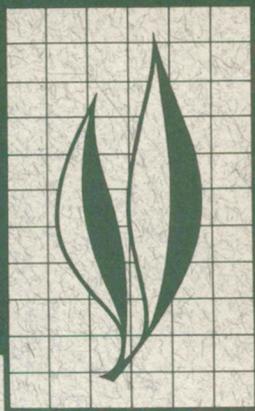


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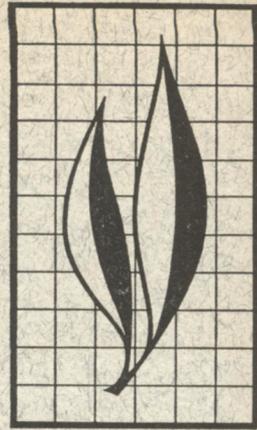
Competition for Food by a Phytophagous Mite

The Roles of
Dispersion and Superimposed Density-independent Mortality

C. B. Huffaker

A Note on Competition

C. B. Huffaker



The experiments described in this paper are part of a continuing series on predator-prey interactions. The six-spotted mite, *Eotetranychus sexmaculatus* (Riley), was used for the study, which involved various ecosystems containing combinations of oranges and rubber balls, over which the mites moved in search of food. Effects of food dispersion on equilibrium level of a population, changes in its numbers, and its utilization of a limited resource were studied. Two main points are emphasized: First, food *may* be a limiting and regulating factor for a given population even if utilization of supply at equilibrium is low. Second, in some particular kinds of ecosystems, where competition for food is the *regulating* factor, superimposition of other mortality factors may alter the density level at which the competition is regulative, and thus result in levels of food utilization varying from low to high. Roles and importance of density-dependent and density-independent factors in the natural control of populations are also discussed.

A note on the definition and ecological implication of the term "competition" is included.

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Competition for Food by a Phytophagous Mite

The Roles of Dispersion and Superimposed Density-independent Mortality^{1,2}

INTRODUCTION

MANY KINDS OF ORGANISMS in communities compete for food, sometimes in ways not immediately apparent. Food is dispersed in the environments in various ways, and competition for it often influences its dispersion and modifies both its quantity and quality. In addition to such regulatory mechanisms as competition for food, many stresses unrelated to population density act on populations of predaceous and phytophagous species. The interplay between such stresses and competition for food by the individuals of a single, primary trophic-level species was therefore examined under controlled conditions in the laboratory. (Competition between two or more species at higher trophic levels would presumably involve an even more complex relationship.)

In complex natural environments, insect populations are often confronted with obstacles to movement, and they may suffer heavy losses during movements. For example, in an area far from commercial acreages of apples, one or two isolated trees may harbor a relatively low population of the codling moth, *Carpocapsa pomonella* (L.), as compared with trees in an orchard situation. Net losses from diffusion may also explain why some introduced colonies of an entomophagous parasite do

not become established when stocked on isolated, single trees or in a single border row, whereas they show strong development in large orchards.

In Australia, detailed monthly censuses showed inordinate mortality of young larvae of the beetle *Chrysolina quadrigemina* (Rossi) because they were required to meander about in dense grasses to find their depauperate host plant, *Hypericum perforatum* L. The larvae, especially small ones, are poor searchers. Furthermore, *H. perforatum* in some Australian and New Zealand environments is of only "intermediate" density on many narrow rights-of-way. In the adjacent fields heavily grazed by sheep, the weed is almost annihilated. Thus, beetles reproduce only on the narrow strips, and their emigration to the fields is not compensated for by a return flow of immigrants to the strips.

Few data are available on the effects of dispersion of favorable habitat units on the equilibrium level of a population, its variations in numbers, and its utilization of a limiting resource. Vouôte (1946), Elton (1958), and others have held that the environment that is biotically heterogeneous is conducive to ecological stability. Earlier experiments (Huffaker, 1958a; Huffaker *et al.*, 1963) and the present study

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show conclusively that spatial heterogeneity affects a population's dynamics, including its interaction with a predator population.

The consensus has been that phytophagous insects' destruction of their own food supply is not a limiting factor in their abundance (reviewed by Huffaker, 1957, 1962a). The cases in which phytophagous insects increase to "outbreak" proportions and cause drastic destruction of their food plants have been considered exceptional (Thompson, 1929; Bodenheimer, 1930; Nicholson, 1933; Smith, 1935; Imms, 1937). The consensus is, however, contrary to the premise assumed for the biological control of weeds. Moreover, because we feel that host-specific insects in either natural or agricultural areas may commonly limit the abundance of their host plants and, in turn, be reciprocally limited themselves, we are concerned with the apparent discrepancies. We feel that in natural situations the shortage of food is usually relative to the organisms' capacities for locating it and using it efficiently. Furthermore, even if a plant is superabundant, it may lack a critical nutrient, and therefore be limiting to some degree (e.g., Kennedy and Stroyan, 1959; Huffaker, 1957; Lauckhart, 1957; Main *et al.*, 1959; Pickford, 1962; Watson, 1964).

In this connection most field ecologists and insect nutritionists would reject Klomp's (1964) statement that

little or no evidence exists for the view that plants or plant parts may be so nutritionally poor that food is limiting even though the apparent food is plentiful.

Evolution in herbivores of such characteristics as dispersal, territoriality, or reduced fecundity, which promote adjustment in the population level before food resources are severely taxed, is important here. "In such cases there may not be an immediate shortage of food every year (or even every five years), but food may still be the ultimate factor limiting the population," said Root (1962).

In describing our present experiments, we wish to stress two main points: First, food *may* be a limiting and regulating factor for a given population even if utilization of supply at equilibrium is low. Second, in some particular kinds of ecosystems, where competition for food is the *regulating* factor, superimposition of other mortality factors may alter the density level at which the competition is regulative, and thus result in levels of food utilization varying from low to high.

The present studies are also concerned with evaluation of the roles and importance of density-dependent and density-independent (conditioning or legislative) factors in the natural control of populations. Although their roles are distinct, these two factors are inseparable components and *codeterminants*.

MATERIALS AND METHODS

The present experiments are part of a continuing series of studies on predator-prey interactions (Huffaker and Kennett, 1956; Huffaker, 1958a; Huffaker *et al.*, 1963). The phytophagous six-spotted mite, *Eotetranychus sexmaculatus* (Riley), was the only organism used in this study, and all references to mites refer to this species.

The general procedures and arrange-

ments of the universes used in this study were the same as those employed by Huffaker *et al.* (1963).

Oranges were used as food for the mite, in some ecosystems, in various combinations with rubber balls. The amount of each orange surface exposed was varied by wrapping the fruit with paper, cutting circular holes in the wrapping, and sealing the edges with

paraffin. By varying both the total amounts of orange surface exposed in the different universes and the dispersion of food in the cabinets, varying degrees of hazard to movement were maintained in relation to "reward" in the form of achievable reproduction when the mites located the exposed surfaces.

Basically, two techniques were employed to alter the degree of density-independent stress faced by the mites, but competition for food remained the only true density-dependent or regulating factor. First, the spatial complexity (dispersion of the food) of the system was varied, so that the available food was more or less difficult to find. Second, two levels of density-independent destruction were superimposed on the hazards already inherent to the "standard" spatial complexity itself.

One-seventh of the oranges was renewed each seven days—complete replacement in 49 days. This renewal pattern was held constant even though the total amount of food available, or its dispersion, was varied. The number of oranges used in each ecosystem had to be a multiple of seven in order that the pattern of renewal could be held constant. The total orange surface used in different universes varied from 0.6 to 12.6 whole-orange equivalents, and the amount of surface exposed on each whole orange of a given universe varied from $\frac{1}{70}$ to $\frac{1}{2}$. The surfaces of the oranges were linted with kapok fibers according to the method of Finney (1953) to furnish a more favorable microenvironment.

The cabinets used as universe enclosures were essentially the same, except that cabinets B, C, D, and E were slightly smaller than cabinets I and II; in the former, 210 oranges or rubber balls were used, and in the latter, 252. This difference apparently was not significant in explaining basic differences in the populations.

The oranges were either placed ad-

jacent in one end of one shelf or dispersed randomly over the three grid-wire shelves. The posts used to support the shelves, the walls of the cabinets, the grid-wire shelves, and the oranges and/or rubber balls permitted the mites free, if hazardous, movement throughout each universe.

As in previous studies, temperature was maintained at approximately 78° to 82° F, and relative humidity usually at 45 to 55 per cent.

Sampling was not a problem in this study. The mites on half the total feeding surfaces were counted weekly.

Because this general study has continued over eight years, several different persons have made the population counts and done the linting of the orange surfaces. Consequently, the question arises of possible variation in the populations, associated either with a basic difference in the mites themselves or with the way in which the operation was handled. The oranges were linted in the same manner, but some variation appeared from time to time in the amount of lint that adhered to the orange surfaces. Different technicians sometimes had different concepts of the amount of lint desired. A check on the counting performance of persons who made population counts indicates that this has been a negligible variable. The method of marking the population areas into "pie-slice" segments has facilitated accurate counting.

The method of stocking the universes with mites has been consistent when the variable nature of the experimental designs of the many universes is considered. The general scheme has been to use one-fourth as many mature female mites as there are oranges in the system, and to place one on each randomly-chosen orange as follows: 252 oranges, 63 mites; 210 oranges, 52 mites; 42 oranges, 11 mites; 21 oranges, 5 mites. The pattern of establishment and the early history of the populations have shown that in all cases the

stocking colonies were sufficient to establish populations fairly soon.

For the populations in universes D-4, D-5, and D-6, which died out rather quickly, three replicates were run to be sure that early annihilation was typical. Ones that went along smoothly for long periods of time were not replicated.

In the continuing experimental studies on predator-prey interactions (Huffaker, 1958a; Huffaker *et al.*, 1963), a "standard" universe, with regard to spatial complexity, has been employed in a series of ecosystems in which different intensities of additional density-independent mortality have been imposed on the populations by weekly destruction of the mites on a fixed fractional area on the oranges. Since the percentage of mites so destroyed is in each case independent of the density of the mites, this artificially imposed mortality is similar to that resulting from a normally occurring, density-independent factor (*legislative* sense of Nicholson, 1933, 1954b; *density-independent* sense of Smith, 1935; *conditioning* sense of Huffaker, 1958b; Huffaker and Messenger, 1964). Results of the experiments relative to the predator-prey interactions (i.e., whether or not greater homeostasis results from the additional imposed mortality) will appear in a subsequent publication. However, two universes subjected to imposed mortality were continued after the predator species had died out, as a means of following the recovery of the prey species, the patterns of fluctuation, and the mean densities at equilibrium, in the *absence* of predation. The continuation of these as nonpredator universes enables us to compare the results of competition of the six-spotted mite for food under (1) standard density-independent hazards and (2) hazards of greater degree inherent in the spatial complexity of the ecosystems. These two universes are also use-

ful for comparing results in which the only population stress other than competition for food was the built-in hazard to movement, with other systems in which variable degrees of fixed additional destruction of density-independent nature were superimposed weekly on the standard built-in degree of stress.

