Ecology of Tetranychid Mites and Their Natural Enemies: A Review

I. Tetranychid Enemies: Their Biological Characters and the Impact of Spray Practices

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II. Tetranychid Populations and Their Possible Control by Predators: An Evaluation

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The two papers presented here were prepared at the request of the Special Committee of the International Biological Program, as part of a broad program on the ecology and natural control of spider mites (Tetranychidae) on a worldwide basis.

Part I is a review of the pertinent literature and a discussion of the biology and ecology of various spider mite enemies, their potential as biological control agents, and the effects of pesticides on their populations.

Part II reviews the literature pertaining to tetranychid abundance, and the evidence supporting various hypotheses concerned with their populations. It evaluates the action of various predators and discusses possible ways of implementing biological control.

A third paper in this series (Part III), by the same authors, will review the literature and discuss the problem of spider mites from the standpoint of their biology, ecology, pest status, and their relationship to host plants. This paper is expected to be published shortly.

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II. Tetranychid Populations and Their Possible Control by Predators: An Evaluation[1,2]

INTRODUCTION

MANY FACTORS interact to affect the abundance of tetranychid mites: (1) features of the life cycle, particularly with regard to movement phases and potentials, reproduction, and diapause; (2) meteorological conditions, including photoperiod effects; (3) the nutrition afforded by the host plant, and its relative susceptibility or resistance to the mites; (4) action of enemies, particularly predators; and (5) the horticultural programs in their entirety, including use of chemicals (and resistance to them), which may operate through or in relation to any of the other factors. Certain of these aspects have been dealt with separately in some detail by McMurtry, Huffaker, and van de Vrie in the first paper of this series. A third paper, to be published separately, will be concerned with biology, ecology, and other significant factors.

Gunther and Jeppson (1960), who have devoted their careers to the study of insecticide toxicology and utilization, in their book *Modern Insecticides and World Food Production,* pointed to the worldwide increase in tetranychids associated with the extensive use of organic pesticides. Chant (1966) stated: "Mites were of decidedly secondary importance in our orchards and fields 30 or 40 years ago. As the use of pesticides in-

tensified in the late 1940's and early 1950's, and as the new organics came into favor, mites began to create damage problems. Today, in many of our states (U.S.A.) mites as a group are rated our most serious pests. In California in 1964, they were so rated and they caused an estimated damage and loss of more than $150,000,000."

Many statements of judgment and research data in the literature suggest that spider mites remain at low levels in situations where their natural enemies are not inhibited by sprays or other factors (e.g., Porter, 1947; Fleschner, Hall, and Ricker, 1955; Lord, Herbert, and MacPhee, 1958; Snetsinger, 1959; Dosse, 1960; Cutright, 1963; Chant, 1963; Putman, 1964; Putman and Herne, 1966; Huffaker and Flaherty, 1966).

The general conclusions in some cases were based on studies in abandoned orchards, as compared with well-managed orchards under fertilizer and pesticide treatments. Such studies can be criticized on the grounds that foliage in such orchards may be deficient in nutrients or injured by disease, so that it is not favorable for spider mites. Kuenen (1946, 1949), Garman and Kennedy (1949), Kuenen and Post (1958), and Post (1962a,b) found marked differences between spider mite reproduction on

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leaves from trees in abandoned orchards and on those from trees in well-kept, fertilized orchards. (See subsequently herein.) Furthermore, the pesticides themselves may alter nutritional quality in the leaves (Rodriguez, Chen, and Smith, 1957; Rodriguez, Maynard, and Smith, 1960; Chaboussou, 1963*a,b*, 1965; Bogdanoff, 1964).

