon the characteristics of the individual parasite and we would expect the same forms as will be postulated for predators at the end of this section. The functional responses of parasites have been studied experimentally by a number of workers (e.g. Ullyett, 1949 a and b ; Burnett, 1951 and 1954; De Bach and Smith, 1941 and 1947). In each case the number of hosts attacked per parasite increased rapidly with initial increase in host density but tended to level with further increase. These results, however, cannot be closely compared to those previously described for the functional responses of small mammals, because the experimental method was different. In every case a surplus of hosts was not provided
so that the curves were determined more by the limitations in the available hosts rather than by the behaviour of the parasites. Basically it seems that the functional responses of parasites are similar to those of predators and the same subsidiary factors (characteristics of hosts, number and variety of alternate hosts and predilections of the parasites) will affect their functional responses.

The numerical response of both predators and parasites is measured by the way in which the number of adults increases with increase in prey or host density. At first thought, the numerical response of a parasite would seem to be so intimately connected with that of its functional response that they could not be separated. But the two responses of a predator are just as intimately connected. The predator must consume food in order to produce progeny just as the parasite must lay eggs in order to produce progeny.

The agents limiting the numerical response of parasites will be similar to those limiting the response of predators. There is, however, some difference. During at least one stage of the parasites' life, the requirements for both food and niche are met by the same object. Thus increase in the amount of food means increase in the number of niches as well, so that niches are never limited unless food is. This should increase the chances for parasites to show pronounced numerical responses. The characteristics of the numerical responses of both predators and parasites, however, will be similar and will range from those in which there is no increase with increase in the density of hosts, to those in which there is a marked and prolonged increase.

A similar scheme has been mentioned by Ullyett (1949 b) to describe parasitism. He believed that "the problem of parasite efficiency would appear to be divided into two main phases viz. (a) the efficiency of
the parasite as a mortality factor in the host population, (b) its efficiency as related to the maintenance of its own population level within the given area". His first phase resembles the functional response and the second the numerical response. The combination of these two phases or responses will determine the changes in the per cent parasitism with changes in host density. Since both the functional and numerical responses presumably level at some point, per cent parasitism curves might easily be peaked, as were the predation curves. If these responses leveled at a host density that would never occur in nature, however, the decline in per cent parasitism might never be observed.

The scheme of predation revealed in this study can explain all types of predation as well as insect parasitism. The knowledge of the basic components and subsidiary factors underlying the behaviour permits us to imagine innumerable possible variations. In a hypothetical situation for example, we could introduce and remove alternate food at a specific time in relation to the appearance of a prey, and predict the type of predation. But such variations are only minor deviations of a basic pattern. The major types of predation will result from major differences in the form of the functional and numerical responses.

If the functional responses of some predators are partly determined by their behaviour, we could expect a variety of responses differing in form, rate of rise, and final level reached. All functional responses, however, will ultimately level, for it is difficult to imagine an individual predator whose consumption rises indefinitely. Subsistence requirements will fix the ultimate level for most predators, but even those whose consumption is less rigidly determined by subsistence requirements (e.g. fish, Ricker, 1941) must have an upper limit, even
if it is only determined by the time required to kill.
The functional responses could conceivably have three basic forms. The simplest would be shown by a predator whose pattern of searching was random and whose rate of searching remained constant at all prey densities. The number or prey killed per predator would be directly proportional to prey density, so that the rising phase would be a straight line. Ricker (1941) postulated this type of response for certain fish preying on sockeye salmon and De Bach and Smith (1941) observed that the parasitic fly, Muscidifurax raptor parasitized puparia of Musca domestica, provided at different densities, in a similar fashion. So few prey were provided in the latter experiment, however, that the initial linear rise in the number of prey attached with increase in prey density may have been an artifact of the method.

A more complex form of functional response has been demonstrated in laboratory experiments by De Bach and Smith (1941), Ullyett (19491), and Burnett (1951, 1956) for a number of insect parasites. In each case the number of prey attacked per predator increased very rapidly with initial increase in prey density, and thereafter increased more slowly approaching a certain fixed level. The rates of searching therefore became progressively less as prey density increased.