In general, if we disregard one unusual example (Huffaker, 1958a, p. 355), the mean population of *Eotetranychus sexmaculatus* at equilibrium under essentially full utilization of the oranges is about 2,800 to 3,500 mites per whole-orange equivalent. Yet the mean population has varied substantially over periods of time due to many different factors. The schedule of complete replacement of oranges each 44 days, employed in the 1958 studies, accounted for a 10 per cent higher mean density at full utilization, than did the schedule of replacement each 49 days, as used in the present study and in 1963 (Huffaker *et al.*). Furthermore, in some universes analyzed by age class (size categories) of individuals in the population, an approximate variation in density as high as 25 per cent (explainable on the basis of approximate biomass) was found from time to time at nearly full utilization of the food. For example, such a general shift in size classes accounted for approximately 25 per cent of the general trend downward in the population reported by Huffaker (1958a). In many universes, variations in such size-class distribution among the individuals of the population were not substantial.

Another, and probably more striking source of variation is related to the specific oranges used as food. The Valencia variety has consistently produced higher populations than the other type used, the California navel. This fact probably accounts for the consistently higher mite populations in the universes of the 1958 study, in which only Valencias were used. In the later

studies, extended over all seasons for several years' work, the California navel had to be used when Valencias were unavailable. Some variation also resulted from the source and general condition of the oranges. Toward the end of the

cold storage period for a given crop, little-understood biochemical changes occur that make the oranges less nutritious. A few are almost unacceptable as food for the mites even though no recognizable change has occurred.

RESULTS AND INTERPRETATIONS

As we have seen (p. 535), two basically different experimental techniques were used at different levels as a test of their effects on population expressions: (1) the choice of the physical materials and their distribution in the systems; and (2) use of two levels of density-independent destruction. Four basically different patterns of dispersion in the systems were employed, and two levels of additional imposed destruction. One of the systems not subjected to additional imposed destruction was equal, in other respects, to those on which additional destruction was imposed, and could therefore be compared with the latter as a level of "additional" destruction (*none*).

In universes or ecosystems B-3, E-2, C-1, D-4, D-5, and D-6, all the density-independent hazards faced by the populations were built-in (inherent) to the systems' spatial designs. The universes had different levels of built-in hazards to movement, but no additional density-independent mortality was imposed by destruction.

In universe I-7, an additional imposed destruction of 25 per cent of the population was applied weekly, and in universe II-6, the amount was 50 per cent.

The greatest source of error in these studies to date has been in the rating of degree of food utilization. This rating has previously been based on a visually formed judgment of the particular operator. Poorly linted oranges, or those that had become partly delinted through handling at counting times, may have been rated as "condi-

tioned," even though additional food was still present, simply because moderate populations had previously been maintained on them, but had declined to low levels. Therefore, in the present paper, we must assume, for purposes of comparison, that the degree of utilization reflects population size. Population size is thus taken as the gauge of degree of utilization.

Populations under varying built-in hazards to movement but no additional imposed mortality

Universe B-3: 21 large areas of food, adjacent; 189 rubber balls; each orange exposing $\frac{1}{2}$ whole-orange equivalent (fig. 1, table 1).

Universe B-3 was started on March 22, 1963, and ended arbitrarily on July 20, 1964. It was intended to present sufficiently low hazards to movement to insure 100 per cent utilization of the oranges while maintaining the same gross physical spaces as those in comparable universes. Mites could move freely throughout the maze of obstacles, or wander off. This resulted in some losses, so that high densities on some oranges were not reached until the fruit was ready to be discarded. On other oranges or at other times, however, heavy utilization occurred quickly, and some oranges were fully used in only a few weeks. Actually, 100 per cent utilization of all oranges had not occurred up to April 13, 1964. At that time, two changes were made in an attempt to bring the degree of utilization closer to 100 per cent: (1) the oranges were placed in a pan, in

TABLE 1
SUMMARY OF EQUILIBRIUM DENSITIES OF *EOTETRANYCHUS SEXMACULATUS*
POPULATIONS WHEN REGULATED BY COMPETITION FOR FOOD UNDER
DIFFERENT DENSITY-UNRELATED CONDITIONING RELATIONS IN
CONTROLLED ECOSYSTEMS

Factor	Only built-in hazards of density-independent nature					Additional imposed hazards of density-independent nature	
	Universe					Universe	
Equilibrium estimates per whole-orange equivalent	B-3. 21 oranges $\frac{1}{2}$ exposed, adjacent, among rubber balls		E-2. "Standard" dispersion, 210 oranges 1/20 exposed, dispersed uniformly (no rubber balls)	C-1. 42 oranges 1/20 exposed, dispersed widely at random among rubber balls	D-4, D-5, D-6. 42 oranges 1/70 exposed, dispersed widely at random among rubber balls	I-7. "Standard" dispersion, 252 oranges 1/20 exposed, dispersed uniformly, 25% killed weekly (no rubber balls)	II-6. "Standard" dispersion, 252 oranges 1/20 exposed, dispersed uniformly, 50% killed weekly (no rubber balls)
	a)*	b)*					
Mean density (no. of mites)	2,000	2,790	1,900	460	Indication less than 90	1,320	290
Food utilization (per cent)	73	100	69	17	Indication less than 3	48	11

* See text p. 537 for explanation of differences.

the cabinet, so that mites either moving downward or dropping could readily regain their original orange or an adjacent one; (2) fine plastic-wire loops were placed over the oranges to provide connecting "bridges" for ready access to new oranges added to the system, and make possible early and presumably complete utilization before discard.

Figure 1 shows that just following the initial upsurge of the population in March, 1963, a very severe, greater-than-normal crash occurred in the population. As indicated, the predator *Typhlodromus occidentalis* Nesbitt had become established in the universe, possibly having come in on the new crop of oranges. For four or five weeks careful examinations were made, and all predators were destroyed, but they nevertheless had a depressing effect at this period. Consequently, this interval of very low densities was omitted in determining the approximate mean density for this population at equilibrium.

By attempting to rate the degree of utilization, by considering the build-up in density, the periods of high population, and the decline, if completed, as a sequence for each orange, and by judging the appearance of the oranges at time of discard, it was estimated that through April 13, 1964, there had been an approximate mean utilization of 73 per cent in this universe at equilibrium.

Up to that time the mean population level was 2,000 mites per whole-orange equivalent. On this basis, complete utilization would give a population of approximately 2,700 mites. Also, the mean of the population following the changes made on April 13 was 2,790 mites per whole-orange equivalent; the degree of utilization of oranges at discard was near 100 per cent. Since either figure includes considerable possibility for error, we may use a population density of approximately 2,750 mites per whole-orange equivalent as a "yardstick" value associated with full utilization under the conditions of the

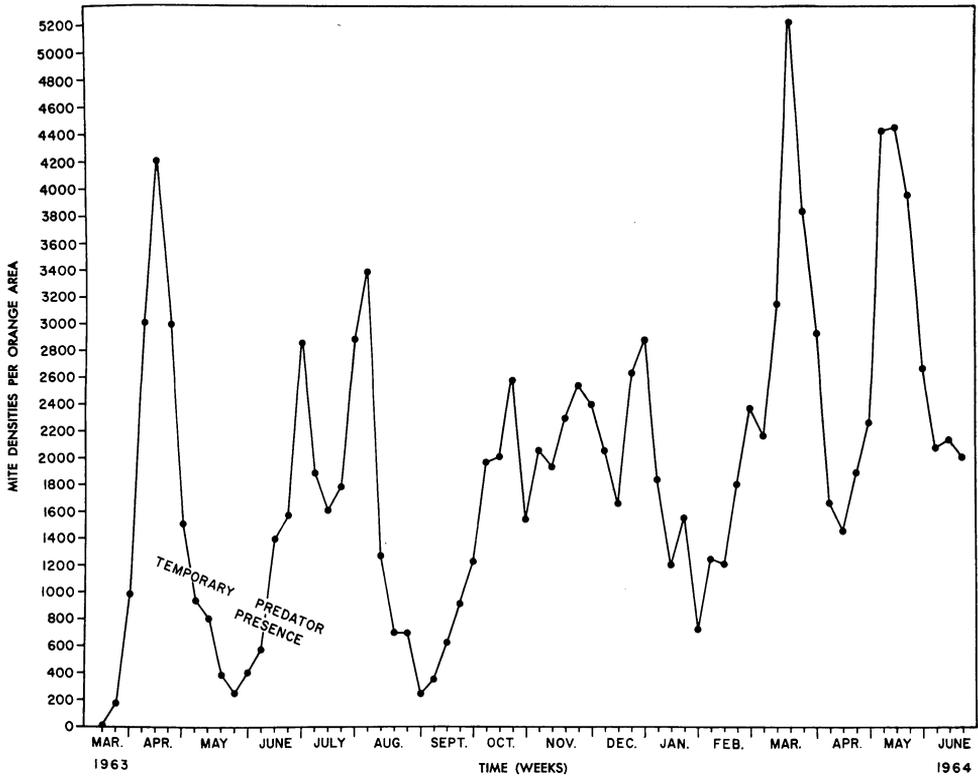


Fig. 1. Universe B-3. Densities per orange area of *Eotetranychus sexmaculatus* when regulated by competition for food under "minimum" hazards of dispersion of the food: 21 large areas of food arranged adjacent in a cabinet (Huffaker *et al.*, 1963) with 189 rubber balls; each orange exposing one-half whole-orange equivalent. Severe drop in April-May caused by predator, *Typhlodromus occidentalis* Nesbitt.

present experiments and the supply of oranges used.

Universe E-2: 210 small areas of food, randomly dispersed; no rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent (fig. 2, table 1).