Huffaker and Flaherty (1966) briefly postulated the post-World War II history of tetranychid outbreaks as follows:

"Generalizations are dangerous and may run counter to specific examples. Nevertheless, it seems to be a well-founded generality that 1) plant feeding mites in natural areas untreated with chemicals or uninfluenced by man, dust, etc., seldom extensively damage their hosts and are often so scarce they are difficult to collect, 2) before introduction of DDT and other synthetic materials, these mites though injurious at times, were not as perennially severe as they became after extensive use of these materials, and 3) the overriding common denominator is that in the natural situations and in our crops previously, the natural enemies were effective natural control agents." The present review has uncovered no substantial disagreement with points (1) and (2) above regarding tetranychids. It has by no means disproved but it has weakened (3), for much evidence exists to the effect that other factors than the destruction of enemies may have profound effects on or be a principal cause of mite outbreaks in some situations. Much of the support for the predator hypothesis is of a correlative nature, and much thorough ecological work is needed if it is to be fully proved that predators are indeed the main factor.

Three main avenues to understanding such outbreaks are: improved nutritional conditions (1) associated with improved care of the crops independent of pesticides; and (2) associated with use of the new pesticides or other agricultural sprays; and (3) the detrimental influences of pesticides on the enemies.

The third paper in this series will examine in detail the physiologically-induced response (mainly in fecundity) of mites that is associated with nutritional condition of the host plants and with use of agricultural sprays. McMurtry, Huffaker, and van de Vrie, in the first paper, considered the direct and indirect effects of spay practices on mite predators, and cited studies that have also shown the capacities of various mite predators to reproduce at a high rate and to consume large numbers of phytophagous mites. Here, however, we are interested in evidence primarily from the field, at the total, interacting *population* level. It has been possible to achieve seasonal control of *Tetranychus urticae* Koch in field strawberries by releases each season of *Phytoseiulus persimilis* Athias-Henriot (Oatman and McMurtry, 1966; Oatman *et al.*, 1967). The predator species in this case is not yet established, and depends on repeated colonizations for its effect. Huffaker and Kennett (1956) were also able to achieve good control of the tarsonemid, cyclamen mite (*Steneotarsonemus pallidus* (Banks)), in strawberries by stocking newly planted fields with both the cyclamen mite and its predators, *Amblyseius aurescens* Athias-Henriot and *Metaseiulus cucumeris* (Ouds.). Since both the presence and absence of predators were achieved without use of a pesticide, the marked differences noted in abundance of the mites cannot be regarded as pesticide-induced.

FIELD EVIDENCE FOR THE HYPOTHESIS
OF PHYSIOLOGICAL INDUCEMENT

As indicated above, the better nutrition provided by well-fertilized, pruned, properly managed, flush-growth fruit trees is, in some situations at least, more conducive to mite increase than is the less favorable nutrition commonly found in abandoned orchards. Henderson and Holloway (1942) and Jeppson, Fleschner, and Complin (1957) also found that the seasons of rapid flush growth in citrus were most conducive to build-up of populations of *Metatetranychus citri* (McGregor). Increase in a given nutritive element that *increases* fecundity in one mite species or on one plant host, or in one season of the year, however, may in fact *decrease* fecundity in certain other situations (see later discussion). Furthermore, use of certain of the chlorinated hydrocarbons, organic phosphates, and carbamates may also alter host-plant physiology to favor spider mite increases. Even more clear is the fact that most of the pesticides now used are moderately to very hazardous to predators of tetranychids, depending on a given situation (see first paper in this series).

Since predators are an inherent element of the ecosystem in undisturbed situations, field analysis of the role of these other factors cannot be viewed in isolation from the predators' potentialities for control. Thus, a number of workers (e.g., Mathys, 1958; Lord and Stewart, 1961; Collyer, 1964b,c; van de Vrie, 1965; Putman and Herne, 1966; Huffaker and Flaherty, 1966; Flaherty, 1967) appear to hypothesize that the enemies would commonly, but not invariably, prevent mite outbreaks even in the presence of factors that promote fecundity if such conditions could be obtained without adverse effects on the enemies. This hypothesis, i.e., the potential of key enemies to maintain control, can be tested under conditions offering the highest possible conduciveness to tetranychid increase relative to nutrition and any presumed pesticide-induced stimulation. The necessary conditions can be established by hydroponic cultures, where feasible, or simply simulated by repeatedly adding eggs or mites to the population, in numbers sufficient to equal maximum fecundity for the parents present. Plots having a full complex of key predators could then be compared with ones in which predators are either removed by hand or otherwise excluded. Such a study on apple has been completed by van de Vrie and Boersma (1970), and a similar study on strawberry is being conducted in Berkeley.

