

## The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly<sup>1</sup>

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### INTRODUCTION

The fluctuation of an animal's numbers between restricted limits is determined by a balance between that animal's capacity to increase and the environmental checks to this increase. Many authors have indulged in the whimsy of calculating the progressive increase of a population when no checks were operating. Thus Huxley calculated that the progeny of a single *Aphis* in the course of 10 generations, supposing all survived, would "contain more ponderable substance than five hundred millions of stout men; that is, more than the whole population of China", (in Thompson, 1929). Checks, however, do occur and it has been the subject of much controversy to determine how these checks operate. Certain general principles—the density-dependence concept of Smith (1955), the competition theory of Nicholson (1933)—have been proposed both verbally and mathematically, but because they have been based in part upon untested and restrictive assumptions they have been severely criticized (e.g. Andrewartha and Birch 1954). These problems could be considerably clarified if we knew the mode of operation of each process that affects numbers, if we knew its basic and subsidiary components. Predation, one such process, forms the subject of the present paper.

Many of the published studies of predation concentrate on discrete parts rather than the whole process. Thus some entomologists are particularly interested in the effect of selection of different kinds of prey by predators upon the evolution of colour patterns and mimicry; wildlife biologists are similarly interested in selection but emphasize the role predators play in improving the condition of the prey populations by removing weakened animals. While such specific problems should find a place in any scheme of predation, the main aim of the present study is to elucidate the components of predation in such a way that more meaning can be applied to considerations of population dynamics. This requires a broad study of the whole process and in particular its function in affecting the numbers of animals.

Such broad studies have generally been concerned with end results measured by the changes in the numbers of predator and prey. These studies are particularly useful when predators are experimentally excluded from the environment of their prey, in the manner adopted by DeBach and his colleagues in their investigations of the pests of orchard trees in California. This work, summarized recently (DeBach, 1958) in response to criticism by Milne (1957), clearly shows that in certain cases the sudden removal of predators results in a rapid increase of prey numbers from persistently low densities to the limits of the food supply. Inasmuch as these studies have shown that other factors have little regulatory function, the predators appear to be the principal ones responsible for regulation. Until the components of predation are revealed by an analysis of the processes leading to these end results, however, we will never know whether the conclusions from such studies apply to situations other than the specific predator-prey relationship investigated.

Errington's investigations of vertebrate predator-prey situations (1934, 1943, 1945 and 1956) suggest, in part, how some types of predation operate. He has

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postulated that each habitat can support only a given number of animals and that predation becomes important only when the numbers of prey exceed this "carrying capacity". Hence predators merely remove surplus animals, ones that would succumb even in the absence of natural enemies. Errington exempts certain predator-prey relations from this scheme, however, and quotes the predation of wolves on deer as an example where predation probably is not related to the carrying capacity of the habitat. However logical these postulates are, they are only indirectly supported by the facts, and they do not explain the processes responsible.

In order to clarify these problems a comprehensive theory of predation is required that on the one hand is not so restrictive that it can only apply in certain cases and on the other not so broad that it becomes meaningless. Such a comprehensive answer requires a comprehensive approach, not necessarily in terms of the number of situations examined but certainly in terms of the variables involved, for it is the different reactions of predators to these variables that produce the many diverse predator-prey relations. Such a comprehensive approach is faced with a number of practical difficulties. It is apparent from the published studies of predation of vertebrate prey by vertebrate predators that not only is it difficult to obtain estimates of the density of predator, prey, and destroyed prey, but also that the presence of many interacting variables confuses interpretation.

The present study of predation of the European pine sawfly, *Neodiprion sertifer* (Geoff.) by small mammals was particularly suited for a general comprehensive analysis of predation. The practical difficulties concerning population measurement and interpretation of results were relatively unimportant, principally because of the unique properties of the environment and of the prey. The field work was conducted in the sand-plain area of southwestern Ontario where Scots and jack pine have been planted in blocks of up to 200 acres. The flat topography and the practice of planting trees of the same age and species at standard six-foot spacings has produced a remarkably uniform environment. In addition, since the work was concentrated in plantations 15 to 20 years of age, the closure of the crowns reduced ground vegetation to a trace, leaving only an even layer of pine needles covering the soil. The extreme simplicity and uniformity of this environment greatly facilitated the population sampling and eliminated complications resulting from changes in the quantity and kind of alternate foods of the predators.

The investigations were further simplified by the characteristics of the prey. Like most insects, the European pine sawfly offers a number of distinct life-history stages that might be susceptible to predation. The eggs, laid in pine needles the previous fall, hatch in early spring and the larvae emerge and feed upon the foliage. During the first two weeks of June the larvae drop from the trees and spin cocoons within the duff on the forest floor. These cocooned sawflies remain in the ground until the latter part of September, when most emerge as adults. A certain proportion, however, overwinter in cocoons, to emerge the following autumn. Observations in the field and laboratory showed that only one of these life-history stages, the cocoon, was attacked by the small-mammal predators, and that the remaining stages were inaccessible and/or unpalatable and hence completely escaped attack. These data will form part of a later paper dealing specifically with the impact of small mammal predation upon the European pine sawfly.

Cocooned sawflies, as prey, have some very useful attributes for an investigation of this kind. Their concentration in the two-dimensional environment of the duff-soil interface and their lack of movement and reaction to predators considerably simplify sampling and interpretation. Moreover, the small mammals'

habit of making a characteristically marked opening in the cocoon to permit removal of the insect leaves a relatively permanent record in the ground of the number of cocooned sawflies destroyed. Thus, the density of the destroyed prey can be measured at the same time as the density of the prey.

