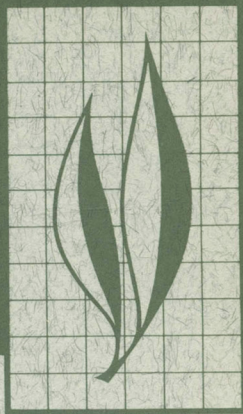


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A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
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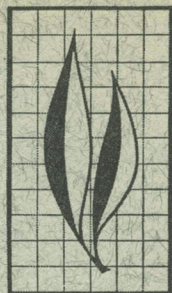


Volume 34, Number 9 • July, 1963

EXPERIMENTAL STUDIES ON PREDATION

**Complex Dispersion and Levels of Food in an
Acarine Predator-Prey Interaction**

C. B. Huffaker, K. P. Shea, and S. G. Herman



Experimental studies on the role of dispersion and level of food supply in predator-prey relations were continued. They were conducted under controlled laboratory conditions using the phytophagous mite *Eotetranychus sexmaculatus* as prey, and the mite *Typhlodromus occidentalis* as predator.

Results give additional support to earlier findings that more stable control of a population results when the environment is spatially more heterogeneous and there is a balance between the extent of heterogeneity and the amount of basic food. An excess of plant food at first generated large numbers of prey, and then an excess of predators which overexploited their prey and then starved.

By using a complex spatial environment consisting of three grid-wire shelves in a cabinet, and a wide dispersion of the basic food material, the predator-prey interaction was continued for 490 days, and the end was brought about by a disturbing disease rather than by overexploitation on the part of the predatory mite.

In contrast, trebling the quantity of basic food while maintaining other factors unchanged apparently created an imbalance between numbers of predators generated in the system and the hazards they faced in covering the areas to be searched—thus, they overexploited in each case at the end of the first prey population crash phase.

These results also suggest the potential role of predation as a means of synchronizing cycle phase in some natural populations.

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The research on which this paper is based was, in part, supported by a U. S. Public Health Service, National Institutes of Health, grant.

Experimental Studies on Predation: Complex Dispersion and Levels of Food in an Acarine Predator-Prey Interaction

(With Theoretical Consideration of Predation as a Synchronizer of Cycle Phase)¹

This paper is the third of a series resulting from experiments intended to shed light on the fundamentals of predator-prey interactions, in particular, and the interrelationships of such interactions with other important factors in populations dynamics, in general.

The first of this series (Huffaker and Kennett, 1956) explored the interaction between the cyclamen mite, *Steneotarsonemus pallidus* (Banks), which attacks strawberries, and its predators, two mite species of the genus *Typhlodromus*. The authors discussed the need for predator-prey studies of this kind and the significance of such results for concepts of natural control. The role of predation in natural control was particularly emphasized.

A significant result of the experiments of Huffaker and Kennett was the elucidation of two distinct types of oscillations in density. Where the predators were excluded there occurred a sequence of regularized fluctuations of *decreasing* amplitude. When predators were present and reduced the prey population to a low density, the prey could not interact in a mutual relation with its host, the strawberry plant, so that both predator and prey underwent regular, reciprocally dependent oscilla-

tions, and both populations were held fairly constant. The cyclamen mite population seemed to be saved from extinction, locally, by the occurrence of refuges in the strawberry plants and by the spatial dispersion created, while the predators were limited by the scarcity of prey. When prey densities were very low, the predators survived by feeding on honeydew and other liquid foods.

The second paper in this series (Huffaker, 1958), hereafter referred to as "the earlier studies" or "the 1958 results," reported on the interactions of the tetranychid mite, *Eotetranychus sexmaculatus* (Riley), and its predator *Typhlodromus occidentalis* Nesbitt. These studies revealed that increasing the spatial heterogeneity also increased the stability of predator-prey interaction. In the most complex system used, where the food (oranges) was widely dispersed, both predator and prey underwent three reciprocally dependent oscillations before the predator overexploited the prey and died out. No refuges were provided for the prey and no predator immigrants were introduced into the system. Increasing the spatial heterogeneity when no predators were present also had an influence on the patterns of utilization of food by the prey species.

¹ Submitted for publication September 4, 1962.

When the food was uniformly distributed in the absence of predation, a much more uniform distribution pattern of the prey species occurred than when the predators were present. Thus, the predators altered—and in that sense controlled—the distribution of the prey population, as well as reducing its density. Thus, in nature, predator action may be suspected if no other factors account for the very irregular distribution of phytophagous insects on uniformly distributed plants or on plants grown in monocultures.

In the present and third work, the 1958 studies on the interaction between *E. sexmaculatus* and its predator, *T. occidentalis*, were continued. Some of the experimental details were varied, however. Open trays, placed in a large room and edged by vaseline to prevent escape of the mites, had been used in the earlier studies. Two-dimensional movement only was possible in these trays. In the present experiments, conducted in closed cabinets having three grid-wire shelves each, three-dimensional movement was possible, since mites could crawl from one shelf to another. A higher level of total basic food was supplied to the prey in these studies, and the manner of dispersion was varied (see "Experimental Design and Procedure," p. 307). The systems used also permit a comparison of the consequences for predator-prey interaction of what may be termed an overabundance of food with a more moderate, balanced level.

The relation between complexity of environment and stability of populations was closely studied in these experiments. Obviously, the rigidly restricted universes used here cannot compare with the complexity of a natural environment. However, in nature, the extreme complexity of predator-prey interactions makes the illucidation of the specific roles of certain factors in rela-

tion to others difficult, if not impossible. It is hoped that the simplified systems can at least throw some light on the complex natural systems. Heterogeneity in nature, of course, has many facets, for example, physical or spatial dispersion, varied causes of mortality, diversity of competitors or allies, and diversity of food (plant or prey).

The ecology of a true predator-prey interaction is fundamentally similar to the ecology of some phytophagous insect-plant host interactions, such as those which occur in the biological control of a plant species. This is true whether the control results from action of a foreign insect which has been imported for control of a weed or from action of endemic phytophagous species on endemic plants (weeds or otherwise). The phytophagous species here acts as a regulator of the plant population in the same way as a carnivorous predator controls its prey. There is no basic difference between the biological control of prickly pears by *Cactoblastis cactorum* (Berg) in Australia, or of Klamath weed by *Chrysolina quadrigemina* (Suffrian), and the control of cottony cushion scale by the Vedalia beetle, *Rodolia cardinalis* (Mulsant), in California, or of rats in Jamaica by the mongoose, *Herpestes auropunctatus* Hodgson. This is one reason why, in studies of this kind, we do not restrict ourselves to study of classical predator-prey interactions. We are equally interested in the interactions resulting between the plant-feeding "predator" (the phytophagous insect) and its "prey" (the plant), for relevance to biological control of plant composition. In addition, an understanding of the interaction between the true predator and its phytophagous prey depends on an understanding of the interactions between the prey and its plant food supplies. One is superimposed on the other.

EXPERIMENTAL DESIGN AND PROCEDURE

General Features

For a study of interactions between *Typhlodromus occidentalis* and *Eotetranychus sexmaculatus* populations in the present work, the general procedures used by Huffaker in 1958 were employed. Oranges were used as food for the prey species. The amount of each orange surface exposed to the mites was varied by wrapping oranges with paper and cutting out circular areas for exposure. The orange surfaces were then linted to provide a more suitable micro-environment for the mites. Furthermore, the dispersion of the food material was an important feature of each study.

The universes used in the 1958 studies were simpler than those used in the present research. In the present studies, the oranges of each universe were dispersed over three different shelves in cabinets, each shelf consisting of a wire grid. These universes provided a three-dimensional sphere of movement. The posts used to support the intermediate shelves, the walls of the cabinets, and the grid itself permitted free, if hazardous, movement throughout each system (fig. 1). It was felt that this would increase the chances for a perpetuating predator-prey interaction. In each universe in the present research, the total amount of food used, expressed in whole-orange-equivalents,

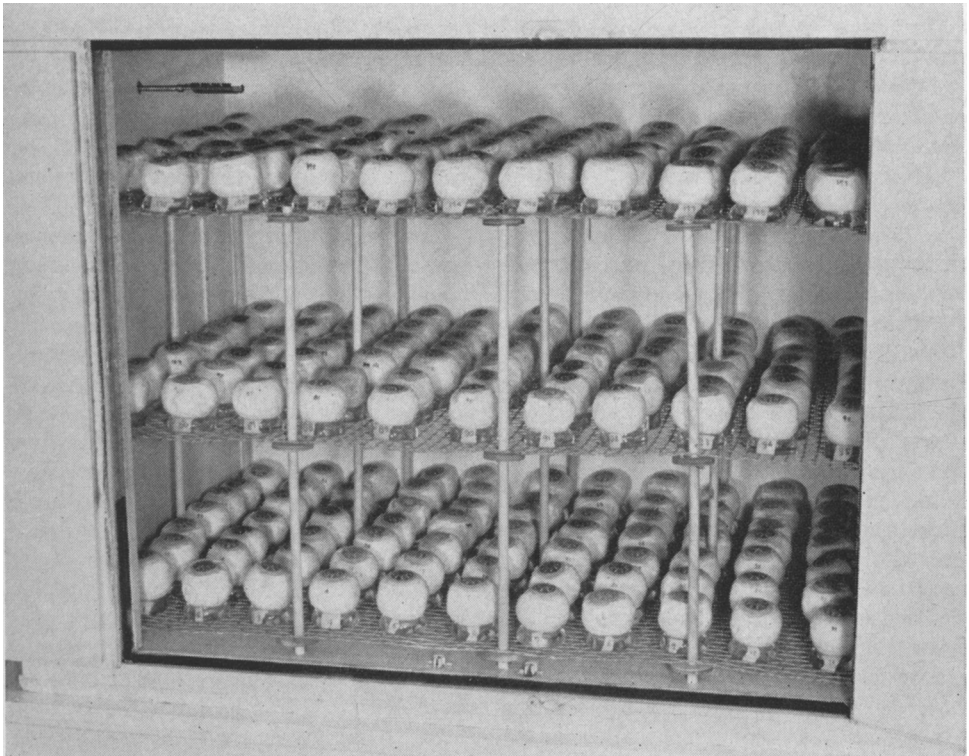


Figure 1. Cabinet universe (with doors open) showing arrangement of oranges used in studies of predator-prey interaction (prey: *Eotetranychus sexmaculatus*; predator: *Typhlodromus occidentalis*). The 252 oranges, each with 1/20 orange-area exposed—a 12.6 whole-orange-equivalent on a 252-orange dispersion—arranged on three grid-wire shelves supported by wood dowel posts. Each orange rests on a glass furniture coaster. The grid wire serves as a maze of impediments. Exact arrangement of systems II-3 and II-4. (Photograph by F. E. Skinner.)

was greater than that used in any universe employed in the 1958 studies. In the most successful universe used in the earlier work, the total areas exposed were equivalent to 6 oranges, while in the present studies exposed areas were equivalent to 12.6 oranges. In one case, areas exposed equaled 37.8 oranges. For ease of comparison, all densities shown in the graphs of Huffaker (1958) and in the present paper are expressed in whole-orange-equivalents.

