PREDATION AND OTHER MORTALITY FACTORS

IN

GRASSHOPPER POPULATIONS

GRASSHOPPER POPULATIONS AT LOW DENSITY - ECOLOGICAL OBSERVATIONS AND THE INFLUENCE OF SOME MORTALITY FACTORS, EMPHASIZING PREDATION

By

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A study of two grasshopper populations at low densities has shown the relative influence of climate, parasites and predators on the mortality of the nymphal and adult stages.

Short term weather fluctuations have a large influence on the mortality, but cannot control a population.

Parasites were scarce and of small importance.

Predators played an important role in the control of grasshopper populations at low densities. A special study has been made of the praying mantis-grasshopper relationship.

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INTRODUCTION

Apart from the many theoretical works on the natural control of animal populations, few researchers have tested the practical problems. Notable exceptions are Varley (1947) and what Milne (1957) calls the "Riverside School", that of P. De Bach and his co-workers in California. The exchange of articles for and against certain theories has assumed large proportions without the backing of basic research into the problems discussed.

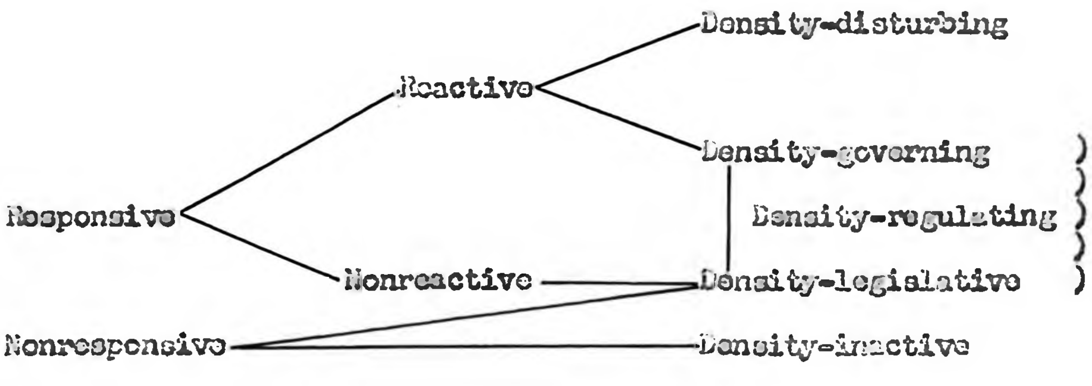
The three main theories, or four if Milne's (1957) theory is to be accepted as a separate entity, instead of a mixture of the three theories herein discussed, are respectively those of Nicholson (Nicholson 1933, 1954 and Nicholson and Bailey 1935), Andrewartha and Birch (1954) and Thompson (1929, 1939, 1956).

The ease with which arguments by one worker can be contradicted by one or more of the others shows one thing clearly that, at this stage, the available knowledge is still scant and before any rigid conclusions can be reached, much more attention must be paid to basic research. Of course this is not easy in such a complicated subject, but the sometimes prevalent tendency of ignoring this problem, just because it is difficult, has to be abandoned.

The basic idea in the Nicholson theory is, that "populations are self-governing systems. They regulate their densities in relation to their own properties and those of their environment. This they do by depleting and impairing essential things to the threshold of favourability, or by maintaining reactive inimical factors, such as the attack of natural enemies, as the limit of tolerance. The mechanism of density governance is almost always intraspecific competition, either among the animals for a critically important requisite, or among the natural enemies for which the animals concerned are requisites" (Nicholson, 1954, p. 10).

The term "density-dependent factor" was first used by Howard and Ficke (1911) and is described by Smith (1935) as destroying a percentage of the population, a percentage which increases when the numbers of the host increases. Nicholson (1933) and Smith (1935) adopted this term, and Smith (1935) used an opposing term, "density-independent", by which he meant all the factors not influenced by changes in density of the host populations.

Nicholson (1954) worked out a scheme for classifying all factors (see below):



Other concepts which he brought forward were the "steady state" and "steady density" described as follows:

Further increase of a population is prevented when all the surplus animals are destroyed, or when the animals are prevented from producing any surplus. When this happens the animals are clearly in a state of stationary balance with their environment (i.e., the steady state) and maintain their population densities unchanged from generation to generation under constant conditions (i.e., steady density).

In nature no environment is constant and the same for long periods. Milne (1957), who rightly points this out, proposes a division of possible densities in three zones:

> Zone 1 comprises the very low numbers with, as the lowest level, the lower extinction level which is never reached because of density-independent factors.
>
> Zone 2 comprises the usual numbers which fluctuate within this zone due to the combined action of density-independent factors and imperfectly density-dependent factors.
>
> Zone 3 has very high numbers with, as the highest level, the upper extinction level which is never reached because of "the one perfectly density-dependent factor" which is intraspecific competition.

Although the concept of the zone 2, of Milne, is a step ahead from the practical point of view, theoretically this is identical with the "steady-density" idea of Nicholson if one considers that, due to the continuous changing of the environment, the value of the densities will change accordingly and over a long period the resulting densities will vary within a band around the theoretical long-term steady-density. In both cases the result is that, under "normal" circumstances due to the influence of perfectly and imperfectly density-dependent factors, the numbers of animals will be regularly restricted between certain limits and will be much lower than would be theoretically possible if the populations were unchecked. A change in weather conditions disturbs this equilibrium but, unless one wants to assume that over a long period the climate is precisely the same, i.e., that favourable and unfavourable influences cancel each other out, the climate in itself is unable to control a population. However, that climatic influences will ever balance each other is unlikely, if one only considers the change in the climate recorded in the relatively short period during which weather observations have been made. Haldane (1955) reasons that, if the populations are not controlled by any other factors, small changes in the rate of survival due to changes in the climate would lead to unchecked increases if the climate becomes more favourable or to extinction if the opposite is the case.

One side of this question is of course why one should reject the idea that a population can be in balance with its environment and at the same time suggest that it is in balance with the climate which is a part of that same environment. Nevertheless, a third important theory is built on this basis. Andrewartha and Birch (1956) claim "that density-independent factors do not exist" and "the concept of competition is not relevant to the ecological problem (of distribution and abundance)."

The first of their statements follows from the observation that no environmental factor kills a constant proportion of a population, irrespective of density as Nicholson, Smith and others claim. This is quite possibly a confusion between what theoretically takes place and what actually happens in nature. If it were possible to have two populations of the same animal present in the same habitat under the influence of the same environmental factors, it could be accepted that an adverse factor, e.g., frost, would kill the same proportion of both populations. On the other hand it is highly improbable that the environment would be constant from year to year, to make it possible to see the influence of the same adverse factor (if this would occur at the same strength) from year to year. If one takes this into consideration, both statements are true and it does not matter which one is used, as long as it is made clear which definition one uses. Apart from this it is also possible to visualize a density-independent factor that affects a varying proportion. But as Milne (1957) points out, there is no reason at all to exclude such a factor from the density-independent category.

The second statement of Andrewartha and Birch (1957) concerning competition is highly erroneous. At every level of density, competition will have an influence on the number of animals. Ultimately competition is the prime reason why a population cannot fulfil its potential reproductive capacity. Because of these two major shortcomings the theory of Andrewartha and Birch cannot be accepted in its present form.

Thompson's theory (Thompson 1929, 1939, 1956) is difficult to describe. A quote from his article in 1929 will illustrate this:

> "Natural control of organisms is primarily attributable not to any complex cosmic mechanisms or regulatory factors, but rather to the intrinsic limitations of the organisms themselves. Every organism has specific characteristics that vary about a mean, but may be considered for practical purposes as fixed. These specific characteristics imply and indeed include specific needs. An environment which meets these specific needs is, for a given species, the optimum environment. Given this optimum environment indefinite increase at a specific rate is possible. But the environmental conditions of the globe vary from point to point and are probably in no two places exactly the same. From this follows that at a given moment, in a given area, the precise environmental complex constituting the optimum for a given species will be found at relatively few points. This is the real reason that organisms and, in particular injurious insects, do not often increase to the point where they are devastating plagues. The fundamental constitution of the universe, composed of a multitude of specifically different and interacting things, living and nonliving, necessarily implies a limited possibility of existence for any particular one of them. The fact that there are species, that is a variety of essentially limited things, means that their ability to increase is necessarily limited. From this

> follows that the causes of natural control, even for a particular species, are essentially multiple and variable: difficult therefore to bring within the compass of any simple definition.
>
> When we recognize the specific intrinsic limitations of organisms we have, in my opinion, arrived at the absolutely fundamental explanation of the fact that no organism increases without limit. This is a philosophical explanation which, indeed, verges on the metaphysical, and this I think is a sign that we have really got to the bottom of the subject" (Thompson 1929).

If an individual animal is reacting to the environmental conditions in the way described in this quote, it can be said that this animal is in balance with its environment. All actions upon it will be followed by a reaction. But if this is the case is it not also true for the population consisting of animals, each of which is in its place and time in balance with its environment? This is one of the main points in Nicholson's theory and basically of the theories of Andrewartha and Birch and of Milne. The difference between the two theories is what the cause of this balance is. Thompson does not give a concrete suggestion. He says in effect "The causes of natural control are essentially multiple and variable". This will be true in most cases, although not in all, but does not give any help in trying to describe those causes. Because of this Thompson's theory is not used much for practical problems and actually would be extremely difficult to use. The recent developments in ecology show that a complex can be studied more extensively by breaking it down into parts. If a series of these have been studied the next step is to try and reconstruct the original problem. Andrewartha and Birch (1956 p. 4) give good reasons why this should be the case.

None of the four theories here discussed can be accepted completely in its present form. An attempt will be made here to resolve their differences.

A population is governed by the action of density-dependent factors. These factors can both be perfectly and imperfectly density-dependent, or a combination of both, according to the density. Intra-specific competition is important especially at high densities and it is one of the perfect density-dependent factors. Interspecific competition can be either imperfectly or perfectly density-dependent. Density-independent factors cannot in themselves control a population. They have, however, a great influence on the level at which the control will take place. This they do by influencing the individual and its environment to make it more or less favourable for the existence of the species. Because of fluctuations in the density-independent factors both in time and place, the steady-density will fluctuate in time and place.

Various animals have been used in studying population dynamics. Insects because of their abundance and reproductive capacity are useful in studies on populations. In this study the grasshopper was used.

Man has been interested in grasshoppers for a long time, if only for the damage they do to crops and to food for livestock. Almost since written history begins grasshopper plagues have been mentioned and in this century a tremendous effort has been put into attempts at control. This effort is mainly directed towards eradication by chemical means and by efforts at predicting outbreaks. The literature abounds in articles describing the effects of new insecticides and, if influences of predators are mentioned, the observations seem to be done mostly under plague conditions. Of course this is understandable from the economic point of view, but the study of this insect under normal conditions (if low densities can be called normal in an insect that almost regularly erupts to high numbers) has been more or less neglected as a result.

The one outstanding contribution to this study is that of Richards and Waloff (1954). They describe the grasshoppers in a grassy heath in England and reasons for the changes in their abundance over a 5-year period. Among the other biotic factors studied, they come to the conclusion that only Scelio, an egg parasite, plays a part in the numerical fluctuations of the populations. There was no convincing evidence that predators played a part in this. As predators they listed birds, spiders, wasps and possibly small animals. Their data on predators were mostly qualitative. They tried to estimate the predation by birds by comparing the numbers of grasshoppers in two enclosures, one of which was divided by poles and threads in such a way that, it was hoped, birds might be kept from entering. No significant difference was found between the two enclosures.

There is a long list of birds that are reported to eat grasshoppers, sometimes in large quantities, but most, if not all, of these observations were made under outbreak conditions, and it is well known that birds tend to aggregate in areas where a prey species occurs in high numbers and for a time feed almost exclusively on that species. In this way they are sometimes responsible for the decline of the prey species (Andrewartha and Birch 1956).

Not much is known of the influence of birds on low densities of prey. The literature consists mainly of qualitative observations and most of these are reports of incidental feedings.

The main difficulty here is that in a quantitative study in a particular area it is impossible to identify the stomach contents by the usual method, because this would kill and remove the bird from the area in which it is being studied excluding longterm research. A method used in Holland by L. Tinbergen (1949, 1960) and later in England by Betts and Gibbs (1955) gives good results. It consists of erecting a blind (hide) near the nest during the breeding period and observing the composition of the food brought to the nestlings. This was used in Europe mainly on nestbox-breeding species, e.g., the Great Titmouse (Parus major L.) and the Blue Titmouse (Parus caeruleus L.). In the case of the Chaffinch (Fringilla coelebs L.), an open nest breeder, this method led to a high mortality of nestlings from predation (L. Tinbergen personal comm.). The hide near the nest tends to reveal it to predators. Nevertheless, this method has great advantages. Although observations are limited to the season when the birds are feeding their young, one gets during that time a good sample of what is used as food by the birds.

The species of small animals listed in Richards and Waloff (1954) as occurring in their field were: Microtus agrestis hirtus (Bellamy), Apodemus s. sylvaticus (L.), Clethrionomys glareolus britannicus (Miller), Sorex araneus castaneus Jenyns, and Sorex minutus L. They quote Sviridenko (1924) as stating that Microtus can do considerable destruction to the grasshopper Dociostaurus maroccanus Thunberg. Wragge (quoted in Richards and Waloff 1954) states that Microtus, Apodemus, Clethrionomys and Sorex araneus castaneus will readily feed on grasshoppers in the laboratory.

It is very difficult and often impossible to identify prey remains in the stomach of mice, because their food is very finely chewed and often wings and hindlegs are rejected. Because of this and also because it will decrease the population appreciably, the usual method of killing and checking the stomach contents is of no use.

Recently there has been a large increase in the use of radioactive materials in biology. As tracers their influence on methods has been great, in both botany and zoology. In simple population problems, especially in entomology, they can be used to mark a portion of the population for estimating size and movements of the population and for finding the predators affecting it. The advantage over painted spots is that moulting has no influence. Baldwin et al. (1955) described their method of using radioactive phosphorus in the study of mosquito larvae and their predators. Relevant to the present study was their experience in measuring the number of prey eaten by each predator. Their method showed great promise but has, of course, its limitations. It is only possible to work with animals that are easily collected, made radioactive and released again. This excludes most of the tree living, and some burrowing species.

The aim of the present investigation was to determine the seasonal change in a grasshopper population at low density, and to examine the influence of mortality factors especially that of predation. As the praying mantis, _Mantis religiosa_ L., is one of the important predators on grasshoppers, this predator-prey relation was studied in detail with the help of radioisotopes.

MATERIALS AND METHODS

The Experimental Plot

Part of the research was done in a 13.75 acre field approximately 2 miles north of the McMaster University campus on the north side of the Dundas Marsh, Hamilton, Ontario. The field is enclosed on the north by the Hamilton-Dundas Canadian National Railway line, east by a wooded gully with a creek running through it, south by the Royal Botanical Gardens and west by a dry gully. The vegetation is mainly grasses with weeds and scattered shrubs and trees. The north side consists of two small hills approximately 20 feet higher than the rest. (Figs. 1-2). There is a gentle slope to the south throughout the whole field. In spring the south part especially is wet, but this dries in late spring. (Figs. 3-4). The field has been unmowed and ungrazed since 1951. (Figs. 5-6). It can be assumed that recently no sudden change in the composition of the vegetation has taken place.

Throughout the flat portion of the field 50 stakes were placed in a grid at constant intervals, the stakes in each row being 25 meters and the rows 30 meters apart. On the hills 25 stakes were spaced 7.5 meters apart and the rows were 20 meters apart. (Figs. 5 and 7). These stakes aided in the census for grasshoppers and for their mantid predators. This will be described in detail later.

Census of Grasshoppers

The grasshoppers were collected with the help of a cage described by Smith et al. (1946). The collecting apparatus consisted of a shallow cage one meter (40") square and 15 cm (6") high, and a separate flat piece of plywood a little larger than the cage (Fig. 8). This cage was used as follows: from near one of the stakes in the field the cage was thrown in such a way that it landed right side up approximately 10 feet away from the person handling it. Care was taken that it was thrown on a spot where the grasshoppers had not been recently disturbed. The flat piece of plywood was inserted just under one side of the cage and the cage was brought slowly over the plywood. Thus the grasshoppers were caught between the cage and the plywood and they could be easily collected. The grass under the cage was carefully examined for any grasshoppers that might not have followed the cage. In 1957, 50 samples were taken in the field and 25 on the hills at 14-day intervals. The frequency was later changed to weekly collections of 50 samples in the field and 25 samples on the hills and beginning with the collection on July 23 and 24, 1958, 100 samples were taken in the field. This change was necessitated by a decrease in the number of grasshoppers after 1957. Each collection of grasshoppers was placed at once into a small vial of 70% alcohol and the date and place, where each was found, was recorded. A number corresponding with the date and the stake near which the grasshoppers were collected was put on the cork of the vial. All of these grasshoppers were stored until the autumn, when identification of species, stage and sex took place. For identification, use was made of the descriptions and keys of Handford (1946).

To estimate at any given time the total number of grasshoppers in the whole area under study, we have to consider the difference in areas of the hills and the field.. The area of the hill is approximately one-tenth the area of the field, respectively 1.25 acres and 12.5 acres. The total number of grasshoppers in the whole area can be calculated by adding the estimated numbers on the hills to the estimated numbers in the field ($\frac{\text{number collected on hills}}{\text{number of sq. m. sampled}} \times$ total sq. meter on hills + $\frac{\text{number collected in field}}{\text{number of sq. m. sampled}} \times$ total sq. meter of field). For ease of calculation the number of grasshoppers in the whole area is calculated by multiplying the area of the field (50,000 sq. m.) by the sum of the number of grasshoppers per sq. m. in the field and one-tenth the number of grasshoppers on the hills.

Labelling Grasshoppers with P^{32}

In the laboratory experiments were done on the feeding of grasshoppers with radioactive phosphorus (P^{32}). In 1958 grasshoppers to be released in the field were dipped in a solution of Sodium Radio Phosphate and water (Chas. Frost and Co., Montreal) and permitted to dry before they were used in experiments. This method had the advantage of speed and ease with which large numbers of grasshoppers could be handled. The obvious disadvantage was that if these grasshoppers were used in the field, rain would quickly remove the radioactivity. Even without rain the radioactivity disappeared rapidly, although after a week, radioactivity was still found to be present and was easily measured. In 1959 the slower method of spraying food, mainly leaves of dandelions, grass and alfalfa, with a solution of radioactive phosphorus in water, was used, and after drying, this was offered to the grasshoppers. A level of approximately 50-100 μc P^{32} was used for 300-400 grasshoppers. In 24 hours approximately half the area of dandelion leaves were eaten. Before radioactive food was offered, the normal food was withheld for a period of 12-24 hours. Time for this method was possible in 1959 because large scale collecting of grasshoppers was impractical due to extremely low densities.

It was shown by Kettlewell (1955), (see also Fuller et al. 1954) that about 50% of the radioactivity ingested by the insect disappeared in 24-48 hours and that after this initial decrease, the radioactivity of each grasshopper declined only slowly. Therefore all grasshoppers used for experiments were, after feeding on radioactive material for 24 hours, fed on normal food for a period of 48 hours, before they were used for further experiments.

For measuring radioactivity use was made of a Tower (Simpson-Sears) geiger counter (model 6157) together with an Industrial Glow Tube Counter from the Atomic Instrument Corporation (Cambridge, Mass., U.S.A.), consisting of the following panels: one of model 1238, two of model 180 and one of model 955. The actual measuring was done by holding the grasshopper against the unsheathed probe which was fastened in a stand and which rested on an aluminum plate. All counts were timed to the full minute after the count of a thousand had passed. When this was obviously too time-consuming, as in counts of the background radioactivity and of nonradioactive substances or animals, the radioactivity was counted for 10 minutes. Counts of the background were taken before and after an experiment or series of experiments. Long series of experiments were regularly interspersed with these 10-minute background counts.

Before releasing the grasshoppers one of two methods of measuring the radioactivity was used. With large numbers ($>$ 100), the radioactivity of a random sample, consisting of 10% of the number released, was measured and the average value of the radioactivity was used as an indication of the average radioactivity of the whole group. Small numbers of grasshoppers ($<$ 50), to be released, were counted individually just before their release and care was taken to use only those grasshoppers that had roughly the same amount of radioactivity).

Collection of Egg-pods

In the autumn of 1957 and the spring of 1958 a collection of sods was made randomly from the position of the stakes in that portion of the field and hill where the main oviposition had taken place. The size of the individual sod was one square foot and each sampling collection consisted of 80 sods (7.2 sq. meter).

In searching for evidence of oviposition each sod was crumbled into particles smaller than an egg-pod.

Examination of Grasshoppers for Parasites

The grasshoppers, collected and preserved earlier, were examined for internal and external parasites.

Censusing Predators and Evaluating their Effect on the Grasshoppers.

Birds.

The method of censusing birds, described in detail by Tinbergen (1946) and Kendeigh (1949), was used. This consists of counting the number of singing males in the spring after they have established their territories. It is assumed that all singing males will attract a female and will rear young. Later in the season the territories are again checked for activity and the nest or the approximate position of the nest is found. The progress in the rearing of the young is followed throughout the season.