Universe E-2 was started March 17, 1961, and ended arbitrarily January 29, 1962. One mature female mite was introduced only at the initiation, on each of 52 oranges taken at random. The mean level of the post initiation population in this universe, 1,784 mites per whole-orange equivalent, is unrealistically low for several reasons. First, a six-week interval of low densities followed the first peak population level of 3,044. One explanation is that, through error, oranges were not

replaced during one of the scheduled weekly periods for changes. Also, the mites apparently were not obtaining full nourishment from the oranges at that time. It is not known if this condition was due to a relatively poor linting of surfaces or to quality of the oranges. Of course, the depressed status reflects, in part, the previous high, or supra-normal, population. Also, during the period of the last population wave some of the oranges were spoiling—a common occurrence toward the end of cold storage for each harvest crop, particularly if the crop had suffered from frost before harvest. Considering these conditions, we have taken the approximate mean of the last four population waves, 1,900, as the equilibrium position

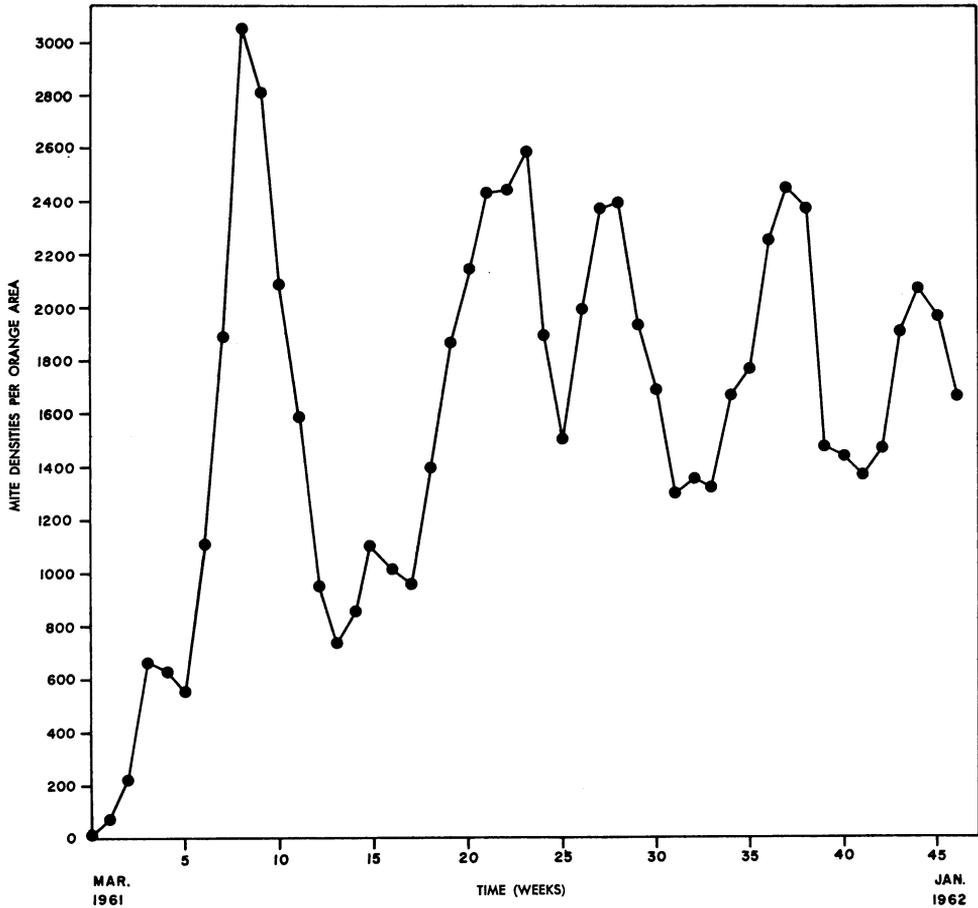


Fig. 2. Universe E-2. Densities per orange area of *Eotetranychus sexmaculatus* when regulated by competition for food under a "standard" hazard of dispersion of the food: 210 small areas of food dispersed in a cabinet (Huffaker *et al.*, 1963) with no rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent.

in this ecosystem after balance was achieved.

The basic pattern of density fluctuations of this population was discussed by Huffaker *et al.* (1963). We note that although 93 per cent of the oranges in the system was then judged as "conditioned," the relative utilization, based on the mean of our yardstick value (see above), was $1,900/2,750$, or 69 per cent.

The intervals of time between peak population levels, which varied from 6 to 14 weeks, apparently had no direct correlation with the intervals of orange change, either partial (weekly) or com-

plete (every 7 weeks), nor with the use of new-crop oranges.

Universe C-1: 42 small areas of food, randomly dispersed among 168 rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent (fig. 3, table 1).

Universe C-1 was started May 6, 1962, and ended arbitrarily in September, 1964. One mature female mite was used as stock on each of 11 oranges chosen at random.

It is obvious that this universe presented considerable hazard to the mites in getting about in the system. They were required to traverse from position

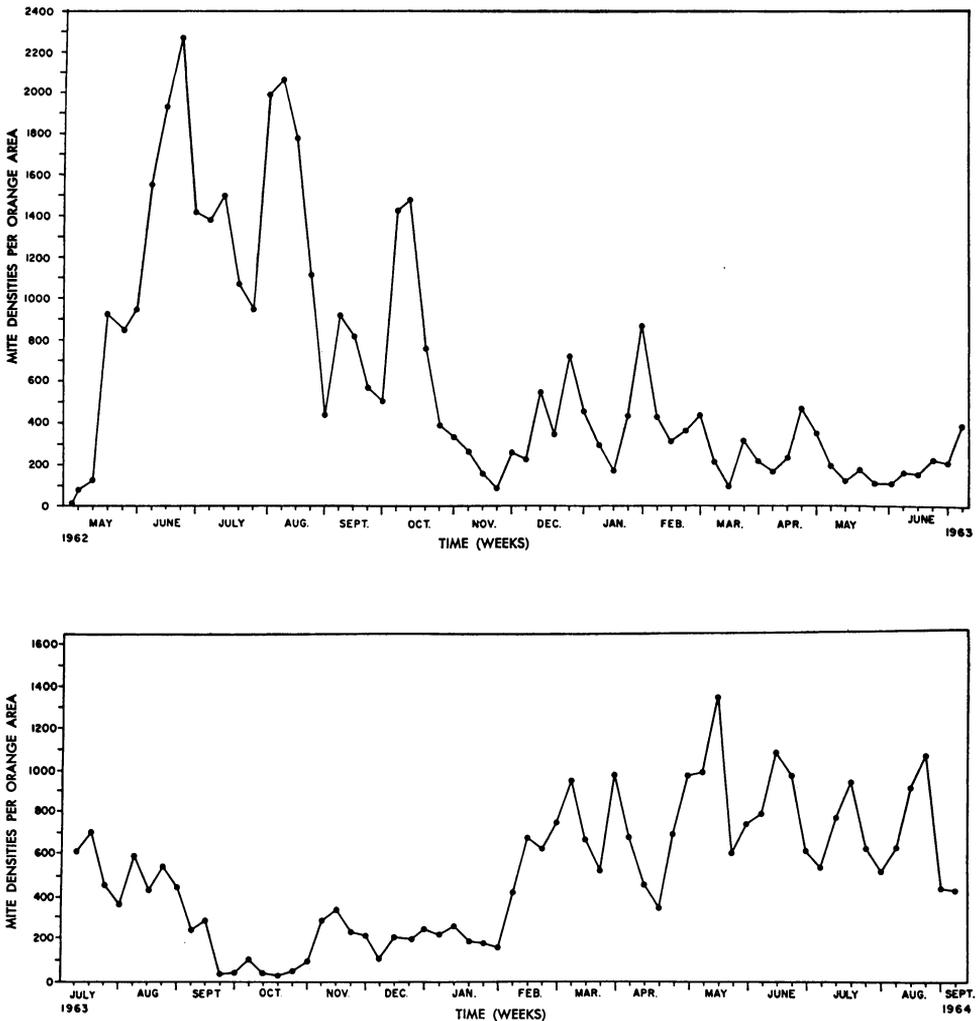


Fig. 3. Universe C-1. Densities per orange area of *Eotetranychus sexmaculatus* when regulated by competition for food under a "hazardous" pattern of dispersion of the food: 42 small areas of food, arranged in a cabinet (Huffaker *et al.*, 1963) among 168 rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent.

to position not only over the grid-wire shelves and from shelf to shelf, but also over and about the 168 rubber balls which, when reached, presented no food. Furthermore, even when a fertilized female⁸ successfully located an exposed orange surface, the amount exposed was so small ($\frac{1}{20}$ whole-orange equivalent) that the reproduction achieved, in relation to the hazards faced by the migrants, was relatively

low. On the other hand, when an equally large (two-orange-equivalent) total feeding area was exposed on only four oranges in a single-tray universe, even when the oranges were dispersed among rubber balls (Huffaker, 1958a) the successful migrating females found enough food so that very large numbers of migrants were produced on each orange. These migrants were sufficient to insure against losses during

⁸ Unfertilized females produce only males.

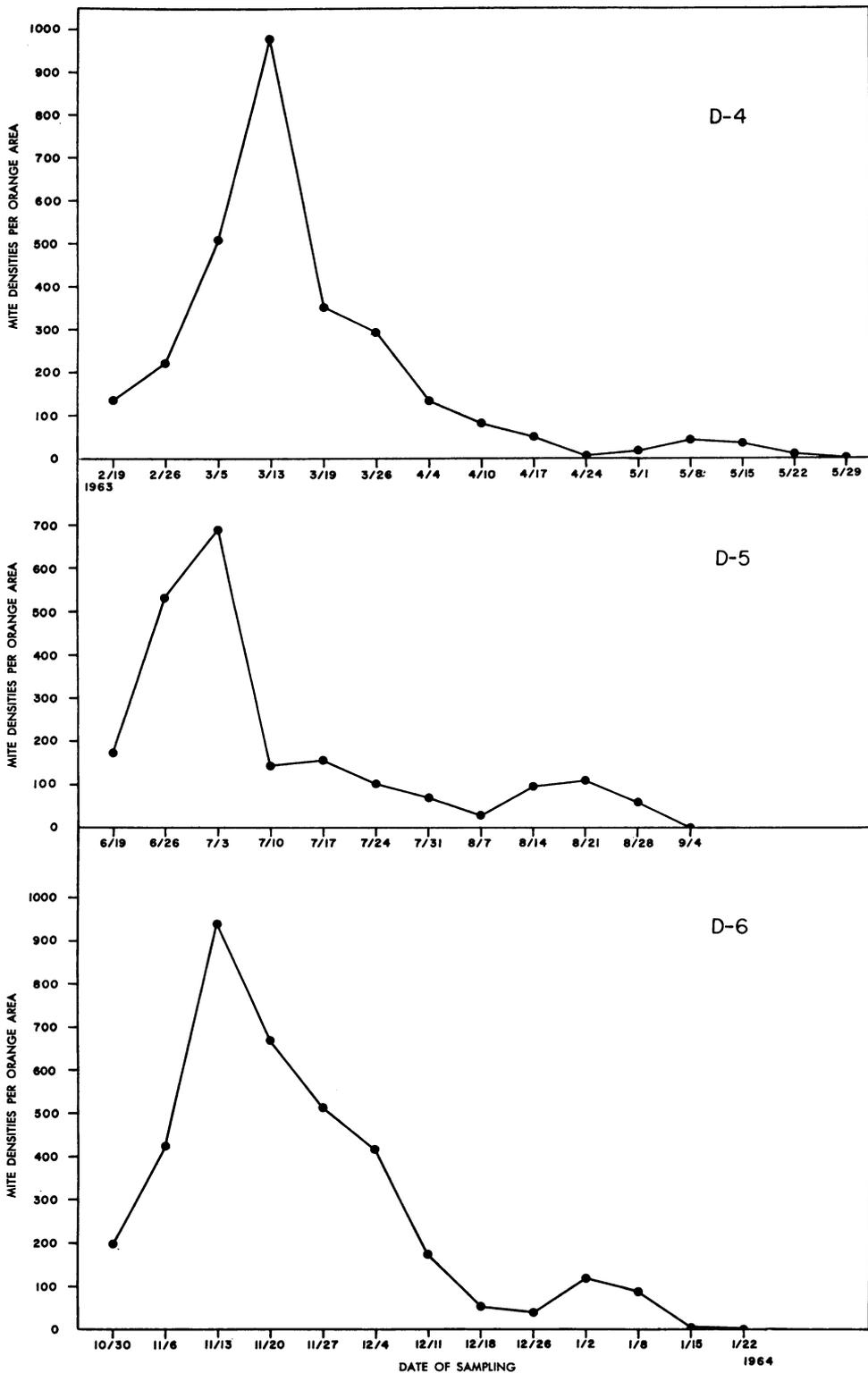


Fig. 4. Universe D-4, D-5, and D-6. Densities per orange area of *Eotetranychus sexmaculatus* "regulated" by competition for food under a "severe" hazard of dispersion of the food: 42 tiny areas of food randomly dispersed in a cabinet (Huffaker *et al.*, 1963) among 168 rubber balls; each orange exposing $\frac{1}{70}$ whole-orange equivalent.

migration too severe to permit discovery of each new orange early enough for nearly full utilization, and to lead to emigration before scheduled removal of the oranges.