Post's (1959, 1962a,b) work on apples presents evidence supporting the hypothesis that mite outbreaks have been physiologically induced by improved host-plant nutrition. In one experiment, in the Netherlands, Post started with a well-cared-for and regularly sprayed young apple orchard with an initial high density of *Panonychus ulmi* (Koch) and virtually no predator complex. She obtained decreases in mite populations in the plots where soil treatment, fertilization, and pruning were then abandoned. This occurred in the plots from which pesticides were deleted as well as in those in which they were continued. In the plots where all the treatments (i.e., soil treatment, fertilization, pruning, and spraying) were practiced, Post found that the effect of the application of pesticides on the excessive increase of *P. ulmi* was less important than that of soil treatment and pruning. The decline in mites was also correlated with an observed decline in nitrogen levels in the leaves. Much of Post's work was primarily descriptive in nature, and the role of enemies was not fully con-

sidered in the experimental part of her work. In a second experiment begun in a neglected orchard in which *P. ulmi* occurred sporadically, increases in this species were associated with increases in nitrogen content of the leaves resulting from introduction of an improved program of soil management. Predatory mites (mainly *Typhlodromus aberrans* Ouds.) were somewhat more numerous in plots having higher densities of *P. ulmi*. Predaceous Hemiptera were present, but were erratically distributed. Post considered that these predators were not sufficient to prevent the observed increases in *P. ulmi*.

A critical consideration is whether Post, in her field studies, was dealing with the best predatory species for preventing the increases. She reported *Typhlodromus aberrans* to be most numerous, and little is known about it, whereas *T. pyri* has been reported to be effective against this species on apple in the Netherlands (van de Vrie, 1964*a;* van de Vrie and Kropczyńska, 1965) and in England (see below). In Post's first experiment, the predator complex had possibly not had sufficient time to develop to normal efficiency.

In any event, it seems almost inconceivable that just after World War II a massive, worldwide, place-by-place, crop-by-crop improvement in cultural conditions took place, so precisely synchronized as to account for the many cases of upsurge of tetranychids which suddenly occurred at that time, and which were associated with the use of many different kinds of chemicals. (See discussion below.) That the increases were induced by the pesticides entering the picture at that time is a much more conceivable general explanation, provided adequate evidence exists that fecundity is so generally increased in both mites and insects, by each of the materials concerned, as to account for the general phenomenon. The evidence seems quite inadequate to support this conception, but Chaboussou's work (see below) suggests this possibility. (It seems more plausible, and consistent with much of the evidence, that the mite enemies, being ubiquitous and generally quite adversely affected by the new materials being introduced, were simply kept from exerting the control previously effected. Furthermore, figures 1 and 2 suggest an important predator component in any event.)

Chaboussou (1960, 1961*a,b*, 1963*a,b, c*, 1964, 1965, 1966) has conducted extensive studies on the effects of pesticides, including fungicides, on internal leaf biochemistry in relation to the nutritional requirements and reproductive response of several species of spider mites. In his 1965 paper, for example, he considers that all the common agricultural pesticides can enter the plant, when applied at the standard dosages, in amounts sufficient to cause physiological effects paralleling those of the growth substances (e.g., 2,4-D) applied in much lesser amounts.

Moreover, Chaboussou also presents very convincing data indicating why responses in mite fecundity or in population size have in some instances followed use of a given pesticide while in other cases no such responses have occurred. The changes arising present altered nutritional possibilities for the mites—they affect, for example, the proportional occurrence of amino acids and of sugars, i.e., nitrogen and carbon. They also affect the potassium and protein nitrogen content of the leaves— considered important in the nutrition of *Panonychus ulmi*. Young, mature, and senescent leaves differ biochemically, and the influence of a given pesticide, as to whether it would induce increased nutritional possibilities for the mite, would depend upon the particular biochemical state of the leaf, the weather, and so forth, as well as on the nature of the pesticide (see also Bogdanoff, 1964). Moreover, different mite species may have different nutritional

optimums with respect to amino acids, sugars, and other biochemical compounds. Chaboussou considers this an explanation for *Tetranychus telarius* following *P. ulmi* late in the season, on apples, and it would theoretically explain why a reproductive response might occur in one mite species but not in another.