In one universe where the predator was not introduced, the total food used was only 10.5 whole-orange-equivalents, since the cabinet was smaller. The pattern of dispersion, however, and the nature of the terrain to be traversed by the mites in moving about in this slightly smaller system was the same as in the larger cabinets. The ecological parameters in the utilization of food under these circumstances were expected to be similar to parameters in the larger cabinets, other conditions being the same.

The scheme for renewal of the oranges in the universes differed from that used by Huffaker in 1958. In the present study, it was not necessary to replace one fourth of the oranges every 11 days, as in the earlier experiments. Instead, one seventh of the oranges in each universe was renewed each week; that is, the oranges were completely renewed every 49 days. Since the time span was still short, the oranges did not deteriorate because of aging processes. Since the 49-day renewal schedule was only 5 days greater than the schedule used in the 1958 studies, this aspect of the two studies is relatively comparable.

In these studies temperature was maintained at $80^{\circ}\text{ F} \pm 2^{\circ}$. Although relative humidity varied over a wider range—and at some times more than at others—it was maintained fairly consistently at from 43 to 55%. Early in the study the humidity exceeded 60% for one rather extended time during which an unidentified viral disease in the six-spotted mite (prey) population

appeared. The virus terminated the systems affected. Subsequently, closer control of humidity was maintained. Relative humidities higher than 60% or as low as 43% occurred very rarely even before that time.

Sampling

The populations in all universes were counted weekly. It was shown by Huffaker (1958, p. 351) that it is best to sample from every orange in such populations. In other words, if the population on half of the total areas exposed is to be counted, it is better to count the mites on half of the exposed sections of every orange rather than to count the mites on the total exposed areas of only half the oranges. Every orange was sampled in the present study whether populations were high or low.

The method employed by Huffaker (1958, p. 352) to determine if such half-area samples could be used to adequately estimate the total populations was again used. Series of six half-area randomized lots of the component items were drawn from total population counts on two dates taken as representative of high-density and low-density levels for both the predator and prey. These counts were made on all the 252 oranges used in the typical universe. The means, standard errors, and coefficients of variation were then compared with the corresponding values based upon the total known population.

The data from system II-3 on March 3, 1959, for the six randomized lots were taken as representative of high population densities. For the *prey* the following subsample statistics were little changed, compared with those of the total population: the standard errors were $\pm 1.23, 1.23, 1.17, 1.30, 1.14$, and 1.24 , respectively, compared with a half-value standard error of 1.18 for the total population; the coefficients of variation were $12.7, 12.3, 11.8, 12.7, 12.3$, and 12.7 , respectively, compared with 12.1 for the total population; and the means, as estimates of the mean of

the total population, averaged only 2.3% higher or lower than the corresponding value for the total population, the range being from 0.2 to 5.0%.

On this same date, the six series of randomly drawn *predator* data from half-areas gave standard errors of .045, .051, .046, .038, .044, and .045, respectively, as compared with .041 for the corresponding half-value standard error for the total population. Coefficients of variation of 22.5, 28.1, 23.2, 28.1, 22.8, and 23.6, respectively, compared with 22.6 for the total population. Means averaged 7.9% higher or lower than the corresponding half-value for the total population, the range being from 0.0 to 19.6%. It is thus obvious that at such high densities the half-area counts were adequate as samples for both the prey and the predators.

The data from system II-3 on September 1, 1959, were taken as representative of moderately low populations. For the prey, the standard errors were .52, .55, .60, .60, .60 and .59, respectively, compared with a half-value of .58 for the total population. The coefficients of variation were 26.1, 27.5, 27.1, 26.9, 27.7, and 27.7, compared with 26.8 for the total population. The means averaged 3.7% higher or lower than the corresponding half-value for the total population, the range being from 0.5 to 8.2%. Again, the sample gave entirely satisfactory results for the prey species.

For the predator, however, the half-area sample was not entirely satisfactory at the low population level. The six lots of data gave standard errors of .014, .017, .013, .017, .015, and .014, respectively, compared with a half-value of .014 for the total population. Coefficients of variation of 39.8, 42.1, 42.3, 39.9, 53.6, and 38.9 compared with 37.9 for the total population. Means averaged 11.1% higher or lower than the half-value for the total population, the range being from 0.0 to 22.2%. However, even for the predator populations at moderately low densities, the data indicate that a half-area sample

gives a fair estimate of the true population. Obviously, at the extremely low densities at times encountered in these studies, such a sample would not give a fair estimate of the population. However, unless these extremely low populations of predators rebounded to higher levels later, their impact on the prey would not be significant at any rate, and the confidence from such time-series data would be much greater than that which rests on the statistical estimate of the population at any single point in time.

It is significant that the coefficients of variation for both the predator and prey populations were roughly twice as high for the low population densities as they were for the high densities.

Rating of Orange Utilization

Records on the degree of orange utilization (conditioning) by the prey species were kept for all universes, whether or not populations reached levels high enough to utilize oranges to a marked degree. The degree of utilization was indicated by the percentage of oranges which at the time of replacement appeared to be fully utilized, or essentially so. This, of course, meant that mean population levels were somewhat higher than is indicated by this measurement of the degree of utilization, since some increase in population resulted from *partial* utilization of a given orange even though it was recorded as unutilized or unconditioned up to the time of its removal.

Complete or nearly complete utilization is the best way to rate utilization with relative accuracy. This method gives a good measure of competition for food. For example, if 50% of each of 50 oranges in a universe was utilized, there was evidently little competition for food. However, if 25 of the 50 oranges were completely utilized and the other 25 entirely unutilized, the stress manifested on the 50 oranges as a whole was undoubtedly much more severe.

RESULTS

Fluctuations and Densities of Prey in the Absence of Predation

One universe in which predators were not introduced was set up as a control. The interaction between the prey species and its food supply could thus be studied under conditions comparable in other respects to the universes where predator-prey interactions were under study.

Predators Absent; Complex 3-Shelf Universe; 210 Small Areas of Food.

Universe E-2 was started on March 17, 1961, and continued until January 29, 1962, at which time the basic pattern of the interaction was established (fig. 2). One mature, female, six-spotted mite (prey) was introduced on each of 52 oranges taken at random, that is, on one

fourth of the total 210 oranges. No additional mites were added thereafter.

The prey species in this universe increased at a fast rate up to April 7, then declined briefly, after which it resumed the rapid ascent. During this first increase period the highest population density by far occurred, that is, 3,044 mites per orange-area (expressed in whole-orange-equivalents) on May 6, 1961. The population then declined to a level of 725. Subsequently (ignoring the small temporary increase), four additional, rather regularized, major fluctuations occurred. These last four waves may be taken as fluctuations about the equilibrium position as governed by the food supply. The mean of these four waves is approximately 2,000 mites per whole-orange-equivalent.

The first and greatest population in-

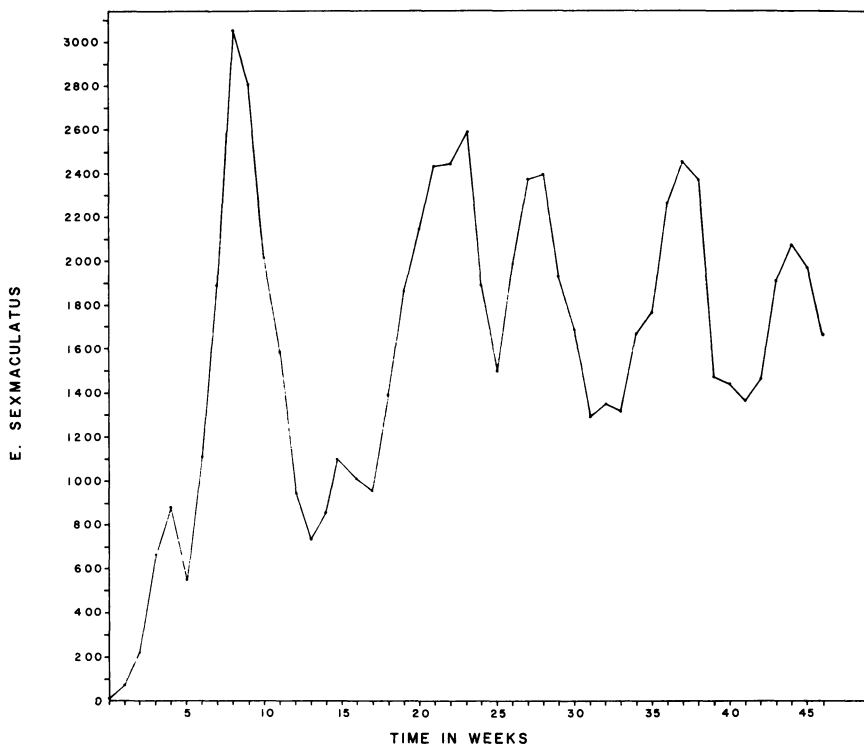


Fig. 2. Control system, E-2. Densities per orange-area of *Eotetranychus sexmaculatus* in the absence of predators with 210 oranges arranged in a cabinet (slightly smaller) as shown in figure 1 and with 1/20 of each orange surface exposed—a 10.5 whole-orange-equivalent on a 210-orange dispersion, with uniform spacing.

crease occurred at a time when no oranges in the system had been utilized previously by mites of an earlier high-level population, although a few of the stocked oranges were utilized fairly early in the increase period. Consequently, in the beginning the ratio of unutilized to utilized food was abnormally high, and this made possible the unusually high first increase. This above-normal level of utilization may have been in part responsible for the very small increase which followed. These two extremes seemed to be steps in the adjustment of the interaction between food and mites. The last four fluctuations reflect a more normal interaction, since they occurred after utilization became stabilized in relation to current *rate of renewal* of the food, that is, the renewal of one seventh of the oranges each 7 days. The pattern of fluctuation was fairly characteristic, with fairly wide amplitude and periods of 4 to 6 weeks between peaks.