The fluctuations in this universe were striking. There were strong influences both of *chance*, acting forcefully on *variations* in density, and of density-gearred *regulation*, acting on average *magnitude* at equilibrium. Following initiation of the universe, population growth was rapid. This was consistent with the facts that no unused oranges were then present and the system of stocking was such as to assure a fairly uniform, random dispersion of mites (that is, on one-fourth of the oranges) throughout the universe. Commonly, in such a system at equilibrium, a substantial portion of the oranges remains uninfested for a considerable period after introduction, a portion maintains good densities of mites, and a small portion becomes fully utilized before removal. In this ecosystem, high utilization occurred only during the preadjustment phase (for about five months after initiation). It is interesting that this sequence of densities during the first five months was similar, in the general trend toward a lower level, with time, to that of a related universe in the earlier 1958 studies (Huffaker, 1958a). A striking difference is the magnitudes involved. It also seems unlikely that the universe of the earlier studies would have fallen much below densities of 2,800 to 3,000 mites per whole-orange equivalent if it had been continued for a longer period, because the hazards of getting about, even after adjustment to equilibrium, were not nearly so severe as in the present universe.

A striking feature of the C-1 universe is that the general mean density for the entire 28-month period, with the exclusion only of the initial establishment phase (two successive dates just after initiation), means very little.

Contrast between pre- and postadjustment densities is so sharp that the mean density covering the period after September, 1962 (i.e., excluding the first four months) has more significance. Even during that time, there was no consistent trend; for several months the density fluctuated around 150 to 300, at other times near 400 to 500, and for the last seven months, at about 750. The general average was 460 (see table 1).

Universes D-4, D-5, and D-6: 42 tiny areas of food, randomly dispersed; 168 rubber balls; each orange exposing $\frac{1}{70}$ whole-orange equivalent (fig. 4, table 1).

Universes D-4, D-5, and D-6 are replicates. In each, 11 oranges were each stocked with one adult female mite. Universe D-4 was initiated February 19, 1963, D-5 on June 12, 1963 (first count, June 19), and D-6 on October 23, 1963 (first count, October 30). These universes terminated by self-annihilation as follows: D-4 on May 29, 1963; D-5 on September 4, 1963; and D-6 on January 22, 1964.

Study of these universes reveals a rather consistent result. In each case an initial surge of population growth almost surely resulted from an above-normal amount of unused food available at the beginning and a favorable pattern of distribution of vigorous gravid mites (comparable for all systems) at the initial stocking. With this favorable beginning, the populations in each replicate universe reached densities of approximately 700 to 1,000 mites per whole-orange equivalent, after which each immediately crashed to very low levels. Establishment of mites on the new oranges being added to the systems was never enough that births equalled deaths. In each case, however, a second, feeble population increase occurred, associated with the first complete change of oranges after the seven-week period.

Although we do not consider that

these universes demonstrate equilibrium positions in any sense, for comparative purposes the mean densities of these second feeble "waves" may perhaps suggest postadjustment levels *higher* than the mean of a conceivable population at equilibrium under comparable dispersion hazards, but embracing such a large universe that survival would be possible (see p. 545).

Interpretations. Figures 1 to 4 inclusive, table 1, and pages 537 to 545 show data from several universes which had different levels of built-in hazards to movement, but in which no additional density-independent mortality was imposed by destruction.

As stated on p. 537, we used four basically different kinds of dispersion, but only three markedly different results were obtained. In two of the universes that were less spatially complex, but in somewhat different ways, population means and the degrees of utilization of the food were comparable (universes E-2, B-3, part "a"). In these two universes, densities of 1,900 and 2,000 mites per whole-orange equivalent, with approximately 69 per cent and 73 per cent utilization, respectively, were achieved. The mean densities of mites in universe E-2, and in B-3 prior to April 14, were thus at near 2,000 per whole-orange equivalent. After April 13, following changes to promote fuller utilization, the mean density in universe B-3 was 2,790, which slightly exceeded the yardstick value, and was associated with approximately 100 per cent utilization of the food.

We may infer that, except for universe B-3, part "b", the mites faced appreciable hazards to movement in these universes, so that some oranges, at discard, still had substantial populations on them and were still not fully utilized. In universe E-2 the exposed feeding areas were dispersed uniformly through the entire universe; there were no rubber balls, and all migrants to the

oranges were separated only by a small amount of space over which they could walk, on a grid-wire base, to other oranges. The competitive utilization in the course of the population fluctuations was such, however, that the nearest oranges sometimes had no food left when found by the mites, while at other times they had.

In universe B-3 a mean density nearly equal to that in universe E-2 was obtained to about April 13, 1964, when the change in experimental conditions was made. Considering the preceding period, the hazards in movement were presumably equivalent, overall, to that in universe E-2, but in this case the oranges were grouped on one of the grid-wire shelves, but were not touching. Only 21 oranges were used, but a half-orange equivalent was exposed on each. There were 189 rubber balls in the other positions. Mites apparently dropped off or wandered away from the congregated group of oranges into parts of the system where hazards to success were far more severe than at normal positions in universe E-2. Thus, the net effect of hazards in the two ecosystems was apparently nearly equal. The total amount of food supplied in each of these systems was also the same.

In the second and more meaningful period of universe B-3, after April 13, 1964, the mean population rose to about 2,790 mites per whole-orange equivalent. Food utilization was thus about 100 per cent. The April 13 change must have reduced losses of mites resulting from dropping through the wire base into lower portions of the cabinet, far away from sources of food. It must therefore have permitted a more rapid infestation of the oranges so that complete utilization was accomplished before discard.

For further comparison of built-in hazards, we have one long-term experiment of a continuing ecosystem, C-1, which represents a high level of haz-

ards, and four replicates of one ecosystem in which, in each case, the stress or hazards were so great that the populations soon died out. In the latter cases, since the initial stocking procedure created an early, unnaturally high utilization of the food, we consider for comparison only the densities following this unnatural period—that is, only the “equilibrium” densities (see pp. 543–544). In universe C-1, with substantial built-in hazards to movement, the mean density after adjustment or equilibrium was 460 mites per whole-orange equivalent. This corresponded to a food utilization of only 17 per cent, as contrasted with 69 per cent and 73 per cent in the low-hazard universes E-2 and B-3, respectively, and with nearly complete utilization in universe B-3, after April 13, and in the simpler universes of Huffaker (1958a).

Although the hazards in the three replicated systems, D-4, D-5, and D-6, were too severe for continued survival, the small rebound wave of population shown by each replicate following the major wave may be considered *indicative* of a value perhaps comparable with that which would be possible at equilibrium if a sufficiently extensive representation of this type of system were run in which continued survival *were* possible. We have taken these rebound values (fig. 4, table 1) to indicate a utilization of the food at less than 3 per cent.

Including the earlier ecosystems run by Huffaker (1958a), we have a series of results in which competition for food has been the only true regulating factor, but in which the varying degrees of built-in hazards to movement resulted in a corresponding density-independent stress which markedly altered the density level and the degrees of food utilization at which the regulation occurred. These ranged from less than 90 mites per whole-orange equivalent to about 3,000, and from less than 3 per cent

utilization of food to approximately 100 per cent.

The high mortality from density-independent stresses in getting about in universe C-1 was such that only a low mortality resulting from competition for food was sufficient to balance births and deaths. Thus, the density at equilibrium under regulation by competition for food was correspondingly low, and the regulation was accomplished even though only 17 per cent of the available food (if it could be found) was utilized. The marked variations in general densities from low levels of 50 to 100 up to 800 and over per whole-orange equivalent occurred at intervals of time and at periods in the year that suggest a possible association between the higher densities and the introduction of new crops of oranges.

Thus, we see that an organism may be limited by its food supply even if a very large portion of it *remains unutilized*. The density level of the resulting balance reflects not only the total rate of supply of the food in an absolute sense, but also its relative availability—the stress imposed on the user in finding it, as balanced against the population realization after finding it. The whole environmental complex is involved.

Populations under standard built-in hazards to movement but different imposed density-independent mortality

The universe here considered “standard” for purposes of comparison is one in which all the positions in the cabinets were occupied by oranges resting on coasters on the grid-wire shelves. Universes E-2, I-7, and II-6 are therefore considered to have standard hazards. In universes C-1, D-4, D-5, and D-6 various, more severe hazards to movement were achieved by spreading oranges at random among rubber balls. Fewer oranges than balls were used, but with the

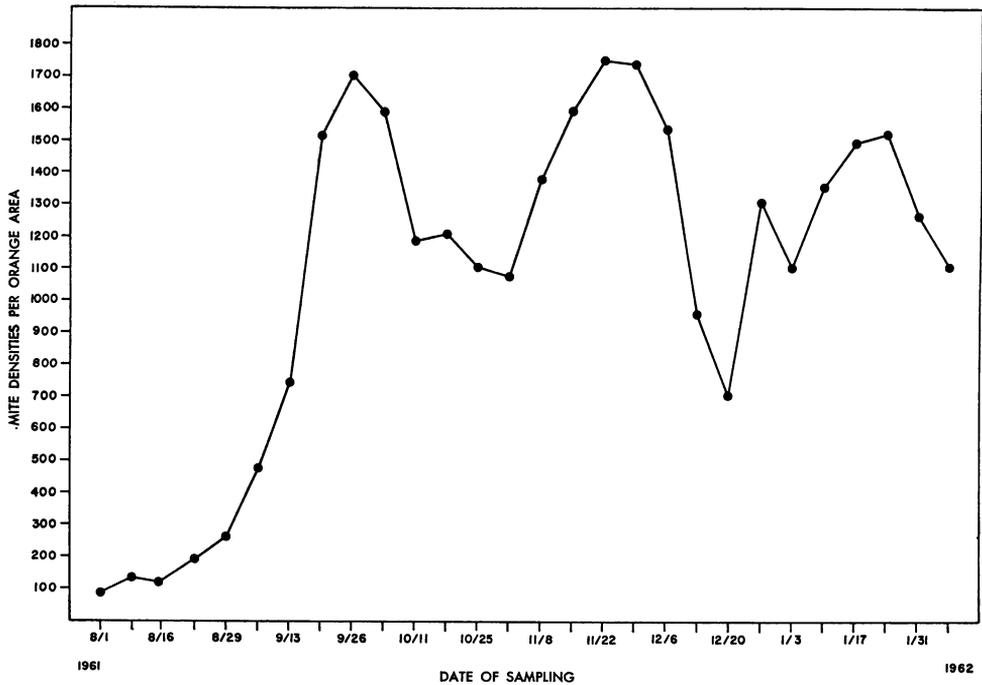


Fig. 5. Universe I-7 Densities per orange area of *Eotetranychus sexmaculatus* when regulated by competition for food under a "standard" hazard of dispersion of the food and a 25 per cent additional imposed density-independent mortality weekly: 252 small areas of food dispersed in a cabinet (Huffaker *et al.*, 1963) with no rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent.

same or smaller areas exposed. Lesser degrees of hazard were achieved by grouping oranges to expose $\frac{1}{2}$ whole-orange equivalent in one area in the cabinets as in universe B-3.