Attention was concentrated upon the three most numerous predators—the masked shrew, *Sorex cinereus cinereus* Kerr, the short-tail shrew, *Blarina brevicauda talpoides* Gapper, and deer mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott. It soon became apparent that these species were the only significant predators of the sawfly, for the remaining nine species trapped or observed in the plantations were either extremely rare or were completely herbivorous.

Here, then, was a simple predator-prey situation where three species of small mammals were preying on a simple prey—sawfly cocoons. The complicating variables present in most other situations were either constant or absent because of the simple characteristics of the environment and of the prey. The absence or constancy of these complicating variables facilitated analysis but at the expense of a complete and generally applicable scheme of predation. Fortunately, however, the small-mammal predators and the cocoons could easily be manipulated in laboratory experiments so that the effect of those variables absent in the field situation could be assessed. At the same time the laboratory experiments supported the field results. This blend of field and laboratory data provides a comprehensive scheme of predation which will be shown to modify present theories of population dynamics and to considerably clarify the role predators play in population regulation.

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### FIELD TECHNIQUES

A study of the interaction 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.

#### Small-Mammal Populations

Since a complete description and evaluation of the methods used to estimate the density of the small-mammal predators forms the basis of another paper in preparation, a summary of the techniques will suffice for the present study.

Estimates of the number of small mammals per acre were obtained using standard live-trapping techniques adapted from Burt (1940) and Blair (1941). The data obtained by marking, releasing and subsequently recapturing animals were analysed using either the Lincoln index (Lincoln, 1930) or Hayne's method for estimating populations in removal trapping procedures (Hayne, 1949). The resulting estimates of the number of animals exposed to traps were converted to per acre figures by calculating, on the basis of measurements of the home range of the animals (Stickel, 1954), the actual area sampled by traps.

The accuracy of these estimates was evaluated by examining the assumptions underlying the proper use of the Lincoln index and Hayne's technique and by comparing the efficiency of different traps and trap arrangements. This analysis showed that an accurate estimate of the numbers of *Sorex* and *Blarina* could be

obtained using Hayne's method of treating the data obtained from trapping with bucket traps. These estimates, however, were accurate only when the populations had not been disturbed by previous trapping. For *Peromyscus*, Lincoln-index estimates obtained from the results of trapping with Sherman traps provided an ideal way of estimating numbers that was both accurate and unaffected by previous trapping.

### *N. sertifer* Populations

Since small-mammal predation of *N. sertifer* was restricted to the cocoon stage, prey populations could be measured adequately by estimating the number of cocoons containing living insects present immediately after larval drop in June. This estimate was obtained using a method outlined and tested by Prebble (1943) for cocoon populations of the European spruce sawfly, *Gilpinia hercyniae* (Htg.), an insect with habits similar to those of *N. sertifer*. Accurate estimates were obtained when cocoons were collected from sub-samples of litter and duff distributed 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 unpractically large number of sample units. It proved feasible in the present study, however, to convert such estimates from a square-foot to an acre basis, by stratifying the forest floor into three strata, one comprising circles with two-foot radii around tree trunks, one comprising intermediate rings with inner radii two feet and outer radii three feet, and one comprising the remaining area (three to five feet from the tree trunks).

At least 75 trees were selected and marked throughout each plantation, and one or usually two numbered 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 four sides of each stake were lettered from A to D and the stake was placed so that the numbered sides bore no relation to the position of the trunk. Samples were taken each year, 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 AB corner, in the second year's at the BC corner, etc. Different-sized screens were used to separate the cocoons from the litter and duff.

Cocoons were collected in early September before adult sawflies emerged and those from each quadrat were placed in separate containers for later analysis. These cocoons were analysed 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. These assumptions proved partly incorrect, however, for some of the cocoons retained their new colour for over one year. Hence the "new" category contained enough cocoons that had been spun before the sampling year to prevent its use, without correction, as an estimate of the number of cocoons spun in the year of sampling. A correction was devised, however, which reduced the error to negligible proportions.

This method provided the best available estimate of the number of healthy cocoons per acre present in any one year. The population figures obtained ranged from 39,000 (Plot 1, 1954) to 1,080,000 (Plot 2, 1952) cocoons per acre.

### Predation

Small-mammal predation has a direct and indirect effect on *N. sertifer* populations. The direct effect of predation is studied in detail in this paper. The

indirect effect, resulting from the mutual interaction of various control factors (parasites, disease, and predators) has been discussed in previous papers (Holling, 1955, 1958b).

The direct effect of predation was measured in a variety of ways. General information 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.

The actual numbers of *N. sertifer* cocoons destroyed were estimated from cocoons collected in the regular quadrat samples described previously. As shown in an earlier paper (Holling, 1955), cocoons opened by small mammals were easily recognized and moreover could be classified as to species of predator. These estimates of the number of new and old cocoons per square foot opened by each species of predator were corrected, as before, to provide an estimate of the number opened from the time larvae dropped to the time when cocoon samples were taken in early September.