In the 1958 studies on a related system (Huffaker, p. 356), although the pattern of fluctuations was similar, the period between fluctuations was only 13 to 18 days. In that case, the oranges were partially renewed every 11 days, and completely renewed every 44 days. In the present universe (E-2), the oranges were partially renewed every 7 days and completely renewed every 49 days. Thus, we see no correlation in these fluctuations with the schedules of food renewal. Furthermore, in another related system used in the 1958 studies (Huffaker, p. 357) where food was also the limiting factor, an initial fluctuation of greater amplitude was obtained. These fluctuations then settled down to ones of minor amplitude, a distinctly different pattern. Approximately 25% of the difference in mean population density is explainable on the basis of the change occurring in size (age) classes in the population (recent analysis of original data), that is, when the population "density" was rated roughly on the basis of mass. The intervals be-

tween the fluctuations varied approximately from 12 to 22 days.

Since universe E-2 is much more complex than those used in the 1958 work, the greater spatial complexity appears to have added to the interval between significant fluctuations. (See also "Discussion," p. 323.)

Population Changes Under Predator-Prey Interactions

Predators Present; 3-Shelf Universe; 252 Small Areas of Food. Systems II-3 and II-4 were run as replicates. System II-3 was started on August 29, 1958, and ended 75 weeks later on February 2, 1960. However, the predator-prey interaction ended after 70 weeks on January 21, 1960, although the graph showing the results (fig. 3) covers only a period of 60 weeks. The additional data, which were not significant, were deleted to facilitate the engraving process.

One mature, female, six-spotted mite was introduced on each of 63 oranges taken at random. These oranges represented one fourth of the total 252 oranges. Twenty-eight days later one mature female *Typhlodromus occidentalis* (the predator) was added to each of 21 oranges chosen at random from the 63 oranges previously stocked with the prey species. Thus one third of the original prey-stocked oranges received predators. No stock was added after this.

The arrangement of oranges in the cabinet is shown in figure 1, and the results of the interaction in this universe are shown in figure 3. Each pictorial chart shows positions of predators and prey in the universe at the time of each count (charts 1 to 60, fig. 3). Each chart is divided by two horizontal broken lines delimiting three sections which represent the three shelves of the cabinet—upper, middle, and lower. Four classes of increased density in the prey are shown by varying degrees of shading at the respective positions of

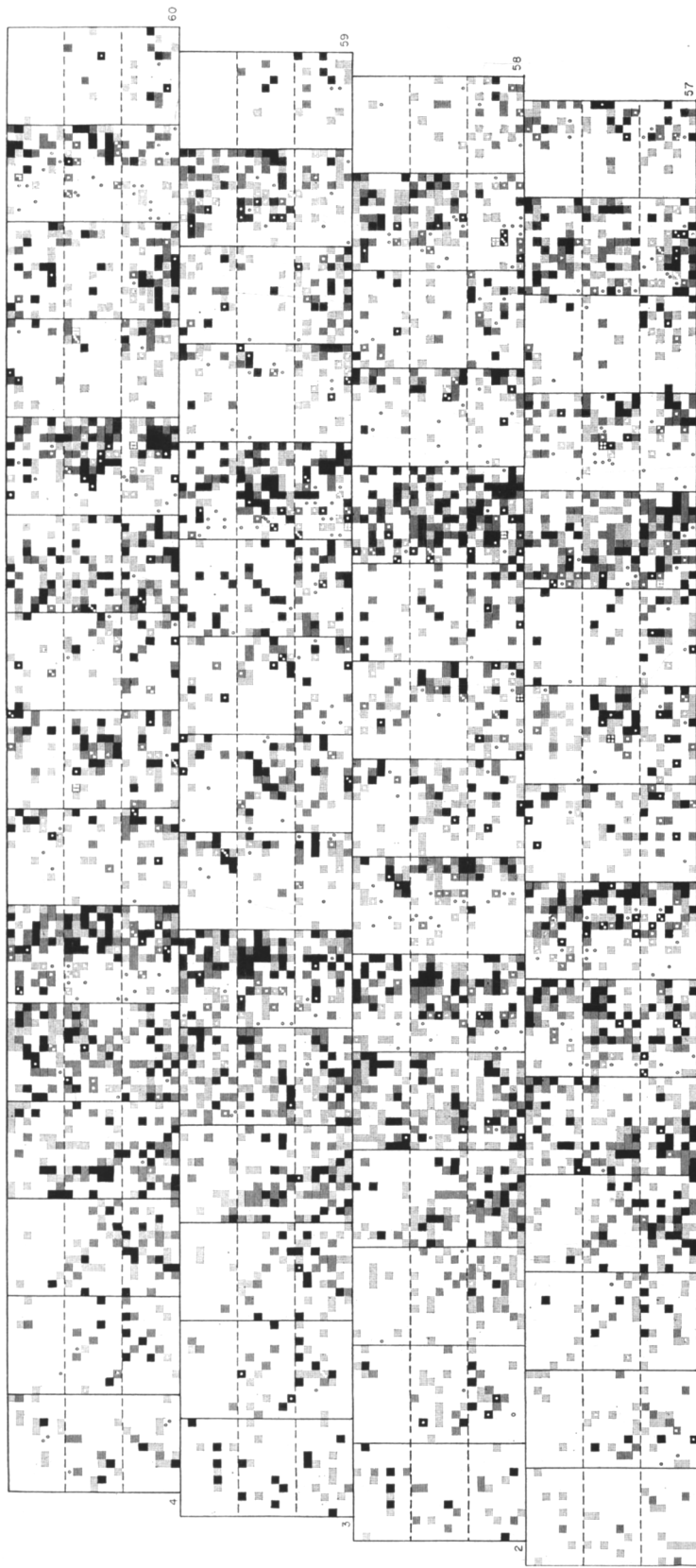
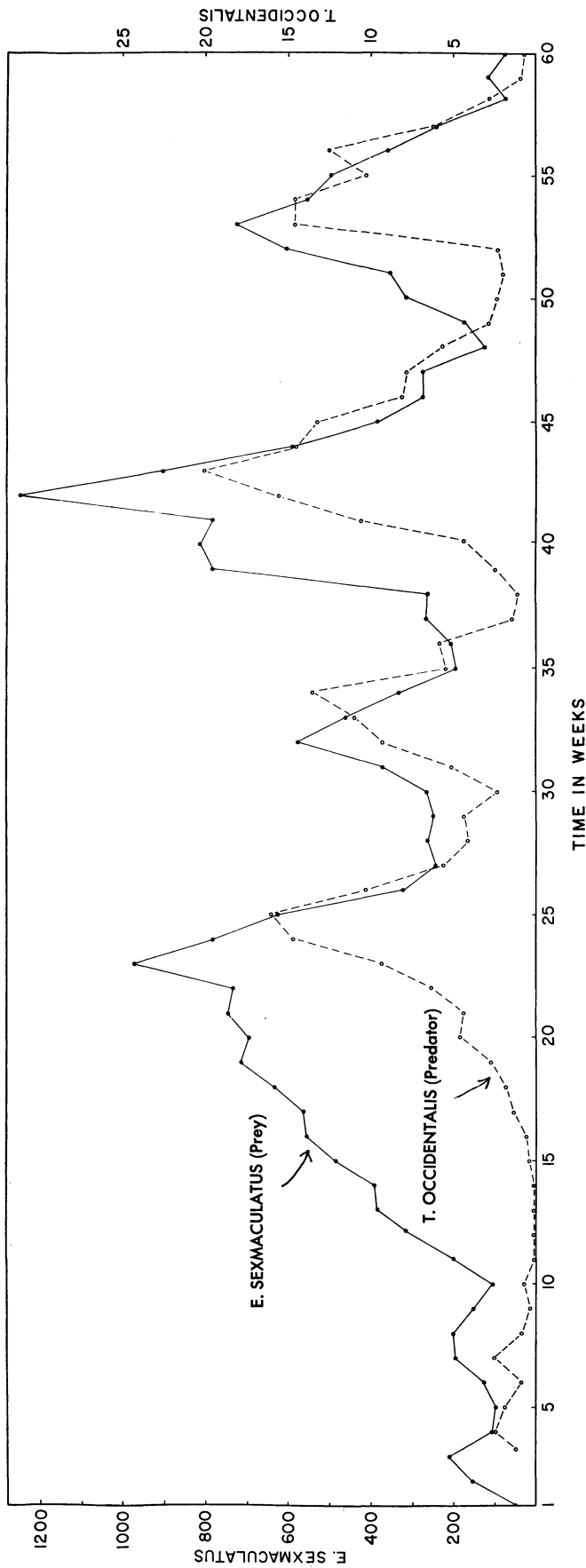


Figure 3. System II-3. Oscillations in density of a predator-prey interaction in which the predatory mite, *Typhlodromus occidentalis*, preyed upon the orange-feeding six-spotted mite, *Eotetranychus sermaculatus*. System with a 12.6 whole-orange-equivalent on a 252-orange dispersion.