Universe E-2, with no imposed destruction, may be considered a control for universes I-7 and II-6 for which imposed destruction of the mites was 25 per cent weekly for I-7 and 50 per cent for II-6.

Universe I-7: 252 small areas of food randomly dispersed; no rubber balls; 25 per cent additional imposed mortality weekly; each orange exposing $\frac{1}{20}$ whole-orange equivalent (fig. 5, table 1).

The mites on one-fourth the total habitable surfaces were destroyed weekly. For the present purpose, this universe was begun on July 26, 1961

(first count, August 1). While the level of density at that time was higher than an original stocking level, the picture of population increase from that position, or a level as low as five gravid females per universe, was little different initially. A solid population growth followed immediately upon the death of the predator population even though the 25 per cent weekly destruction was continued. The universe was ended arbitrarily on February 7, 1962, at which time the pattern and the equilibrium density were fairly well established.

In this system the fluctuations were moderate and the mean density at equilibrium was 1,320 mites per whole-orange equivalent. Based on the yardstick density value of 2,750, this is 48 per cent utilization of the food. The 1,320 mites resulting under the 25 per

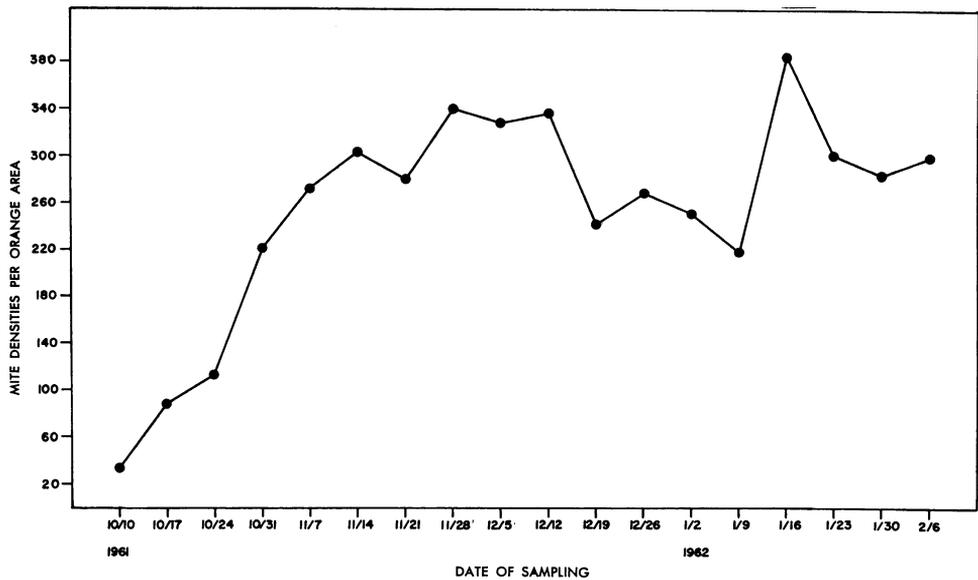


Fig. 6. Universe II-6. Densities per orange area of *Eotetranychus sexmaculatus* when regulated by competition for food under a "standard" hazard of dispersion of the food and a 50 per cent additional imposed density-independent mortality weekly: 252 small areas of food dispersed in a cabinet (Huffaker *et al.*, 1963) with no rubber balls; each orange exposing $\frac{1}{20}$ whole-orange equivalent.

cent weekly destruction may be compared with the 1,900 mites found at equilibrium in universe E-2 (comparable in all respects except that in E-2 there was no imposed additional mortality).

Universe II-6: 252 small areas of food, randomly dispersed; 50 per cent additional imposed mortality weekly; each orange exposing $\frac{1}{20}$ whole-orange equivalent (fig. 6, table 1).

The mites on one-half of each orange (approximately 50 per cent of the population) in this universe were destroyed weekly. For present purposes, the universe was begun on October 10, 1961, and ended arbitrarily on February 6, 1962, after the equilibrium position and the pattern were fairly established.

In this universe, a severe mortality was imposed, and an appreciable hazard was built into the spatial complexity itself (the latter true also with universes I-7 and E-2).

The mean density in universe II-6,

after the initial growth phase, was approximately 290 mites per whole-orange equivalent, and the degree of food utilization was only 11 per cent. Furthermore, there was a most pronounced reduction in the mean density and degree of food utilization, as compared with universe E-2 (no imposed destruction), or with universe I-7, in which the degree of imposed mortality was only half as heavy, i.e., 25 per cent weekly.

Interpretations. Table 1 summarizes the data of systems I-7 and II-6, in which arbitrary destruction of 25 and 50 per cent, respectively, was imposed weekly, and in the comparable system E-2, with no imposed destruction.

In universe II-6, an additional purely density-independent destruction of 50 per cent of the mites weekly resulted in an equilibrium density of 290 mites and only 11 per cent utilization, as compared with 1,900 mites and 69 per cent utilization in the control. The imposition of 25 per cent destruction in universe I-7

produced a mean density of 1,320 mites and a utilization of 48 per cent, a position between the two extremes and considerably nearer the result in universe E-2 than that in universe II-6.

The results indicate that, up to the point at which destruction is rather severe, the population can compensate to a considerable extent (see p. 550).

A comparison of regulation when additional mortality was imposed and when not imposed

The results of these experiments suggest that: the hazards built into the spatial complexity of these ecosystems are of a *conditioning* or legislative nature; the stress resulting does not in itself *regulate* the population; and the stress is similar in its role and action to that resulting from the arbitrary destruction of a fixed fraction of the respective populations at given intervals. The data are consistent with and suggest the interpretation that in these experimental systems, as the density-independent stress is increased through spatial complexity causing hazard to movement, a lower density-dependent stress is required at the point of balance between births and deaths. Hence, equilibrium is reached at a lower population level and at lower levels of food utilization.

The results illustrate that, as certain density-independent factors are varied in intensity, the expression of the regulating factor(s) is modified, so that different mean densities at equilibrium are maintained even when the same basic agent is the inherent regulating instrument in each case. Furthermore, some populations may possess remarkable compensatory powers, and adjust for marked increase in density-independent stresses, thus maintaining essentially the same densities at different levels of stress. Other populations, or the same populations under different conditions, however, may not possess such marked

compensatory ability in the sense suggested by Nicholson (1954a). (See also p. 549).

In the competitive use of food, some self-induced modification of the degree of stress in each ecosystem is undoubtedly caused by the spatial complexity of the design. Yet all the stress (as a sequence in time) resulting from the problems of getting about and finding food is by no means density-independent and therefore strictly equatable with the arbitrary weekly destruction. However, a good part of the problems in getting about in the systems is associated with the spatial complexity of the respective system, or is random in occurrence and therefore density-independent in nature, and *can* be equated with the arbitrary imposed destruction. This is shown by contrasting the results in different ecosystems having definitely different built-in hazards of a spatial nature.

A noteworthy feature of universe II-6, with 50 per cent imposed destruction, is an apparent increase in stability of the population density resulting from the additional stress. Changes in this universe from week to week were, on the whole, much less variable in an absolute sense than were those in either E-2 or I-7. The departures were normally no greater than 50 mites per whole-orange equivalent, above or below the mean, but with two departures of 70 below and 90 above, respectively, representing values 25 per cent lower and 31 per cent higher. On the other hand, under a lighter, 25 per cent imposed mortality (universe I-7), the changes from week to week on an absolute basis were very much greater, and even if expressed as a percentage variation about the mean (1,320), there was also some greater variation, from about 47 per cent lower to about 33 per cent higher, under the lower level of imposed mortality.

If we compare universe II-6 with another (universe C-1, fig. 3, table 1)

which had a relatively low equilibrium value entirely because of the much greater built-in hazards, and in which there was no application of a constant level of mortality week to week, we again see that the fixed 50 per cent level of mortality weekly tended to lessen the violence of the changes in density. In universe C-1 the mean density for a long period was about 400. Departures from this mean on an absolute basis were much greater (true also for the comparison systems), and the maximal departures on a relative basis, after the initial period, were also considerably greater, being 375 per cent higher and 88 per cent lower. Thus, the addition of a mortality factor that has some inherent constancy in its operation may add to homeostasis. Additive density-dependent factors may also tend to depress the fluctuations, as seems evident in the biological control of olive scale (Huffaker and Kennett, 1966).

On the other hand, if either constancy in occurrence or a tendency to increased intensity with increasing density is lacking in the mortality, presumably two such entirely chance-operating factors (in contrast to one) could result in more violence in the *extreme range* of fluctuation, although, on the average, each tended to lessen the variation in impact caused by the other. The maximal and minimal depressive powers of the two factors could (but rarely would) fall at the same time, whereas maximal or minimal occurrences of one of the factors would usually coincide with a more steady pressure by the other.

These studies support Nicholson's (1933, 1954b) view that populations adjust their densities *in relation to* prevailing conditions, but that the regulation itself is some form of density-induced reaction, and that populations possess a power to compensate for stresses encountered. The results may be compared with the data of Nicholson (1954a, 1957), Watt (1955),

Slobodkin and Richman (1956), Davis and Christian (1956), and Nakamura (1962, 1963) to the effect that populations possess marked abilities to compensate for stresses in the environment that cause destruction or reduce fertility, and that under appropriate circumstances, this compensation is sufficient to negate much if not most of the stress encountered.

Compensation relative to maintaining a given equilibrium density may, however, be marked in some instances and very limited in others, as our present data illustrate. In the above-mentioned experiments, known percentages of selected stages in the life cycle were destroyed. So long as the destruction was not too extreme, the organisms not only maintained themselves in each instance, but they did so at higher densities than might be expected from the proportionate destruction imposed. It is interesting that in a typical result, the age structure changed in such a way that more individuals of the stage under destruction appeared, and of those, the numbers left to reach the next stage were not reduced proportionately to the degree of destruction, as compared with the control. Under some conditions, an "overcompensation" may occur if the number of adults is taken as the criterion (Nicholson, 1954a; Nakamura, 1963).