It has proved difficult to obtain a predation and cocoon-population estimate of the desired precision and accuracy. The corrections and calculations that had to be applied to the raw sampling data cast some doubt upon the results and conclusions based upon them. It subsequently developed, however, that a considerable margin of error could be tolerated without changing the results and the conclusions that could be derived from them. In any case, all conclusions based upon cocoon-population estimates were supported and substantiated by results from 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 *Peromyscus* at different cocoon densities. These experiments were conducted at room temperature (ca. 20°C) in a screen-topped cage, 10' x 4' x 6". At 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 levelling 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. Consumption by 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, the consumption at each density being measured for three to six consecutive days. Ideally the size of the cage should remain constant at all densities but since this would have required over 1,400 cocoons at the highest density, practical considerations necessitated a compromise whereby the cage was shortened at the higher densities. In these experiments the total number of cocoons provided ranged from 88 at the lowest density to 504 at the highest. At all densities, however, these numbers represented a surplus and no more than 40 per cent were ever consumed in a single experiment. 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. Sound cocoons from either source were then segregated into those containing healthy, parasitized, and diseased prepupae using a method of X-ray analysis (Holling, 1958a). The small male cocoons were separated from the larger female cocoons by size, since this criterion had previously proved adequate (Holling, 1958b). 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 x 8 x 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 were 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 has been shown (Holling, 1955, 1958b) that a seven-day period is more than ample to permit complete learning.

#### THE COMPONENTS OF PREDATION

A large number of variables could conceivably affect the mortality of a given species of prey as a result of predation by a given species of predator. These can conveniently be classified, as was done by Leopold (1933), into five groups:

- (1) density of the prey population.
- (2) density of the predator population.
- (3) characteristics of the prey, e.g., reactions to predators, stimulus detected by predator, and other characteristics.
- (4) density and quality of alternate foods available for the predator.
- (5) characteristics of the predator, e.g., food preferences, efficiency of attack, and other characteristics.

Each of these variables may exert a considerable influence and the effect of any one may depend upon changes in another. For example, Errington (1946) 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. First, the characteristics of cocoons do not change as the other factors vary and there are no reactions by the cocooned sawflies to the predators. We therefore can ignore, temporarily, the effect of the third factor, 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 density and quality of alternate foods, can therefore be initially ignored, as can the fifth factor, characteristics of the predator, which is really only another way of expressing factors three and four. There are thus only two

basic variables affecting predation in this instance, i.e., prey density and predator density. Furthermore, these are the only essential ones, for the remainder, while possibly important in affecting the amount of predation, are not essential to describe its fundamental characteristics.

### The Basic Components

It is from the two essential variables that the basic components of predation will be derived. The first of these variables, prey density, might affect a number of processes and consumption of prey by individual predators might well be one of them.

The data which demonstrate the effect of changes of prey density upon consumption of cocooned sawflies by *Peromyscus* were obtained from the yearly cocoon quadrat samples in Plots 1 and 2. In 1951, Dr. F. T. Bird, Laboratory of Insect Pathology, Sault Ste. Marie, Ont., had sprayed each of these plots with a low concentration of a virus disease that attacked *N. sertifer* larvae, (Bird 1953). As a result, populations declined from 248,000 and 1,080,000 cocoons per acre, respectively, in 1952, to 39,000 and 256,000 in 1954. Thus predation values at six different cocoon densities were obtained. An additional sample in a neighbouring plantation in 1953 provided another value.

Predation values for *Sorex* and *Blarina* were obtained from one plantation, Plot 3, in one year, 1952. In the spring of that year, 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 at the other. An area at one end, not sprayed, served as a control. When cocoon populations were sampled in the autumn, 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 densities. Thus, in this one plantation in 1952, there was a sufficient number of different cocoon densities to show the response of consumption by *Sorex* and *Blarina* to changes of prey density.

The methods used to estimate predator densities in each study plot require some further comment. 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 mammals. The populations determined from these trapping procedures were plotted against time, and the number of "mammal-days" per acre, from the start 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 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 caged *Sorex* per day, i.e. 101. Since the number of cocoons opened at the highest cocoon density was

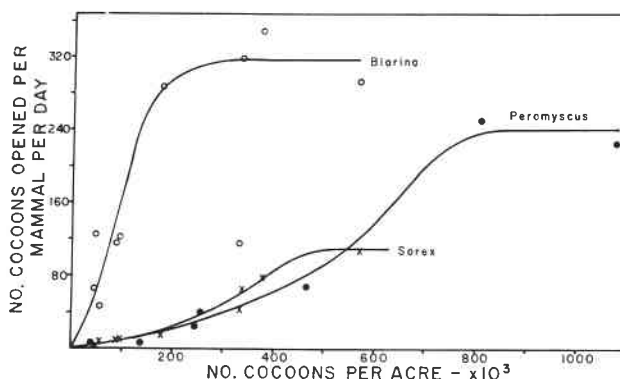


Fig. 1. Functional responses of *Blarina*, *Sorex* and *Peromyscus* in plots 1, 2, and 3.

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, estimates from Sherman trapping were shown to underestimate the numbers of *Sorex* by about the same amount, i.e. one-tenth.

With estimates of the numbers of predators, prey and destroyed prey available, the daily number of prey consumed per predator at different cocoon densities can be calculated. As seen in Fig. 1, the number of cocoons opened by each species increased with increasing cocoon density until a maximum daily consumption was reached that corresponded approximately to the maximum number that could be consumed in any one day by caged animals. 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.

The existence of such a response to cocoon density may also be demonstrated 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 I. 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

TABLE I

Stomach contents of *Peromyscus* trapped immediately before larval drop and two months later

Time trapped	Approx. no. cocoons per acre	No. of stomachs	Analysis	Plant	<i>N. sertifer</i>	Other insects	All insects
June 16-21	600,000	19	% occurrence	37%	95%	53%	100%
Aug. 17-19	300,000	14		79%	50%	64%	86%
June 16-21	600,000	19	% volume	5%	71%	24%	95%
Aug. 17-19	300,000	14		47%	19%	34%	53%



TABLE II

Occurrence of food items in stomachs of *Microtus* trapped before and after larval drop

Time trapped	Plant		<i>N. sertifer</i>		All insects	
	No. of stomachs	% occurrence	No. of stomachs	% occurrence	No. of stomachs	% occurrence
before larval drop	25	100%	2	8%	2	8%
after larval drop	29	100%	8	28%	11	38%

*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 acted as buffer or alternate foods. *Microtus*, even though they 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 II). 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 this response to changes in prey density by *Microtus* is extremely low.