The graphic record below shows the sequence of densities per orange-area while the pictorial record, charts 1 to 60, above, shows both *densities* and *positions* within the universe in a time-series. Each chart is divided by broken lines separating areas representing the oranges of each shelf, and



PREDATOR-PREY INTERACTION WITH 1/20th ORANGE EXPOSED ON 252-ORANGE DISPERSION

each chart is arranged with the center directly above the time of occurrence on the horizontal time scale. The physical arrangement of oranges and the nature of the dispersion are detailed in figure 1. Density classes at each orange position are:

Prey: 0-5, nil density (white); 6-25, low density (light stipple); 26-75, medium density (dark lining); 76 or over, high density (solid black).
 Predator: 1-8 (one white circle, ringed in white areas, unringed in shaded areas).

each orange in the universe. Predator densities are shown by small white or black circles. Actual densities per orange-area in the universe as a whole are shown graphically in figure 3.

From figure 3 it may be seen that there were two minor fluctuations in density which occurred before the population increases of either the predator or prey got well under way. By chance, the predators were at first favorably located on some of the oranges having the highest prey densities, and they apparently caused an early slight decline in the prey. This was then followed by a decline in the predators and a subsequent gradual increase in the prey. Predators then again increased slightly, followed by a second minor decline in both prey and predators. It is unlikely that predator increase alone caused the second prey decline, since the predators evidently lost adequate contact with their prey or both the prey and other predators, and declined simultaneously.

Although a rather explosive increase in prey population might then have been expected, this did not occur. In fact, the prey increased only gradually from the 13th week to the 22nd week, a rather long period. Undoubtedly, the predators had declined to such low levels that they had been unable either to find mates with sufficient success or to locate areas of favorable prey densities. It is remarkable that the predators survived at all. Substantial predator pressure was not again exerted until the 19th or 20th week, and such pressure did not become dominant even then. Two possible reasons for this are suggested. During that period the oranges being used were of rather poor quality, and although outright spoilage did not occur, they developed an offensive odor and flavor. This appears to be correlated with biochemical changes which cause the mites to wander off rather than settle down to feed and reproduce. Also, possibly an accumulation of air pollutants of unknown nature, perhaps

associated with overripening, may have acted to prevent normal feeding and reproduction. Munger (1956) reported that in small, tight rooms or cabinets related species of mites do not thrive unless the air is circulated over activated-carbon filters. C. A. Fleschner (personal communication) has also found this method essential in maintaining cultures of such mites in the insectaries of the Department of Biological Control at Riverside. At any rate, following the installation of an activated-carbon filter system and a change to better-quality oranges, the mites in this universe, and in others, began to perform more satisfactorily. In the absence of predator pressure on given oranges or in given universes, the prey reproduced rather uniformly at their usual accelerating rate.

The latter half of the first major population oscillation and the succeeding three oscillations occurred without any apparent disturbing factor. The predator and prey populations interacted in a characteristic reciprocating density-dependent manner (Huffaker, in press; Huffaker and Messenger, in press). An increase in the prey population was followed by an increase in predators to a point which then caused sharp decreases in the prey. Through feed-back mechanics, the new low densities of the prey then caused corresponding declines in the predator populations.

In each oscillation there was a definite lag in the recovery of the predator populations after the prey had begun to increase again. Only during the first major oscillation was this lag unduly long.

The data from the control universe can be used to appraise the amplitude and the degree of biological control of the prey population in the predator-prey universe. The measure of degree of control is the difference between population levels in system II-3 and in the control universe. In the control universe, food alone was the limiting requisite for the prey. Other nonregulating

stresses, although important, were the same in the II-3 universe and the control universe. As previously stated, the mean density when food alone limited the prey population was 2,000 mites per whole-orange-equivalent. The mean in the predator-prey universe was about 500, which illustrates the substantial degree of control exerted by the predators. Records on the utilization of oranges, which were made at renewal times, show that food shortage did not contribute appreciably to the lower densities in this predator-prey universe. Only about 15% of the oranges were completely utilized.

The pattern of utilization of the oranges in system II-3 was similar to that in system II-4 except that utilization averaged approximately 15.0% in system II-3 and only 11.3% in system II-4. The mean population levels were approximately equal at 500 in both. (See "Discussion," p. 322.)

A period of higher utilization (about 20%) followed the first major oscillation maximum in system II-3. There was then a period of less utilization (from 8 to 20%) from weeks 31 through 42. At each period there was a time lag between the actual utilization and the date it showed up in the renewal records. From weeks 43 through 46, utilization varied from 20 to 33%, the highest recorded, just following the highest prey density recorded. Another period of low utilization (5 to 11%) followed, then a final period of higher utilization (from 11 to 20%) and a final period of low utilization (3 to 14%).

The termination of system II-3 seemed definitely the result of a previously unknown disease. The causative pathogen was diagnosed by M. E. Martignoni as of an undescribed viral nature. Both predator and prey populations had survived the last crash phase shown at week 60 in figure 3 and, during the next 5 weeks, had increased to densities which assured an additional oscillation had the disease not appeared. The disease reduced the prey population to such a low

level that the predators were unable to survive, the interaction thus terminating at the 70th week (not shown in fig. 3). The prey population then began a slow recovery which was followed until the 75th week, and observations were then arbitrarily ended.

The results of the second replicate of this universe are shown in figure 4. System II-4 was started on June 1, 1960, and ended on December 15, 1960. Two major oscillations occurred. The initial small oscillations recorded in the replicate system (II-3) did not occur. The positions of the mites, illustrated in figure 4, show that although the predators were reduced to low levels in the initial crash phases of the two oscillations, the remaining predators were located close to adequate prey populations in the first oscillation but not in the second. As a result, the predators died out shortly after the second crash phase. Because the poor quality of the oranges used prevented the prey population from increasing rapidly, the predators did not reestablish significant contact with prey once it had been lost. Had this occurred the predators may have survived. Green, grove-picked oranges were then substituted as food in place of commercially available ripe oranges, and this problem was greatly reduced in subsequent universes.

These two replicate runs of interacting systems clearly illustrate that, even in relatively complex systems, chance plays an important role in the survival of the predator after a sharp population decline. However, the chance for survival seems to be improved when the environment is more complex. (See "Discussion," p. 323, and Huffaker, 1958, p. 376.)

The orange utilization record of the six-spotted mite in system II-4 shows that for the first population wave the percentage of oranges utilized was negligible up to July 7 (week 6), at which time only 13.9% was fully utilized. One week later, renewal records showed utilization at its highest peak, that is,