The study of fundamental biochem-ical changes in plants associated with use of pesticides is a new field, and Chaboussou's work is a major attempt to relate those changes to mite outbreaks. The changes are not yet fully understood, but Chaboussou has found certain correlations between the effects of pesticides on plant biochemistry and the known nutritional needs of certain spider mites. He has also found that mites respond reproductively, in either the laboratory or field, to such materials as carbaryl, DDT, parathion, diazinon, and even Bordeaux mixture.

An interesting feature of these studies (inconsistent with the predator hypothesis) has been the finding that sometimes a great increase in the mite population has followed either a light or heavy treatment, and that the greater increase has been associated with the lower dosage. Also, carbaryl has given higher responses in some cases than has DDT, even though both would presumably have interfered rather completely with effective predator action. The results unquestionably indicate that more than repressed predator action is involved in many mite outbreaks, and Chaboussou thinks that destruction of predators is certainly not the main explanation.

Chaboussou's studies were short-term ones, however, as he deliberately shifted plots year by year. The studies were thus primarily physiological, not ecological. Chaboussou made no adequate study of influences on predators and their possible action or lack of action in his field populations. This conclusion is suggested by his (1963) state-ment that phytoseiids are not affected by DDT. The results, therefore, are hardly a general answer to the question of whether or not really effective predators could have prevented the observed increases had they not been simultaneously rendered ineffective in the environment, nor whether predators were, in fact, significant factors in the low densities prevailing before the more powerful "stimulative" pesticides were introduced. The results do strongly suggest, however, that in many situations where effective predators are either absent or rendered ineffective by use of chemicals, the rise and decline of spider mites can be a function of the chemicals used. Those chemicals may result in both direct toxic effects and, subsequently, in many cases, indirect physiological inducement to increase. But increase in fecundity does not automatically mean increased densities—at least not to outbreak status—for this assumption ignores compensatory mortality.

Other work by Kuenen (1946, 1949), Huffaker and Spitzer (1950), Fleschner (1952), Hueck (1953), and Kuenen and Post (1958) at least in part supports the hypothesis of physiological stimulation in one or more respects. Huffaker and Spitzer did not find destruction of predators by DDT to be the principal cause of the marked increase in spider mites on pears in northern California following World War II, nor did the predators considered appear to be effective. (Too little attention was probably paid to phytoseiids in that study.) They did find that the deletion of oil (used as a "spreader" in the old lead arsenate program) was a key factor in the build-up, as the oils were effective against *Panonychus ulmi* in the spring. Those authors, as well as Fleschner (1952) and Hueck (1953), also reported DDT to stimulate spider mite increase to greater or lesser degree.

FIELD EVIDENCE FOR THE HYPOTHESIS
OF PREDATOR INHIBITION

At present, the evidence tends to support predator inhibition as the main, but not the only, reason for the *world-wide* upsurge of spider mites since World War II. This seems true in spite of the evidence cited above that cultural, fertilizing, and pesticide-control practices do stimulate mite fecundity in some, perhaps even in a great many, situations. Endemic enemy complexes, when uninhibited, appear to possess a substantial compensatory ability to control spider mites, whether or not the latter's fecundity is stimulated (within limits), if they are not themselves simultaneously rendered ineffective. Those possessing good powers of searching and specialization, relative to their food requirements, appear particularly effective in maintaining low prey densities, while those having higher powers of consumption are often effective in quick suppression of "escape" situations, but not in maintaining low densities.

The broad scope of pesticide effects on predators was recently reviewed (Huffaker, van de Vrie, and McMurtry, 1969; and the first paper in this series). The adverse effects are certainly sufficient, in general, to interfere greatly with predator efficiency. The question primarily raised, then, is whether existing predators were, in general, significant factors in the low levels of mites prevailing before such treatments came into practice. Obviously, if the plant hosts simply were not nutritionally conducive to support of high numbers of mites, the predators present may have had little meaning.