The graphs presented in Fig. 1 and the results of the analyses of stomach contents leave little doubt that the consumption of cocooned sawflies by animals in the field increases with increase in cocoon density. Similar responses have been demonstrated in laboratory experiments with three *Peromyscus*. As shown in Fig. 2, the number of cocoons consumed daily by each animal increased with increase in cocoon density, again reaching a plateau as did the previous curves. Whenever the number of prepupae consumed did 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

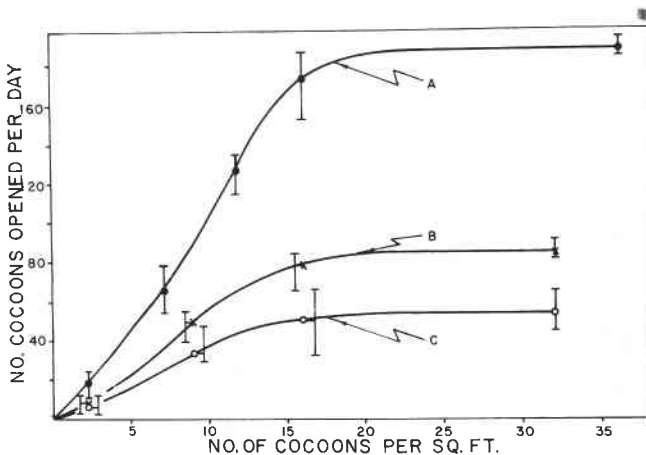


Fig. 2. Functional responses of three caged *Peromyscus* (means and ranges shown).

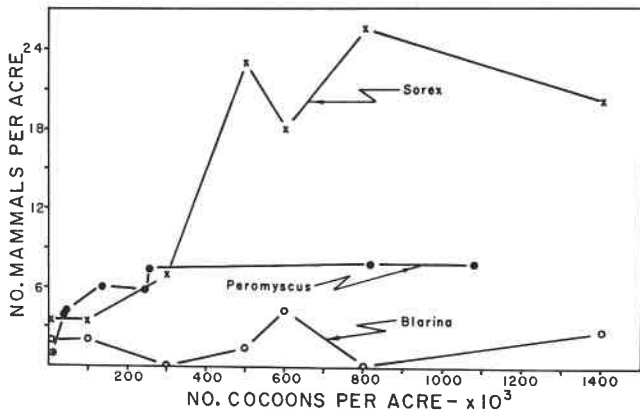


Fig. 3. Numerical responses of *Blarina*, *Sorex* and *Peromyscus*.

less than one-half the number of sawflies they would 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 another paper, 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 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. These curves are very similar to the ones based upon field data. All show the same form, the essential feature of which is an S-shaped rise to a plateau.

The effect of changes of prey density need not be restricted exclusively to consumption of prey by individual predators. The density of predators may also be affected and this can be shown 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 data for the three most important species of predators are shown in the curves of Fig. 3, where each point represents the highest summer population observed either in different plantations or in the same plantation in different years.

The densities of *Blarina* were lowest while those of *Sorex* were highest. In this situation, *Blarina* populations apparently did not respond to prey density, for its numbers did not noticeably increase with increase in cocoon density. Some agent or agents other than food must limit their numbers. Populations of *Peromyscus* and *Sorex*, on the other hand, apparently did initially 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.

Thus two responses to changes of prey density have been demonstrated. The first is a change in the number of prey consumed per predator and the second is a change in the density of predators. Although few authors appear to recognize the existence and importance of *both* these responses to changes of prey density, they have been postulated and, in the case of the change of predator density,

demonstrated. Thus Solomon (1949) acknowledged the two-fold nature of the response to changes of prey density, and applied the term *functional response* to the change in the number of prey consumed by individual predators, and the term *numerical response* to the change in the density of predators. These are apt terms and, although they have been largely ignored in the literature, they will be adopted in this paper. The data available to Solomon for review did not permit him to anticipate the form the functional response of predators might take, so that he could not assess its importance in population regulation. It will be shown, however, that the functional response is as important as the numerical.

It remains now to consider the effect of predator density, the variable that, together with prey density, is essential for an adequate description of predation. Predator density might well affect the number of prey consumed per predator. Laboratory experiments were designed to measure the number of cocoons opened by one, two, four, and eight animals in a large cage provided with cocoons at a density of 15 per square foot and a surplus of dog biscuits and water. The average number of cocoons opened per mouse in eight replicates was 159, 137, 141 and 159 respectively. In this experiment, therefore, predator density apparently did not greatly affect the consumption of prey by individual animals. This conclusion is again suggested when field and laboratory data are compared, for the functional response of *Peromyscus* obtained in the field, where its density varied, was very similar to the response of single animals obtained in the laboratory.

In such a simple situation, where predator density does not greatly affect the consumption by individuals, the total predation can be expressed by a simple, additive combination of the two responses. For example, if at a particular prey density the functional response is such that 100 cocoons are opened by a single predator in one day, and the numerical response is such that the predator density is 10, then the total daily consumption will be simply  $100 \times 10$ . In other situations, however, an increase in the density of predators might result in so much competition that the consumption of prey by individual predators might drop significantly. This effect can still be incorporated in the present scheme by adopting a more complex method of combining the functional and numerical responses.