In the destruction of the mites in the present experiments, there was not so strong a tendency to homeostasis in the sense of Nicholson (1954a). No overcompensation occurred. In fact, a strong reflection of the degree of destruction is seen in the corresponding equilibrium densities of the mites, but certain of the ecosystems do reveal a tendency to compensate in Nicholson's sense. Although we have not completed all experiments with the various degrees of imposed destruction, a tentative curve plotting degree of "additional" imposed destruction against equilibrium density indicates that the

relation is not too far from linear, which would mean that no compensatory response to the additional destruction is exhibited. Yet the departure from linearity appears to be greatest at the lowest level of weekly destruction for which we presently have data (25 per cent).

It may also be significant that, as previously stated, the population was under a fairly high level of stress in-

herent to this ecosystem even where no *additional* destruction was imposed, and also in the universes where 25 per cent or 50 per cent destruction was imposed. Apparently, this intense built-in stress may have been enough to have largely "absorbed" the compensatory ability of the organism, so that the *additional* mortality was then rather more directly reflected in *alteration* in the equilibrium density.

RELATIONSHIP OF EXPERIMENTS TO GENERAL THEORY OF NATURAL CONTROL

The general relationships

These experiments have a bearing on several questions relative to the general theory of natural control of populations. They illustrate the emphasis of Huffaker (1958*b*) and Huffaker and Messenger (1964) that the density-independent and conditioning forces and the density-dependent regulating forces occur together and are best thought of as parallel, inseparable co-determinants of population size in natural control. This concept is also inherent in Nicholson's classical works (1933, 1954*b*, 1958) even if the emphasis is somewhat different. In our definition, natural control, or population *determination*, as the results differ in comparing two different situations or areas, is a function of the joint operation of density-dependent and density-independent factors even though the density-dependent factors which operate in the given situation *do* the regulating or account for the maintenance of the population equilibrium in the real sense. Nicholson (1958) stated: "In addition, logical deduction from certain well established facts has shown that density-induced governing [regulating] reaction must necessarily play this role of adjustment in each persistent population. This inescapable conclusion is completely consistent with the knowledge that many factors

which do not react in this way play very important parts in contributing to the *determination* [italics added] of population levels."

The results of the study point to a clearer understanding of what is meant by *regulation* on the one hand and population *determination* on the other. Either Andrewartha and Birch (1954) apparently feel that Nicholson (1933, 1954*b*) and others of similar views do not recognize this distinction, or else Andrewartha and Birch do not recognize it. Consequently, we may infer that the latter authors consider that, since density-dependent factors *alone* do not determine population levels, these factors can have no distinct role in such determination. Andrewartha and Birch claim that their model of population dynamics is superior, and adequate, without including the concept of density-dependence. In fact, they state that this concept is not within the scope of the model, although, as we have seen, such regulation plays an ever-present, key role in population *determination* in constantly favorable physical environments. Moreover, density-related regulation comes into play, now and then, in populations which are more variable or even subject to tremendous buffeting about in ways unrelated to their densities. Even if specific departures, in time, from any given magnitude are greatly independ-

ent of densities, occasional actions by such regulating forces are necessary to restore the correlation or connection between *magnitude* and the capacity of the environment.

The results of these experiments illustrate that in some types of ecosystems, there is not so much internal self-adjustment or compensation in the sense of Nicholson; in some cases, at least where high stress is already being endured, the degree of additional density-independent stress that the population faces in still more rigorous situations alters more or less directly the level at which the density-dependent factors regulate or govern the population density.

We believe that the two kinds of stress—the density-dependent actions, and density-independent or legislative stress imposed on the population and inherent to the overall conditions of the environment—have different roles in natural control. These two kinds of stress were first emphasized by Woodworth (1908) and later by Howard and Fiske (1911). We appreciate Andrewartha and Birch's (1954) attempt to arrive at a simple, clear classification of factors and to consider only the direct action on the individual, thus relegating to environmental history the action of all indirect factors or modifiers, but we do not believe that this permits a rewarding, or full understanding. The attempt to merge, confuse, or ignore either of these two classes of stress or to disregard their fundamental distinction would be most unrewarding. We agree with Andrewartha and Birch (1954) that in the day to day occurrences of stresses on individuals, there are usually strong reflections of density-dependent actions.

We disagree that since density-dependence is so universal the solution is to abandon the use of the entire concept. The task is to untangle the complex where possible and to remain alert to the operation of forces or facets of

the whole, in nature, that operate in ways either related or unrelated to density. The way in which these two basically different but mutually compatible forces operate together in simplified laboratory universes to determine and explain population levels and natural control will help us remember that the same roles tend to be expressed in much more complex field situations even though partially masked by superimposed relations or conflicting tendencies of many factors.

The general concept of Nicholson (1933, 1954b), Smith (1935), and many others is that, although the regulation of population density is the result of density-governed reaction, the different legislative factors (Nicholson), density-independent factors (Smith), or conditioning factors (Huffaker, 1958b; Huffaker and Messenger, 1964), which operate independent of density, alter the levels at which density is regulated. (See also Wilbert, 1962; Bakker, 1964.) The work of Holdaway (1932), which showed that under different conditions of humidity, populations of the flour beetle (*Tribolium confusum* Duval) grew from initial stocking densities at different rates and ultimately attained different asymptotes or equilibrium densities (fig. 7), clearly illustrates this concept of natural control. Terao and Tanaka's (1928) work also illustrates this same concept. In any given universe, their water fleas (*Moina macrocopa* Strauss) grew when at low densities until, at some higher density, no further growth was possible and equilibrium was attained. In the universe having a moderate temperature (24.8° C), a higher mean density (429) at equilibrium was attained than at either a lower (19.8° C) or a higher (33.6° C) temperature, where densities of 199 and 271, respectively, were attained. Temperature thus served in some way to affect the response to "crowding."

The results of the present study are fundamentally related to those of

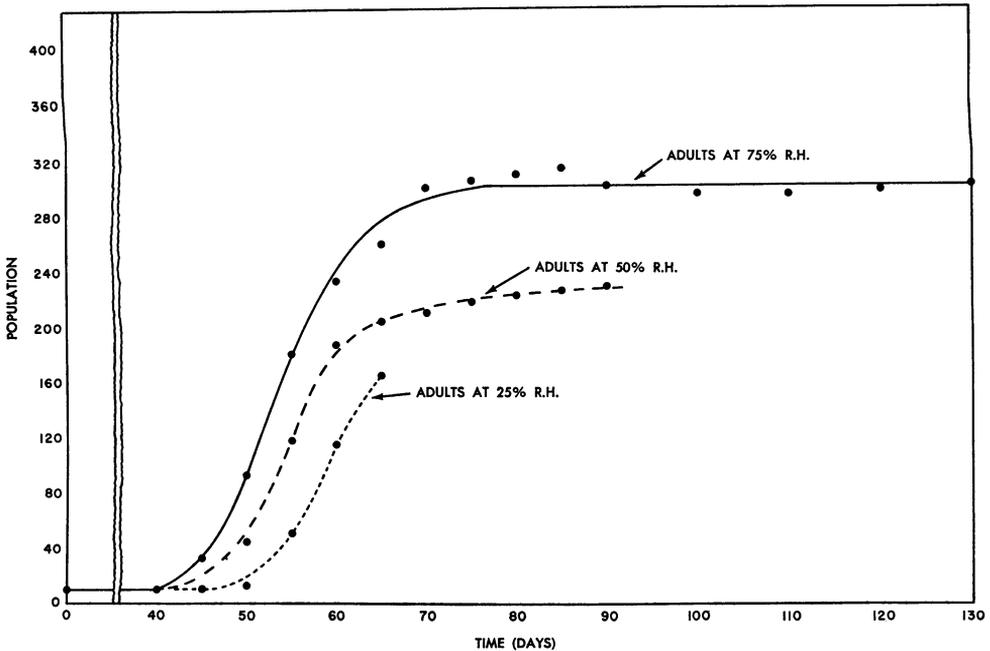


Fig. 7. Logistic growth of populations of the flour beetle, *Tribolium confusum*, from initial stocking densities, and regulation at respective equilibria positions characteristic for the respective humidities employed as the variable—a clear demonstration of the roles of *conditioning* and *regulating* features in natural control or population determination. All temperatures at 27° C. (Redrawn from Holdaway, 1932.)

Holdaway (1932) and Terao and Tanaka (1928), but we have varied a different sort of density-independent, conditioning factor. With competition for food as the only true regulating factor, we varied the conditioning environment in which this factor operated in two ways: (1) by use of different patterns of built-in spatial complexity of the ecosystems; and (2) by destroying fractions of the populations of mites in a manner independent of density (see above).

Food-limited herbivores and herbivore-limited plants

The results also support the general observation that the point of equilibrium between a true regulating, host-specific, food-limited phytophagous insect and its host plant will automatically be at a density where a degree of disengagement of the intensity of at-

tack has occurred, as contrasted to that at higher host densities. Thus, the equilibrium at which the control comes to rest represents a status at which a much lower percentage of utilization is common, and other factors have even greater, comparative increased impact; yet food supply is still the regulating factor for the insect's abundance, and the insect's attack is the regulating factor for the plant's abundance.

Although we do not care for the sharp distinction made by Andrewartha and Birch (1954) and Andrewartha and Browning (1961) between *relative* and *absolute* shortage of food because we believe that, in natural situations, shortage of food is *commonly* relative to the capacities of the organisms to locate and use it efficiently, we do agree that food can certainly be limiting to a population while still relatively common in the absolute sense.

Mortality and population density are of course reflections of both the quantity and dispersion (availability) of an animal's food (Andrewartha and Birch, 1954). Dethier (1959) showed that losses during dispersal may be very high. Mortality of the larvae of the butterfly *Melitaea harrisii* Scud. may be as high as 80 per cent due to inability to find hosts. Morris (1964) suggested that the higher mean density of the fall webworm (*Hyphantria cunea* Drury) at Perth, in contrast to that at Fredericton, New Brunswick, Canada, may be "... associated with more favorable occurrence of the main webworm host plants." A vast literature exists in support of this view.

Smith (1954) concluded, from a review of many examples, that large animals, in contrast to small animals, live in a rather benign world, and that physical factors (such as diffusion) related to the problems of *getting* to favorable places or *staying* in favorable places presented a greater potential danger to very small organisms. We would add that possession versus lack of a means of rapid and directed movement against currents in air or water tends to reduce the latter correlation. The mites in this study were limited in movement to dropping down or crawling. The more efficient method of movement available to them in nature, namely, drifting in the wind on silken strands over great distance, was not a factor here. Thus, the problem of getting about served to greatly reduce the effective power of increase. As the data show, from generation to generation and from place to place, variation of such hazards may be expected to strongly alter population expressions.

Whether herbivores in general are commonly limited or regulated by their food supply has long been a source of divergent opinion. Certain early opinions were discussed previously (p. 534). Brues (1920, 1946, 1952) held that host-specific, phytophagous insects are

a prime factor in regulating the abundance of specific plants, particularly flowering plants. Huffaker (1957, 1959, 1962), Wilson (1964), and others have discussed examples of successful control of weedy plants as the result of introduced phytophagous insects to illustrate the consequent limitation of the insects concerned by self-induced shortage of food. This does not include the many phytophagous insects which are limited by their own enemies at densities too low for them to exert controlling effects on their host plants.