The third and final form of functional response has been demonstrated for small mammals in this study and was postulated for insectivorous birds by L. Tinbergen (1955). These functional responses are S-shaped so that the rates of searching at first increase with increase in prey density, and then decrease.

The different characteristics of these functional responses produce different types of predation. There are four major types conceivable and these are shown in Fig. 18. Three possible numerical responses are


Fig. 18 - Major types of predation. Functional response: abscissa $=$ prey density, ordinate $=$ no. of prey killed per predator. Numerical response: abscissa $=$ prey density, ordinate $=$ predator densityo Total response: abscissa $=$ prey density, ordinate $=$ percent predation.
postulated for each type - a positive response (a), no response (b), and an inverse response (c). In type 1 , the number of prey consumed per predator is assumed to be directly proportional to prey density, so that the rising phase of the functional response is a straight line. In type 2, the functional response is presumed to rise at a continually decreasing rate. In type 3, the form of the functional response is the same as that observed in this study. Type 4, is the compensatory predation of Errington. The vertical dotted line represents the "threshold of security" below which the strength of stimulus from prey is low and above which it is high. The functional response curve at these two strengths of stimulus are given the form of the functional responses observed in this study.

The combination of the two responses gives the total response shown in the final graphs of Fig. 18. Both peaked (la, 2a, 3a,b, c, $4 a, b, c$, ) and declining (lb, $c, 2 b, c$, ) types of predation can occur, but regulation is possible only in the former type.

## SUMMARY AND CONCLUSIONS

The simplest type of predation is affected by only two variables - prey and predator density. Predation of cocooned N. sertifer by small mammals is such a type, for prey characteristics, the number and variety of. alternate foods, and predilections of the predators do not vary in the plantations where N. sertifer occurs. In this simple example of predation, the basic components of predation are responses to changes in prey density. The increase in the number of prey consumed per predator, as prey density rises, is termed the functional response. The increase in the density of predators, as a result of increase in prey
density, is termed the numerical response.
The three important species of small mammal predators (Blarina, Sorex, and Peromyscus) each showed a functional response, and each curve, whether it was derived from field or laboratory data, showed an initial S-shaped rise up to a constant, maximum consumption. The rate of increase of consumption decreased from Blarina to Sorex to Peromyscus while the upper, constant level of consumption decreased from Blarina to Peromyscus to Sorex. The characteristics of these functional responses could not be explained by a simple relation between consumption and the proportion of prey in the total food available, nor did different rates of learning at different densities seem important. Their characteristics are determined very early in the feeding behaviour, before the animals dig for cocoons. The final explanation probably involves changed in the neural circuits mediating the feeding behaviour -- changes that operate together with changes in prey density and so determine the form of the functional response curves.

The form of these functional response curves is: such that the proportion of prey consumed per predator increases to a peak and then decreases. This peaked curve was emphasized by the positive numerical responses of Sorex and Peromyscus, since their populations rose initially with increase in prey density up to a maximum that was maintained with further increase in cocoon density. Blarina did not show a numerical response. The increase in density of predators resulted from increased breeding, and because the reproductive rate of small mammals is so high, there was an almost immediate increase in density with increase in food.

The two basic components of predation - the functional and numerical responses - can be affected by a number of subsidiary components: prey
characteristics, the number and variety of alternate foods, and predilections of the predators. It was shown experimentally that these components affected the amount of predation by lowering or raising the functional and numerical responses. Decrease of the strength of stimulus from prey, one prey characteristic, lowered both the functional and numerical responses. On the other hand, the number and variety of alternate foods affected the two responses differently. Increase in the palatability or in the number of kinds of alternate foods lowered the functional response but promoted a more pronounced numerical response.

The peaked type of predation shown by small mammals can theoretically regulate the numbers of its prey if predation is high enough to match the effective reproduction by prey at some prey density. Even if this condition does not hold, however, oscillations of prey numbers are damped. Since the functional and numerical response differs for the different species of predator, predation by each peaks at a different prey density. Hence, when a large number of different species of predators are present, the declining phase of predation is displaced to a higher prey density, so that the prey have less chance to "escape" the regulation exerted by predators.

The scheme of predation presented here is sufficient to explain all types of predation as well as insect parasitism. It permits us to postulate four major types of predation differing in the characteristics of their basic and subsidiary components.

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