This section was introduced with a list of the possible variables that could affect predation. Of these, only the two operating in the present study — prey and predator density — are essential variables, so that the basic features of predation can be ascribed to the effects of these two. It has been shown that there are two responses to prey density. The increase in the number of prey consumed per predator, as prey density rises, is termed the functional response, while the change in the density of predators is termed the numerical response. The total amount of predation occurring at any one density results from a combination of the two responses, and the method of combination will be determined by the way predator density affects consumption. This scheme, therefore, describes the effects of the basic variables, uncomplicated by the effects of subsidiary ones. Hence the two responses, the functional and numerical, can be considered the basic components of predation.

The total amount of predation caused by small mammals is shown in Fig. 4, where the functional and numerical responses are combined by multiplying the number of cocoons opened per predator at each density by the number of effective mammal-days observed. These figures were then expressed as percentages opened. This demonstrates 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

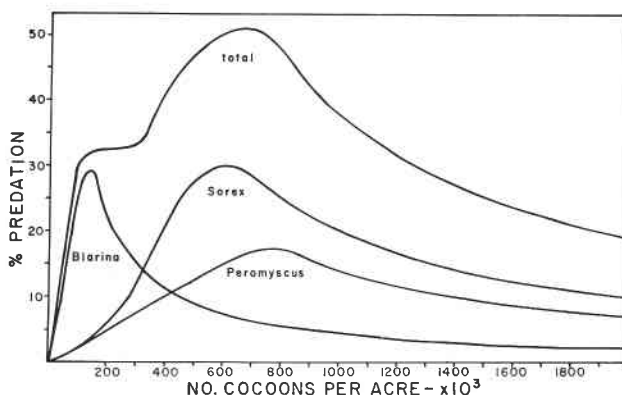


Fig. 4. Functional and numerical responses combined to show the relation between per cent predation and cocoon density.

from this figure. The general conclusion, that per cent predation by each species shows an initial rise and subsequent decline as cocoon density increases holds, however. For this conclusion to be invalid, the numerical responses would have to decrease in order to mask the initial rise in per cent predation caused by the S-shaped form of the functional responses. Thus from zero to some finite cocoon density, predation by small mammals shows a direct 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 has 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. Unfortunately 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 the several curves to be presented in the following section all suggest a point of inflection. The positive numerical responses shown by *Sorex* and *Peromyscus* also promote a direct 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 dome-shaped curves for the proportion of insects destroyed by birds. His data were only partly published (1949, 1955) before his death, but Klomp (1956) and Voûte (1958) 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. 4, we see that the form of the peaked curve for *Blarina* is determined solely by the functional response since this species exhibited 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 *Peromyscus*, but the numerical response, unlike that of *Sorex*, was not marked, and the maximum consumption of cocoons was reached only at a relatively high density; the result is a low per cent predation with a peak occurring at a high cocoon density.

Predation by 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 particularly 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 and if the prey had a sufficiently high reproductive capacity its density might jump this vulnerable range 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 considered.

### The Subsidiary Components

Additional factors such as prey characteristics, the density and quality of alternate foods, and predator characteristics have a considerable effect upon predation. It is necessary now to demonstrate the effect of these factors and how they operate.

There are four classes of prey characteristics: those that influence the caloric value of the prey; those that change the length of time prey are exposed; those that affect the "attractiveness" of the prey to the predator (e.g. palatability, defence 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. Since small mammals detect cocoons by the odour emanating from them (Holling, 1958b), the strength of this odour perceived by a mammal can be easily changed in laboratory experiments by varying the depth of sand covering the cocoons.

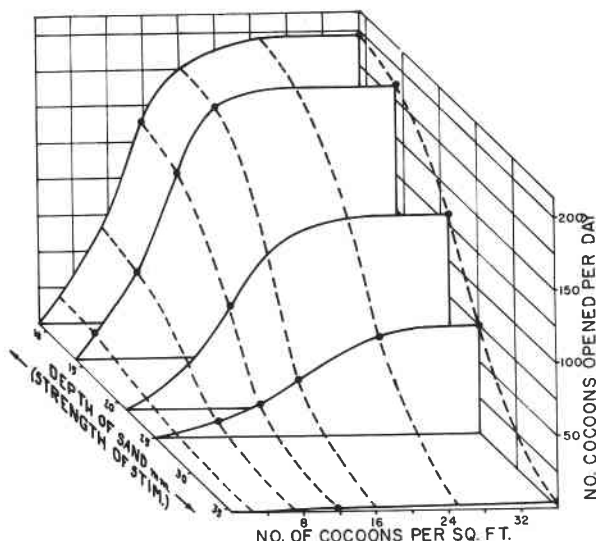


Fig. 5. Effect of strength of stimulus from cocoons upon the functional response of one caged *Peromyscus*. Each point represents the average of three to six replicates.

One *Peromyscus* 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. 5. Since the relation between depth of sand and strength of stimulus must 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. Decreasing the strength of the perceived stimulus by increasing the depth of sand causes a marked decrease in the functional response. A 27 mm. increase in depth (from nine to 36 mm.), for example, causes the peak consumption to drop from 196 to four cocoons per day. The daily number of calories consumed in all these experiments remained relatively constant since dog biscuits were always present as alternate food. The density 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. For the moment, however, 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.

In the plantations studied, cocoons were not covered by sand but by a loose litter and duff formed from pine needles. Variations in the depth of this material apparently did not affect the strength of the perceived odour, for as many cocoons were opened in quadrats with shallow litter as with deep. This material must be so loose as to scarcely impede the passage of odour from cocoons.