This would imply that they are rather ineffective controlling agents in the situations concerned; else they would have reduced their prey's abundance to levels below what the available nutrition would support. Possibly in some neglected orchards or in certain unfavorable host-plant situations, the low numbers of mites could have been due to a combination of both factors. Thus numbers might have been relatively low even if no predators were present, but not so low as they would have been if predators had not been inhibited. The possibility of pesticides increasing the fecundity of the mites and also inhibiting the predators is very real.

Cases suggesting, albeit not proving, the predator-inhibition hypothesis are worldwide, and relate to a great variety of spider mites, predators or predator complexes, crops, management practices, and climatic conditions. A reliable capacity to keep mites suppressed under such a wide variety of field situations almost surely means the ability to control them even if their reproductive proclivity were inherently high at the time, as when fecundity is stimulated (figs. 1 and 2).

While some of the earlier work was done before it became rather generally recognized that both fertilizer programs and other cultural methods, as well as the pesticides used in the spray program, can increase the reproductive proclivity of spider mites, most of the studies here listed were conducted later. Their evidence suggested efficiency of predators, with inhibition a real factor in the mite increases involved.

The Worldwide Record

Support for this hypothesis includes, for *Panonychus ulmi, Tetranychus urticae* and/or *T. telarius,* and other species, on apple: *Austria* (Dosse, 1961a); *Canada* (Lord, 1949; Herbert, 1953; Lord, Herbert, and MacPhee,

1958; Lord and Stewart, 1961); *England* (Massee, 1958; Collyer, 1964*a;* Muir, 1965*a,b*); *Germany* (Andersen, 1947; Dosse, 1956, 1960; Berker, 1956, 1958); *Japan* (Hukusima, Tsugawa, and Taneichi, 1958); *Lebanon* (Dosse, 1967); *The Netherlands* (Kuenen, 1947; van de Vrie and Kropczyńska, 1965; Kropczyńska and van de Vrie, 1965); *New Zealand* (Collyer, 1964*d*); *Poland* (Wiackowski and Suski, 1962; Niemczyk and Wiackowski, 1965; Niemczyk, 1966*a,b*); *Switzerland* (Günthart and Clausen, 1959); *United States* (L. F. Steiner, Arnold, and Summerland, 1944; Steiner, Summerland, and Fahey, 1946; Clancy and Pollard, 1952; Clancy and McAlister, 1958; Snetsinger, 1959); for *Bryobia redikorzevi* Reck and *Tetranychus crataegi* Hirst on apple (Begljarov, 1957); and for various species: citrus (DeBach, Fleschner, and Dietrick, 1950; Fleschner, 1958*b;* McMurtry and Johnson, 1966; Dosse, 1967); avocado (Fleschner, Hall, and Ricker, 1955; Fleschner, 1958*b;* Chant and Fleschner, 1960); grape (Mathys, 1955, 1956, 1958; Huffaker and Flaherty, 1966; Flaherty, 1967); various miscellaneous hosts (English and Tinker, 1954; Chant, 1963); and, if a tarsonemid is admitted, on strawberries (Huffaker and Spitzer, 1951; Huffaker and Kennett, 1953, 1956). In these studies, several different species of phytoseiids effectively preying on various spider mites on a variety of plant hosts were involved, e.g., *Metaseiulus occidentalis* (Nesbitt) preying on either six-spotted mite or two-spotted mite on oranges and strawberries, *Typhlodromus pyri* (Scheut.) preying on *Panonychus ulmi* on apple and plum, and *Phytoseiulus persimilis* preying on *T. urticae* on beans, cucumbers, and strawberry.