Some ecologists object to these examples because they represent action by *introduced* enemies against *alien* plants in *unnatural* communities. Although this is true, there is no overwhelming evidence that such action does not represent what actually occurs in some natural situations. It is difficult to believe, for example, that St. Johnswort (*Hypericum perforatum* L.) would be as scarce as it is in favorable environments in Eurasia except for the attacks of a horde of endemic, host-specific insects that feed on it. Some of these insects have similarly reduced the plant's abundance in many other areas of the world where it has become an important weed in seminatural grazing lands (western North America, Chile, Australia, New Zealand, South Africa). Likewise, it is difficult to believe that the attacks of insects on puncture vine (*Tribulus terrestris* L.) in their native environments in Eurasia and Africa, or on lantana (*Lantana camara* L.) in Mexico and Central America have had no role in determining the relative scarcity of these plants in those areas.

Jansen (1965) made an elaborate study of the impact of phytophagous insects and of grazing animals on the success and abundance of a "fugitive" type, or early successional-stage, native tree species, *Acacia cornigera* L., in eastern Mexico. This plant is strongly protected from otherwise annihilative pressure from a broad complex of phy-

tophagous species, predominantly insects, by the action of the ant *Pseudomyrmex fulvescens* Emery, which inhabits the enlarged thorns of this plant. When the ant was excluded or just naturally absent, early loss in the competitive struggle with other kinds of plants was the overwhelming fate of the young acacias.

This concept of food-limited animals, here applied to plants as the hosts, has been appreciated for many years relative to biological control of insect pests by entomophagous parasites. The host-specific parasite's numbers are restricted by the density of their hosts. In situations in which a pest is under good control by a parasite, the degree of utilization of *its* food (the host) by the parasite (percentage parasitization) is much less than during periods when, for one reason or another, the host has previously escaped from the action of the parasite, but the parasite, having then regained its status as a regulator, is in the process of bringing the host population back under control. It seems, then, rather strange that the fact that living plants are not destroyed *en masse*, season after season, has been taken as *a priori* evidence that the organisms which depend on them are not limited by their food supply, or that such plants likewise are not limited or controlled by the phytophagous enemies.

Hairston *et al.* (1960) presented logical argument based on the observation that, in terrestrial environments, herbivores, as a gross trophic-level category, are not limited by their food supply since most of the primary food, green plants, is not utilized by the herbivores but goes instead to the decomposers. As pointed out by Huffaker (1962), this viewpoint may apply in a gross sense, to vegetation in general, to many of the dominants and other species, and yet not apply to some or many of the less-abundant plants in that same vegetation.

Even if the view of Hairston *et al.* (1960) is true in the general sense, which seems logical, this does not necessarily mean that host-specific, phytophagous animals cannot be regulated by their food supply. The total overall vegetation could remain rank and abundant and be relatively little damaged or used by the total feeding of herbivores, yet a great many of the species of plants in that assemblage could exist at varying densities and in patterns of dispersion which are a function of the action of the monophagous (or oligophagous) phytophagous animals which perhaps utilize the plant species only very moderately at any given time and place; this would be more likely if the plant species exist at relatively low densities.

The results of the present experiments suggest that, with competition for food as the regulating factor in two contrasting situations, if dispersion of the food makes availability relatively difficult, this can act in a density-independent way to alter the specific pattern of regulation and the equilibrium density. The manner of dispersion of such food may itself be a result, in part at least, of the pattern of density-dependent utilization, and thus may enter, not only as a density-independent factor, but also as a density-dependent one. Density-dependent actions, of course, may alter the dispersion pattern (e.g., Ito *et al.*, 1960).

The populations in this study utilized their orange food to a heavier degree when at high densities than at low densities, even though a constant weekly rate of replenishment of oranges was maintained. Thus, to some extent the difficulty the mites had in finding food following waves of above-normal utilization was a result of prior usage. The fluctuation in the opportunities the mites had within a given universe is not only, in part, a chance feature, but is also normal to the density-dependent regulation in the utilization of the

food. Greater numbers of mites automatically use up more food and create shortages in both the absolute and relative senses, the latter being associated here with a self-induced alteration in the "norm" of the dispersion pattern as set by the experimental design. When the rate of supply of the food itself is a strong function of the pattern of density-dependent use, as is very common (reciprocally controlling predator-prey relations—Huffaker and Messenger, 1964), the interdependence is even greater.

On the other hand, we can say, that, on the average, in comparing different universes with different fixed patterns of dispersion which offer different degrees of potential modification of this dispersion by the population itself, there is a density-independent, conditioning, or legislative stress imposed on the population that is inherent to the spatial complexity of the ecosystem. In other words, a basic difference in dispersion patterns of habitat units between given universes exists, and the way in which the dispersion pattern in a given universe is modified in time, in a density-dependent way, is a relation superimposed upon the basic condition of spatial complexity of each design itself. This appears to support the view of Andrewartha and Birch (1954) that it is difficult to conceive of a mortality factor that does not act in a density-dependent way. However, as previously mentioned, we believe that the density-dependent actions and the density-independent or legislative stress have different roles in natural control.

**Density-dependent factors
(competition for food)
as related to density-unrelated,
conditioning factors**

As stated previously, in the present experiment the only factor that was truly regulating the population was something associated with higher den-

sity because the initiating, or lowest populations in all these universes (except for a few in which the mite could not have survived following crash phases) invariably grew and eventually fluctuated, even if rather violently, about a definitely higher mean level. Factors operating in any other way could not have given this result. The only reasonable possibility was the competition for food. Natural enemies were not present in these universes except for the case of accidental establishment of a predatory mite (soon removed) and the suspected occurrence of a disease pathogen at one short period of time in one universe in each case. In every universe there was also a similar rate of replenishment of food regardless of whether a small or large fraction had been utilized at the scheduled renewal. These experimental examples, then, all illustrate regulation through competition for food.

The basic interpretation is that, in general, low populations, in contrast to high populations, experienced less intense competition. Thus, there was a decreased chance that each individual would die prematurely, or an increased chance that it would produce a given number of offspring. The fact that beginning and low populations did more commonly grow rather than decline further to extinction, and high populations did more commonly decline rather than increase further (to levels above their food supply potential) shows a rough general density-dependent relation. The strong interactions between the population of users and the supply of unused food available at a given time, even though a constant rate of supply of the food was built into the experimental design, apparently produced strongly fluctuating population densities as a feature of the competitive use itself.

Significantly, since pressures of varying intensity from density-independent, chance occurrences operated

within each ecosystem, in time, and varied according to the experimental design from one ecosystem or universe to the other, many of the specific fluctuations observed are more suggestive of, and probably more related to, chance factors than to density-dependent action. The fact that the populations exhibited a marked degree of balance (whether at densities that used most of the food or only a small portion of it) while at the same time being buffeted about rather relentlessly by chance factors of destruction or repressed natality, implies that density-dependent forces *were* in operation. Such factors prevented self-annihilation from sudden depletion of all the food at conceivable high densities and alleviated enough of the total stress, by relaxing competition for food, to make annihilation at the low or "floor" densities much less likely.

Regardless of the varying fluctuations, regulation resulted from a balance in births and deaths. In these cases, perhaps typical of a type in which the rate of food supply is not modified by its competitive use, and where the population still has available a relatively limited compensatory power, as the density-independent component of total stress was increased, the amount of density-dependent stress resulting from competition for food, and required to balance births and deaths, was lower. Thus, with a fixed, high density-independent stress the population could not grow beyond relatively low levels because shortage of food would cause either too many deaths or too few births. Likewise, with a low density-independent stress the population growth would proceed to a point at which a higher density-dependent stress would then effect a balance in births and deaths, and this would occur only at a higher density. Intermediate levels of density-independent stress were associated with intermediate mean densities, and thus

with intermediate levels of competition for food and its utilization.

It is important to point out that in cases more typical of biological control of living populations, if the rate of food supply is responsive and reactive to use by the user (terms of Nicholson, 1933) we may not have the relations just stated. For example, when an effective natural enemy is the key regulating factor for a host species, rate of supply of new recruits of the host species in the whole ecosystem (reproduction on an absolute density basis) would vary with the varying efficiency, in time, of the natural enemy population. Here we have reciprocally-gearred regulation of both populations through the medium of the enemy.

According to Nicholson (1933), who assumed parasites to have a constant area of discovery in their searching, when some of the hosts are destroyed by a new factor other than the regulating parasite, the steady density of the parasite is lowered, because if it remained as abundant as before it would reduce its host's density below the level necessary for its own survival. Where the assumption of a constant area of discovery is realistic, this would be true. Also, if the other factor operates *before* the parasite, both the initial and final steady densities of the host species would be higher; and if it operates *after* the parasite, both these values would be lower than when the parasite operates alone. Nicholson also assumes that if the other factor operates simultaneously with the parasite, the values for host density remain the same. Without going into the possibilities, this will serve as a warning not to apply our present results to situations that are fundamentally different.

The present results illustrate an important point with respect to the differing appraisals of the roles of density-dependent and density-unrelated factors in the natural control of field pop-

ulations. Under very complex situations of diversity of biotic habitat, in which physical conditions and a multiplicity of mortality-causing and natality-suppressing factors are operating vicariously, the role of a key regulating factor (or key factor causing *change*) may well be masked unless powerful tools for detection are used.

Thus, even in relatively simple monocultures where the weather is favorable, with no extremes beyond what the species can withstand, high densities are followed by depletion of resources, filling of available shelters, or attacks by enemies, and thus decline. At the density-induced lower densities these pressures become increasingly disengaged. Therefore, in considering only what happens during an epidemic ("outbreak"), we see only one side of the picture (Morris *et al.*, 1963) as we do when we look only at the very lowest populations. Populations in endemic equilibrium status are commonly partly or markedly disengaged from the *most intense* action of their key regulating factors. The absolute intensity of regulative action is thus relaxed, but its relative importance may nevertheless still be high (Huffaker, 1957).

For example, when an effective enemy is introduced into an environment where a prospective host species exists at very high densities, the enemy would have an opportunity for much more intense action than it would ever enjoy after the new equilibrium density (under regulation by the enemy) is attained. Even the maximal densities of the fluctuations, if under continuing regulation, and assuming no real "escape" (Solomon, 1949), would present only moderately improved opportunities for more intense action. Also, the characteristic level of destruction by a regulating factor may be only 20 per cent to 40 per cent at such times, and yet control may be maintained, provided the *other* mortality is steadily

heavy, as illustrated by Chamberlin (1941) and emphasized by Dowden (1962). Thus, even in relatively simple situations, at existing endemic or equilibrium densities, the intensity of action of the key regulating factor(s) as commonly measured is diminished decisively and becomes more difficult to demonstrate.