The remaining subsidiary factors, the density and quality of alternate foods and predator characteristics, 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 of quality of alternate foods on the functional response, however, was demonstrated experimentally using one *Peromyscus*. 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, or 200 sunflower seeds.

Fig. 6 shows the changes in the number of cocoons opened per day and in the amount of alternate foods consumed. The functional response decreased with an increase in the palatability of the alternate food (Fig. 6A). Again the functional response curves showed an initial, roughly sigmoid rise to a constant level.

As cocoon consumption rose, the consumption of alternate foods decreased (Fig. 6B) at a rate related to the palatability of the 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.

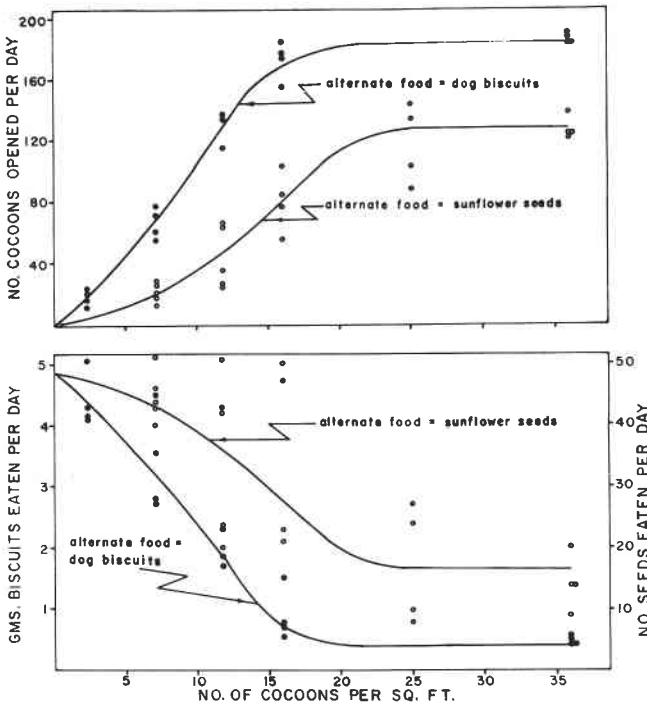


Fig. 6. Effect of different alternate foods upon the functional response of one *Peromyscus*. A (upper) shows the functional responses when either a low (dog biscuits) or a high (sunflower seeds) palatability alternate food was present in excess. B (lower) shows the amount of these alternate foods consumed.

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. L. Tinbergen (1949) observed a similar phenomenon in a study of predation of pine-eating larvae by tits in Holland. He presented data for the consumption of larvae of the pine beauty moth, *Panolis griseovariegata*, and of the web-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 anthropocentric 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 proper 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

TABLE III

The effect of alternate foods upon the number of cocoons consumed per day by one *Peromyscus*

Alternate food	No. of exp'ts	No. of cocoons opened	
		$\bar{X}$	S.E. $\bar{x}$
none . . . . .	7	165.9	11.4
dog biscuits . . . . .	5	143.0	8.3
sunflower seeds . . . . .	8	60.0	6.2
sunflower seeds and dog biscuits . . . . .	8	21.5	4.2

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 III. This table again shows that fewer cocoons were consumed when sunflower seeds (high palatability) were present than when dog biscuits (low palatability) were present. In both cases, however, the consumption was lower than when no alternate foods were available. When two alternate foods were available, i.e., both sunflower seeds and dog biscuits, the consumption dropped even further. Thus, increase in both the palatability and in the number of different kinds of alternate foods decreases the functional response.

## DISCUSSION

### General

It has been argued that three of the variables affecting predation—characteristics of the prey, density and quality of alternate foods and characteristics of the predators — are subsidiary components of predation. The laboratory experiments showed that the functional response was lowered when the strength of stimulus, one prey characteristic, detected from cocoons was decreased or when the number of kinds and palatability of alternate foods was increased. Hence the effect of these subsidiary components is exerted through the functional response. Now the numerical response is closely related to the functional, since such an increase in predator density depends upon the amount of food consumed. It follows, therefore, that the subsidiary components will also affect the numerical response. Thus when the functional response is lowered by a decrease in the strength of stimulus detected from prey, the numerical response similarly must be decreased and predation will be less as a result of decrease of the two basic responses.

The density and quality of alternate foods could also affect the numerical response. Returning to the numerical responses shown in Fig. 3, if increase in the density or quality of alternate foods involved solely increase in food "per se", then the number of mammals would reach a maximum at a lower cocoon density, but the maximum itself would not change. If increase in alternate foods also involved changes in the agents limiting the numerical responses



(e.g. increased 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. Voûte (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 be affected by that part of the third subsidiary component — characteristics of the predators — that concerns food preferences. Thus an increase in plants or animals other than the prey will most likely affect the responses of those predators, like the omnivore *Peromyscus*, that are not extreme food specialists. Predation by the more stenophagous shrews, would only be affected by some alternate, animal food.

Food preferences, however, are only one of the characteristics of predators. Others involve their ability to detect, capture, and kill prey. But again 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. 1 undoubtedly reflect differences in their abilities to detect, capture, and kill. The amount of predation will similarly 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 investigating 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 (1940). As N. Tinbergen (1951) remarked, localization of direction is developed to the highest degree in the eye. Thus the 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 one that locates its 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 prey densities, suggesting that the functional responses of these “visual predators” did indeed reach a maximum at a low density.