A number of these examples are discussed in the following section, and others are referred to in relation to various aspects of predator control considered later. Valuable supporting evidence from population interactions in laboratory, growth-chamber, or greenhouse studies is also presented with respect to the potential of certain predators for control of spider mites (Huffaker and Kennett, 1956; Huffaker, 1958; Collyer, 1958, 1964*a,b;* Chant, 1961*a;* Herbert, 1926*b;* Bravenboer and Dosse, 1962; Bravenboer, 1965; Huffaker, Shea, and Herman, 1963; F. F. Smith, Henneberry, and Boswell, 1963; Hussey, Parr, and Gould, 1965; van de Vrie and Kropczyńska, 1965; Huffaker and Flaherty, 1966; McMurtry and Scriven, 1966*a,b;* Begljarov, 1967; Laing, 1968; Laing and Huffaker, 1969).

Post's (1959, 1962*a,b*) results, furthermore, do not refute the hypothesis that a single good enemy or a full complex of adapted enemies, uninhibited by sprays, may have prevented prey increase even though fecundity is increased. Collyer's (1964*a,b*), van de Vrie and Kropczyńska's (1965) and Flaherty's (1967) studies strongly indicate that considerable time may be required after cessation of pesticide treatments before an effective complement of enemies or a balanced situation can be established. Also, Lord and Stewart (1961) failed to obtain an increase either in *Panonychus ulmi* or other tetranychids when increased levels of nitrogen were applied in apple orchards in Nova Scotia long held under a modified spray program designed to favor natural enemies. Such a test would have had additional value if supplemental tests had been conducted where mite predators were removed, and a response to nitrogen shown. Moreover, Putman (1964) found that *P. ulmi* laid as many eggs on peach leaves from abandoned orchards as on those from well-managed and fertilized ones. These results, however, are not inconsistent with Chaboussou's hypothesis.

Collyer (1964*d*) found that in previously well-managed and treated apple

orchards at Auckland, New Zealand, re-
duction in treatments with materials
known to be toxic to predators of mites
and use of less toxic materials resulted
in initial increases in *Panonychus ulmi,*
but that after a time the populations
declined to acceptable economic levels.
Collyer wrote: "*Stethorus bifidus* Ka-
pur is usually the first predator to
become abundant and is often the spe-
cies responsible for the decline of the
phytophagous species, but being de-
pendent on mites, cannot survive after
they are reduced to a low level; the
predacious mites *Typhlodromus pyri*
Scheuten and *Agistemus longisetus*
Gonzalez then become established and
prevent a resurgence of the harmful
species."

An established sequence such as this
means that since the tetranychid did
not maintain the initial high densities
even though the cultural conditions
shown to be nutritionally favorable to
its increased fecundity (see previous
section herein) were continued, means
that some *other* factor was preventing
the realization of a continued high
abundance. The predator action ob-
served was postulated as a sufficient ex-
planation. Also, the omission of treat-
ments with DDT and other materials
known to have a stimulative effect on
tetranychid fecundity at times did not
result in a decline in mites, as required
under this hypothesis, but rather the
reverse. Since some time is required
after cessation of such treatments be-
fore a predator complex can become
established or reach a favorable ratio
of abundance (van de Vrie and Krop-
czyńska, 1965), subsequent declines are
consistent with Collyer's claim of ene-
mies (including disease) as sufficient
cause. A. D. Pickett (personal com-
munication) has long claimed that de-
finitive studies conducted in the ab-
sence of disturbing treatments must be
continued over a long period of years
if the true potential of an enemy com-
plex is to be ascertained.

Some of the material in the preceding
section that is opposed to the view that
mite outbreaks in general have been nu-
tritionally or physiologically induced
is also pertinent to this section.