At the beginning of May several early morning counts were made. From the time of sunrise and for 2 hours afterwards the species and the position of each singing male was recorded. This not only gave the numbers of birds present but gave also an indication of the size of the territory of each individual bird. Special care was taken to evaluate the influence of those birds nesting at the edge or just outside the field. As far as possible the amount of time spent foraging in the field was given. A bird which spends half the time foraging in the field and half outside is given the index 1/2.

When the young were being reared, a blind consisting of a collapsible frame and a canvas cover was gradually brought into position two feet from the nest. Daily observations of the food brought to the young was made to distinguish both the species of grasshopper and the instar. This was only possible in few instances because of the speed with which the young were fed. The disadvantage of this method was the mortality of the birds from predation. The position of the blind near the nest revealed the nest to people wandering through the field as well as to mammalian predators.

Mice.

To determine which species of small mammals were in the experimental plot, a grid of modified Sherman livetraps was used.

The meadow vole, Microtus p. pennsylvanicus (Ord.), found commonly in grasslands in Southern Ontario, is a vegetarian according to the literature (Allee et al. 1949). An attempt was made to verify this by supplying a surplus of vegetable food and providing live grasshoppers.

Radioactive grasshoppers were fed to mice to determine the amount of radiation appearing in their droppings after certain time intervals. In order to assess whether grasshoppers were an important part of the diet of the vole, droppings were collected in the field after a number of radioactive grasshoppers had been released in part of the field. A grid of flat aluminum squares (4" x 4") was put out in the field andthe droppings deposited on them collected at regular intervals and measured for radioactivity.

Emlen et al. (1958) elaborated a suggestion of Eady (1948) and found that mice tend to concentrate their droppings on smooth surfaces. They evaluated the properties of different materials in this respect and concluded that, although the material had some influence, the main point was that the surface was horizontal and smooth.

Aluminum plates were used in this study because they are easily cleaned, an advantage when there is a possibility of radioactive contamination.

Twelve rows of 12 aluminum squares each were set out in the field. The rows and the individual squares were 7.5 metersapart. If droppings were found on a plate it was exchanged for a clean plate and the old one was taken to the laboratory and checked for radioactivity and cleaned. The ratio of radioactive and nonradioactive grasshoppers at the beginning of the experiment was found by making the release of the radioactive grasshoppers. coincide with the weekly census. The census gave the number of nonradioactive grasshoppers, and a known number of radioactive were released. After an interval of a week (the duration of the experiment) the grasshoppers collected in the regular census were checked for radioactivity. This gave the ratio at that time.

Praying Mantis.

In the field, praying mantis (Mantis religiosa L.) were censused at the same time and in the same way as the grasshoppers. Other mantis were reared in the laboratory. After hatching,the small mantis were fed on fruit flies (Drosophila melanogaster Meigen). The fruit flies were reared on a malt-molasses medium in pint bottles. The wild (winged) type was used at first but later it was found easier to use flies with vestigial wings. Every day a number of fruit flies was released in the cages in which the small mantis were being reared. Large mantis were kept individually in pint bottles with a cheesecloth top. A piece of paper was provided to give a foothold. Their food was house flies and grasshoppers. Mantis were fed grasshoppers of known radioactivity and then their own radioactivity was measured after three days. Measuring the radioactivity was done by pressing the whole animal with the ventral side against the probe of the Geiger-Müller Counter. The counts were done to the full minute after the count of a thousand had been reached. In cases of low radioactivity and nonradioactivity, the insect was counted for 10 minutes.

Outdoor Experiments on the Predator-Prey Relation between Mantis and Grasshoppers

In the field use was made of cages, measuring 2½ x 2 x 1 meter, constructed of wooden supports 2" x 1" thick and green-painted, 16 mesh-per-inch window screening (Fig. 9). These were set up near the woodside edge of an open field on the McMaster University campus. Each cage was stocked with three adult mantis and a varying number of radioactive adult and late nymphal red-legged grasshoppers (Melanoplus femur-rubrum (De Geer)). Care was taken to prevent escape of either species. After three days the remaining mantis and grasshoppers were collected and after a further three day interval their radioactivity was measured.

RESULTS

General

The area chosen for this study being an uncultivated, unmowed field was less populated by grasshoppers, and apparently by other insects, than surrounding mowed areas. Nevertheless in the first two years of the investigation it was practical to make a regular census throughout the season of grasshopper abundance and to study the factors responsible for mortality in the population. In 1959 and 1960 however, the number of grasshoppers was so low that it was impractical to study the seasonal change in the grasshopper abundance. In these years the relation between praying-mantis and different prey-densities was examined more critically making use of radioactive phosphorus.

Grasshoppers

Seasonal Change in Abundance in Different Instars

Data on the seasonal change in abundance of the five nymphal instars and of the adults in two species of grasshoppers, Melanoplus femur-rubrum (DeGeer) and Melanoplus bivittatus (Say), were obtained by a periodic sampling of grasshoppers from one square-meter areas, which were distributed according to a stratified randomness (see Materials and Methods). The change in density in numbers/sq. m. both on the hill and in the field for 1957 are illustrated in Figs. 10-13 and for 1958 in Figs. 14-17. The actual numbers of each instar of each species collected on the hills (in 25 sq. m.) and in the field (in 50 sq. m.) is shown in Tables I-VIII. The numbers in the collection taken during the latter part of the 1958 season had to be halved, as they were based on 100 one sq. m. samples. The total number of grasshoppers in the study area are shown in Figs. 18-21.

Average Rate of Mortality.

If the total number of grasshoppers per collection is plotted against time, the slope of the curve will give an indication of the average mortality per time unit. Richards and Waloff (1954) describe a method to determine this mortality. The following is a quote:

> "The analysis of the data is based on the assumption that once the nymphs have hatched there is an approximately steady mortality, so that the population can be represented by a formula after the type $Y = nK^t$, where $\underline{Y}$ is the population on day $\underline{t}$, $\underline{n}$ the peak number (ideally the number which hatched) and $\underline{K}$ the fraction of the population which survives to the end of a unit of time (in this case a day). After the peak has been passed, the logarithm of $\underline{Y}$ should follow a straight line, since $\log Y = \log n + t \log K$.
>
> The logarithm of successive population estimates can be used in conjunction with the value of $\underline{t}$ (= day number) to determine a linear regression equation. The regression coefficient is the logarithm of the average fraction surviving per day and by putting in the equation a value of $\underline{t}$ which corresponds to the beginning of hatching, a value of $\underline{\log Y}$ is obtained which gives an estimate of the size of the initial population (pg. 111)".

In Table IX and X this method has been used for the calculation of the field populations of *M. femur-rubrum* and *M. bivittatus*. In the formula $\log Y = \log n + t \log K$, *Y* is the accumulated number of grasshoppers of all instars and as these were collected in the field, it is expressed as the number per 50 sq. meter. The numbers in the collections made later in the season, when 100 one sq. m. samples were taken, were halved which explains the occurrence of half grasshoppers in the tables. The number of grasshoppers in the initial population ($t = 0$) is *n*, *t* is the time in weeks since the beginning of the hatching with one week before the first grasshoppers were found as the beginning of the hatch, and *K* the fraction that survives at the end of each time unit. In the regression line $y = \bar{y} + b(t - \bar{t})$, $y = \log Y$ and $b = \log K$.

The So-called Species C.

1. Morphological Evidence for its Validity.

In the collection of 1952, specimens not readily identified as either *M. femur-rubrum* or *M. bivittatus*, were found among the first instars. These grasshoppers were tentatively designated as species C.

The first and second instar of *M. femur-rubrum* and *M. bivittatus* are distinguished by the following characteristics (Handford 1946):

In the first and second instar of *M. femur-rubrum* the whitish crescent on the pronotal lobe is always present and it continues partway across the gena, while in those of *M. bivittatus* the crescent is less pronounced and does not reach the head region. The black band on the posterior femur in *M. femur-rubrum* covers the upper third of the lower chevrons and the lower margin is somewhat irregular. In both species the black band is unbroken.

Species C differed from the first instar of the two common species in that it did not have the whitish crescent of the pronotal lobe continue partway across the gena, as in M. femur-rubrum, and the banding of the posterior femur was unlike that of M. bivittatus and more like that of M. femur-rubrum, sometimes broken and often obscure or even lacking.

All second and older stages found were those of the two common species.

2. Ecological Evidence for its Validity

The temperature in June 1958 was much below average (see Table XVI) and this influenced the mortality during that time and also delayed the emergence of the later-hatching grasshoppers. The main portion of the first instars collected in early July was of species C and the main hatching took place in the northern part of the field. Because the later stages of M. femur-rubrum appeared to be concentrated in the same locale, the following study of the data was made. The field was divided into ten parts of which each consisted of a group of five stakes. Exceptions were groups 6 and 7 which had respectively a group of four and six stakes. This was done solely for convenience, as any other division would have been awkward, due to the arrangement of the stakes, which was dictated by the shape of the field. This grouping had no influence on the results however. The location and numbering of the groups as well as the individual stakes in the field are shown in Fig. 7. The number of each instar of grasshopper collected on July 10, 16, 23 and 30 and the position of each collection in the field are presented in Table XI.

Sex-ratios in Nymphs and Adults

The sex of the grasshoppers was recorded for all collections. The numbers for 1957 were too low to be reliable. The data for 1958 are summarized in Tables XII and XIII. These tables give the numbers of males and females collected in the two species. The last column expresses the number of males as a percentage of the number of females. In both species there was a consistent excess of females in the younger nymphal stages. In the older stages, namely in the fourth, fifth and adult of M. femur-rubrum, the ratio was approximately one to one. In the adults of M. bivittatus there was an excess of males.

The females hatch earlier than the males, for instance the percentage of males over females in the first instars of M. femur-rubrum in the collection of May 23 is 25% and the combined percentage of males over females in the collection of June 4 and June 10 is 76%.

Evidence of Oviposition of Grasshoppers and Mantis

On the sods of the fall collection of 1957, three egg-pods were found. One egg-pod was found in the spring collection of 1958. Two praying mantis oötheca were present in the fall collection and two in the spring collection.

Climate

The climatological observations were made, in part by the author, at the Royal Botanical Gardens, approximately two miles from the experimental plot. Observations were taken at 7 a.m., 1 p.m. and 7 p.m. Eastern Standard Time (12, 18 and 24 hours G.M.T.). The average monthly temperature for 1957 and 1958 are listed in Tables XIV and XV. The column headed "Deviation" lists the departure from the 20-year average.

In June 1958, the month with a high mortality in M. femur-rubrum (Fig. 12), the temperature averaged much below normal. The average temperatures for the month in the ten-year period 1948-1957 is summarized in Table XVI. The average temperature in June 1958 is 6.2° F. below the average of the ten preceding years. Also the winter of 1958-1959 was severe, as the following quote will illustrate (from the Monthly Meteorological Summary of the Meteorological Division, Department of Transport Canada for December 1958 at Hamilton, Ont.):

> "Temperature averaged much below normal. Not since 1918 had December been so cold (December 1918 mean temperature was 19.6° F.). Cold spell began on November 26th and lasted until December 26th with only brief warm intervals. The ten-day cold period from the 6th to the 16th was unusual for so early in the winter. Precipitation was much below normal. The mild spell on the 3rd and 4th melted most of the 4" snow carried over from November. The heaviest snowfall of the month was 2" on the 16th".

Parasites of the Grasshoppers

The most abundant parasite was the larva of the grasshopper mite, Eutrombidium trigonum (Hermann). In 1957 the infestation of mites occurred from July 19 to August 16 and reached a peak on August 2 when 22% of M. femur-rubrum and 28% of M. bivittatus were infested with larval mites. Most grasshoppers had only one or two mites with eight being the maximum. In 1958 the incidence of mites was much lower, only a few per cent of the grasshoppers of both species were infected.

The examination for internal parasites showed that less than one per cent of the grasshoppers were parasitized. Two mermithid nematodes infected one grasshopper and eight sarcophagid larvae were found.

Predators of the Grasshoppers

Birds

In 1958 a series of observations was made at the nest of a Catbird (Dumetella carolinensis L.). For a period of seven days (July 3 - July 10, 1958) the feeding of the three young in the nest was watched for a total of 27 hours, during which the young were fed 125 times. The food included 25 grasshoppers. In the same period the parents themselves were twice seen catching and eating a grasshopper. Other food fed to the young was: moths, caterpillars, spiders, aphids, beetles, an unidentified red flower and possibly praying-mantis.

The density of the grasshoppers in the territory of the Catbird in the beginning of July was 0.40 grasshoppers/sq. m. The approximate size of the feeding territory of the Catbird was two acres (8000 sq. m.).

The species and number of birds nesting in the field are summarised in Table XVII. The nests of some of these were watched from a blind but predation destroyed the nest before any significant data were obtained. Apart from the species breeding in the field, the following species were regularly seen near or in the field: Mourning Dove (Zenaidura macroura carolinensis (L.)), Hairy Woodpecker (Dendrocopus villosus villosus (L.)), Downy Woodpecker (Dendrocopus pubescens medianus (Swainson)), Crested Flycatcher (Myiarchus crinitus (L.)), Wood Peewee (Contopus virens (L.)), Blue Jay (Cyanocitta cristata cristata (L.)), Crow (Corvus brachyrhynchos brachyrhynchos Brehm), Black-capped Chickadee

(*Parus atricapillus atricapillus* (L.)), Red-breasted Nuthatch (*Sitta canadensis* L.), Cedar Waxwing (*Bombycilla cedrorum* Vieillot), Starling (*Sturnus vulgaris* L.), Bobolink (*Doliochonus oryzivorus* L.), Baltimore Oriole (*Icterus galbula* (L.)), Bronzed Grackle (*Quiscalus quiscala aeneus* (L.)), Cowbird (*Molothrus ater ater* (Boddaert)), Cardinal (*Richmondena cardinalis cardinalis* (L.)), American Goldfinch (*Spinus tristis tristis* (L.)). Infrequent vicitors were several species of Hawks, Owls, Heron, Killdeer, etc. Of the above mentioned birds the following are known to eat grasshoppers: Heron, several Hawks, Killdeer, Hairy Woodpecker, Downy Woodpecker, Blue Jay, Crow, Catbird, Brown Thrasher, Robin, Starling, Meadowlark, Redwing, Bronzed Grackle, Cowbird, Field Sparrow, Song Sparrow.

Meadow Vole

The only species of small mammals collected in the livetraps, was the Meadow Vole (*Microtus p. pennsylvanicus* (Ord)). Also just one type of droppings corresponding to that of the Meadow Vole was found on the "Emlen" squares.

The experiment done in the laboratory showed that voles, kept in cages with an oversupply of vegetable food, readily ate grasshoppers. They made a considerable effort to catch a live grasshopper and as soon as it was caught they ate it rapidly. When a radioactive grasshopper was fed to a mouse, its droppings became radioactive after a two-hour period. The radioactivity gradually increased, reaching a peak after approximately 24 hours. After 52 hours the droppings were still slightly radioactive but after this the radioactivity did not differ significantly from the background counts.

From August 18 - 21, a total of 2604 radioactive grasshoppers was released on the two acres in the north-west sector of the field. The census of August 20 showed 35 grasshoppers in 24 sq. meter, while on August 26 this number was 55. Assuming an average number of 45 grasshoppers per 24 sq. meter, this would mean that of the total population (radioactive + nonradioactive grasshoppers) 14.8% were radioactive. The following week of the 55 grasshoppers collected, 7 or 12.7% were radioactive. The small difference in these percentages indicates that the mortality of the radioactive grasshoppers was approximately the same as that of the nonradioactive grasshoppers and that the use of radiophosphorus at these concentrations has no deleterious effect on the grasshoppers. This is confirmed by Fuller, Riegert and Spinks (1954) for laboratory populations.

From August 20 - September 9 mouse droppings were collected every other day. However there was no significant difference in the level of the radioactivity of the droppings and that of the background.

Praying Mantis

1. Seasonal Change in Abundance.

The collection of the praying mantis (Mantis religiosa L.) was made at the same time and in the same way as the grasshopper collections. In 1957 and 1958 they occurred in large numbers over the whole study area. The numbers in 1959 and 1960 were much lower. The emergence was much later than that of M. femur-rubrum and the peak numbers were reached, both on the hills and in the field, in the beginning of July (Fig. 22 and Table XVIII). The last unhatched oöthecae were found on

July 9, which indicates the end of the hatching. At the end of July the first adult praying mantis were collected and on August 28 the population comprised only adults. The first and only new egg case collected was found on that same date.

The mortality in the field in the period from July 3 to September 23 is calculated in the same way as already described for the grasshopper populations (see p. 14) and the results are presented in Table XIX.

2. Radioactivity in Mantis Fed Radioactive Grasshoppers.

For the experiments with radioactive grasshoppers, it was of great interest to know the amount of radioactivity taken up by the praying mantis. To each of a group of ten praying mantis, kept in separate pint-size bottles, a radioactive grasshopper was fed. The radioactivity in each praying mantis was measured on ten consecutive days, beginning one day after the feeding, the average radioactivity being expressed as the percentage of the radioactivity of the grasshopper fed (Fig. 23). Three days after feeding, the radioactivity was approximately 50% of the initial amount. Another group of three praying mantis was fed radioactive grasshoppers at three-day intervals, and the resulting radioactivity was measured before each feeding. The results are summarised in Table XX. Although there is a small difference in the average percentage radioactivity retained, the assumption in the following experiments that 50% of the radioactivity is lost during the three-day period, is justified as an approximation.

The distribution of radiophosphorus in the body is presented in Table XXI. In this table the radioactivity of the different parts is expressed as a percentage of the sum of the radioactivity of all parts. The sum of the radioactivity of the parts is approximately double of that of the intact animal, for the obvious reason that the radioactive material is not concentrated in a small space but distributed through the whole body, i.e., parts farther away from the probe of the Geiger-Müller Counter register lower than parts that are nearer.

Predation Experiments with Grasshoppers

The experiments in the field have to be described rather extensively. The main difficulty in this type of experiment is to recognize whether the praying mantis have eaten one, two or more grasshoppers in the three-day period. The distinction between eating grasshoppers or not is easy. Every grasshopper that might have been in the cages before the experiment started was removed and only radioactive grasshoppers were released in the cages. If after the three-day period the praying mantis proved to be radioactive, it meant that one or more grasshoppers had been eaten. To ensure that the day on which the grasshopper(s) had been caught would not influence the amount of measured radioactivity, the praying mantis were counted three days after the end of the experiment. Any difference in residual radioactivity from grasshoppers caught on the first day and from those caught on the last day of the experiment would be small. In all cases it was assumed that the radioactivity measured in the praying mantis at the end of the experiments was half that of the grasshoppers that were eaten.

Care was taken that the grasshoppers used in each cage were approximately of the same radioactivity. Under ideal conditions, if all the grasshoppers are of the same radioactivity, it would be possible to predict the radioactivity of the praying mantis after they had eaten one, two or more grasshoppers. It was not possible to supply the praying mantis with grasshoppers that were identical in their radioactivity, but in most cases the difference between the grasshopper with the highest and the lowest radioactivity, was not greater than the radioactivity itself. Because in the field the Geiger-Müller Counter had to be used without the electronic counting apparatus and the deflection of the needle fluctuated, it was necessary to interpolate the values. As the scale was divided in one-tenth divisions, all counts were given to the nearest division. This will explain the occurrence of many grasshoppers with the same radioactivity. In reality it means that the grasshoppers are classed in multiples or 50 counts. Some examples of the relation between the radioactivity of the grasshoppers and that of the praying mantis in three experiments with five, ten and twenty grasshoppers per five sq. meter are given in Table XXII. As in all experiments three praying mantis were put in at the beginning.

Because the amount of solar radiation is lessened by the use of screened cages, the temperature near the ground in the cage was lower than that outside. This may have increased mortality. The cages were inspected for possible openings before the experiment started, and it was felt that the escape of grasshoppers and praying mantis made little or no contribution to the change in numbers. The influence of predation differs with the density of the grasshoppers. It is relatively high at low densities and lower at high densities. From the number that were put in and that were removed after the experiment, total mortality can be calculated. The numbers were rounded to the nearest whole number.

A total of 35 cage-experiments were made. Most of the experiments with low numbers per cage (i.e., 5, 10 and 20) and some experiments with 40 grasshoppers were done in 1959. From the results of these, it was found necessary to experiment at a higher density and in 1960 experiments with 80 grasshoppers per cage were made.

The average density of the grasshoppers (D_G), the number eaten (N_G) by a certain number of praying mantis (N_P) and the number eaten per praying mantis ($N_G/N_P = C$) are collected in Table XXIII. Also given is the average density of the praying mantis (D_P) for the duration of the experiments.

The change in consumption with different densities of grasshoppers is shown in Fig. 24. From the form of the curve it is possible to gain the impression that the maximum consumption of praying mantis is approximately one and a half grasshoppers. However from actual observation it is known that this is much too low. This was substantiated by further tests. A group of praying mantis in the laboratory, which were kept in pint-size containers, was presented with a surplus of grasshoppers and the consumption in terms of three-day periods calculated. Although there was a difference in the capacity of the individuals, with the males especially eating less than the females, it was found that the average number eaten in three days was approximately two to four times higher than the highest found in the outdoor cage-experiments.