### **The Effect of Predation on Prey Populations**

One of the most important characteristics of mortality factors is their ability to regulate the numbers of an animal — to promote a “steady density” (Nicholson, 1933; Nicholson and Bailey, 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, i.e. it requires a direct density-dependent mortality (Smith, 1935, 1939). Density-independent factors can affect the numbers of an animal but alone they cannot *regulate* the numbers. There is abundant evidence that changes in climate, some aspects of which are presumed to have a density-independent action, can lower or raise the numbers of an animal. But this need not be regulation. Regulation will only result from an interaction with a density-dependent factor, an interaction

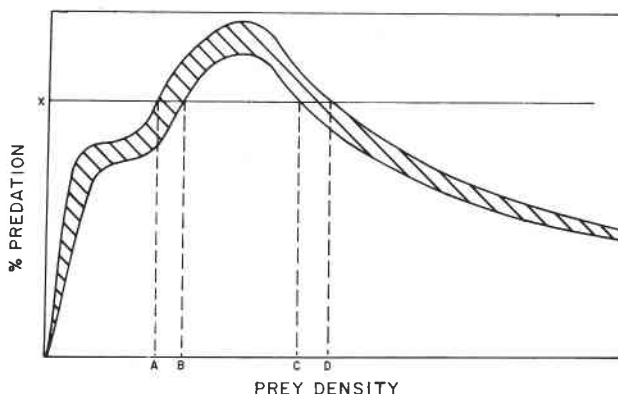


Fig. 7. Theoretical model showing regulation of prey by predators. (see text for explanation).

that might be the simplest, i.e. merely additive. Recently, the density-dependent concept has been severely criticized by Andrewartha 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 changes 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 direct density-dependent 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 shown 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 cannibalism became common. Such changes in the rate of reproduction have been shown for experimental populations of *Tribolium confusum* (MacLagan, 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. 7. The curve that describes the changes in predation with changes in prey density is taken from the actual data shown earlier in Fig. 4. It is assumed that the birth-rate of the prey at any density can be balanced by a fixed 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,  $x\%$ , 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 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 B and C, 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 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 D. If densities A and D were far apart, there would be less chance of this occurring. This spread is in part determined by the number of different species of predators that are present. Predation by each species peaks at a different density (see Fig. 4), 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 equal the effective birth-rate. When the prey is an insect and predators are small mammals, 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, Voûte's (1946) observation that insect populations in mixed woods are less liable to show violent fluctuations.

I cannot agree with Voûte (1956 and 1958) that factors causing a peaked mortality curve are not sufficient for regulation. He states (1956) that "this is due to the fact that mortality only at low densities increases 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". All that is necessary for regulation, however, 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 I 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 number killed with increase in prey density is so marked as to result in a heavy proportion of prey destroyed; a proportion that, furthermore, increases initially with increase of prey density. Thompson depreciates the importance of the numerical response of predators 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 inter-

action between parasitic flies and their insect hosts but they can be applied equally well to predator-prey relations. Thompson (1939) assumes that a predator has a limited appetite and that it has no difficulty in finding its prey. Nicholson (1933) assumes that predators have insatiable appetites and that they have a specific capacity to find their prey. This searching capacity is assumed to remain constant at all prey densities and it is also assumed that the searching is 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, it was obvious that predators did have difficulty in finding their prey and that their searching ability did not remain constant at all prey densities. Searching by small mammals was not random. Hence in the present study of predator-prey relations, the remaining assumptions of both Thompson and Nicholson do not hold.

Klomp (1956) considers the damping of oscillations of animal numbers to be 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. In particular he ignores the important possibility of an S-shaped functional response of the type shown by small mammal predators. If the parasites did show an S-shaped functional response, there would be an *immediate* increase in per cent predation when host density increased, an increase that would modify the effects of the delayed numerical response of parasites emphasized by Nicholson and Varley. Under these conditions the amplitude of the oscillations would not increase as rapidly, and might well not increase at all. An S-shaped functional response therefore acts as an intrinsic damping mechanism in population fluctuations.

Oscillations undoubtedly do occur, however, and whether they increase in amplitude or not, any extrinsic damping is important. The factor that damps oscillations most effectively will be a concurrent density-dependent factor that reacts immediately to changes in the numbers of an animal. Predation by small mammals fulfils these requirements when the density of prey is low. The consumption of prey by individual predators responds immediately to increase in prey density (functional response). Similarly, 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 immediately 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 assess precisely 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 and 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 1, 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 population had obviously increased in this plot, before the virus disease could cause much mortality. It happened, however, that *Peromyscus* was the only species of small mammal 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 shrews was effectively 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 predator-prey 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 "noncompensatory" 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, he does not believe that predation of ungulates by canids is compensatory and 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. Non-compensatory predation is easily described by the normal functional and numerical responses, for predation of *N. sertifer* by small mammals is of this type. Compensatory predation can also be described using the basic responses and subsidiary factors previously demonstrated. The main characteristic of this 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.

Compensatory predation will occur (1) when the prey has a specific density level near which it normally operates, and (2) when the strength of stimulus perceived by predators is so low below this level 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 upon insects is probably uncommon.

Entomologists studying the biological control of insects have largely concentrated their attention on a special type of predator — parasitic insects. Although certain features of a true predator do differ from those of a parasite, both predation and parasitism are similar in that one animal is seeking out another. If insect parasitism can in fact be treated as 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 responses 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 finite 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 might expect some of the same forms that will be postulated for predators at the end of this section. To summarize, I do not wish to imply that the characteristics of the functional response of a parasite are identical with those of a predator. I merely wish to indicate that a parasite has a response to prey density — the laying of eggs — that can be identified as a functional response, the precise characteristics of which are unspecified.