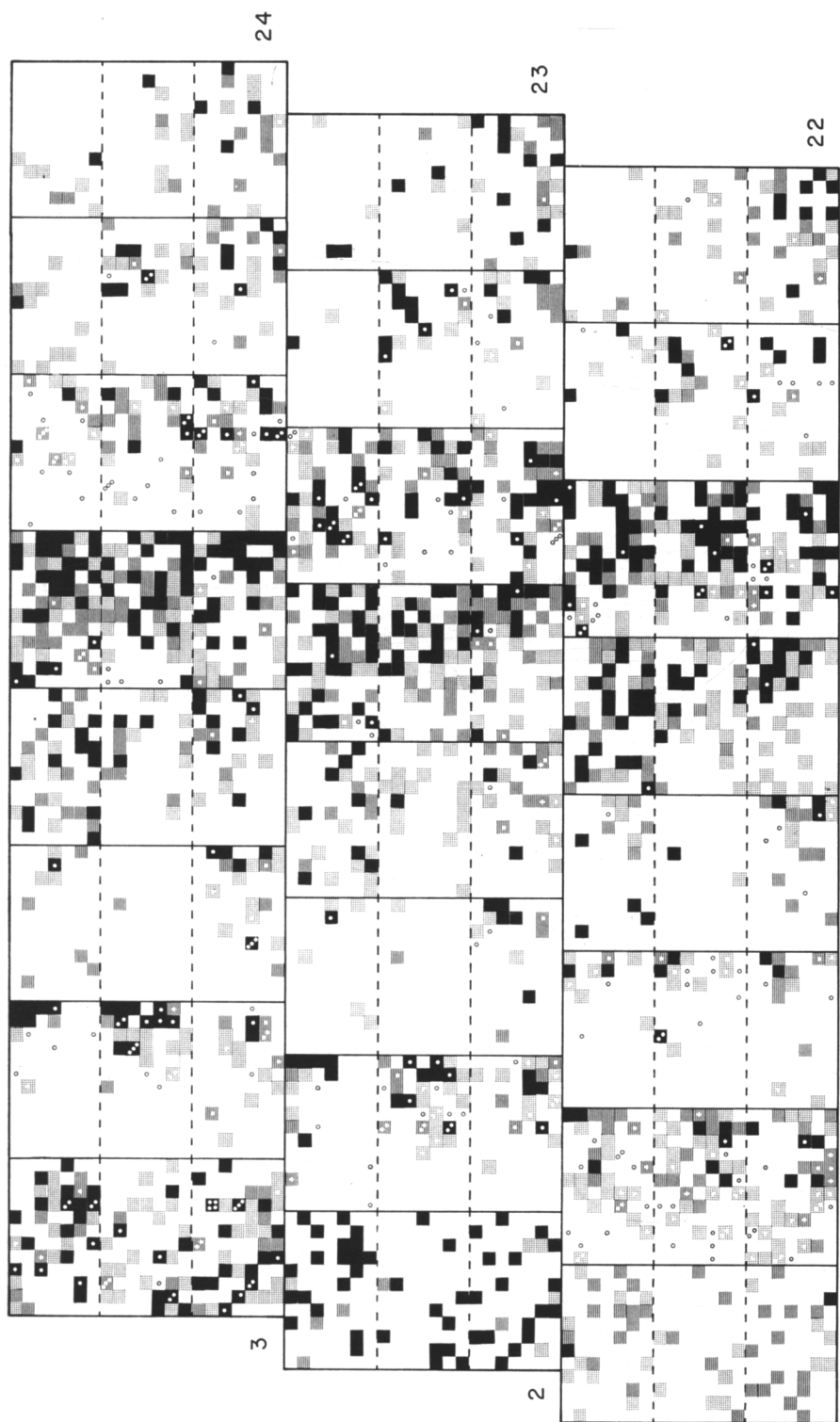
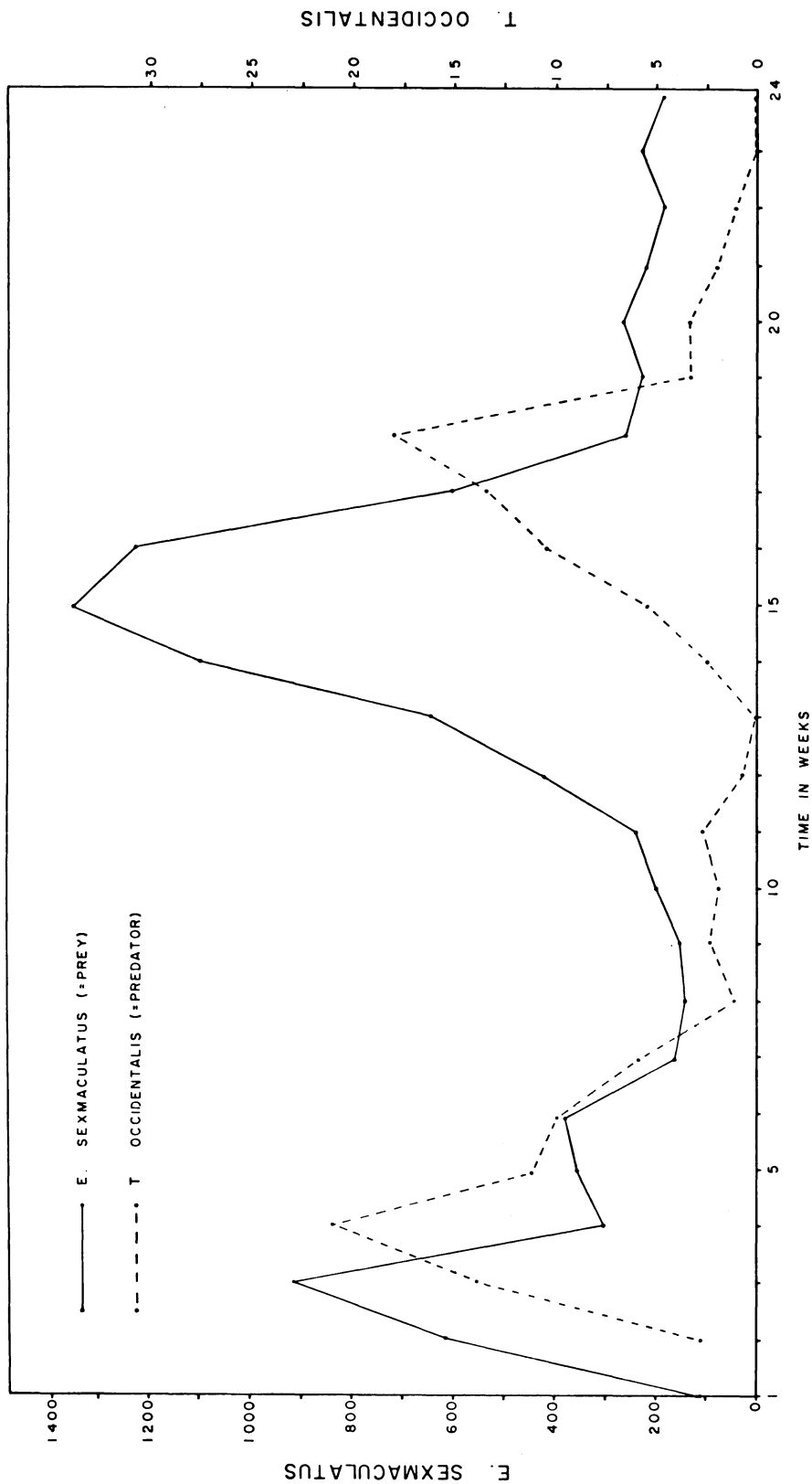


Figure 4. System II-4. Replicate of system II-3. Oscillations in density of a predator-prey interaction in which the predatory mite, *Typhlodromus occidentalis*, preyed upon the orange-feeding six-spotted mite, *Eotetranychus sermaculatus*.

The graphic record below shows the sequence of densities per orange-area, while the pictorial record, charts 1 to 24, above, shows both *densities* and *positions* within the universe in a time-series. Each chart is divided by broken lines separating areas representing the oranges on each



PREDATOR-PREY INTERACTION WITH 1/20th ORANGE EXPOSED ON 252 ORANGE DISPERSION

shelf, and each chart is arranged with the center directly above the time of occurrence on the horizontal time scale. The physical arrangement of oranges and the nature of the dispersion are detailed in figure 1. Density classes at each orange position are:

Prey: 0-5, nil density (white) ; 6-25, low density (light stipple) ; 26-75, medium density (dark lining) ; 76 or over, high density (solid black).

Predator: 1-8 (one white circle, ringed in white areas, unringed in shaded areas).

27.8%. However, the period of actual peak utilization had been 3 weeks earlier, even though the records did not reflect this immediately. The next period of low recorded utilization followed the corresponding decline in the mite population. The second-wave population again reached a peak utilization, but it was some 3 weeks before this was reflected in the renewal records. The highest single recorded utilization in this wave was 44.3%. However, since the utilization figures for a single date are based on only one seventh of the total group of oranges, it is best to consider a group of consecutive records as a more accurate measure of the previous actual use by the mites. The five consecutive higher utilization records for this second wave averaged 26.6%.

For the entire interaction in system II-4, the average for completely utilized oranges was only 11.3%. The mean population density of the prey was about 500, as was the density in the twin system, II-3. The population density and the percentage of utilization are similar to those from system II-3. In systems II-3 and II-4, predation held down prey density to about 500 per whole-orange-equivalent whereas in the control universe (system E-2), which had no predators, prey density per whole-orange-equivalent was approximately 2,000, and mean full utilization was approximately 93%.

Predators Present; Complex 3-Shelf Universe; 252 Larger Areas of Food. Three replicate systems, I-4, I-5, I-6,

were run in chronological order in a cabinet identical to the one used for the universes just discussed. However, the area of orange surface exposed to the mites on each of the 252 oranges was three times that exposed in the two former cases. The same dispersion pattern, total areas, and obstacles in the physical systems were used. Figures 5a, b, and c present the results of these universes.

Although there was some variation in the patterns of increase in each prey population and in the predator responses, results were generally similar in each replicate. In system I-4 (fig. 5a), the prey density reached a level of approximately 800 per whole-orange-equivalent; in system I-5 (fig. 5b), a level of 900; and in system I-6 (fig. 5c), a level of 800. Although the predator response varied greatly (figs. 5b and 5c illustrate the extremes), the differences may well have been less had counts been made twice weekly rather than weekly. It is probable that the predator population rose to a level considerably higher than that shown in figure 5c between the counts on December 1 and December 8 (weeks 9 and 10).