Also of interest was the time spent in eating. If this was very long, the time available could be a limiting factor in the consumption of prey. Also the amount of satiation could have an influence on the time spent eating.

To a group of praying mantis that had been starved for ten days, grasshoppers were supplied at a rate insuring that two grasshoppers were always available to the praying mantis. The impression was that the level of satiation had a small effect on the time spent in consuming the grasshoppers. Only on the first day of the experiment did the mantis eat two or more grasshoppers in rapid succession. For example, a praying mantis which ate three grasshoppers in a five-hour period, took one hour for the first and one hour and 45 minutes for the second and third, subsequent grasshoppers eaten at greater time intervals were consumed in little more than one hour. It can be said that on the average the time spent in the consumption of one grasshopper is one hour and a half. It can also be concluded from data that the time interval between feedings becomes longer when the satiation level rises.

There is also a marked change in behaviour with a rising satiation level. When the praying mantis had been starved, they showed a positive hunting reaction when a grasshopper is introduced. They stalk their prey from relatively large distances and catch it in a short time. When they have been feeding for some days, they do not show the hunting reaction as much and the stalking is over much shorter distances and often terminated without capture of prey.

DISCUSSION

Grasshoppers

Many environmental factors affect the size of a population of animals. The interpretation of these influences has been discussed fully in the INTRODUCTION. Such factors as food, weather, competition, parasites and predators all may be of varying importance depending on the conditions. The influence of predators on insect populations, especially on those at low density, is seldom examined quantitatively. In this study one of the most important factors influencing the low-density grasshopper population was predation. Thus, the role of predators was emphasized, although other factors were considered as well.

It was known from local sources that in 1956 the year before this study started, there had been a relatively high number of grasshoppers probably due to the warm, dry spring and summer that had been experienced. Although in the beginning of the 1958 season the number of first instar larvae promised a considerable increase over the numbers in 1957, this number was drastically reduced because of a high mortality in the early instars, and the resulting density was on the whole only slightly higher than in the preceding year. In 1959 and 1960 the density dropped to such a low level that it was of little value to continue the weekly censuses. The grasshopper population was at low level generally throughout Ontario in these two years (Mac May 1959, 1960).

M. femur-rubrum showed a preference for a slightly different habitat than M. bivittatus. These two species are reported to have in principle the same habitat preference with possibly a wider range for M. femur-rubrum, both being most numerous in moister pastures (Brooks 1958). The spatial distribution of the two species in the present study is given in Table XI. Only the results of the collections on July 3, 10, 16 and 23, 1958 are given, but all the other collections show the same trend. Although there was a certain mixing, it could be said that M. bivittatus occurred more or less evenly distributed in the field, whereas M. femur-rubrum frequented the north western part. The southern part of the field is moister in the spring and has a denser and higher cover of grasses. The cover in the northern part is more patchy, with quite low vegetation and a higher incidence of bare patches. The height of the cover will have an influence on the microclimate in which the insect lives. It is thought that at the densities at which the grasshoppers occur, interspecific competition is negligible, and it must be concluded that M. bivittatus has a lower temperature tolerance and a lower temperature optimum than M. femur-rubrum. This will be confirmed by further data which will be discussed below.

Because of the southern exposure of the hills the emergence there is earlier than in the field. It was felt that the two-week interval between censuses in 1957 was too long. For instance, in Fig. 10 in the 5th stage of M. bivittatus the peak in the 5th instar is missed. As the time interval between collections nears the average duration of the instars, the chance that a large portion of an instar will be missed, will be larger and larger. The time necessary for a complete census of the hill and the field was from two to three days. In the later part of 1958 it often took three days to take 125 one sq. m. samples. If it rained on the day a collection was scheduled, the collection was postponed to the next day, as it was found that when the grass was wet the grasshoppers were much more difficult to find and it was thought this would bias the results. On only one occasion was it necessary to postpone the collection for more than two days, namely at the beginning of September 1958, when in the period between September 3 and 10 it rained for five out of seven consecutive days. Because of the above reasons it was found impossible to increase the frequency of collections above that reached in 1958.

M. femur-rubrum occurred in higher numbers than *M. bivittatus* and there was a marked difference in the seasonal occurrence of the two species. In both 1957 and 1958 *M. bivittatus* hatched a week to fourteen days earlier than *M. femur-rubrum*. It had a rapid growth and had completed its cycle at the beginning of August, no *M. bivittatus* being found after August 16, 1957 nor after August 13, 1958. *M. femur-rubrum* was still found on September 4, 1957 and September 23, 1958. This may result in the same instar in each of the species being influenced by different environmental conditions.

The mortality in 1958 from week to week was rather high, especially in *M. bivittatus*. After a rather high early hatch in *M. femur-rubrum*, as compared with the preceding year, the mortality in the beginning of June was almost complete and only in the beginning of July, when the temperature rose appreciably, did the hatching of the rest of the population, which no doubt had also been delayed by the cold weather, take place. The later hatching *M. femur-rubrum* grew from egg to adult under more favourable conditions. Because a sizeable portion of the eggs of *M. femur-rubrum* were delayed in their hatching until a normally warmer season, the mortality in the remaining population of this species tends to be lessened. If the mortality in a population of *Chorthippus brunneus* (Thunb.), described by Richards and Waloff (1954), is calculated for a period of a week instead of a day, it compares readily with the weekly mortality in the two *Melanoplus* species in the present study. The fraction of the total population that survives at the end of a week is in *C. brunneus* approximately 0.73 as against respectively 0.81 and 0.66 in *M. femur-rubrum* and *M. bivittatus*.

The summer of 1958 presented a good example of the great influence the weather can have on the size of a population. The average temperature in June was far below normal and this lead to the high mortality in *M. femur-rubrum*. No doubt *M. bivittatus* was influenced by these adverse conditions, but the fact that mortality in this species was much lower, points again to what has been concluded before, that this species has a lower temperature tolerance than *M. femur-rubrum*.

After an early spring with temperatures much above normal, the hatch in 1958 was early and development especially in *M. bivittatus* was rapid. On May 10, 1958 a check for grasshoppers was made in the field but no grasshoppers were found. On May 20, after subsequent checks had shown that hatching had started, the first collection was made. In

M. bivittatus the hatch was practically completed and high numbers of the second instar of the species were found. During the whole month of June the temperature was much below average, although towards the end the temperature slowly increased, and the mortality of both species was great. *M. femur-rubrum* disappeared completely in the field.

While the precipitation in the early part of the 1958 season had been deficient, there fell, during July, August and September much more rain than average, which had a detrimental influence on the oviposition. This is one of the main reasons that the number of grasshoppers in 1959 was far below that in each of the two preceding years.

The data collected by Richards and Waloff (1954) for *Chorthippus brunneus* in 1948 - 1951 in England show a significant positive correlation between nymphal mortality and temperature. This is unexpected if this is compared with laboratory experiments where it was found that for most species of insects there is an optimum temperature at which growth is the highest and mortality the lowest (Allee *et al*, 1949). Richards and Waloff mention the possibility of a wilt disease. This was suggested from their observations on the nymphs in cage-experiments. On the other hand, in a study of the climatology of *Melanoplus M. mexicanus* (Sauss.) done in Saskatchewan, MacCarthy (1956) found that the most critical months for the development of a large adult population were June, August and September of the previous year and June in the current year. July was less important than any of the other months mentioned. Temperature, especially daily minima, were most important in June and August of the previous year and daily maxima influenced the populations more in the previous August and the current June. Sunshine was important during August and more especially in September. The correlation of numbers with the rainfall in the previous August and September was high and negative. The hatching and development of the nymphs of M. mexicanus take place in June and July, while the oviposition takes place in August and September. A significant positive correlation of temperature in the previous June and the current number suggest a lower mortality with higher temperatures in the young stages. That the weather in July is not as important as in June seems to point to a lesser influence of the weather on the older stages. August and September have the greatest influence on the egg laying.

From what is known of the mortality in M. femur-rubrum and M. bivittatus it can be pointed out that these species seem similar to M. mexicanus. That M. bivittatus did not react as much to the low temperatures in June as M. femur-rubrum, could also be because of the difference in development. M. bivittatus at that time occurs in later instars than M. femur-rubrum.

Although at the low densities of grasshoppers encountered in the experimental field it was impossible to collect enough different eggpods to judge the influence on them of parasites and predators, and of weather during the winter, it was apparent that the abnormally low temperature during early December 1958, at a time of meagre snow cover, might have created a considerable mortality of eggs, another possible factor resulting in the low numbers of first instars in the spring of 1959.

The almost absolute mortality of the young nymphal M. femur-rubrum in the beginning of the season was an unexpected aid in determining the identity of the species C. The delayed hatching of the rest of the eggs took place at a time when no *M. femur-rubrum* were present and when the main portion of *M. bivittatus* had reached the later stages. As no later stages of the unknown species were found, there were only two possibilities, first that the mortality in the first instar was 100% and no later instars were produced and second that the first instar of species C was an unknown form, at least in comparison with the western grasshoppers described by Handford (1946), of either *M. femur-rubrum* or *M. bivittatus*.

Table XI, which gives the number of grasshoppers in each group of five sq. m. in the collections taken respectively one week before, during the two weeks and one week after the main emergence of species C, shows a large number of second stage *M. femur-rubrum* in the collections on July 16 and 23, especially in that part of the field containing the groups one to five, the same area where the main emergence of species C took place. The collection on July 30 contains an appreciable number of third and fourth instars of *M. femur-rubrum*. There was a small number of second, third and fourth instars of *M. bivittatus* in these same collections but this was small compared to those of *M. femur-rubrum*. From this circumstantial evidence it has to be concluded that species C was an unknown form of the first instar of *M. femur-rubrum*. Unfortunately the identification of first instar grasshoppers is difficult because of a great variability in characteristics. Before the ecological evidence was available, the species C was sent to R.H. Handford (Kamloops, B.C.) and R.C. Smith (Belleville, Ont.), who were of the opinion that it was *M. bivittatus*, no doubt from the taxonomic point of view the only possible conclusion. It is quite possible that a few of the species C were wrongly classified as such, and were really first instars of *M. bivittatus*, but that this number must have been small is shown in Fig. 13. In this graph it appears that in the second and third instar, after most of the grasshoppers had moulted, there are few that are delayed in their development.

Criddle (1933) and Faure (1933), working with *Melanoplus bilituratus* (Walker), produced much variation in colour, size and wing length by changing temperature, population-density and food. Brooks (1958) mentions the occurrence of climatically induced forms which differ qualitatively in *M. bilituratus* and *M. borealis* (Fieber). In a memorandum Putnam (1957) realises the occurrence of geographic variations in *Melanoplus m. mexicanus* (Sauss.) collected in British Columbia, Saskatchewan and Manitoba.

A distinction has to be made between phase and form. According to Brooks (1958) a phase can be described as "a variation due to different degrees of stimulation between individuals composing populations of different densities,leading to the appearance of distinct physical types that typically also differ in their physiology and behaviour" and a form is "a variation due to climatic factors, especially those of temperature and humidity, leading to the appearance of a physical type that may also differ in behaviour".

At the densities of grasshoppers encountered in this study, it is highly unlikely that a change in physical type would have taken place. However, according to Putnam (1954) no Canadian species develops a true phase.

In this study no changes in behaviour were observed, and it must be concluded that, probably due to climatic influences, a previously unknown form of M. femur-rubrum occurred. This was noticed because of the change in a characteristic used for identification. No doubt other variations in characteristics occur in grasshoppers that would be identified as M. femur-rubrum. Variation in the banding of the hind femur has already been mentioned.

In both species there was a consistent excess of females in the younger nymphal stages. In the older stages, namely the fourth, fifth and adult of M. femur-rubrum, the ratio was approximately one to one and in M. bivittatus adults there was an excess of males. The high number of females in the first and second instars of M. femur-rubrum is partly related to a difference in time of hatching. The females hatch earlier than males. Also, the period just after hatching is very critical (Parker 1957). Because later in the hatch the temperature dropped, the mortality among hatching males was larger than in the females. In the later instars the mortality of the females must have been higher than that of the males to explain the changes in the sex-ratios. One possible factor is the observed greater reaction to disturbances by the males, which might have had an influence on the predation by making it more difficult for predators to catch them.

It is considered that at the levels of infestation found, the mites had little or no effect on the longevity, activity, fecundity and mortality of the grasshoppers (Severin 1944). At these low densities of grasshoppers, internal parasites played a small role in the regulation of the numbers. This, of course, does not exclude the possibility that at higher densities the parasites will play a major role in the control of the grasshopper.

Predators

Birds

The species nesting in the field are all common to this type of habitat. The nests of most species are of necessity only slightly above the ground level. Some, as for instance the Meadow lark and the Sparrows, nest in or on the ground while others prefer low shrubs and trees. All spend a considerable time in or just above the grassy cover of the field.

From work done by L. Tinbergen and his co-workers (L. Tinbergen 1949, 1955, 1960, Mook, Mook and Heikens 1960) it was known that certain prey-species were only taken in appreciable numbers after they had occurred for some time in high enough numbers. Another interesting phenomenon was that at higher densities, after an optimum had been reached, a prey-species would consume a progressively smaller portion of the total food.

The grasshopper density around the Catbird nest was from the economic point of view low although it could be compared with the densities found for Bupalus piniarius L. as reported by Mook, Mook and Heikens (1960). It is interesting to know that at this density twenty per cent of the food of the nestlings consisted of grasshoppers. If we can assume that the data are representative for the period, it would mean that with a consumption of one grasshopper per hour and a feeding day of 16 hours the mortality due to Catbird predation would be 112 out of 3200 or 3.5% per week. In a period of one month the mortality due to the Catbird family will be of the order of 25%. The whole population of birds, if their feeding behaviour is comparable to that of the Catbird, will eat an appreciable percentage of the available grasshoppers. It is well known that birds are keen hunters. If one has seen the ease and speed with which birds detect and catch, which for the human eye are very well camouflaged, prey-species, e.g., the Eupalus moth, it is difficult to believe that any species, if acceptable as food by the birds, will be free from their predation.

The above shows that birds can play an important role as predators of grasshoppers and that more research has to be devoted to this predator-prey relationship. It will be necessary to devise new methods or modify the old ones to a large degree. Only in nestbox breeders has the use of a blind shown good results. If a method can be evolved to exclude losses due to predation of nestlings, then this will also show good results with open nest breeders. A method using radioactive materials for labelling grasshoppers combined with the use of mistnets to catch the birds at regular intervals to measure their radioactivity would make it possible to study the bird predation during the whole season. It was unfortunate that due to low numbers of grasshoppers in 1959 and 1960 it was impossible to collect enough grasshoppers to use this method, although the equipment was in readiness.

Voles

In the literature the Meadow Vole is described as being completely vegetarian (Allee et al. 1949) and it was therefore interesting to find that in the laboratory it readily ate grasshoppers. This was also noted for another species of vole and for other small mammals by Wragge, quoted in Richards and Waloff (1954). Very few records of small mammals eating grasshoppers exist, no doubt because of the great difficulty experienced in the identification of the food remains in the stomach.

The experiment done in 1958 showed that the Meadow Vole does not eat grasshoppers in great numbers. From the use of the "Emlen" squares it was found that the number of voles was low in the area used. Under these circumstances intraspecific competition for food will have been low. Although nothing is known about the reaction of voles to different densities of grasshoppers, Holling (1959) mentions the reaction of Microtus to changes in density of the cocoon of the European Pine Sawfly, Neodiprion sertifer (Geoff.). The incidence in the stomachs increased three and a half times after the larval drop when the density of cocoons was much higher than before. It must be noted, however, that even at this higher consumption N. sertifer comprised less than one percent of the volume of the stomach contents, and also that the densities of the cocoons were many times higher than the highest density of grasshoppers found in this study. From the data collected, it must be assumed that Microtus does not, or very seldom, eat grasshoppers under natural conditions, and that it plays no role in the regulation of the grasshopper population.

Praying Mantis.

The European praying mantis has been introduced only recently into North America. It was first found in the United States at Rochester, N.Y. in 1899, and in Ontario it was first reported at Carrying Place, north of Rochester in 1914 (James, 1948). Judd (1947) reported that the mantis was unusually abundant at Hamilton, Ontario in 1946, the first mention of the occurrence of it in this locality. In 1947 and 1948 the mantis was newly recorded in Ancaster, Burlington and Aldershot (James, 1948). Although the actual appearance was probably earlier, these records show that the mantis is only recently established in Hamilton and the outlying districts.

The numbers in the experimental field showed that the mantis is by now well adapted to the habitat in which it occurs and that it can be important in the control of pasture and field crop insects. Furthermore it was apparent that, as the mantis was generally almost as abundant as the grasshoppers, it was one of the most important, if not the most important predator of the grasshoppers at least at the low prey densities encountered. Therefore the mantis-grasshopper relationship was studied in greater detail.

As far as could be ascertained, no study of the predator-prey relationship with grasshoppers had been made. The only other predator-prey information is that of L. Tinbergen (1949, 1955, 1960) on birds and forest insects, and of Holling (1959) on small mammals preying on sawfly cocoons. On the other hand a considerable amount of parasite-host information is available in the literature (e.g., Burnett 1951, 1954, 1958; De Bach and Smith 1941, 1947; Ullyet 1949a, b).

Consideration was given to assessing the predation of mantis on grasshoppers in the experimental field using radioactive grasshoppers. However, this would give an indication of the consumption of prey at only one or a few levels of predator and prey, and in order to make reliable determinations of the predation many radioactive grasshoppers would have had to be released and a large number of mantis assessed for their level of radioactivity. In order to explore the mantis-grasshopper relation with different ratios of predators to prey large outdoor cages were used so that the experimental habitat would be close to the natural as far as weather, vegetation and other invertebrate life.

For a study of this kind it is necessary to measure the densities of both prey and predator as well as the number of prey attacked in a given period of time. These measurements are relatively easy to do in laboratory experiments, but in simulated field experiments and in field experiments the latter will often be difficult, especially when no remains of the prey can give an indication of the number attacked or consumed.

No remains of dead grasshoppers were found in the outdoor cages. This is also commented upon by Putnam (1947), who mentions the acquisition of radioactivity by several soil-inhabiting wireworms (Elateridae), ground beetles (Carabidae) and darkling beetles (Tenebrionidae) in an experiment with radioactive grasshoppers. The radioactivity was most probably picked up by scavenging.

Baldwin, James and Welch (1955) describe a study of the predation of mosquito larvae and pupae with a radioactive tracer. They concluded that due to the difference in the amount of radioactivity in the prey, it was not possible to assess predation accurately. In their experiments the amount of radioactivity in the individual mosquitoes that were released in a group, differed in some instances as much as a factor 125 and this was, in all groups, not less than a factor 3.

In the study herein described, this has to some extend been overcome by using groups of grasshoppers that were more consistent in their amount of radioactivity and by using a short period of time for an experiment. The latter meant that especially at the lower densities it was most often a question of deciding whether a praying mantis had or had not eaten one grasshopper. This meant that a comparatively high number of experiments had to be done.

In the study of host-parasite relations it was reported that at higher densities the parasites were attacking a lower percentage of the host and the relation between number of eggs laid and the host-density can be described by a curve of continually decreasing slope.

The reaction of the individual predator (or parasite) to changes in prey-density can be called the functional response, as compared to the increase in number of the predators with a higher food supply (or increase in parasites with increasing host-density) which can be termed the numerical response. In nature these two responses will work together. Most laboratory experiments have studied the functional response and the field studies are mostly concerned with the numerical response (e.g., Morris _et al._ 1958, but see also Tinbergen 1949, 1955 and 1960).

A number of mathematical equations have been worked out to describe the effect of prey-density on the number of prey attacked. Some of these will be discussed below and in the light of these, the results of the mantis-grasshopper experiments will be examined.

In 1935 Nicholson and Bailey published a theory on the regulation of numbers using a mathematical approach. This was based on a number of simplified assumptions regarding the properties of animals. They assumed among others that animals search at random with respect to each other and that the searching activity is constant and independent of host-and parasite-densities, and concluded that if a population of parasites traverses an area s, and a number u of the objects sought remain undiscovered, while u' = the number of objects present in the area at the beginning of searching, then the number of undiscovered objects in part of the area ds = uds and this is equivalent to the decrease $-du$ in the number of undiscovered objects, i.e.,

$$uds = -du$$

and since $u = u'$ when $s = 0$

then it follows that

$$u = u'e^{-s} \qquad (1)$$

The area s = also bP, where b = the area searched per female and P the number of female parasites. The number of eggs available is $x = aP$, where a = the average number of eggs per female which is considered constant. It follows that

$$s = \frac{bx}{a} \text{ or } a'x \qquad (2)$$

and the more hosts are available, the smaller will be the area in which a parasite can lay its complement eggs, or

$$s = \frac{a'x}{u'} \qquad (3)$$

If (3) is inserted in (1)

$$u = u'e^{-\frac{a'x}{u'}} \qquad (4)$$

and the fraction of the original object discovered can be written as

$$\frac{(u' - u)}{u'} = (1 - e^{-\frac{a'x}{u'}}) \qquad (5)$$

A similar equation has been proposed by Thompson (Watts 1959). From (1) it follows that

$$s = \ln (\frac{u'}{u}) \qquad (6)$$

Nicholson and Bailey refer to the area traversed as *s*, and the area covered by one parasite is the area of discovery

$$\text{A.O.D.} = \frac{1}{P} \ln \frac{u'}{u} \qquad (7)$$

This is considered a constant, and in nonselective parasites the mean number of eggs laid per parasite per host equals the area traversed. This implies that there is a linear response between the density of the prey and the number attacked. This has not been shown in most of the experiments done (Burnett, 1951, 1954, 1958; De Bach and Smith, 1941, 1947; Ullyet, 1949a and b).*

In all these experiments the response could be described by a curve with a continually decreasing slope. This is also the case in the mantis-grasshopper experiments. This implies either that animals do not search at random or that Nicholson's mathematical method is not complete.