The effects of host density upon the number of hosts parasitized have been studied experimentally by a number of workers (e.g., Ulliyett, 1949a and b; Burnett, 1951 and 1954; De Bach and Smith, 1941). 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. Hence these functional response curves showed a continually decreasing slope as host density increased and gave no indication of the S-shaped response shown by small mammals. Further information is necessary, however, before these differences can be ascribed solely to the difference between parasitism and predation. It might well reflect, for example, a difference between an instinctive response of an insect and a learned response of a mammal or between the absence of an alternate host and the presence of an alternate food.

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 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 Ulllyett (1949b) 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. Both phases or responses will be affected, of course, by subsidiary components similar to those proposed for predation—characteristics of the hosts, density and quality of alternate hosts, and characteristics of the parasite. The combination of the two responses will determine the changes in per cent parasitism as the result of 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 levelled at a host density that would never occur in nature, however, the decline of per cent parasitism might never be observed.

The scheme of predation revealed in this study may well 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 mathematically 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 of 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 attacked 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), Ulyett (1949a) 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. These functional responses are S-shaped so that the rates of searching at first increase with increase of prey density, and then decrease.

Numerical responses will also differ, depending upon the species of predator and the area in which it lives. Two types have been demonstrated in this study. *Peromyscus* and *Sorex* populations, for example, increased with increase of prey density to the point where some agent or agents other than food limited their numbers. These can be termed direct numerical responses. There are some cases, however, where predator numbers are not affected by changes of prey density and in the plantations studied *Blarina* presents such an example of no numerical response. A final response, in addition to ones shown here, might also occur. Morris *et al.* (1958) have pointed out that certain predators might decrease in numbers as prey density increases through competition with other predators. As an example of such inverse numerical responses, he shows that during a recent outbreak of spruce budworm in New Brunswick the magnolia, myrtle, and black-throated green warblers decreased in numbers. Thus we have three possible numerical responses — a direct response, no response, and an inverse response.

The different characteristics of these types of functional and numerical responses produce different types of predation. There are four major types conceivable; these are shown diagrammatically in Fig. 8. Each type includes the three possible numerical responses — a direct response (a), no response (b), and an inverse response (c), and the types differ because of basic differences in the functional response. 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. These three types of predation may be considered as the basic ones, for changes in the subsidiary components are not involved. Subsidiary components can, however, vary in response to changes of prey density and in such cases the basic types of predation are modified. The commonest modification seems to be Errington's compensatory predation which is presented as Type 4 in Fig. 8. In this figure 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 curves at these two strengths of stimulus are given the form of the functional responses observed in this study. The forms of the responses shown in Types 1 and 2 could also be used, of course.

The combination of the two responses gives the total response shown in the



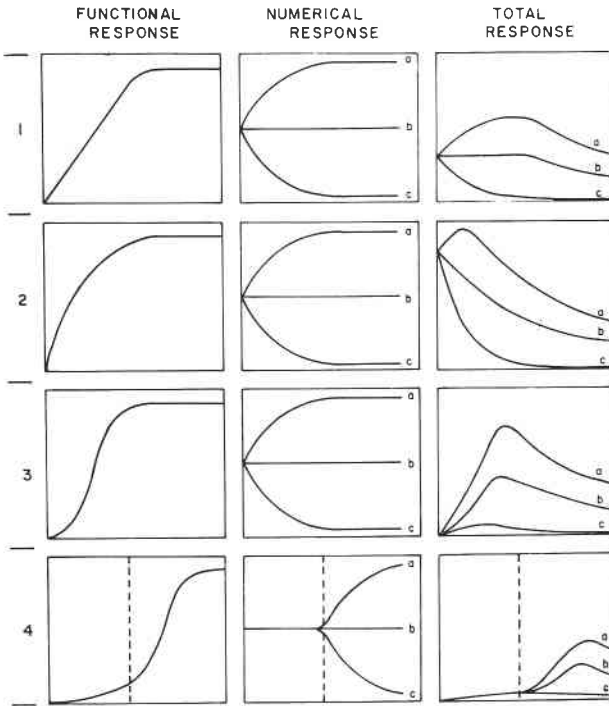


Fig. 8. Major types of predation.

final column of graphs of Fig. 8. Both peaked (curves 1a; 2a; 3a, b, c; 4a, b, c) and declining (1b, c; 2b, c) types of predation can occur, but in the absence of any other density-dependent factor, regulation is possible only in the former type.

This method of presenting the major types of predation is an oversimplification since predator density is portrayed as being directly related to prey density. Animal populations, however, cannot respond *immediately* to changes in prey density, so that there must be a delay of the numerical response. Varley (1953) pointed this out when he contrasted "delayed density dependence" and "density dependence". The degree of delay, however, will vary widely depending upon the rate of reproduction, immigration, and mortality. Small mammals, with their high reproductive rate, responded so quickly to increased food that the delay was not apparent. In such cases the numerical response graphs of Fig. 8 are sufficiently accurate, for the density of predators in any year is directly related to the density of prey in the same year. The numerical response of other natural enemies can be considerably delayed, however. Thus the density of those insect parasites that have one generation a year and a low rate of immigration results from the density of hosts in the preceding generation.

In these extreme cases of delay the total response obtained while prey or hosts are steadily increasing will be different than when they are steadily decreasing. The amount of difference will depend upon the magnitude and amount of delay of the numerical response, for the functional response has no element of delay.

#### SUMMARY AND CONCLUSIONS

The simplest and most basic 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 change 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. The form of the functional response curves is such that the proportion of prey consumed per predator increases to a peak and then decreases.

This peaked curve was further emphasized by the direct numerical response 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 density and quality of alternate foods, and characteristics 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 quality 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 responses undoubtedly differ for different species of predator, predation by each is likely to peak 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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