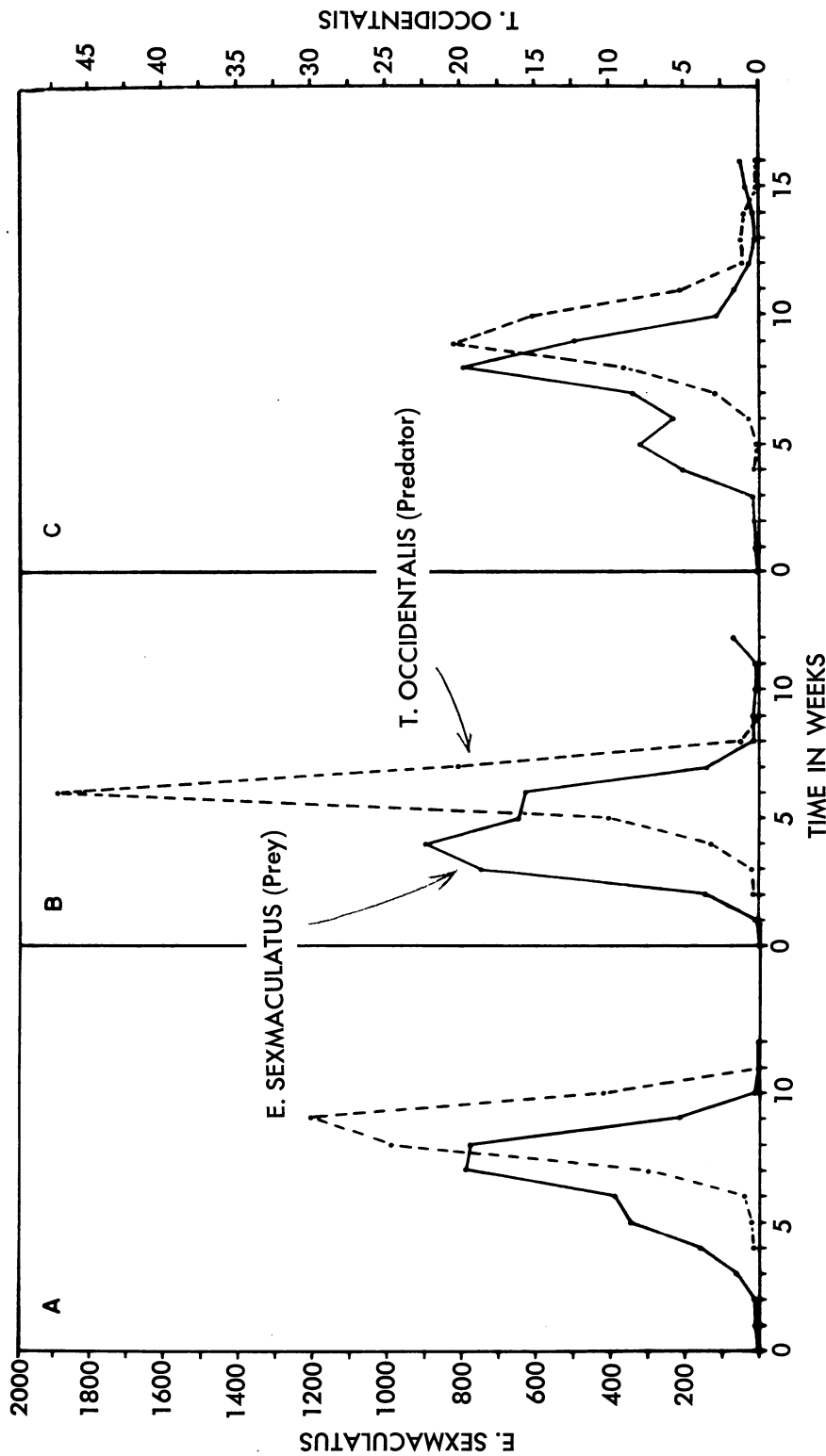
In each of the replicates the interaction ended as a result of the single crash phase of each population wave. The predators reduced the prey populations to extremely low levels, too low to offer appreciable chance of predator survival, and so low that the prey itself recovered only very slowly. (See "Discussion," below.)

DISCUSSION

Effect of Spatial Complexity on Mean Densities Under Predator-Prey Interaction

The mean densities attained by six-spotted mite populations in the *absence* of predation (in universes used in these and similar studies in 1958) vary greatly according to the nature of the

dispersion and physical complexity employed, among other causes. This fact is important to remember in considering the mean levels attained by prey populations in the *presence* of predators. Also, the amplitudes of fluctuations about the mean levels and the patterns of such fluctuations are markedly affected by these same factors (Huffaker, 1958). Particularly if the predator



Figures 5 a, b, c. Systems I-4, I-5 and I-6 (replicates). Oscillations in amount of area was exposed on each orange. The 252 oranges, each with density of a predator-prey interaction in which the predatory mite, *Typhlodromus occidentalis*, preyed upon the orange-feeding six-spotted mite, *Eotetranychus sexmaculatus*. Each system identical with system II-3 except that three times the 3/20 orange-area exposed, arranged on three grid-wire shelves supported by wood dowel posts, a 37.8 whole-orange-equivalent on a 252-orange dispersion with the grid wire serving as a maze of impediments.

(*Typhlodromus occidentalis*, in these universes) does not restrict the prey to such low densities that the latter cannot interact significantly with its own food supply, such prey-food interactions would then affect the total population dynamics observed in the predator-prey universes. Both mean levels and population fluctuations would be affected. In the present studies, maximal prey densities under predation reached levels of 800 to 1,200 occasionally, while in comparable systems free of predators minimal prey densities were only moderately higher. Thus, prey-food interaction undoubtedly did affect the population dynamics in the predator-prey universes.

When the predator controls its prey at a level far too low to allow significant prey-food interaction, the predator-prey dynamics is largely divorced from this factor (Huffaker and Kennett, 1956, p. 199). In these 1956 studies, the mean population level of the cyclamen mite under predation by *Typhlodromus* spp. was much too low to allow significant interaction with the host plants so that food supply did not appear to be a limiting factor for the prey species at any time.

In the present studies, however, densities of the prey, *Eotetranychus sexmaculatus*, under predation by *Typhlodromus occidentalis*, fluctuated so greatly that some food depletion occurred at local foci. In the systems used, the hazards to movement were maximal, so that even relatively little stress from food depletion very likely had a proportionately greater impact on the determination of population densities than might be true in systems where movement is easier. Additional experiments designed to test this hypothesis are now in progress.

Thus, in the more complex physical system, significant action of food depletion for the prey came into play at lower densities; the action of predation on the

prey may be seen as a supplement, in a sense, to the degree of stress already inherent on the prey in its getting about to locate food. In such complex systems, the equilibrium reflects the results of all stresses: predation (density-dependent); food depletion by members of the same species (also density-dependent); and hazards to movement built into the system (density-independent²).

In the less complex, single-tray predator-prey system used by Huffaker (1958, p. 370), the mean of 1,000 to 1,100 prey per whole-orange-equivalent at equilibrium was also the result of the combination of these stresses. However, in that case the amount of stress caused by hazards to movement was less than that in the more complex 3-shelf system (II-3) used in the present studies. In cases of this kind, since the density-independent stress was low in the simpler system, the increase in prey was more favored. Equilibrium in that system was achieved only by a proportionately greater degree of density-dependent stress, either by depletion of food or by predation.

Huffaker (1958, p. 374) reported that following a third oscillation in density, approximately 38% of the oranges were fully utilized in the less complex system. Food depletion undoubtedly caused a substantial part of the stress in the third oscillation, and also some of the stress, although less, in the second oscillation. However, this was not enough to cause the subsequent crash; this must have resulted from predation. Actually, as was pointed out, the partial food depletion probably served as a damping factor against a more severe crash which might have been expected had the prey increased to higher levels and thus produced more predators.

Presumably, the added complexity in the present systems also caused losses in the predators during their movements, even though they have greater vagility than the prey.

² The percentage of losses is density-independent (nonregulating) even though at higher densities the absolute number of losses is higher.

In another system used by Huffaker (1958, p. 357), which is nearest to that just discussed except that predators were not present, the approximate mean prey density per whole-orange-equivalent was 3,250—that is, when governed by food alone. It is evident, then, that the mean prey density was altered from a level of approximately 3,250 in the predator-free universe to only 1,000 to 1,100 under predator action. Thus the equilibrium of the prey population was reduced to about one third the level reached when governed by food alone.

We may now compare two corresponding 3-shelf systems employed in the present studies with the systems used in the 1958 work. In the 3-shelf universes, where more severe losses of a density-independent nature occur during movements, less density-dependent (regulating) stress is required to balance births and deaths, and hence, in cases of this kind, equilibrium is achieved at lower densities. In system E-2, no predators were present; thus all the density-dependent stress was due to food depletion, and the approximate mean prey density per whole-orange-equivalent was 2,000. In system II-3, which had predators, the approximate corresponding mean was about 500. The same was true for the replicate system (II-4). Thus, in systems with comparable hazards the addition of the predatory *Typhlodromus occidentalis* caused a reduction in the mean prey density from 2,000 to 500, that is, to about one fourth the level reached when governed by food alone.

The percentage of oranges fully utilized by the prey in the complex universe was about half that used in the simpler predator-prey universe. In no oscillation did utilization of oranges in system II-3 (fig. 3) approach 38% as an average for consecutive records. In fact, the percentage of oranges which were fully utilized at time of replacement averaged only 15% for the four major oscillations. In system II-4, the average was only 11%.

Although food depletion was lower in the present complex universes than in the 1958 universe, a heavier relative stress was caused by the same level of food depletion in the present systems having the greater general hazards. However, the degree of food depletion was sufficiently lower in systems II-3 and II-4 than in the system used by Huffaker in 1958 (p. 370), that it is safe to conclude that the impact of predation as a *component* of regulation increased and the impact of food depletion decreased.

Where food alone governed the prey species the mean density in the earlier, less-complex system was 3,250, while in the more complex present study it was only 2,000—an approximate ratio of 3:2. On the other hand, when the predator was present the prey density in the less complex system was about 1,050, while it was only 500 in the two complex systems (II-3 and II-4)—an approximate ratio of 2:1. This may mean that the predators overcome added hazards to movement better than the prey do. This explanation is supported by observations on the movements of individual predators and prey. As stated in the earlier study, in systems where the prey cannot be carried on their silken strands by the wind over great distances, the predators (which lack this mechanism) have greater vagility since they are better adapted to crawling as a means of locomotion.

The mean densities of the prey in the absence of predation were greatly affected by the method of linting used. In system E-2 (predator-free), the mean density per whole-orange-equivalent of the prey species was considerably less than in the somewhat comparable systems reported by Huffaker (1958, p. 355–357). This was undoubtedly due in part to the linting method. Although approximately 93% of the oranges were rated fully utilized at removal from system E-2, there is evidence that true full utilization did not actually occur. The linting of the orange surfaces was less

complete than in the earlier studies. As a result, the mites did not build up to as high levels initially nor did the population decline so rapidly as it would have if the oranges had been completely utilized. Instead, there was a moderately quick increase on well-linted areas, followed by sporadic, lingering fluctuations as the mites forged outward to partially utilize relatively unlabeled areas. As a result, although classed as utilized at removal, such orange rinds may have contained much unutilized food.

Variations in the nutritional quality of different lots of oranges may have also caused variations in mean densities. The high densities obtained in the earlier studies occurred from March through July, 1955, a period when Valencia oranges were used exclusively. *Eotetranychus sexmaculatus* usually reproduces more efficiently on Valencias than on the Navel variety, which was used for about half the longer intervals in the present studies. Also, the Valencias obtained in 1955, from a local source no longer available, were of unusual nutritional quality.