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* Klomp (1956) interprets the relation between number of eggs laid per female parasite and the number of hosts in *Carcelia obesa* searching for *Bupalus piniarius* in a pine forest as rectilinear. It is interesting to note that the densities of the host described in his study are far below those in the present investigation. Any deviation from a linear relationship will therefore be difficult to detect.

Watts (1959) developed an equation in which it was realised that there is an upper limit to the number of hosts a parasite or predator can attach. This equation is as follows:

$$N_a = PK\ (1 - e^{-aN_oP^{1-b}}) \qquad (8)$$

where N_a is the number attacked, N_o the initial number of hosts or prey, P the number of parasites, K the maximum number of attacks that can be made per parasite and a and b are positive constants. In this equation the effect on the number attacked is explored. In its simplest form, when the number of parasites is constant, it can be written

$$N_a = K'\ (1 - e^{-a'N_o}) \qquad (9)$$

If P is a constant, PK will be a constant K' and also aP^{1-b} will be a constant a'.

In no experiments has K' been measured and it will be influenced by temperature, presence of alternate hosts, etc.

Where only N_o and N_a are measured as in most parasite data, equation (9) is changed to

$$\ln \frac{K'}{K'-N_a} = a'N_o \qquad (10)$$

and K' has to be found by trial and error as that value that will straighten the line if $\ln \frac{K'}{K'-N_a}$ is plotted against N_o.

In the mantis experiments $K' = K$, because $P = 1$ and it is arbitrarily set at $K = 1.45$ and 1.50 (Fig. 25). That this value is far below the value found in the laboratory ($K' = 3 - 6$, see p. 35) is because of the influence of alternate prey.

Of the total time spent in hunting, only a fraction will be spent in hunting for grasshoppers and the rest is spent hunting flies, crickets, etc. It will depend on the stimulus from the alternate prey-species how much this factor will be, but as it can be assumed that the density and number of alternate species available is constant during the experimental period, this will be the same in all the experiments with different grasshopper densities. As a result the total number of all prey increases and this is not a linear relationship but again can be described by a curve with a continually decreasing slope. This implication will be further discussed below.

That the hunting behaviour of animals can be divided into different phases was recognized by Holling (1959). This had been known by ethologists (N. Tinbergen 1951) and was described for the praying mantis by Rilling et al. (1959) and was also noted in laboratory experiments by the author.

Holling postulated that in the simplest situations the time spent in hunting can be at least divided into two components, the time spent in searching and the time spent in handling the prey, and the handling of the prey will result in a shorter time available for searching at higher densities. The simplest possible relationship between the number attacked and the number available is

$$y = aT_s x \qquad (11)$$

where y = the number attacked, T_s the time spent searching, x the density of the prey and a a constant equal to the rate of searching multiplied by the probability of finding a given prey (a = comparable with the risk-factor R proposed by L. Tinbergen 1960, see below.).

If the total time available for hunting = T_t, then a fraction = by, where b = the time spent in handling one prey, will be spent in the handling of all attacked prey and

$$T_t - by = T_s \qquad (12)$$

if (12) is substituted in (11)

$$y = a(T_t - by)x \qquad (13)$$

or

$$y = \frac{T_t ax}{1 + abx} \qquad (14)$$

When the constants a and b are not measured, they can be calculated from the straight line equation (from 14)

$$\frac{y}{x} = -aby + T_t ax \qquad (15)$$

When equation (14) is used to describe the mantis-grasshopper relationship, a remarkably good fit between the observed and the calculated values is shown (P 0.95, Fig. 26).

The time spent in hunting by the mantis has to be divided at least into three portions, the time spent in searching, presumably at random (or the time spent in ambush until a prey comes within its sphere of vision), the time spent in the attack (i.e., the directed movement from the moment the praying mantis sees its prey) and in addition the time spent in eating and possibly resting. The time spent in attacking will be a function of the number attacked and it will shorten the time available for searching with an additional amount $-dy$ if d = the time taken for one prey. If this is included in (13), then

$$y = a'(T_t - (b+d)y)x \qquad (16)$$

or

$$y = \frac{T_t a' x}{1 + a'(b+d)x} \qquad (17)$$

This was found by Holling to exist in an experiment in which a human "predator" preyed upon sandpaper discs that were presented in different densities. When the disc had to be found by touch, the time to identify the disc was zero. When they had to be found by the sound of scratching, there was a distinct identification time, which was constant and it was seen that $\underline{a}$, the instantaneous rate of discovery, became smaller with rising densities. If it is possible for equation (14) to describe accurately the relation between number of prey attacked and density of the prey, even when $\underline{a}$ is not constant, then $\underline{a}$ must behave, according to Holling, in a certain fashion. From equation (13) $\underline{b}$ can be expressed in terms of $\underline{x}$, $\underline{y}$ and $\underline{a}$

$$b = \frac{T_t ax - y}{ayx} \qquad (18)$$

and this substituted in (16) and simplified gives

$$a = \frac{a'}{1 + a'cx} \qquad (19)$$

This means that only when $\underline{a}$ is constant or is related as in (19), it will describe the response between density and number of attacks on the prey accurately. In the experiments with sandpaper discs by Holling, this was the case.

Most of the experiments done neglect the influence of alternate prey or hosts, mainly because they are designed in such a way that no alternate hosts are available or because the densities and consumption of the alternate hosts could not be measured.

L. Tinbergen (1959) working with birds preying on forest insects presented the following "probability of encounter" hypothesis:

$$\frac{N_a}{N_a + N_o} = \frac{R_aD_a}{R_aD_a + R_oD_o} \qquad (20)$$

or

$$\frac{N_a}{N_a + N_o} = \frac{D_a}{D_a + \frac{R_oD_o}{R_a}} \qquad (21)$$

where N_a = the number of the prey a, D_a and D_o the respective densities and R_a and R_o = the respective risk indexes. The risk index is the proportionality factor which, in the probability of encounter hypothesis, relates the number of captives $\underline{N}$ to the density $\underline{D}$ and the searching time $\underline{t}$, i.e.,

$$N = RDt \qquad (22)$$

This is similar to the instantaneous rate of discovery as used by Holling (1959).

Tinbergen reasons that, during a short period of time, changes in the density of the other species will be small and that $\frac{R_oD_o}{R_a}$ is a constant. It was found that this possibility of encounter hypothesis alone cannot explain the relation between the density of a prey and its percentage in the food. At low densities the consumption is too low. At moderate densities it is high and at high densities it is again below expectations. Only one other experiment comes to mind in which a similar response was found and that is that by Holling (1959) in which mice searched for a number of buried cocoons and the alternate food was presented in surplus. This is possibly not directly comparable to the bird-insect data, because in the latter the alternate food had to be searched for, which will have an influence on the total amount of food that can be collected.

From the data presented by Holling (1959, Fig. 6, p. 307) it seems that the total amount of food eaten is approximately constant for all densities of the prey. The functional response of the mice under these conditions shows an S-shaped rise to a maximum consumption. From an experiment in which the cocoons were buried for different distances under the sand one can assume that the area in which the mouse can detect the cocoon is appreciable. This will have an influence on the time available for searching. If the density of the cocoons rises, then there will be a relatively larger portion of the time available for searching and there is a certain density at which the mouse will always be influenced by the stimulus of the cocoon. There are two factors here working against each other, the time needed for handling, which tends to shorten the time available for searching at higher densities, and the decrease in the time spent searching per host due to the stimulus range of the host. The influence that each will have will depend upon its relative value. If the time spent in handling is large compared to the decrease in time due to the stimulus range of the host, as it is probably in the praying mantis, then the influence of the latter will be masked by the former. If, on the other hand, the total amount of food eaten is not constant, because of a low number of alternate prey, one will expect a curve with a continuously decreasing slope, the actual form depending on the amount of alternate food available. Also it was seen in the laboratory experiments that if the mantis had been starved, the intensity of the attack was higher and the prey was stalked from a greater distance.

The different mathematical models in relation to the mantis-grasshopper experiment will be summarised below.

The assumption that an animal searches at random for the things they require for existence (Nicholson, 1933) does not seem to fit the mantis-grasshopper relation. If searching is at random and the area of discovery is constant, then a linear relationship between number attacked and the density of the prey would be expected, and there would be no upper limit to the number that could be attacked. From Fig.24 it can be seen directly that there is an upper limit to the number of grasshoppers the mantis can attack, and this limit can be calculated using the model proposed by Holling (1959b).

From equation (15) $\underline{a}$ and $\underline{b}$ can be calculated. In the mantis-grasshopper studies it is not known if $\underline{a}$ is a constant but it can be assumed that $\underline{b}$ is, especially at the higher densities. From the data it follows that $\underline{b}$ = approximately 1.8. The maximum number of grasshoppers that can be attacked in the time available will then be $\frac{T_t}{b} = \frac{3}{1.8} = 1.67$. From these data $\underline{b}$ is much larger than can be explained by the time needed for handling the prey. This probably is because $\underline{b}$ stands for a combination of different time consuming activities, i.e., eating, resting, grooming, etc. Of these, eating and resting will be influenced by the satiation level.

The influence of the satiation level is strongly exemplified in the praying mantis. A starved mantis will actively pursue a potential prey, whereas a satiated mantis does not react or reacts negatively by moving away from a grasshopper.

From this it can also be concluded that, at least under extreme conditions, the satiation level also influences the stimulus range. The satiation level will differ at different densities of grasshoppers when the number of alternate prey is low. From the good fit of the mantis-grasshopper data to the calculated values using equation (14) (Fig. 26), it must be concluded that this was not the case or that the influence of the change in the stimulus range will change a in such a way that, analogous to equation (16), equation (14) still accurately describes the set of data. Of course, when in equation (16) c is small compared with b, the influence of c will be masked by b and a deviation from equation (14) cannot be detected. This is probably the case in the mantis-grasshopper data. It is interesting to note that Holling assumes the predator or parasite to search at random (this follows from equation (11)) if the prey is distributed at random. It now seems logical to amend the assumption of random searching and state that the actual searching of animals is at random but that the response to changes in the density of the objects sought is not linear because of a density-dependent time consuming behaviour.

The complexity of the model described by Watts (1959) makes it difficult to explain the deviation from the straight line in Fig. 25. If the maximum number of grasshoppers that can be eaten, as calculated above from equation (15) is 1.67, then this would mean an even greater deviation from the expected.

Miller (1954), describing the interaction of the spruce budworm and the parasite _Apantelus fumiferanae_ Vier., could explain 71% of the sets of data with Watts' mathematical model. It is not known if this same group of data has been described using Holling's model.

In the mantis experiments it was not possible to measure the density and the consumption of alternate species. This excludes direct comparison of Tinbergen's model with the foregoing. Of the above mentioned models, that of Holling describes the data most accurately and the mantis-grasshopper relationship can be described as follows:

1) Initially the praying mantis searches at random.
2) The activity is slowed down temporarily after each prey-capture under influence of the satiation level, as a result the mantis is more active at low densities than at medium densities.
3) The upper limit of prey consumption is a function of the total capacity for food under the environmental circumstances encountered.
4) The actual form of the curve, describing the mantis-grasshopper relationship, will be influenced by the weather, and the density and relative risk of alternate prey-species.

The effect of the praying mantis under natural conditions must be considerable. From the cage experiments it can be seen that even at low densities the mortality due to the mantis predation is high. The densities of grasshoppers and of mantis in the study area in 1957 and 1958 was comparable to that in the experiments with three grasshoppers per cage, and in some parts of the field the density was equivalent to that in the cages with six grasshoppers per cage. It must be concluded that at these densities of grasshoppers and praying mantis, this predation is one of the most important mortality factors, if not the most important one.

SUMMARY

In this thesis a study of the populations of two species of grasshoppers, Melanoplus femur-rubrum (de Geer) and M. bivittatus (Say), carried out in an uncultivated field near Hamilton, Ontario, is described.

The period of 1956-1960, in which the study was made, was one of low grasshopper densities. There was a marked difference in the seasonal occurrence and the habitat preference of the two grasshopper species. M. bivittatus could complete its life cycle in a lower temperature range than M. femur-rubrum. The mortality in both species was high, with the influence of the weather appreciable.

In 1958 an undescribed form of a grasshopper was present in the study area. On the basis of ecological evidence this was identified as an undescribed form of the first instar of M. femur-rubrum.

In 1958 there was an excess of females in the young stages of both species. In the older stages the percentage of males/females became gradually higher.

Besides the weather, predation was an important mortality factor, while parasitism was of minor importance.

Of the predators studied, the praying mantis and birds are the most important. Voles ate few, if any, grasshoppers.

The praying mantis is the most important predator. The relation between the density of grasshoppers and the number consumed by the mantis is discussed. Several mathematical models were tested and that of Holling (1959) described the data the most accurately.

The relation between density and consumption is explained by assuming a decrease in the hunting-drive under the influence of the satiation level after each prey capture.

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TABLE I THE ACTUAL NUMBERS OF M. FEMUR-RUBRUM COLLECTED FROM 25 ONE SQ. METER SAMPLES ON THE HILLS IN 1957.

DATE		I	II	III	IV	V	Ad.
May	10	-	-	-	-	-	-
	24	8	1	-	-	-	-
June	5	19	3	-	-	-	-
	20	23	5	1	-	-	-
July	4	6	11	4	2	-	-
	18	-	9	8	-	1	-
August	2	-	-	4	3	1	7
	16	-	-	1	-	1	8
September	2	-	-	-	1	1	2
	17	-	-	-	-	-	-

I - V = nymphal stages

Ad. = adult stage

TABLE II THE ACTUAL NUMBERS OF *M. BIVITTATUS* COLLECTED FROM 25 ONE SQ. METER SAMPLES ON THE HILLS IN 1957.

DATE		I	II	III	IV	V	Ad.
May	10	-	-	-	-	-	-
	24	16	8	-	-	-	-
June	5	1	11	10	7	1	-
	20	1	7	5	4	2	1
July	4	-	4	2	-	1	3
	18	-	1	2	-	1	4
August	2	-	-	-	-	-	-
	16	-	-	-	-	-	-
September	2	-	-	-	-	-	-
	17	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE III THE ACTUAL NUMBERS OF *M. FEMUR-RUBRUM* COLLECTED FROM 50 ONE SQ. METER SAMPLES IN THE FIELD IN 1957.

DATE		I	II	III	IV	V	Ad.
May	10	-	-	-	-	-	-
	25	1	2	-	-	-	-
June	7	-	1	2	-	-	-
	21	10	2	1	-	-	-
July	5	6	1	2	1	-	-
	19	7	4	1	-	-	-
August	1	-	5	8	2	1	-
	16	-	-	3	6	12	-
September	4	-	-	-	-	1	4
	17	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE IV THE ACTUAL NUMBERS OF M. BIVITTATUS COLLECTED FROM 50 ONE SQ. METER SAMPLES IN THE FIELD IN 1957.

DATE		I	II	III	IV	V	Ad.
May	10	-	-	-	-	-	-
	25	12	-	-	-	-	-
June	7	1	3	4	-	-	-
	21	-	-	5	3	1	-
July	5	1	-	1	1	3	4
	19	-	1	-	-	-	3
August	1	-	-	-	1	1	4
	16	-	-	-	-	-	2
September	4	-	-	-	-	-	-
	17	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE V THE ACTUAL NUMBERS OF *M. FEMUR-RUBRUM* COLLECTED FROM 25 ONE SQ. METER SAMPLES ON THE HILLS IN 1958.

DATE		I	II	III	IV	V	Ad.
May	13	-	-	-	-	-	-
	20	95	15	-	-	-	-
	28	31	17	7	-	-	-
June	3	19	15	8	-	-	-
	11	3	3	9	1	-	-
	19	8	4	2	1	-	-
	27	16	-	-	-	-	-
July	3	4	-	4	1	-	1
	9	7	-	-	-	-	-
	17	2	6	2	-	-	-
	22	-	3	3	-	-	-
	29	-	2	6	1	-	-
August	5	8	-	7	4	1	-
	12	1	2	1	6	3	1
	20	No collection					
	26	-	-	-	1	1	-
September	9	-	-	1	1	-	1
	23	-	-	-	-	-	-
	30	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE VI THE ACTUAL NUMBERS OF *M. FEMUR-RUBRUM* COLLECTED FROM 50 ONE SQ. METER SAMPLES IN THE FIELD IN 1958.

DATE		I	II	III	IV	V	Ad.
May	13	-	-	-	-	-	-
	21	36	4	-	-	-	-
	27	22	1	-	-	-	-
June	4	12	9	2	1	-	-
	12	1	7	12	8	2	-
	18	5	2	1	-	-	-
	24	-	-	-	-	-	-
July	3	-	-	-	-	-	-
	10	3	-	-	-	-	-
	16	35	9.5	-	-	-	-
	23	23.5	17	2	-	-	-
	30	1	3	12	2.5	1	-
August	6	0.5	4	13	1.5	-	-
	13	-	0.5	4	1.5	1	0.5
	20	-	-	7.5	8	1.5	1.5
	28	-	-	6.5	9	5	9.5
September	10	-	-	0.5	3	0.5	5.5
	23	-	-	-	0.5	0.5	3
	30	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE VII THE ACTUAL NUMBERS OF M. BIVITTATUS COLLECTED FROM 25 ONE SQ. METER SAMPLES ON THE HILLS IN 1958.

DATE		I	II	III	IV	V	Ad.
May	13	-	-	-	-	-	-
	20	13	16	7	-	-	-
	28	-	20	11	3	-	-
June	3	5	18	11	1	-	-
	11	1	-	4	1	-	-
	19	2	3	11	8	2	-
	27	1	-	6	-	3	-
July	3	-	-	-	2	5	1
	9	-	1	-	-	2	-
	17	-	2	2	1	1	4
	22	-	2	1	-	-	2
	29	-	-	1	1	-	3
August	5	-	-	1	1	-	1
	12	-	-	-	-	-	-
	20	No collection					
	26	-	-	-	-	-	-
September	9	-	-	-	-	-	-
	23	-	-	-	-	-	-
	30	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE VIII THE ACTUAL NUMBERS OF M. BIVITTATUS COLLECTED FROM 50 ONE SQ. METER SAMPLES IN THE FIELD IN 1958.

DATE		I	II	III	IV	V	Ad.
May	13	-	-	-	-	-	-
	21	3	12	1	-	-	-
	27	1	20	8	1	1	-
June	4	2	9	14	1	1	-
	12	-	3	3	1	-	-
	18	1	3	14	10	7	1
	24	-	3	9	7	7	-
July	3	-	-	2	2	10	8
	10	-	2	-	1	8	8
	16	-	-	2	1	1	6
	23	-	0.5	-	-	1	12.5
	30	-	-	3	1	1	0.5
August	6	0.5	1.5	3	-	0.5	0.5
	13	-	-	0.5	-	-	-
	20	-	-	-	-	-	-
	28	-	-	-	-	-	-
September	10	-	-	-	-	-	-
	23	-	-	-	-	-	-
	30	-	-	-	-	-	-

I - V = Nymphal stages

Ad. = Adult stage

TABLE IX MORTALITY IN *M. FEMUR-RUBRUM* FIELD 1958

DATE		t	Y*	y = log Y
May	13	-	-	
	21	1	40	
	27	2	23	
June	4	3	24	
	12	4	30	
	18	5	8	
	24	6	-	
July	3	7	-	
	10	8	3	
	16	9	44.5	1.6532
	23	10	42.5	1.6284
	30	11	19.5	1.2900
August	6	12	19	1.2788
	13	13	7.5	0.8751
	20	14	18.5	1.2672
	28	15	30	1.4771
September	10	17	9.5	0.9777
	23	19	4	0.6021
	30	20	-	

* Total number all instars/50 sq. meter

· See also text

TABLE IX (continued)

MORTALITY IN *M. FEMUR-RUBRUM* FIELD 1958

$S(t) = 120$

$n = 9$

$\bar{t} = 13.3333$

$S(t^2) = 1686$

Correction = 1600

$S(t-\bar{t})^2 = 86$

$S(y) = 11.0496$

$\bar{y} = 1.2277$

$S(ty) = 140.0228$

Correction = 147.7328

$S(t-\bar{t})(y-\bar{y}) = -7.7100$

$b = -0.0897$

$\log K = b$

$K = 0.8133$

For explanation see text

TABLE X MORTALITY IN *M. BIVITTATUS* FIELD 1958

DATE		t	Y*	y = log Y
May	13	0	0	
	21	1	16	
	27	2	30	
June	4	3	27	
	12	4	7	
	18	5	36	1.5563
	24	6	26	1.4150
July	3	7	22	1.3424
	10	8	19	1.2788
	16	9	10	1.0000
	23	10	14	1.1461
	30	11	5.5	0.7404
August	6	12	6	0.7782
	13	13	0.5	0.6990 - 1
	20	14		
	28	15		
September	10	17		
	23	19		
	30	20		

* Total number all instars/50 sq. meter
See also text

TABLE X MORTALITY IN *M. BIVITTATUS* FIELD 1958

$S(t) = 81$

$n = 9$

$\bar{t} = 9.0000$

$S(t^2) = 789$

Correction = 729

$S(t-\bar{t})^2 = 60$

$S(y) = 8.9562$

$\bar{y} = 0.9951$

$S(ty) = 69.9295$

Correction = 80.6058

$S(t-\bar{t})(y-\bar{y}) = -10.6763$

$b = -0.6639$

$\log K = b$

$K = 0.6639$

For explanation see text

TABLE XI DISTRIBUTION OF ALL STAGES OF *M. BIVITTATUS* (b), *M. FEMUR-RUBRUM* (f) AND THE SO-CALLED SPECIES C (c) IN THE FIELD DURING 1958.