If we consider much more complex situations involving strong interactions of factors operating in a density-dependent way and those operating in a density-independent way, detecting a key regulating factor becomes even more difficult. The work of Morris (1959), Neilson and Morris (1964), and Morris *et al.* (1963) illustrates the use of powerful statistical methods of indication, as does that of Varley and Gradwell (1960), Hughes (1962), Smith (1961), and Huffaker and Kennett (1966). An entirely different and, to some, a more convincing approach is the use of a "check-method" in which a suspected key factor is removed in order to compare the populations subsequently with "controls" in which the same factor is left functioning (DeBach, 1946; Huffaker and Kennett, 1956; Huffaker *et al.*, 1962; Huffaker and Kennett, 1966).

Both these methods have limitations. The former relies on correlation analysis and cannot fully *prove* a case since the correlation can be one of common association rather than one of direct cause and effect. The latter relies on the common scientific use of paired experimentation with a "control," and the result shows directly as a difference. The method seems primarily useful, and again with limitations, in evaluating the role of certain natural enemies. Morris's (1959) data suggest key roles of parasites in causing changes in population density of the black-headed budworm (*Acleris variana*), even when the mean mortality caused by the parasites was comparatively low. Other causes of

variation appeared to be remarkably constant from generation to generation. The work of Davidson and Andrewartha (1948*a, b*) on populations of the rose thrips in South Australia point up the high degree to which changes in density of a population may be correlated with, and caused by, changes in weather. Because of this, and the "apparent" absence of correlation with any density-dependent factor, Andrewartha and Birch (1954) concluded that density-dependent factors were in no way limiting or regulating the population, but that this was a function of weather variation. In this connection Smith (1961), using the powerful tool of regression analysis, concluded that the thrips data did in fact strongly indicate that *some* density-dependent factor was acting to regulate the population.

If natural enemies did not act effectively at the superabundant densities of their hosts, they could not reduce their hosts' populations. There is no assumption here that all of them do. If they maintained *equal* effectiveness at in-

creasingly lower densities, they would annihilate their hosts.

These aspects of natural control processes make it obvious why adequate field data are seldom obtained to demonstrate conclusively the operation of density-dependent factors (Huffaker and Kennett, 1966). They also explain why one group of workers stresses *changes* in densities and their correlations with variations in weather and another group wishes to learn the relationship between *magnitude* of mean density and whatever regulating factors may be operating, regardless of other, superimposed factors causing wide fluctuations. The general picture described here of very intense action of natural enemies when first introduced into a profusion of their hosts, followed by less intense, if still adequate, action after host densities have been reduced, has been seen many times and is an unquestionable fact of biological control of pest species. The corollary of control by endemic enemies of endemic hosts in natural environments may be assumed to exist, but, by its very nature, this is a less *apparent* occurrence.

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A Note on Competition¹

“COMPETITION” AS A concept in population ecology and natural control continues to be debated in the literature (Nicholson, 1933, 1954; Andrewartha and Birch, 1954; Birch, 1957; Solomon, 1957; Huffaker, 1958; Milne, 1961; Bakker, 1961; Huffaker and Messenger, 1964; Klomp, 1964; and others). Unfortunately, many ecologists use the word in its narrow etymological sense, “together seek,” rather than in its broadest ecological implication. Obviously, simple “seeking together” does not, in itself, necessarily connote competition.

Nicholson (1954) writes, “This state of reciprocal interference which occurs when animals having similar needs live together and which influences their success is here called *competition*.” Odum (1959), referring here to interspecific competition only, applies the term to the state of interaction “. . . in which each population adversely affects the other in the struggle for food, nutrients, living space or other common need.” Plant ecologists have for many years used the term in a sense other than “seeking together,” for plants do not *seek* anything. Even though such usage has been criticized, and terms such as “inhibition” and “interference” have been suggested to cover the comparable concept of processes in plant development and reproduction, competition has remained quite acceptable to plant ecologists in general, for it is a convenient, very meaningful term connoting reciprocal interference as embraced by the above broad definition involving *any need*. As Huxley (1953) emphasized,

words are mere tools, and many words or terms, such as “natural selection,” “survival of the fittest,” and “improvement” are only convenient shorthand expressions for meaningful biological processes or complex sequences of processes. So it is with competition.

In most instances, however, the term competition has been used to indicate a reciprocal interference arising from a shortage in some material resource—water, soil, nutrients, sunlight, space, shelter, nesting sites, food, mates, and the like (Clements and Shelford, 1939; Allee *et al.*, 1949; Andrewartha and Birch, 1954).

Weaver and Clements (1938) clearly stated the nature of competition and the difference between competition and the struggle for existence. They considered that competition always occurs when two or more organisms (in their study, plants) make demands on the environment in excess of the available supply, and that competition thus increases as population density increases. These authors also stated, “There is no competition between a host plant and the parasite upon it, but two or more parasites upon the same host may compete with one another.” In this they are in accord with Darwin’s (1859) statement regarding the relationship of mistletoe plants to their host tree and to each other.

Furthermore, competition, a basically ecological term, has seldom been taken by ecologists to mean anything other than an organism-to-organism relation. The struggle of the organism to survive and reproduce *in the presence* of ad-

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verse physical conditions cannot be taken as competition *against* those conditions. Ecologists in general thus agree with Birch's (1957) objection to Schmalhausen's (1949) notion of individuals competing against harmful physical factors (climate).

As Odum (1959) has stated, Birch (1957) and Williamson (1957) have objected (as have Milne, 1961, Klomp, 1964, and others) to the broad use of the word competition to indicate simply a mutually negative interaction between organisms. They wish to restrict the term to cases in which the negative influences are due to a shortage of materials or of places used by both organisms, thus leaving out other types of mutual interference, such as the secretion of harmful substances and the generation of heat, enemies, or disease. I agree with Odum that the basic meaning should remain broad in scope but should be precisely defined. Nicholson's definition, quoted above, is precise and adequate. I believe, however, that Birch's basic definition and those of Odum and Nicholson are not far apart; the main difference lies in how they interpret the process involved in certain cases, in terms of the definition, and what, in their opinion, constitutes a resource.

I agree with Birch's (1957) objection to Nicholson's (1937) inclusion of predation, as such, as illustrating competition. The predators and the prey do not have similar needs. There is no competition between them in the sense of Nicholson's own definition (see above). Ecologists would commonly agree also with Birch's reluctance to accept, as competition, interference that is not a mutual interference. Again, predation, as such, is a form of nonmutual interference, with reference to the interspecific relation.

My own view of competition, as it is involved in the control of a prey species by a predator, does not differ fundamentally from that of Birch or of

Nicholson. However, as stated previously (Huffaker, 1958), regulation of a population's density by its natural enemies results from competitive processes, even though the predator and prey species do not compete with one another. The prey individuals compete among themselves for security from harm—for living space more or less free of marauding predators. Just as Birch indicated that a suitable tree hole for a tree-hole mosquito should, for example, include the proper pH as a prescribed requirement (resource), in the predator-prey situation the requirement may be a habitat sufficiently free of predators. Increase in density of the tree-hole mosquito may alter the pH unfavorably as granary insects may unfavorably alter the temperature of their medium. Thus, the individuals adversely affect the chances of other individuals' survival and/or reproduction. In the case of the prey population in a reciprocally related predator-prey system, increase in density of the prey generates a greater density of predators and thus causes a decrease in the security of the habitat for the prey. The mere presence of more individuals thus decreases the chance of a given individual's success. This is mutually negative interference—competition.

The individuals of the predator population also compete with one another for their food, the prey, in the usual manner. The process of regulation is thus density-dependent, and results from the interaction of two mutually interlocked systems of intraspecific competition.

In another example, Birch (1957) considered Brian's (1952) observations on ants in which *Formica* sp. displaced *Myrmecia* sp. in a cut-over pine wood. The *Formica* attacked and destroyed the *Myrmecia*. Birch considered that this type of competition fit his precise meaning, although it was by interference rather than superior competition for a resource (exploitation). I assume,

however, that there is direct competition for a resource—the habitat—including elements of food which both species of ants exploit to some extent at least. The predatory action of *Formica* is simply a tool used by the species to achieve competitive superiority with which to exploit the habitat resources.

Fine distinctions have also been made as to whether or not the deleterious effect of competition should be separated from the process itself, and therefore, whether or not it should be included in the definition (Milne, 1961). Furthermore, if the effect is to be included, is the deleterious effect resulting from sociopsychological or mutual interference properly covered by the term competition (Birch, 1957; Christian, 1957; Solomon, 1957; Chitty, 1960; Milne, 1961; Klomp, 1964)? These fine distinctions were ignored (Huffaker, 1958) in inferring that whichever term, inhibition or competition, is more appropriate (etymologically), the concept of a density-induced mutual interference which increases in intensity as density increases, and which we think of as competition, is nevertheless common to all these processes.

For example, Milne (1961) wished to restrict the definition to the searching *process* itself, excluding the result. He nevertheless included in his definition the phrase, "...when that supply (of the resources) is not sufficient for both (or all)..." It is clear that if there were plenty of the resource for all, or if there were no deleterious result, the searching endeavor would not then constitute competition. The process of searching cannot, therefore, be separated from the deleterious result if the meaning ecologists have given to competition is to be retained.

Huffaker (1958) and Huffaker and Messenger (1964) considered that in viewing the overall, and very general, relation involved in the concept of regulation of animal numbers, the focus should be on the density of the popula-

tion under control, rather than on the specific factor or instrument causing the mortality, depressed natality, or emigration. The regulatory mechanism of population density fits the concept of competition in the broad ecological sense of density-induced inhibition or interference. Furthermore, this mechanism applies regardless of what causes the reciprocal interference or deleterious effect(s)—competition for a material resource, mutual or sociopsychological interference, or unfavorable influences on habitat, such as generated heat, waste accumulation, or induced parasitism, predation, or disease. This concept of competition differs from that of Nicholson and Odum only in considering security from harm to be a need. Thus, if increased density causes increased natural enemy action, there is competition in the sense of reciprocal interference—disoperation as opposed to cooperation.

Klomp (1964), Wynne-Edwards (1959), Chitty (1960), and Wellington (1960), on the other hand, apparently regard the density-induced stress of sociopsychological interference as inherently different from competition for space, and therefore, not true competition. However, in the broad general view of competition taken here, we need not be concerned with the problem of whether or not space is actually competed for in such a situation.

Obviously it is practically impossible to test which factor is operating, competition for space, or mutual disturbance. In any hypothetical experiment in which living space were successively reduced, we might find that in some cases, such reduction alone would not reduce the rate of increase until the amount of space reached some critically small point beyond the minimum essential to the health and well-being of the organism—for example, insufficient for mating or normal exercise.

Finally, we feel that if ecologists re-

strict application of the term competition to those cases of mutually deleterious endeavors to obtain needed material resources, we shall simply be forced to adopt other terms to connote: (1) the general concept of competition herein defined (and apparently acceptable to ecologists); and (2) the other aspects of the general concept not covered by the restricted usage. To avoid further, unnecessary proliferation of ecological

terms, we hope that ecologists will continue to regard competition in its broad sense of mutual interference. The term will then retain its greatest usefulness in defining this particular aspect of population dynamics and natural control. (See also Odum, 1959.) Workers wishing to refer to more restricted concepts could either describe the type of example involved, or include proper descriptive adjectives.

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