Consequently, because both the linting techniques and the quality of oranges varied somewhat, the mean densities obtained in the earlier study cannot be compared strictly with those reported in this work, even when food alone was the limiting factor in both studies.

Effect of Increasing Food Availability for Prey on Predator-Prey Interaction

Systems I-4, I-5, and I-6 were designed to show the effect of varying the basic food supply on the predator-prey interaction. In these systems, identical with systems II-3 and II-4 except that three times as much food was supplied to the prey species, the interaction was brought to a halt at the end of the first crash phase in each instance (figs. 5a,

b, c) because of intense predator exploitation.

As in each instance, densities in the graphs are expressed in whole-orange-equivalents rather than by absolute volume or cabinet. Thus, the high prey densities *per whole-orange-equivalent* attained in these universes were somewhat comparable to those attained in universes where only one third the amount of food was available. Yet, the peak prey densities attained *per cabinet* were nearly three times as great. The peak densities for systems II-3 and II-4, shown in figures 3 and 4, averaged 900, while those for systems I-4, I-5, and I-6, shown in figures 5a, b, and c, averaged 2,500 per cabinet.

The high predator densities *per cabinet* in systems I-4, I-5, and I-6 averaged 98, while in systems II-3 and II-4, the average was only 17. The predator density per cabinet, hence, was nearly six times as great in the universes with the greater food supply. Thus, there was a much greater differential in predator populations than in prey populations, a fact which might be expected because of the density-dependent nature of such predator action.

Since there was no change in the total surface areas to be searched or in the dispersion of the oranges in the cabinets, but only changes in the areas exposed, the predators apparently covered the areas much more thoroughly. In addition, the predators have considerable longevity even after their food supply has diminished below that necessary for adequate maintenance and reproduction. The result was *near annihilation* of the prey through overexploitation. In each case the prey itself crashed to much lower numbers than ever occurred under predator pressure in the otherwise comparable systems where only one third as much food was supplied. Although the prey recovered in each case, such recovery was at first very slow.

Thus, a simple increase in the food supply of the prey without a corresponding expansion in the dispersion

may lessen the chances for the perpetuation of a predator-prey interaction. However, in nature, localized overexploitation and annihilation of prey (or host) species by their natural enemies may result in a fragmentation of the prey species into disjunct patches. When repopulation of the prey (pest species) is slow, greater economic control of the pest may result (Huffaker and Messenger, in press).

Effect of Spatial Complexity on Homeostasis and on Period and Amplitude of Fluctuations

The universes used in the present study were designed to maintain predator-prey interaction over a long term without employing absolute refuges for the prey and without adding immigrants at intervals, such as was done by Gause (1934) and Gause *et al.* (1936). In the simplest sense, stability of such an interaction is greater if it continues for a longer period, even though a greater number of oscillations may occur. Stability is also a function of the length and number of major oscillations, and the degree of security against violent oscillations caused by overexploitation.

The data obtained by Huffaker (1958), combined with the present results, help to clarify significant biological factors relating to homeostasis in the predator-prey universes. The mites moved in the universes by walking, a rather slow, hazardous process, particularly in the more complex systems where 3-shelf arrangements were employed and a wire grid formed the floor of each shelf. Spread of the prey species to all positions in the universe was dependent in part on their depleting the food at least in some local arenas. In their undirected movements away from these local arenas, they often died before finding food. Also, the scheme of orange renewal was fixed. The mites, varying from none to many on oranges which were removed, were brushed off and

returned to the cabinet but not placed on new oranges. Most of these mites, including many eggs and young, did not reach suitable food. The time spent in unsuitable areas (for example, on paper coverings on the oranges, on rubber balls, or on the walls or shelves of the cabinets) resulted in an inhibited population increase for that period, even if the mites later found food and reproduced.

To survive and reproduce, the predatory species had to contact the prey and their opposite sexes. At very low prey or predator densities, contact was so difficult that this caused predator extinction in some systems. Predators survive 3 or more days with no food so that if they were present in large numbers (for example, as in systems I-4, I-5, and I-6; figs. 5a, b, c), in 3 days they could reduce the prey population far below the density usually required to *produce* or *maintain* such an abundance of predators. This lag effect maintained predator pressure at a high level beyond the point "called for" by the prey density. Thus, engagement persisted after decline in prey density would otherwise cause disengagement. This is an important feature of the severity of such crash phases in general. In these systems there were no absolute refuges and thus no corresponding *cushioning* of the crashes. There is only relative security occasioned by the hazards to the predator in getting about.

In the very simple universes used by Waters (1955), consisting of single whole oranges (1 large area of food), overexploitation of the prey and death or dropping off of all the predators occurred in 6 to 8 days, and sometimes in only 3 or 4 days.

In the simplest universe used by Huffaker (1958, p. 347), a 2 whole-orange-equivalent feeding area was dispersed on 4 closely adjacent oranges (each orange half covered—that is, 4 large areas of food). Again, predator-prey interaction lasted for only a single wave of prey increase and decline, and the

total time prior to overexploitation and death of the predators was only 15 days. The maximal density attained was 250 prey per whole-orange-equivalent area. When the orange surface exposed was doubled and twice as many oranges were used (that is, 8 areas of food massed at one general position in the universe), the single wave before both species were annihilated occurred 25 days after introduction of the predators. The maximum density of prey per whole-orange-equivalent was about two thirds as high in the universe with 8 areas of food as in the one with 4 areas, but density per universe was one and one-third higher. Furthermore, maximal predator density per whole-orange-equivalent was lower, but for the universe as a whole (physical area) it was higher.

Still other relatively simple systems used in the 1958 study, where greater spatial heterogeneity was employed, showed a wide variation in maximal densities of prey and predators per whole-orange-equivalent area and per universe. However, in all these simpler systems, overexploitation resulted in death of all predators just subsequent to the first crash phase, and in some instances the prey was also annihilated. Prey annihilation never occurred when spatial dispersion was much more complex, even when the total food potential was no greater than that in some of the simpler systems.

When the orange food supply was exactly the same as in the simplest system of Huffaker (1958, p. 347), but the 4 oranges were widely dispersed rather than grouped in the tray, the approximate time of the interaction was 25 days, as contrasted to 15. When a 4-orange area was used on 8 oranges widely dispersed, the single population wave lasted 30 days. In another replicate of this universe the period was about 25 days. When the smallest food supply (a 2 whole-orange-equivalent area) was used on a 20-orange dispersion, the single wave again lasted about

30 days. With a further increase in spacing to a 40-orange dispersion (one twentieth of the surface area exposed on each of 40 oranges, but not interspersed with rubber balls, since all 40 positions were occupied by oranges), the period of the single wave was again 30 days.

The maximal densities of both predators and prey attained in these latter, widely dispersed systems were decidedly higher than those in which the food was massed, as previously discussed. This was because the predators did not "overtake" the prey until after they had spread around and reached a point of substantial utilization of the food supply.

The most complex system used by Huffaker (1958, p. 370) employed a 6-orange feeding area on a 120-orange dispersion, with the 120 oranges arranged in three trays which were joined lengthwise. In one universe, the single wave lasted 35 days. Overexploitation then resulted in the annihilation of predators before they had dispersed into all areas of the universe. In another universe in which the initial population of mites was more widely dispersed at stocking, three successive population waves or oscillations occurred. These waves occurred with some degree of regularity, the average period of a cycle lasting roughly 65 ± 5 days. The total interaction lasted 233 days.

Thus, by increasing spatial heterogeneity, and also food supply to some extent, the continuity of the predator-prey interaction was increased from a minimum of 3 or 4 days to a maximum of 233 days when the oranges were arranged on a single horizontal level in the universe. Another indication of stability was that minimal densities of the prey under predation were much higher in the more complex systems.

The experimental data presented in the present paper confirm and add to these conclusions regarding spatial heterogeneity and stability. However, it is now seen that there must be a balance

between the nature of the spatial heterogeneity and the potential for production of large numbers of predators. If predators become sufficiently numerous, they may search even complex environments so successfully when the prey population is in the crash phases that they threaten their own survival. To prevent this, either dispersion must be wider or the universe must be made more extensive or complex.

In the complex, 3-shelf, wire-grid universe (experimental results shown in figure 3), the total continuity of one replicate (system II-3) was 490 days. Furthermore, in this case the termination of the interaction was definitely not the result of overexploitation by the predator. Had a disease of the prey not appeared, at least one additional oscillation of approximately 75 days seemed assured. Thus, in the absence of this disturbance, the interaction would undoubtedly have lasted a minimum of 600 days. This is much longer than the longest time of any interaction where the 1-level arrangement was used.

The second replicate of this same complex 3-shelf system (system II-4) had a rather short duration (fig. 4). Only two oscillations occurred. Exploitation in the cabinet as a whole did not seem excessive—that is, the general minimal density of the prey following both decline phases was as high as that in system II-3, which continued much longer. Yet, as previously discussed, the predator did locally overexploit, lost contact with the main masses of the prey, and failed to regain that contact. Possibly the opposite sexes also lost contact with one another.* The few predators still alive survived for a rather prolonged period before death but produced no eggs.

It seems likely also that had the prey rebounded in normal fashion when stress from the predator was significantly lessened, but not so completely

so, the predator may have been able to locate the expanding prey population, and thus this replicate, too, *may* have continued.