	JULY 10			JULY 16		
GROUP	b	c	f	b	c	f
1	1-II	2-I		1-III	16-I	8-II
2				1-III 2-Ad.	6-I	
3	1-II 1-Ad.	2-I			4-I	
4					1-I	
5	2-V 2-Ad.			1.5-Ad.	1-I	
6	2-V				2-I	
7	1-V			1-IV 1-Ad.	4-I	1-II
8	1-Ad.			0.5-V	0.5-I	
9	2-V			0.5-V 0.5-Ad.	0.5-I	0.5-II
10	1-IV 1-V 3-Ad.			1-Ad.		

I - V = nymphal stages
Ad. = adult stage

TABLE XI (continued)

DISTRIBUTION OF ALL SPECIES OF M. BIVITTATUS (b), M. FEMUR-RUBRUM (f) AND THE SO-CALLED SPECIES C (c) IN THE FIELD DURING 1958

JULY 23			JULY 30			
b	a	f	b	c	f	GROUP
0.5-II 0.5-Ad.	15.5-I	8.5-II 1-III	1.5-III 0.5-IV		1-II 5.5-III 2.5-IV	1
1-Ad.	4.5-I	1.5-II	1-III 0.5-IV		0.5-II 3.5-III	2
1-V 1-Ad.	0.5-I	1-II	0.5-III		0.5-II 2.5-III 1-V	3
1-Ad.	0.5-I	0.5-II	0.5-V		0.5-III	4
1.5-Ad.	1-I	0.5-II 0.5-III				5
0.5-Ad.						6
1-Ad.	1-I	3-II 0.5-III			0.5-V	7
3.5-Ad.		0.5-II	0.5-III 0.5-V 0.5-Ad.			8
0.5-Ad.					1-II	9
2-Ad.	0.5-I	0.5-II			1-I	10

I - V = nymphal stages
Ad. = adult stage

SEX - RATIO IN NYMPHS AND ADULTS

TABLE XII M. FEMUR-RUBRUM 1958

Instar	♂	♀	% ♂♂/♀♀
1	99	247	40
2	53	98	54
3	66	89	74
4	37	39	95
5	12	14	86
Ad.	20	23	87

TABLE XIII M. BIVITTATUS 1958

Instar	♂	♀	% ♂♂/♀♀
1	6	23	26
2	30	86	35
3	49	73	67
4	26	29	90
5	27	27	100
Ad.	44	21	210

TABLE XIV MONTHLY TEMPERATURE AND RAINFALL 1957

MONTH	AVERAGE TEMP. °F	DEVIATION[1] °F	RAINFALL[2] INCHES	HUMIDITY % 1 P.M. E.S.T.
JAN	19.8	-3.2	2.10	65
FEB	28.2	+5.7	2.56	67
MAR	35.9	+5.1	1.29	57
APR	47.2	+3.6	3.05	60
MAY	54.1	-0.4	4.20	59
JUN	67.1	+2.1	4.84	62
JUL	70.1	-0.9	2.07	59
AUG	67.4	-0.6	1.71	59
SEP	61.9	+0.1	3.51	60
OCT	50.2	+0.3	1.10	59
NOV	41.3	+3.8	1.72	66
DEC	33.8	+6.8	2.89	67
YEAR	48.2	+2.0	31.04	62

1) Deviation from 20 year average

2) 10" snow taken as equivalent to 1" rain

TABLE XV MONTHLY TEMPERATURE AND RAINFALL 1958

MONTH	AVERAGE TEMP. °F	DEVIATION[1) °F	RAINFALL[2) INCHES	HUMIDITY % 1 P.M. E.S.T.
JAN	25.8	+2.8	1.50	67
FEB	20.4	-2.1	1.63	62
MAR	36.0	+5.2	0.48	60
APR	47.7	+4.1	1.93	49
MAY	55.1	+0.6	1.70	45
JUN	60.7	-4.3	2.45	57
JUL	69.5	+1.5	4.37	59
AUG	68.5	0.0	3.32	57
SEP	62.2	+1.2	6.08	63
OCT	50.7	+2.2	1.11	61
NOV	41.6	+4.1	1.96	63
DEC	21.8	-5.2	0.63	66
YEAR	46.8	+0.6	28.35	59

1) Deviation from 20 year average

2) 10" snow taken as equivalent to 1" rain

TABLE XVI AVERAGE TEMPERATURE (°F) IN JUNE

1948	65.2	1954	67.5
1949	70.6	1955	67.1
1950	65.3	1956	66.2
1951	65.0	1957	67.1
1952	67.5	1958	60.7
1953	67.2	1948-1957	66.9

TABLE XVII BIRD POPULATION IN THE IMMEDIATE LOCALE OF THE AREA UNDER STUDY

CLASSIFICATION (Family, genus and species)	1957	1958
Picidae		
Flicker (*Colaptes auratus* (L.))	-	0.5
Tyrannidae		
Eastern Kingbird (*Tyrannus tyrannus* (L.))	-	1
Mimidae		
Catbird (*Dumetella carolinensis* (L.))	4	2
Brown thrasher (*Toxostoma rufum rufum* (L.))	1 or 2	1
Turdidae		
Robin (*Turdus migratorius* (L.))	2	1.5
Parulidae		
Yellow Warbler (*Dendroica petechia* L.)	-	1
Icteridae		
Meadowlark (*Sturnella magna* (L.))	2	1
Redwing (*Agelaius phoeniceus* (L.))	2	0
Fringillidae		
(Eastern) Field Sparrow (*Spizella pusilla pusilla* (Wilson))	2	3.5
Song Sparrow (*Melospiza melodia* (Wilson))	2	4.5

TABLE XVIII NUMBER OF PRAYING MANTIS COLLECTED IN 1958

DATE	HILL per 25 sq. m.	FIELD per 50 sq. m.
JUNE 4	3	0
12	9	22
18	17	15
24	11	36
JULY 3	36	60
10	28	47
16	7	20.5
23	3	13
30	1	10.5
AUG 6	3	5
13	0	3.5
20	no collection	4.5
28	4	4.5
SEPT 10	0	2
23	0	0.5

TABLE XIX MORTALITY IN PRAYING MANTIS IN 1953

DATE	N_p*	LOG N_p
JUNE 12	22	
18	15	
24	36	
JULY 3	60	1.7782
10	47	1.6721
16	20.5	1.3118
23	13	1.1139
30	10.5	1.0212
AUG 6	5	0.6990
13	3.5	0.5441
20	4.5	0.6532
28	4.5	0.6532
SEPT 10	2	0.3010
23	0.5	0.6990 - 1

*N_p = accumulated number of praying mantis

TABLE XIX (continued)

MORTALITY IN PRAYING MANTIS IN 1958

$S(t) = 135$

$n = 11$

$\bar{t} = 12.2$

$S(t^2) = 1759$

correction $= 1657$

$S(t-\bar{t})^2 = 102$

$S(y) = 9.4467$

$\bar{y} = 0.8578$

$S(ty) = 93.8047$

correction $= 115.9368$

$S(t-\bar{t})(y-\bar{y}) = -22.1321$

$b = -0.2174$

$K = 0.6062$

TABLE XX TOTAL RADIOACTIVITY IN PRAYING MANTIS THREE DAYS AFTER FEEDING ON RADIOACTIVE GRASSHOPPERS

DAYS	% OF RADIOACTIVITY OF GRASSHOPPERS FED		
	#1	#2	#3
3	50	55	40
6	50	59	42
9	58	57	44
12	50	56	52
15	51		45
18	54		46
21	47		42
Average	51.4	55.5	44.4

TABLE XXI DISTRIBUTION OF RADIOACTIVITY IN PRAYING MANTIS 10 DAYS AFTER FEEDING ON RADIOACTIVE GRASSHOPPERS

HEAD	5%
FORELEGS (2)	13%
MID and HINDLEGS (4)	12%
PROTHORAX	11%
THORAX	16%
WINGS	8%
ABDOMEN	35%

TABLE XXII LEVEL OF RADIOACTIVITY OF GRASSHOPPERS RELEASED AND OF PRAYING MANTIS AT THE END OF A THREE-DAY EXPERIMENT (COUNTS PER MINUTE ABOVE BACKGROUND)

CAGE	RADIOACTIVITY OF GRASSHOPPERS RELEASED IN CAGES		RADIOACTIVITY IN PRAYING MANTIS
#1	250		158
	300		N.R.A.*
	300		N.R.A.
	300		
	300		
#2	250	300	108
	250	300	N.R.A.
	250	300	
	300	300	
	300	400	
#3	250	300	108
	250	300	170
	250	300	
	250	300	
	250	300	
	300	300	
	300	350	
	300	350	
	300	350	
	300	400	

*N.R.A. = Not radioactive

TABLE XXIII AVERAGE GRASSHOPPER DENSITY IN OUTDOOR CAGES AND CONSUMPTION BY ONE PRAYING MANTIS

D_G	D_P	N_G	N_P	C
3	2.4	6 - 7	15	0.43
6	2.3	10 - 11	14	0.75
13	2.5	16 - 18	16	1.06
28	2.8	16 - 18	13	1.30
58	3.0	12 - 14	9	1.44

D_G = Average density of grasshoppers per 5 sq. m. (i.e., average of those at the start and those at the end)

D_P = Average density of praying mantis per 5 sq. m. (i.e., average of those at the start and those at the end)

N_G = Number of grasshoppers consumed by N_P

N_P = Number of praying mantis

C = Average consumption by one praying mantis

Fig. 1	North west part of the study area, with hill.

Fig. 2	North east part of the study area, with hill.

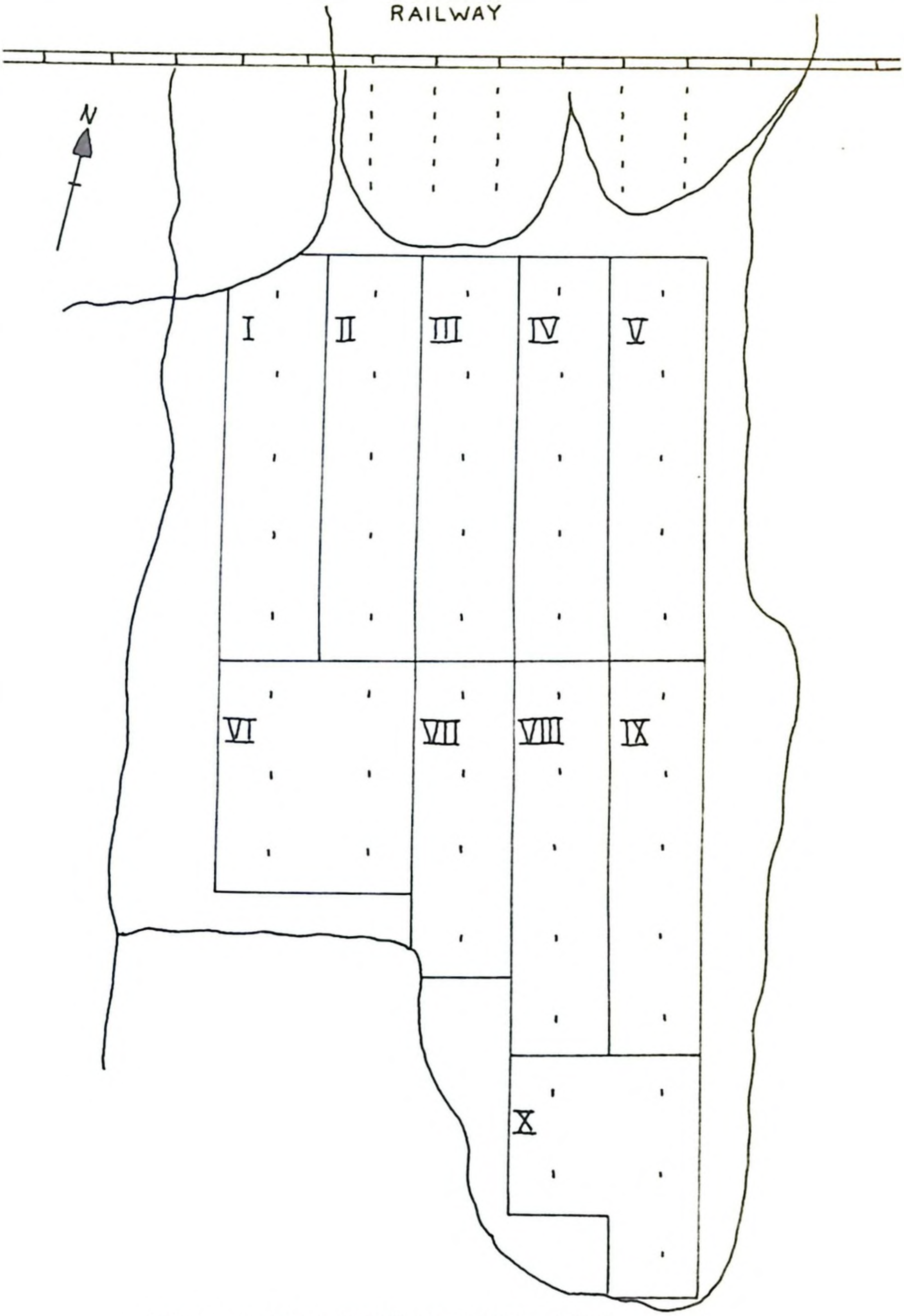
Fig. 3 South west part of the study area.

Fig. 4 South east part of the study area.

Fig. 5 Vegetation in the south part of the field with one of the stakes used for the grasshopper census.

Fig. 6 Bare patch in the north west part of the field.

Fig. 7 Map of the experimental area showing the position of the stakes used in the census of the grasshopper and praying mantis populations.
The field is divided in 10 parts (I - X), (see text).



MAP OF THE EXPERIMENTAL AREA

Fig. 8 Cage for the collection of grasshoppers and praying mantis. Screen removed to show detail.

Fig. 9 Outdoor cage for the predation experiments with praying mantis.

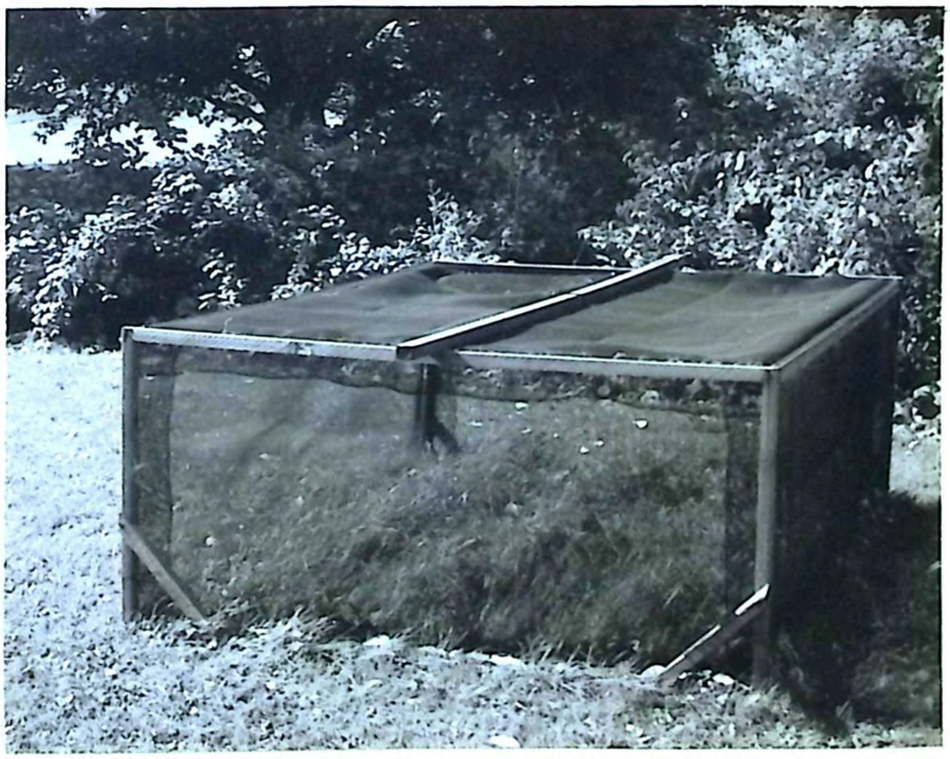


Fig. 10 The estimated numbers of M. femur-rubrum per sq. meter on the hills in 1957.

I - V = nymphal stages

Ad. = adult stage

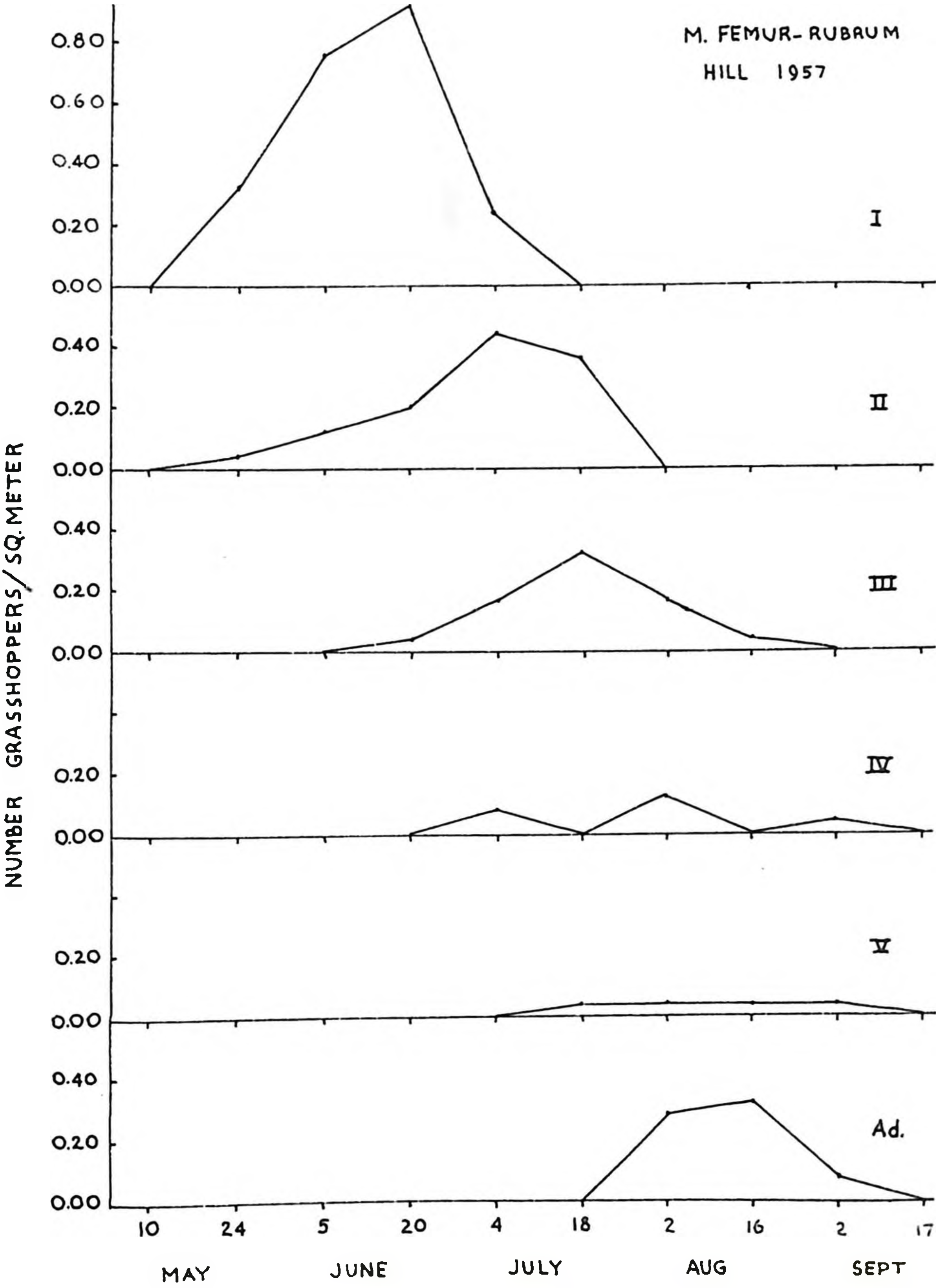
M. FEMUR-RUBRUM
HILL 1957
NUMBER GRASSHOPPERS/SQ.METER
0.80
0.60
0.40
0.20
0.00
I
II
III
IV
V
Ad.
10
24
5
20
4
18
2
16
2
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 11 The estimated numbers of *M. femur-rubrum* per sq. meter in the field in 1957.

I - V = nymphal stages

Ad. = adult stage

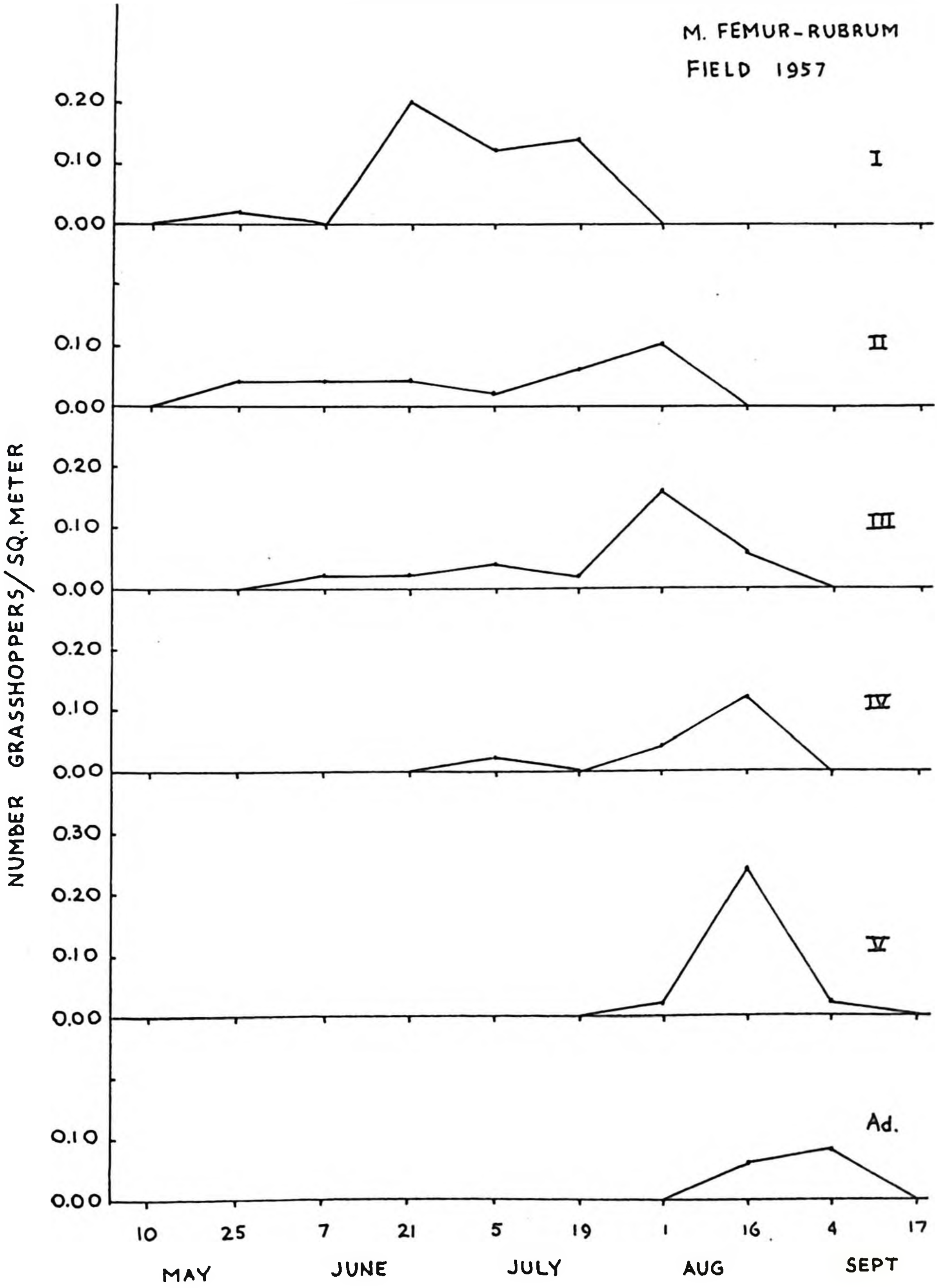

M. FEMUR-RUBRUM
FIELD 1957
NUMBER GRASSHOPPERS/SQ.METER
0.20
0.10
0.00
I
0.10
0.00
II
0.20
0.10
0.00
III
0.20
0.10
0.00
IV
0.30
0.20
0.10
0.00
V
0.10
0.00
Ad.
10
25
7
21
5
19
1
16
4
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 12 The estimated numbers of *M. bivittatus* per sq. meter on the hills in 1957.

I - V = nymphal stages

Ad. = adult stage

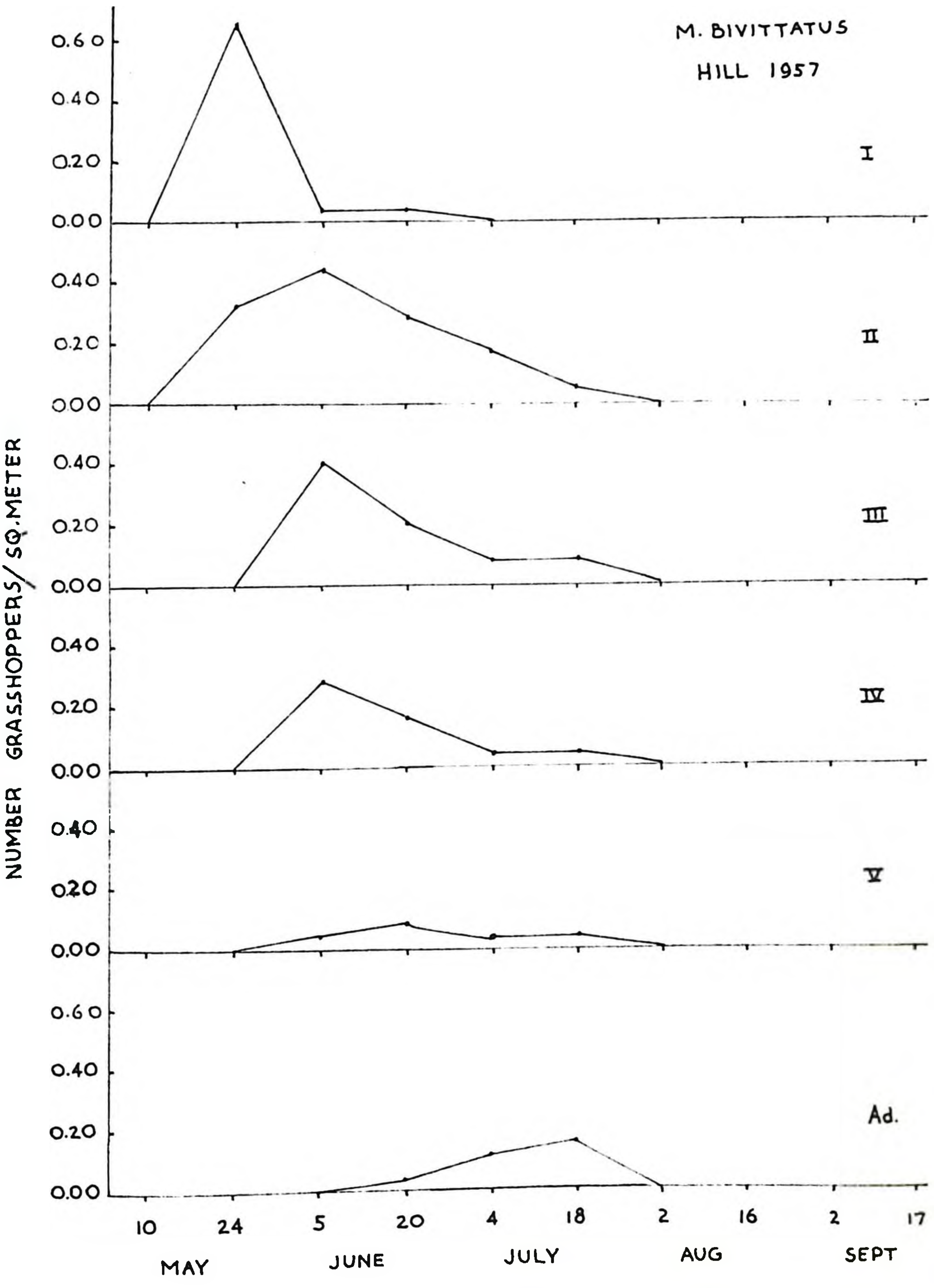

M. BIVITTATUS
HILL 1957
NUMBER GRASSHOPPERS/SQ.METER
I
II
III
IV
V
Ad.
0.60
0.40
0.20
0.00
10
24
5
20
4
18
2
16
2
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 13 The estimated numbers of M. bivittatus per sq. meter in the field in 1957.

I - V = nymphal stages

Ad. = adult stage

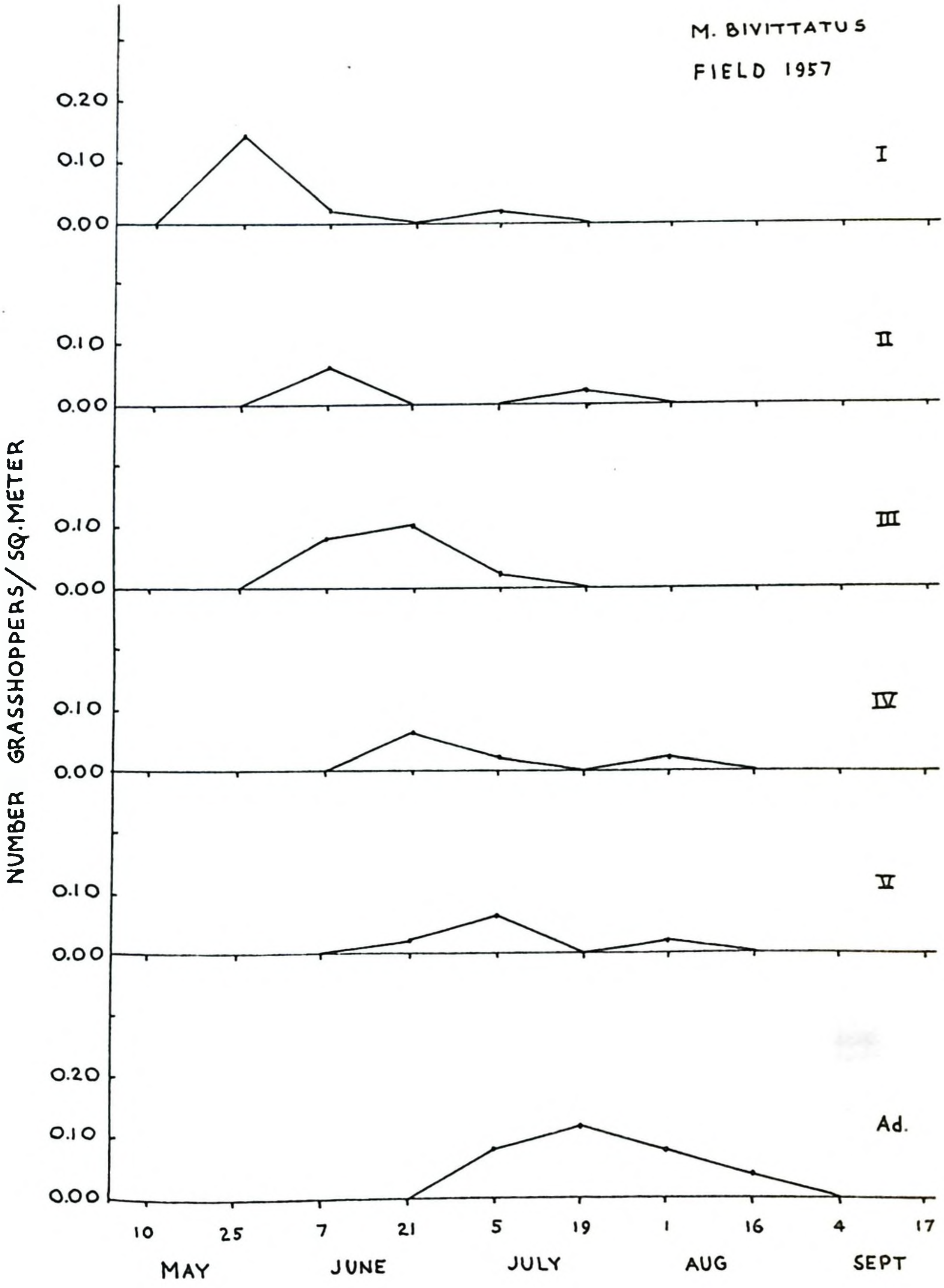

M. BIVITTATUS
FIELD 1957
NUMBER GRASSHOPPERS/SQ.METER
0.20
0.10
0.00
I
0.10
0.00
II
0.10
0.00
III
0.10
0.00
IV
0.10
0.00
V
0.20
0.10
0.00
Ad.
10
25
7
21
5
19
1
16
4
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 14 The estimated numbers of M. femur-rubrum per sq. meter on the hills in 1958.

I - V = nymphal stages

Ad. = adult stage

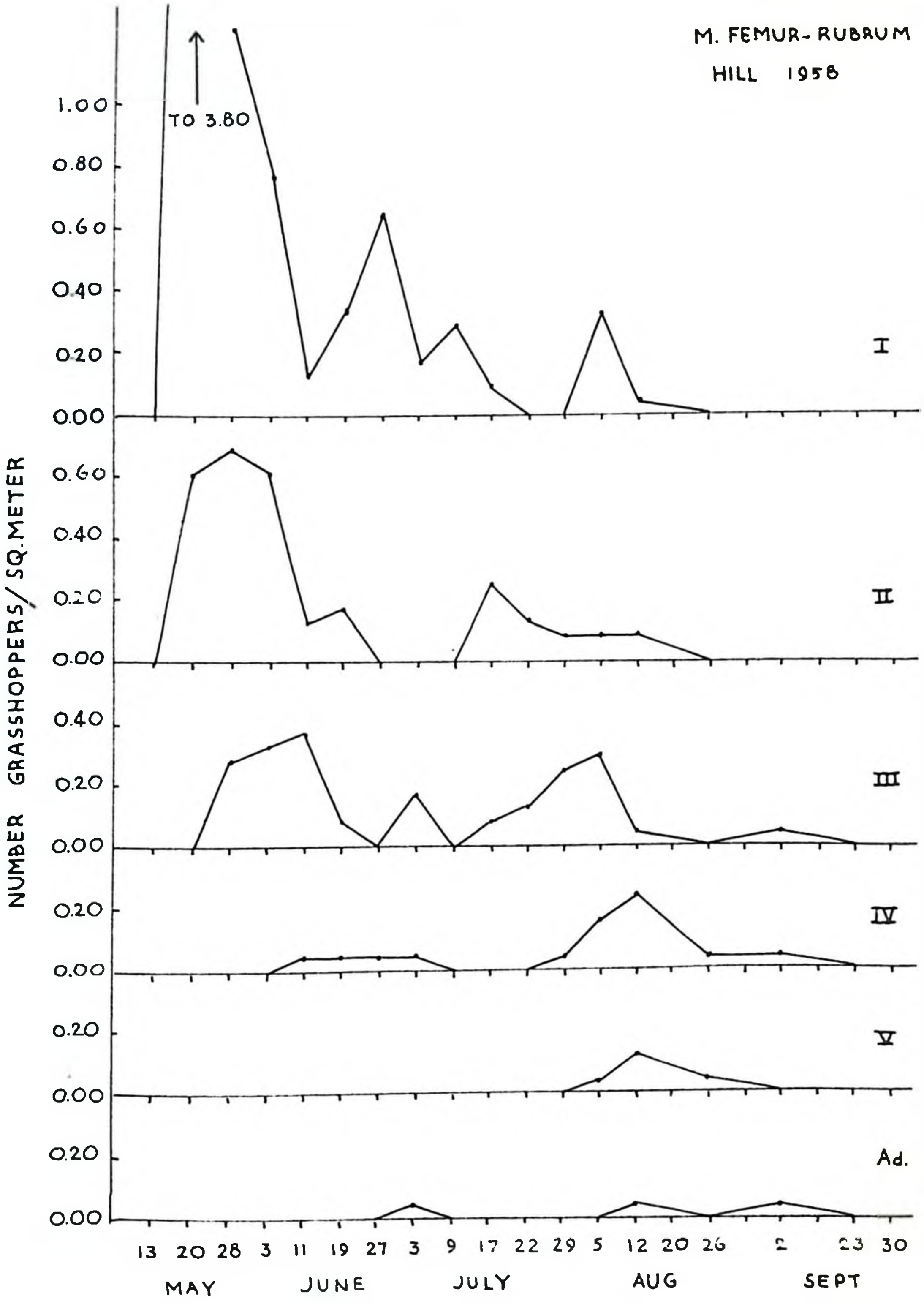

M. FEMUR-RUBRUM
HILL 1958
TO 3.80
NUMBER GRASSHOPPERS/ SQ.METER
1.00
0.80
0.60
0.40
0.20
0.00
I
0.60
0.40
0.20
0.00
II
0.40
0.20
0.00
III
0.20
0.00
IV
0.20
0.00
V
0.20
0.00
Ad.
13 20 28 3 11 19 27 3 9 17 22 29 5 12 20 26 2 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 15 The estimated numbers of *M. femur-rubrum* per sq. meter in the field in 1958.

I - V = nymphal stages
Ad. = adult stage

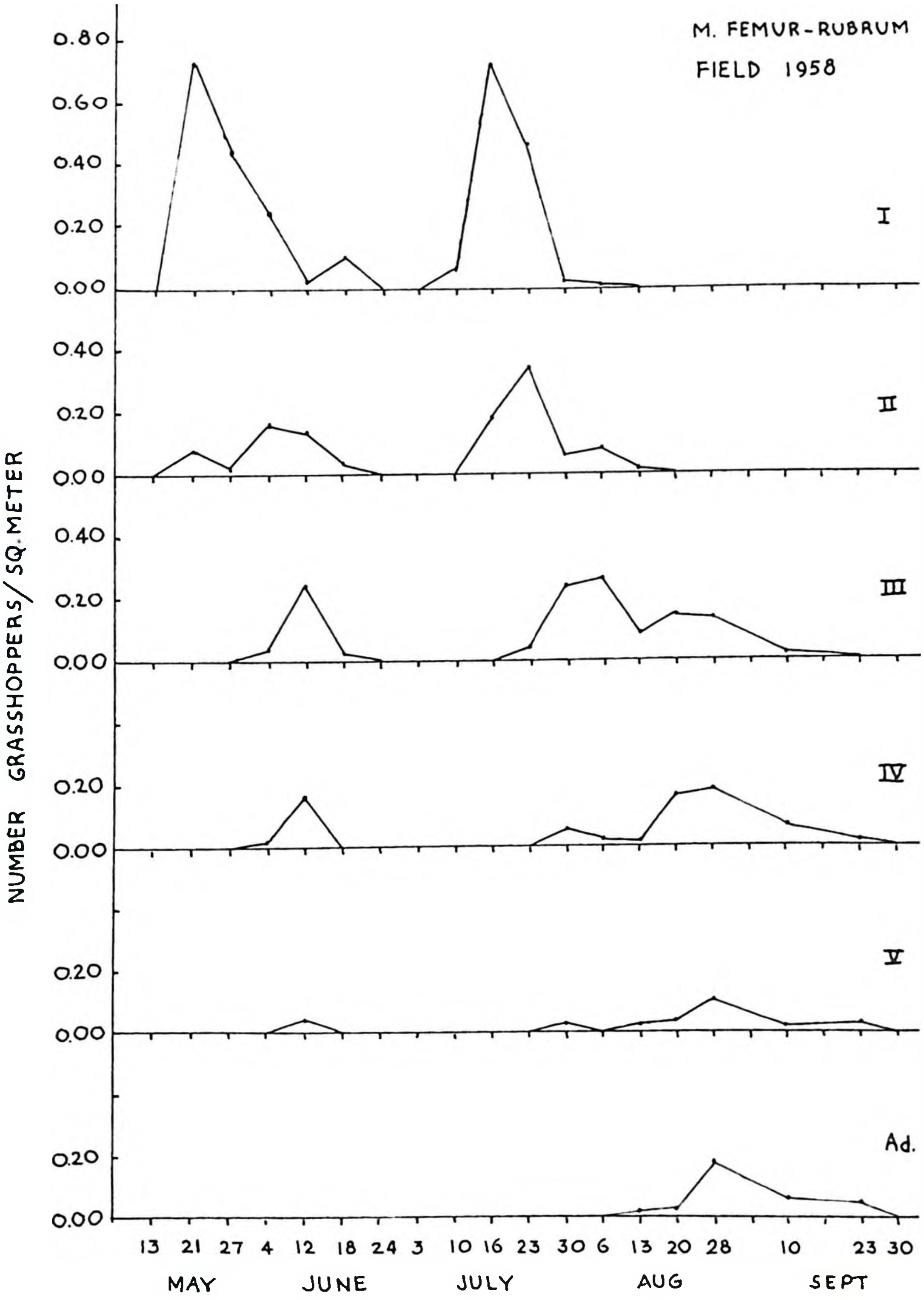

M. FEMUR-RUBRUM
FIELD 1958
NUMBER GRASSHOPPERS/SQ.METER
0.80
0.60
0.40
0.20
0.00
I
0.40
0.20
0.00
II
0.40
0.20
0.00
III
0.20
0.00
IV
0.20
0.00
V
0.20
0.00
Ad.
13 21 27 4 12 18 24 3 10 16 23 30 6 13 20 28 10 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 16 The estimated numbers of *M. bivittatus* per sq. meter on the hills in 1958.