Maximal and minimal prey densities per whole-orange-equivalent are a further measure of differences in stability between the most complex of the 1-level systems and the still more complex 3-shelf systems. Densities per universe cannot be compared since the surface areas in the 1- and 3-shelf systems were very different. In the 1-level system (Huffaker, 1958, p. 370), the maximal prey densities were 1,500 to 2,000 for the three oscillations, and the minimal densities following the three corresponding crash phases were roughly 100, 400, and zero, respectively. On the other hand, the four major oscillations in the successful 3-shelf universe (system II-3) had maximal prey densities varying from only 600 to 1,200 (meaning less potential for generation of too many predators), and corresponding minimal densities of 300, 200, 150, and 100, respectively. Prey and predators alike survived all of these crash phases. Both were entering a phase of rapid increase (not shown in figure 3) at the time disease ended the system.

Theoretical Considerations of Predation as a Synchronizer of Cycle Phase in Some Prey Populations

The experimental data presented here serve to explain the role of predation in synchronizing otherwise separate cyclic phases of acarine prey populations in the laboratory systems described. The authors realize that results obtained in such restricted laboratory conditions, in which only a single predator-prey interaction is studied, are far removed from more complex natural conditions spread-

* Unmated females of the prey produce only male offspring, while unmated females of the predatory species do not produce young.

ing over whole geographic areas. It is not claimed that the present findings can be strictly applied to such diverse conditions. However, the results do suggest that *perhaps* predation does play a role in limited synchronization of cycle phase in natural populations. For example, in a single arena, comprised, say, of six oranges in the same general location in the cabinet or trays, the rise and fall of both prey and predator numbers was characteristically far more rapid than was the more steady march of events for the whole system. While certain small local arenas are out of phase at given time periods, the majority of local arenas are either in high- or low-density phases.

Although localized densities in the laboratory universe may be dominated by chance appearance of immigrants, food utilization, or predation—in various combinations—the general pattern of changes in the whole system is more directly controlled by predation. Partial food depletion plays some part in governing changes, and, of course, the role of chance cannot be ignored even when considering the total population.

The predator was the major factor which served to synchronize events between distinct parts of the systems. The predators are more wide ranging than the prey, per individual, and when a surplus of predators builds up in one arena, some move fairly soon to nearby arenas if prey are available there. At low predator densities the increase and decline of the prey population is less synchronized from area to area, except that food depletion in local areas forces the prey to adjacent areas, until eventually the whole system is too heavily populated for the dwindling food supply. At somewhat higher predator densities, the predators multiply in local arenas of high prey density; this, in turn, reduces the prey in these arenas and synchronizes prey densities at very low levels throughout the entire system. Yet, this does not result in annihilation of prey except in localized arenas. Grad-

ually the prey population begins to recover throughout the system. The predators in the meantime have declined to extremely low levels and subsist at only a few areas. As the prey population recovers, the predators at first control it in these local areas before spreading the control to adjacent areas and, eventually, to other areas of the universe.

There is, of course, a limit to the areal scope of any synchronizing action of predators. Because their vagility is quite limited, the predators in these experiments can exert their synchronizing influence within only a very limited sphere. The universes used were sufficiently restrictive that predators could move about quickly enough to accomplish such synchronization. Also, the vagility of the prey species concerned is an important factor.

As pointed out by Slobodkin (1961, p. 158), population fluctuations may result from either direct environmental influences or intrinsic physiological forces somewhat independent of environment. It is a much debated question whether specific fluctuations observed in vertebrate populations are really cyclic. It is also debated whether, if such cycles exist in specific populations, they are broadly synchronized with those in other specific populations. Pitelka (1957) commented that the cyclic character of patterns has been generally accepted for phenomena in the tundra latitudes, which have a short-term cycle of three- to four-year intervals, and for phenomena in the boreal-forest latitudes, which have a long-term cycle of nine- to ten-year intervals. He states, however, that patterns in more southerly areas remain more open to debate. Pitelka also presented raw data on the brown lemming at Point Barrow, Alaska. The data show cyclicality, but do not indicate that crashes are caused by predation, although variations in predator pressure may shorten or lengthen the typical cycle interval.

Our own laboratory data concerning acarine populations and various other

considerations suggest that, even when overutilization of food causes severe crashes in a prey population (Lack, 1954; Pitelka, 1957), higher predator densities are generated or attracted before or during the crashes of the prey. The lingering predator pressure will tend to spread the areas of severely low prey density throughout the system. In cases where predator pressure causes the crashes the synchronizing role is more obvious.

It is of interest that Lack (1954, p. 220) suggests that predators may possibly serve to synchronize the cycles of two major prey groups, rodents and gallinaceous birds, with the action being dependent on the rodents and controlling for the birds. Thus, following a sharp decline in rodent numbers the predators are faced with a food shortage and react by turning to their favorite alternate prey, in this case gallinaceous birds, which normally exist in maximum densities far below those attainable by the rodents. Also, wide-ranging predators (such as raptors) of small vertebrate prey, may possibly serve as synchronizers of various prey populations which are otherwise sufficiently distinct to have independent cycle phases.

Thus, cycle phases in two microtine populations which have no direct interaction may be synchronized through the medium of wide-ranging predators. To accomplish this, severe predator pressure which builds up in the declining phases of one microtine population must be shifted to the second microtine population rapidly enough and with sufficient intensity to cause a comparable sharp decline. If the second prey population is in an early increase phase but densities are still low, the new predator pressure slows down this increase. At the same time, a higher predator population can be maintained by the second prey population than by the first decimated population. The predators would be slow to shift back again to the previous area until the prey populations there built up, and thus a tendency to

synchrony in the two areas would exist.

This moderation of increase phases in the prey, combined with biological factors which govern recovery of both food plants and prey populations (Pitelka, 1957; Huffaker, in press), may well be enough to cause synchronized resurgence of the prey species over areas subject to such effective predator pressure.

Furthermore, since such predators are long lived and attack a variety of prey, they can shift from one prey species to another as well as from one area to another. When a new predator population moves into an adjacent area, it may, through competition, force a secondary shift further on of a part of the new combined predator population. Broad general shifts in predator pressure may synchronize greater areas than indicated by the behavior and movement potentials of individual predator populations, and certainly of individual prey populations. Of course, prey populations are often so far removed from one another and predator movement so restricted that predator pressure could not serve as a synchronizer.

In the northern hemisphere, the prey complexes available to the respective predators in arctic and subarctic latitudes differ from those of the more southern latitudes. The predators in the more complex southern latitudes are much less dependent on the density of a specific prey species.

There may be no single key herbivore in southern latitudes, as there is in many of the more northern latitudes. Many environmental conditions which vary widely and somewhat independently may suppress or enhance alternate prey species in the southern areas. For this reason, predators do not always exert the same severe pressure on a given prey species in its low density phases. Also, the pressure exerted may vary from area to area. Hence, the potential synchronizing role of predators is undoubtedly much more feeble, perhaps a mere tendency, in the southern latitudes.

It may be of interest that such syn-

chronization by predator action is similar to that caused by severity of weather over a broad area. In either event, when the pressure is reduced, the many distinct populations increase somewhat synchronously at first, although the peaks may vary. If distinct control mechanisms then come into play, the synchrony is short lived.

It appears that broad cyclic synchrony between distinct natural populations does not exist for prey populations of very low vagility which are attacked only by predators of low vagility, unless they are subject to common impact of weather or other adverse events. The classic examples of broad synchronies in insect abundance concern species of unusual vagility, not ones which depend entirely on crawling for locomotion.

Usually, also, entomophagous parasites or predators do not exert a powerful influence in areas distant from the

source of numerical response to prey density. The numbers of such enemies which successfully move into the distant environments are usually too few to have a significant immediate effect, even though their descendants may later do so. This might help to synchronize cycles in insects with long life spans, but undoubtedly the phasing would be poor. However, little effect would be expected on short-lived hosts unless the enemy species had a favorable vagility and generation time relative to that of the host. Thus, localized populations of cyclamen mites in different areas of the same strawberry patch may persist in entirely different phases, even though predatory *Typhlodromus* mites keeping them under control are present in all the localized areas of the field. They can control locally but cannot synchronize over such a wide area (Huffaker and Kennett, 1956; Huffaker, 1958).

SUMMARY

This paper is the third of a series on the nature of predator-prey interactions. The role of spatial heterogeneity in stability and other aspects of predator-prey relations was studied under controlled laboratory conditions. The phytophagous mite *Eotetranychus sexmaculatus* was used as prey, and the mite *Typhlodromus occidentalis* as predator. In the control systems, no predators were introduced so that prey-food interactions could be studied. The results help to clarify some of the principles of population ecology.

The predator-prey systems employed were spatially more complex than those used in the previous study of Huffaker (1958). In the former study, prey and predator could move about on only one level, while, in the present study, they could move freely throughout a cabinet of three horizontally arranged shelves made of wire grating. Stability of interaction was greater in the spatially more complex system. In the earlier, less complex systems, interaction lasted a maxi-

mum of 233 days, while in the most complex system used in this study it lasted 490 days. Disease, rather than predator-prey interaction ended the more complex system. In addition, minimal prey densities were higher, maximal prey densities were lower, a greater number of oscillations occurred, and the average period of the cycles was longer.

In additional studies, food for the prey was tripled without increasing the dispersion of oranges or the total areas required to be searched by the predators. In each of three replicates, over-exploitation occurred at the end of the first crash phase of the prey population. This was apparently the result of generation of too many predators at times of high prey density, in relation to the complexity of the places to be searched. Thus, the areas were then searched "too well." Although the populations survived a much longer *time* than those in previously used simpler systems, in both types of systems the populations ended after a single wave. This is just

another expression of too little spatial heterogeneity.

Lastly, the potential role of predation as a synchronizer of cycle phase in prey populations was considered theoretically. The acarine predator under study synchronized prey cycles by moving to new areas following exploitation in one locality. Thus the pattern of low prey density became rather synchronized

throughout the universe. Once the predator population began to decline because the prey was scarce, a somewhat synchronized resurgence of prey populations then occurred. These findings may have some bearing on the much-debated subject of synchrony in cycle phases of small vertebrate populations in the northern hemisphere.

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