I - V = nymphal stages

Ad. = adult stage

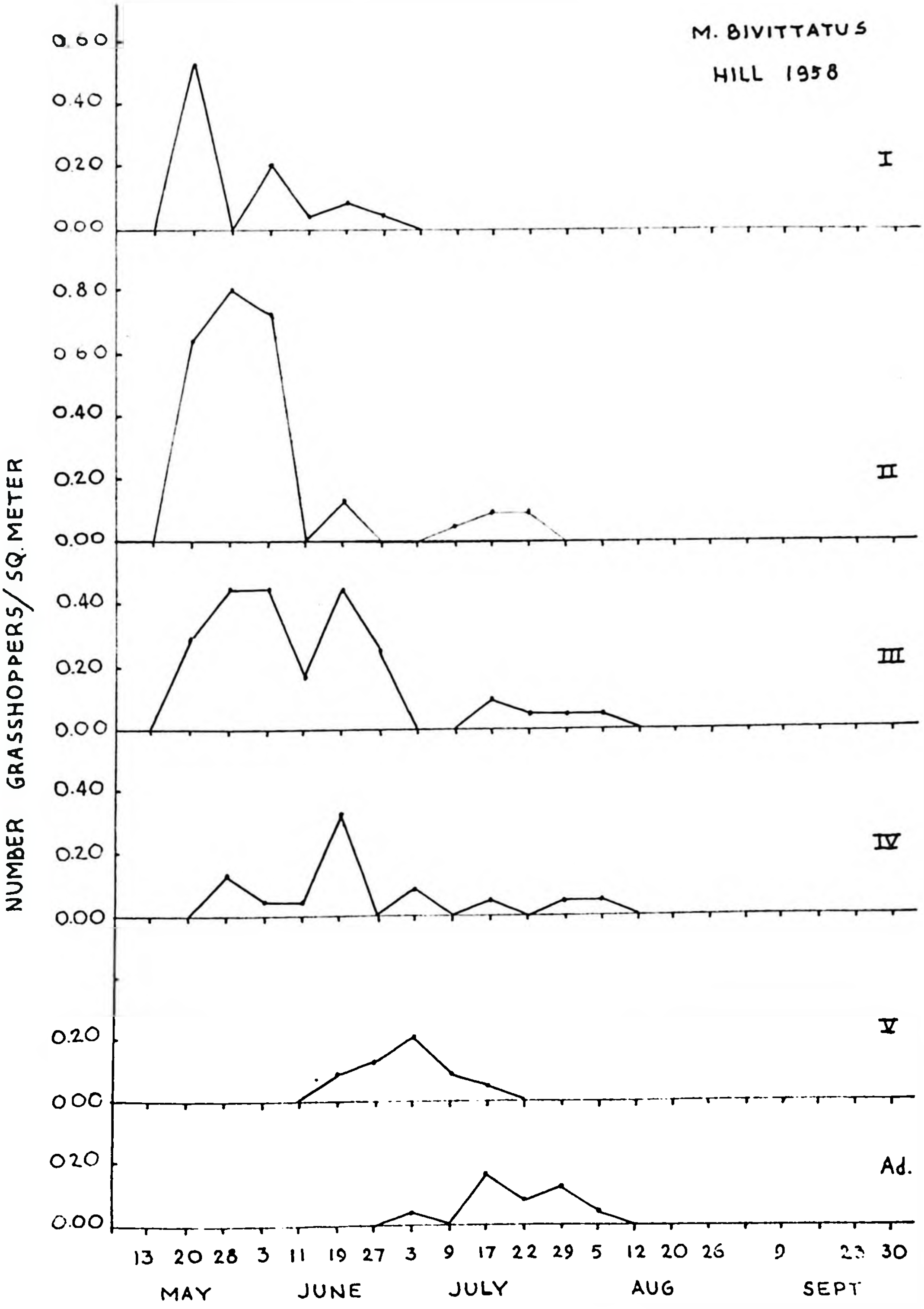

M. BIVITTATUS
HILL 1958
NUMBER GRASSHOPPERS/ SQ. METER
0.60
0.40
0.20
0.00
I
0.80
0.60
0.40
0.20
0.00
II
0.40
0.20
0.00
III
0.40
0.20
0.00
IV
0.20
0.00
V
0.20
0.00
Ad.
13 20 28 3 11 19 27 3 9 17 22 29 5 12 20 26 9 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 17 The estimated numbers of M. bivittatus per sq. meter in the field in 1958.

I - V = nymphal stages

Ad. = adult stage

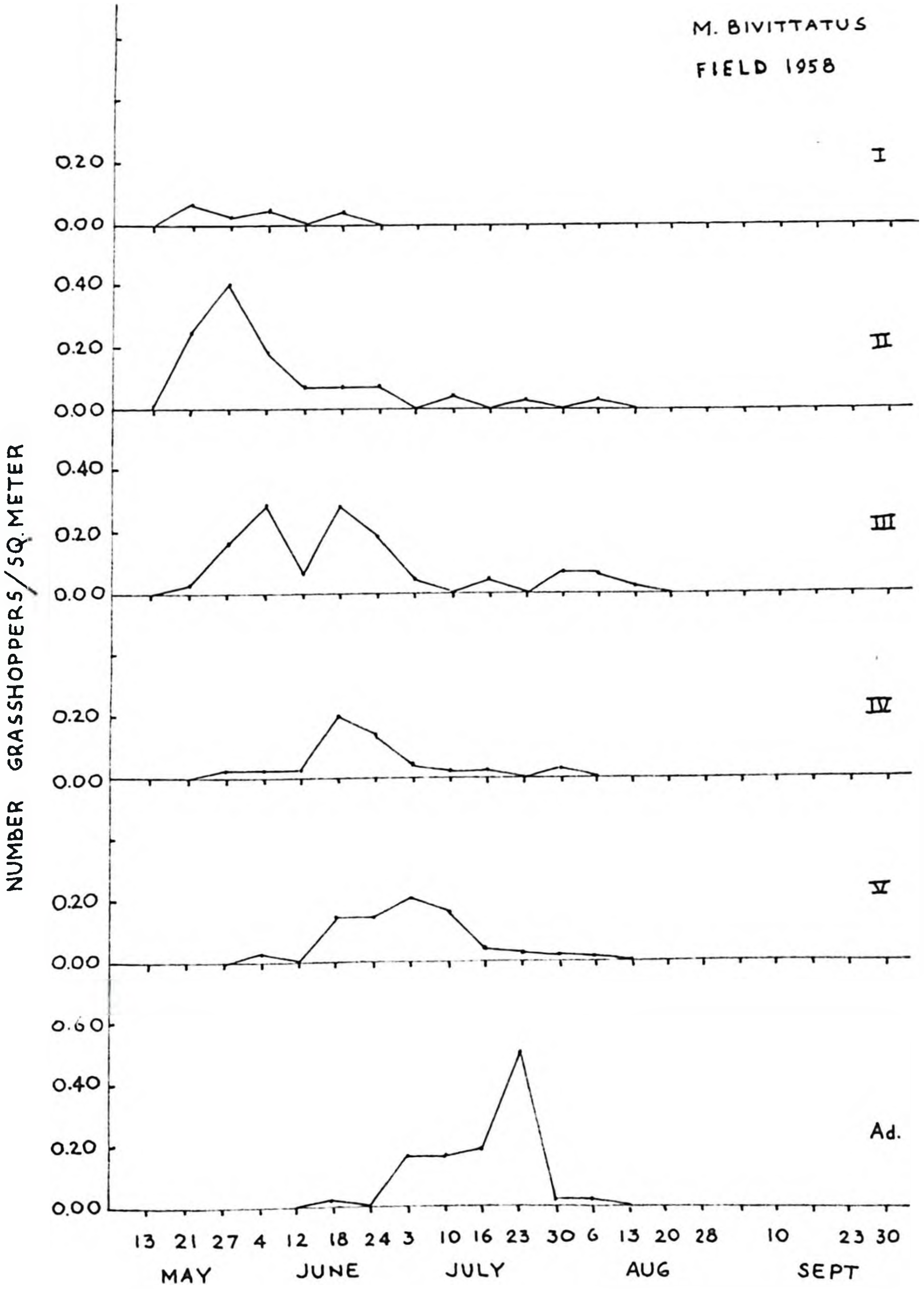

M. BIVITTATUS
FIELD 1958
NUMBER GRASSHOPPERS/SQ. METER
I
II
III
IV
V
Ad.
0.00
0.20
0.40
0.60
13
21
27
4
12
18
24
3
10
16
23
30
6
13
20
28
10
23
30
MAY
JUNE
JULY
AUG
SEPT

Fig. 18 The estimated numbers of M. femur-rubrum in the total area (hills and field) in 1957.

I - V = nymphal stages

Ad. = adult stage

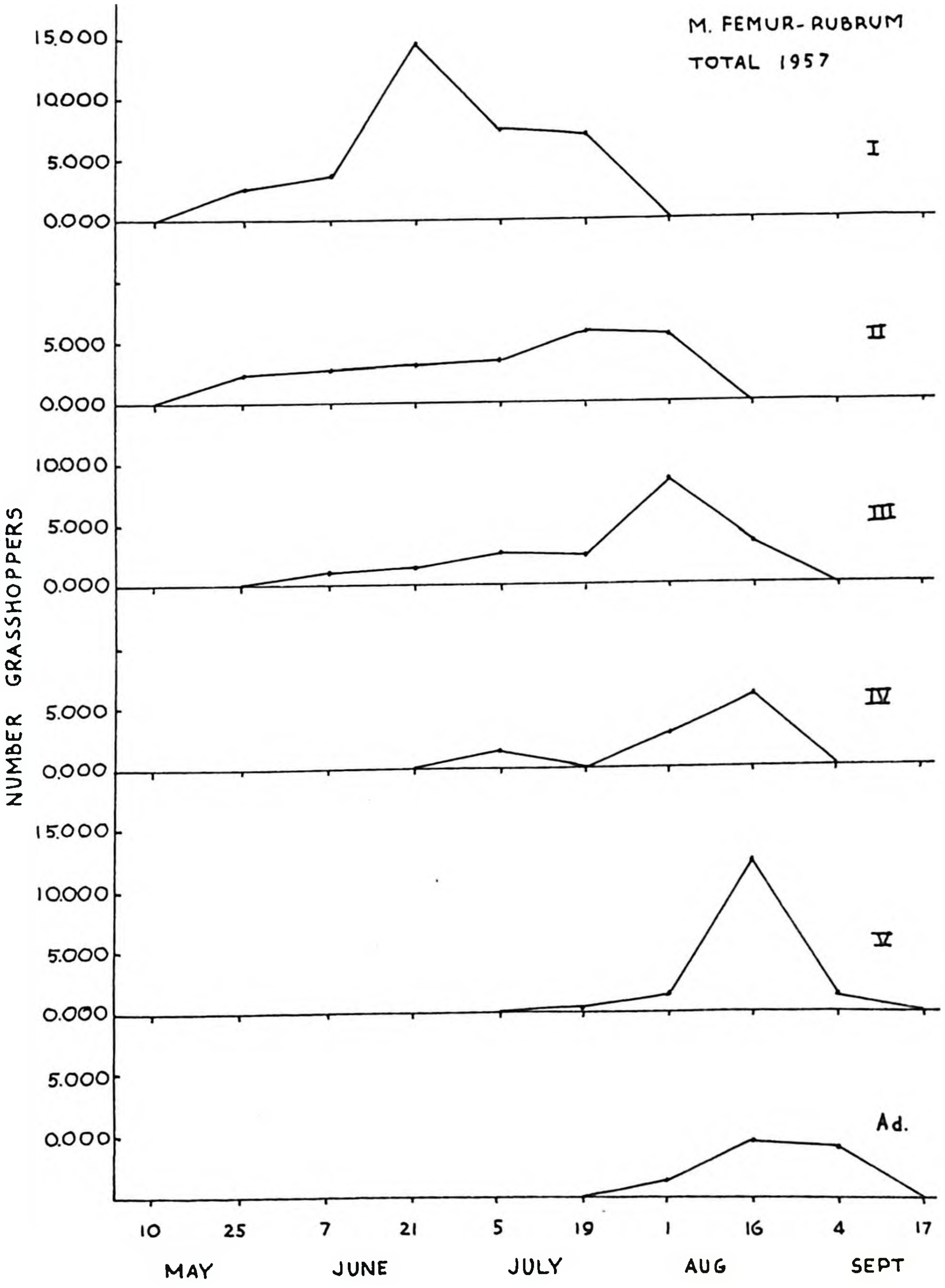

M. FEMUR-RUBRUM
TOTAL 1957
I
II
III
IV
V
Ad.
NUMBER GRASSHOPPERS
15.000
10.000
5.000
0.000
10
25
7
21
5
19
1
16
4
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 19 The estimated numbers of *M. bivittatus* in the total area (hills and field) in 1957.

I - V = nymphal stages

Ad. = adult stage

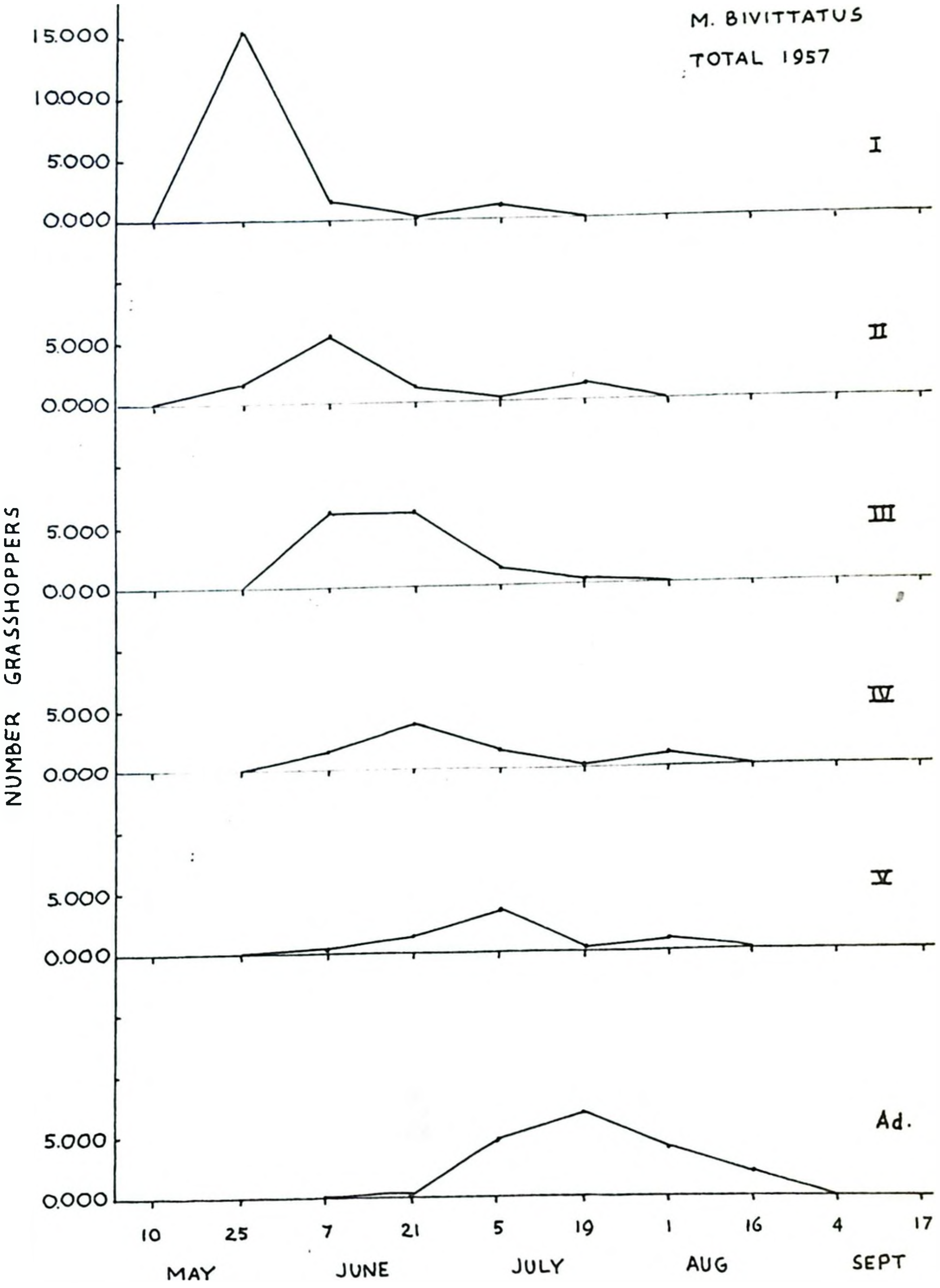

M. BIVITTATUS
TOTAL 1957
I
II
III
IV
V
Ad.
NUMBER GRASSHOPPERS
15.000
10.000
5.000
0.000
10
25
7
21
5
19
1
16
4
17
MAY
JUNE
JULY
AUG
SEPT

Fig. 20 The estimated numbers of M. femur-rubrum in the total area (hills and field) in 1958.

I - V = nymphal stages

Ad. = adult stage

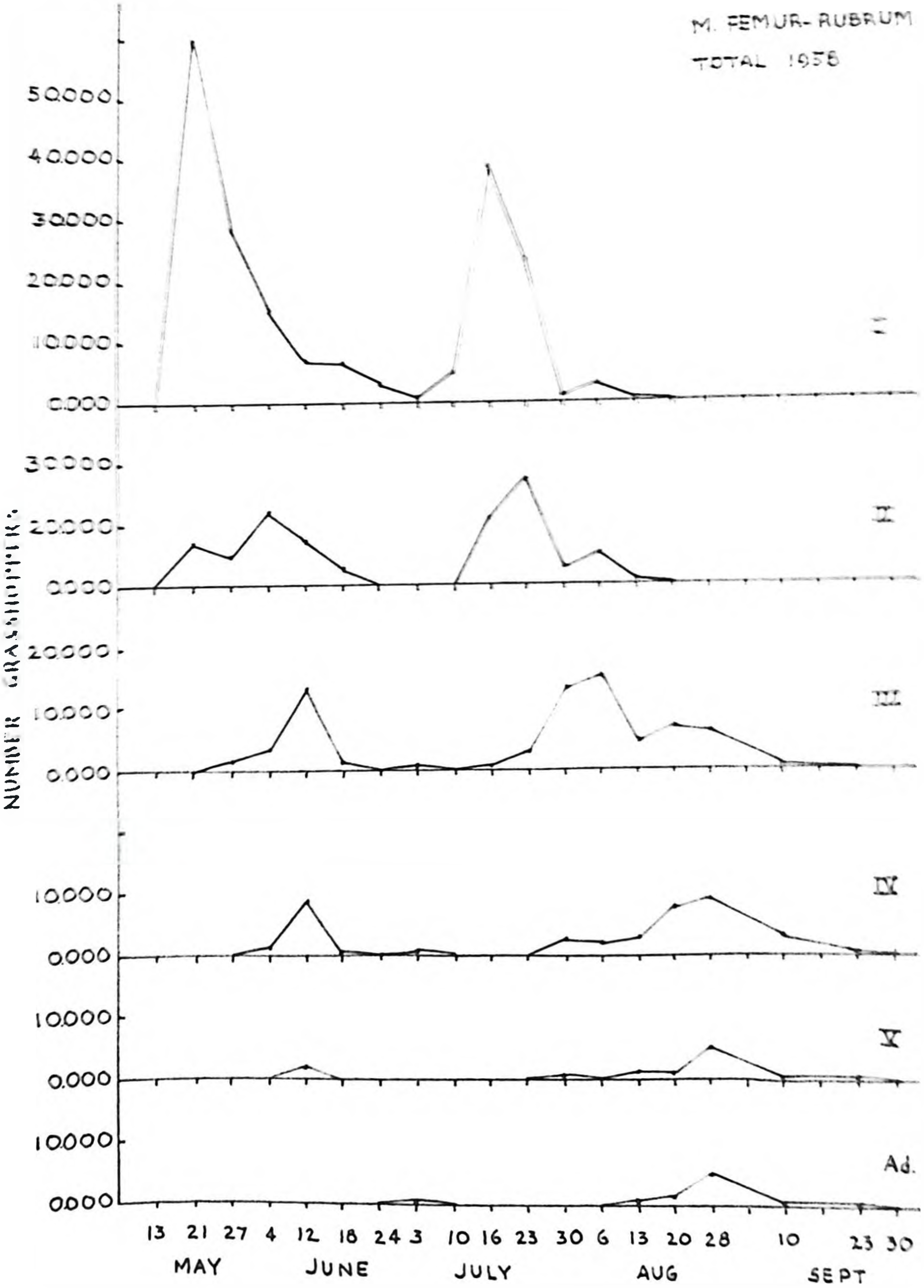

M. FEMUR-RUBRUM
TOTAL 1958
NUMBER GRASSHOPPERS
50.000
40.000
30.000
20.000
10.000
0.000
I
30000
20000
0.000
II
20.000
10.000
0.000
III
10.000
0.000
IV
10.000
0.000
V
10.000
0.000
Ad.
13 21 27 4 12 18 24 3 10 16 23 30 6 13 20 28 10 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 21 The estimated numbers of M. bivittatus in the total area (hills and field) in 1958.

I - V = nymphal stages

Ad. = adult stage

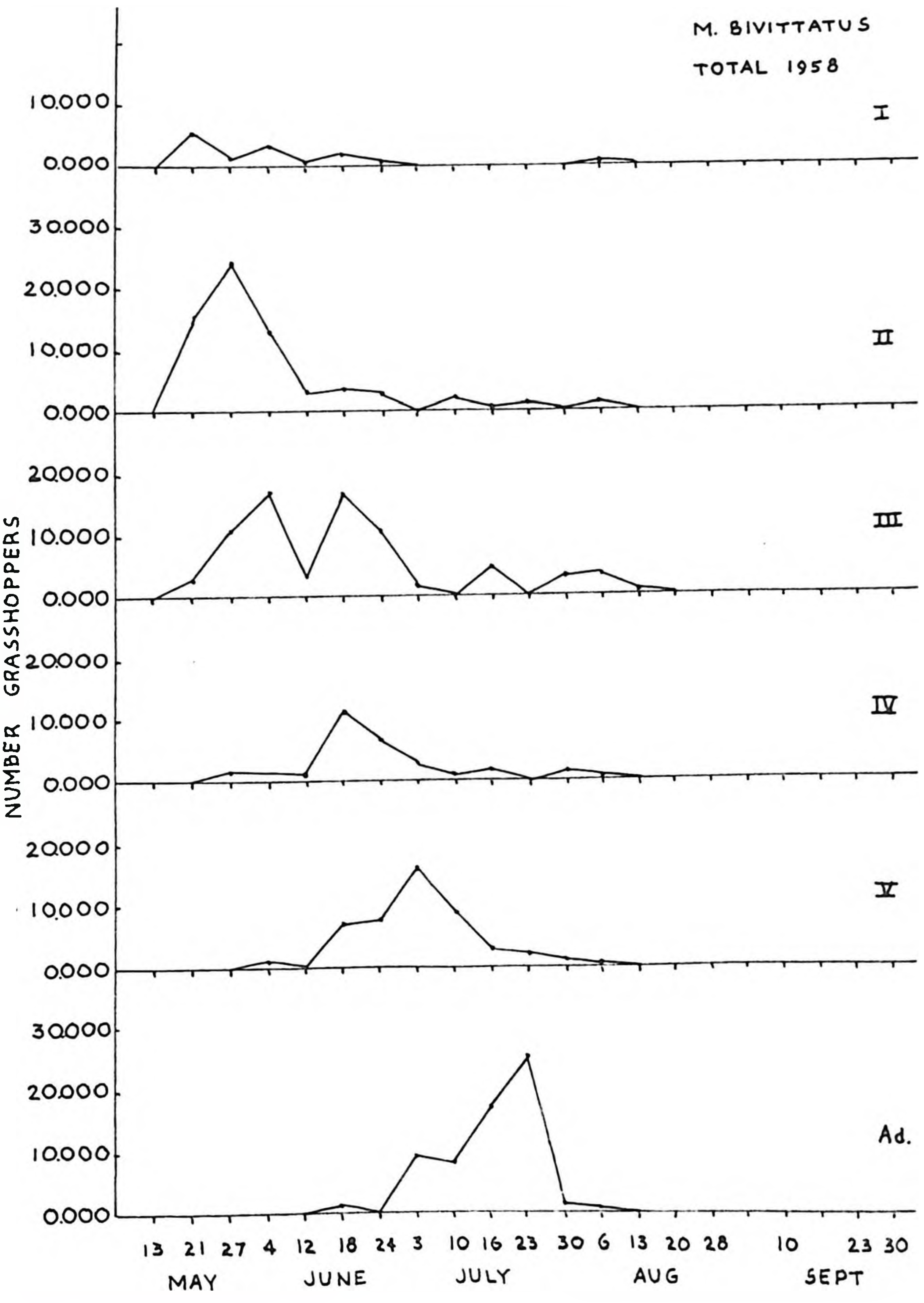

M. BIVITTATUS
TOTAL 1958
I
II
III
IV
V
Ad.
NUMBER GRASSHOPPERS
10.000
0.000
30.000
20.000
10.000
0.000
20.000
10.000
0.000
20.000
10.000
0.000
20.000
10.000
0.000
30.000
20.000
10.000
0.000
13 21 27 4 12 18 24 3 10 16 23 30 6 13 20 28 10 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 22 Estimated number of praying mantis per square meter in the field and on the hill, 1958 collection.

(top two)

Estimated number of praying mantis in the study area, 1958 collection.

(bottom)

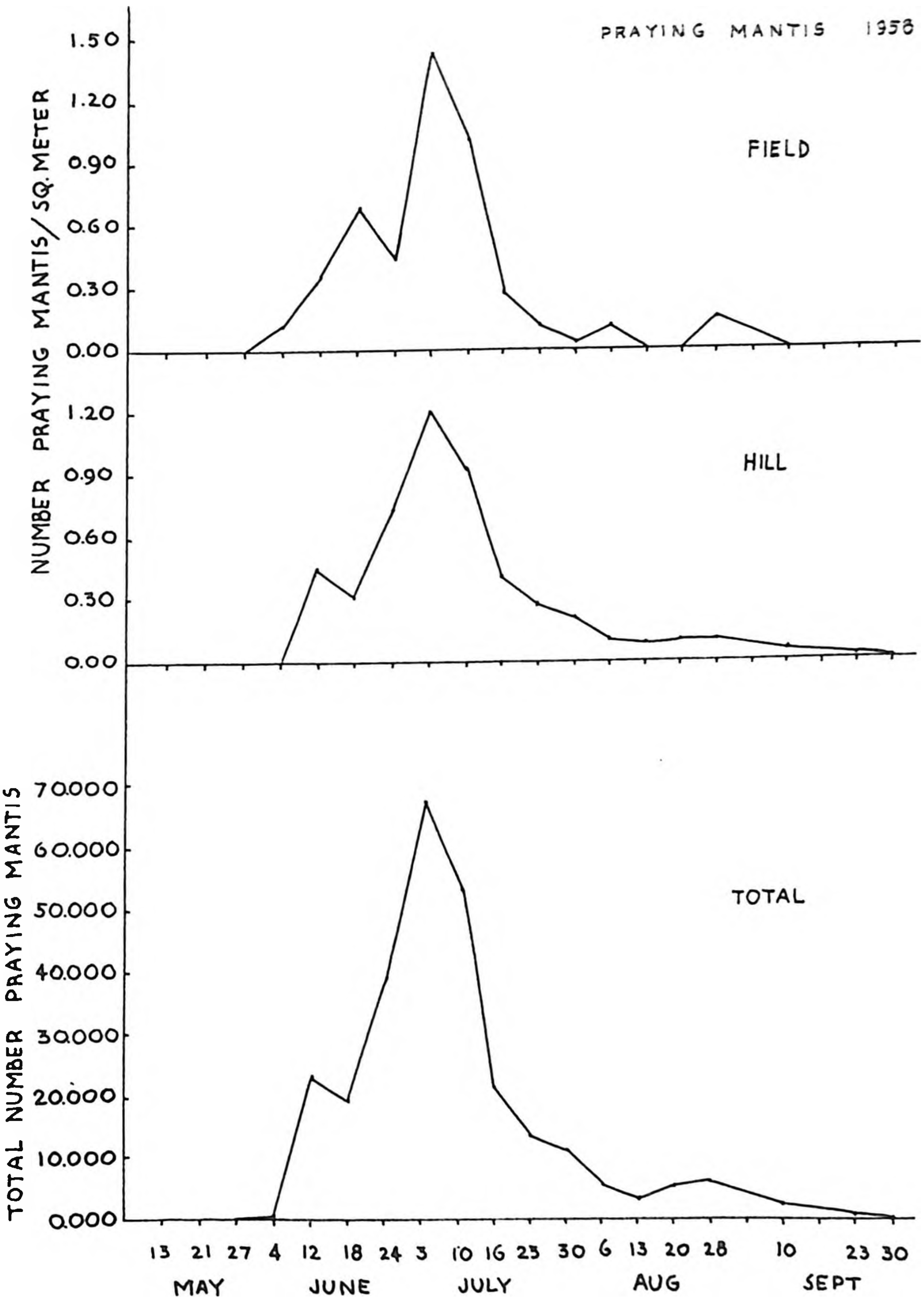
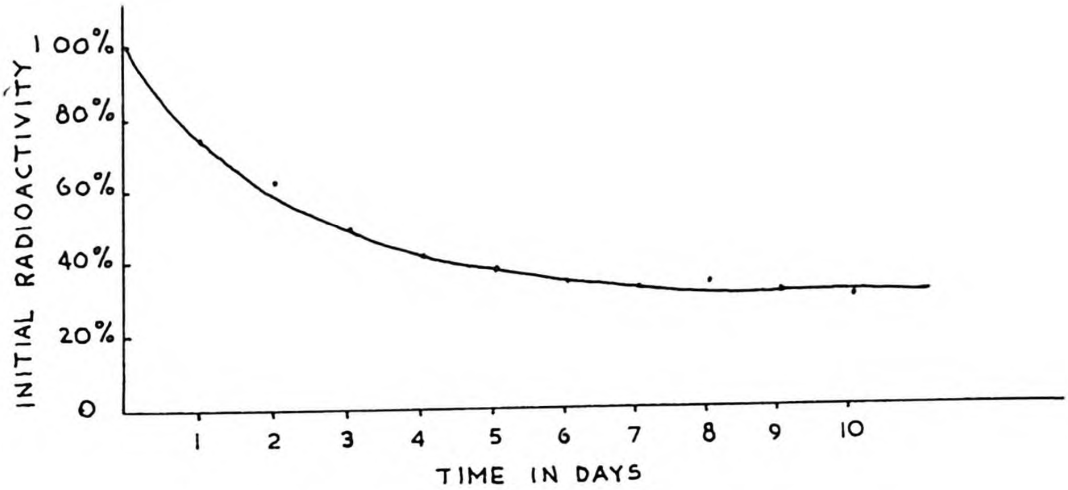

PRAYING MANTIS 1958
NUMBER PRAYING MANTIS / SQ. METER
1.50
1.20
0.90
0.60
0.30
0.00
FIELD
1.20
0.90
0.60
0.30
0.00
HILL
TOTAL NUMBER PRAYING MANTIS
70.000
60.000
50.000
40.000
30.000
20.000
10.000
0.000
TOTAL
13 21 27 4 12 18 24 3 10 16 23 30 6 13 20 28 10 23 30
MAY
JUNE
JULY
AUG
SEPT

Fig. 23	Average radioactivity in praying mantis in time after feeding on a radioactive grasshopper. Radioactivity expressed in per cent of radioactivity of the grasshopper fed, and corrected to date of feeding.
Fig. 24	Functional response of praying mantis searching for grasshoppers in outside cages.


INITIAL RADIOACTIVITY
100%
80%
60%
40%
20%
0
1
2
3
4
5
6
7
8
9
10
TIME IN DAYS

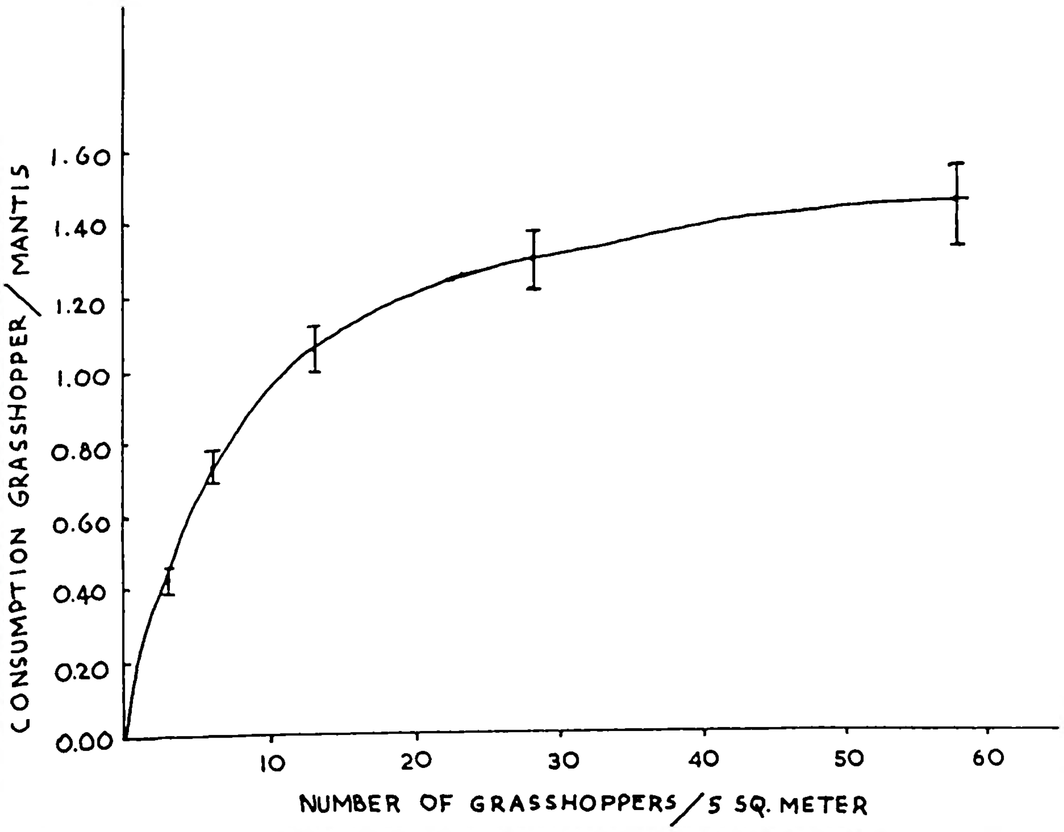
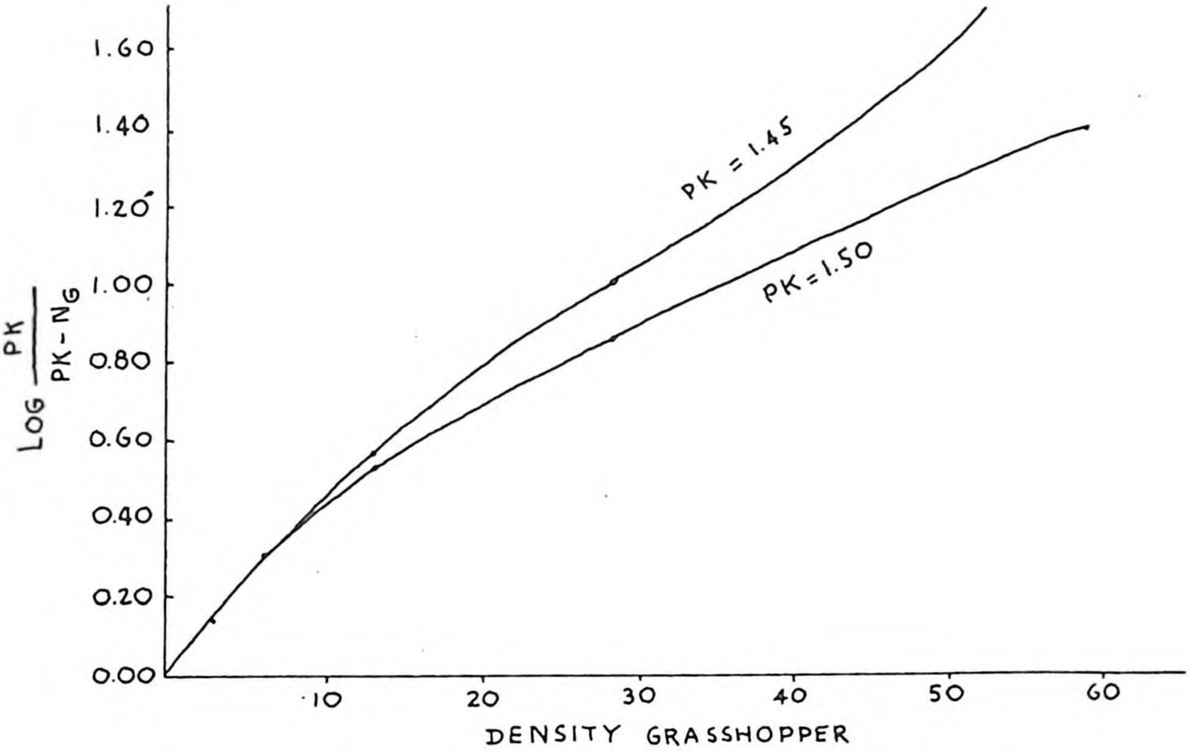

CONSUMPTION GRASSHOPPER/MANTIS
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
10
20
30
40
50
60
NUMBER OF GRASSHOPPERS/5 SQ. METER

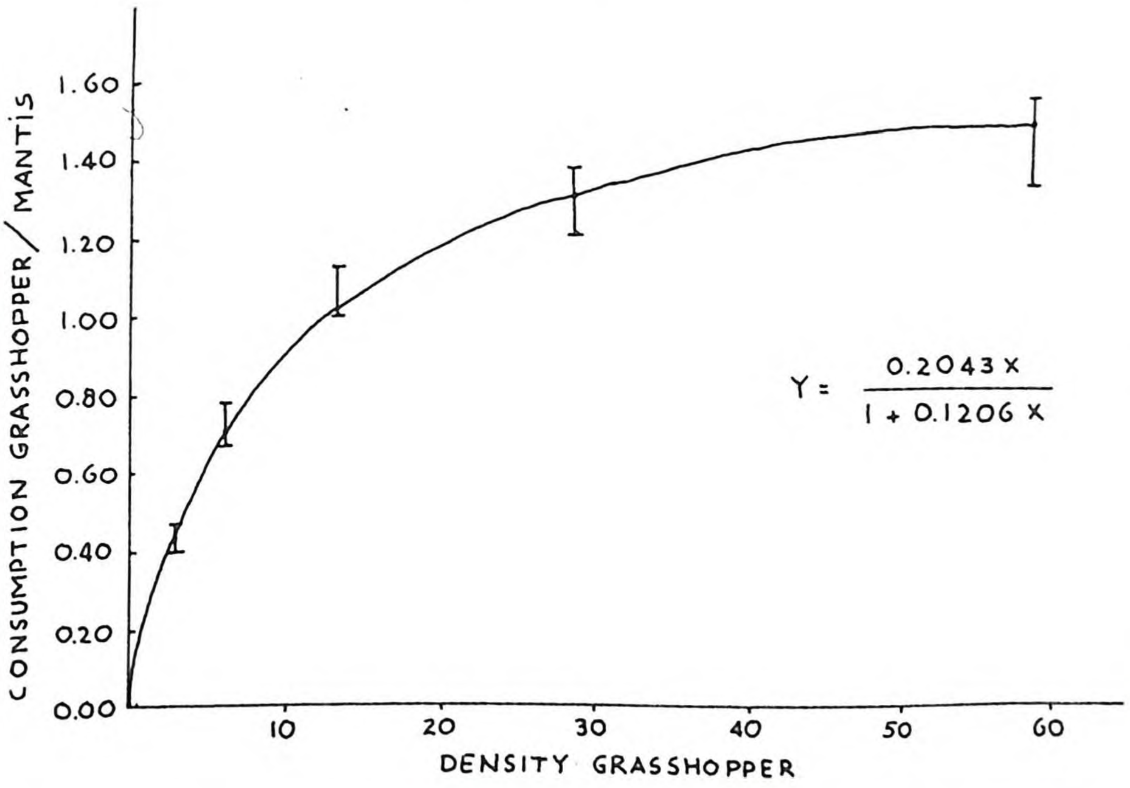
Fig. 25 Test of the hypothesis that $\log \frac{PK}{Pk - N_G} = AN_G$ is a straight line; PK is equal to 1.45 and 1.50 respectively.

Data from Fig. 24.

Fig. 26 Test of the equation $y = \frac{T_t ax}{1 + abx}$ (P 0.95).

Data from Fig. 24.


$\mathrm{LOG}\ \frac{PK}{PK - N_G}$
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
PK = 1.45
PK = 1.50
10
20
30
40
50
60
DENSITY GRASSHOPPER


CONSUMPTION GRASSHOPPER / MANTIS
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
$Y = \frac{0.2043X}{1 + 0.1206X}$
10
20
30
40
50
60
DENSITY GRASSHOPPER