Many studies throughout the world
suggest, although they do not prove, the
predator-inhibition hypothesis, as indi-
cated by the predators' power to control
mites, and the increase in mites follow-
ing suppression of predators by treat-
ments. Such cases pertain to a great va-
riety of spider mites, predators, crops,
and climatic conditions. Reliable ability
to control mites under a variety of field
conditions almost surely means ability
to control them even when their fecun-
dity is near a maximum, for example,
when stimulated. While much evidence
is fragmentary, other evidence is the
result of elaborate studies conducted
over many years. Most of the recorded
outbreaks have accompanied use of
pesticides. Collectively, and weighed
against the limited evidence for the
alternative hypothesis, destruction of
predators by pesticides appears to be
the more commonly accepted explana-
tion of such mite outbreaks. The very
great number of workers who have
drawn such conclusions on the effective-
ness of predators, either from critical
or limited data or based largely on ex-
perience, cannot be taken lightly. Vast
collective experience lies behind these
conclusions. We do not imply that
predator inhibition has been the only
reason for mite outbreaks. Other causes
have also been involved. But data indi-
cating that predators have, on so many
occasions, kept mites under control ex-
cept when pesticides were applied, gives
collateral support to the predator-inhi-
bition hypothesis, if we may assume
that predators could prevent increases
in numbers, in spite of an augmented
prey fecundity, if they were not, in
fact, incapacitated by the treatments.
We believe that many of the good ones
have such abilities. Also, compounds
that both stimulate fecundity and de-

stroy the predators could act in a two-fold manner to cause outbreaks. If fecundity of mites is increased at the same time that the predators are destroyed, the predators will be less likely to recover in time to prevent serious damage. Such materials would be likely to cause more serious outbreaks than ones that destroy predators but do not stimulate fecundity.

Especially pertinent, figures 1 and 2 clearly show the capability of the phytoseiid *Amblyseius potentillae* to compensate for a much increased fecundity in the prey species, *Panonychus ulmi*. Van de Vrie conducted tests on the population development of *P. ulmi* on apple grown under three levels of nitrogen and with *A. potentillae* (1) absent and (2) present. Figure 1 shows that the total prey eggs produced on the high-nitrogen trees in July was more than four times that under the low level of nitrogen, and that the females lived one-third longer on the high-nitrogen trees. Figure 2 shows the efficiency of *A. pyri* (right) in curtailing the *P. ulmi* population increase in spite of this inherently increased fecundity in July (assumed near a maximum). In the absence of predators, the high-nitrogen, intermediate-nitrogen, and low-nitrogen trees developed damaging populations, strikingly so for the high- and intermediate-nitrogen levels. It is most significant that in the presence of the predators, on the contrary, the *P. ulmi* population never attained economic densities even under the highest nitrogen level. The fact that the prey populations under the high, intermediate, and low levels of nitrogen in the presence of predators still stood in the same order, or sequence of pattern, although differing only slightly, means that the predators did not *completely* compensate in the ecological sense, although the compensation was all that was required in the economic sense.

Putman and Herne (1966) consider that outbreaks of phytophagous mites under the use of broad-spectrum pesticides (largely without proved stimulation of fecundity) constitute the most cogent argument for the hypothesis of predator control. Support for this view is widespread even among those who recognize that other factors form a meaningful part of the picture in given situations. Yet, use of the "check method" (DeBach, 1946, 1955; Huffaker and Spitzer, 1951; Fleschner, Hall, and Ricker, 1955; Huffaker and Kennett, 1956; Huffaker and Flaherty, 1966; Flaherty, 1967; and others) for removal or inhibition of predators in one set of plots, while leaving them undisturbed in others, has furnished the most concrete support concerning both insect and mite outbreaks. This evidence is particularly strong in cases where associated tests have employed some method of removal in addition to the pesticide (e.g., by hand—Fleschner, Hall, and Ricker, 1955; Huffaker and Kennett, 1956; physical exclusion—Smith and DeBach, 1942; Huffaker and Kennett, unpublished data; Dosse, 1960; use of a biotic check method (ants)—DeBach, Dietrick, and Fleschner, 1951; DeBach, 1958) and also where tests have failed to demonstrate any stimulation by the pesticide (Warren and King, 1959; Pielou, 1962; van de Vrie, 1964a). In many instances the pesticide associated with a later increase had a direct adverse rather than stimulative effect on the pest species (e.g., Huffaker and Spitzer, 1951; Huffaker and Kennett, 1956; Collyer and Kirby, 1959).

Where such check methods are not employed, the problem of appraisal is most complex, for the situation does not lend itself to long-term analyses such as those of Morris (1959, 1963a, b), Varley and Gradwell (1963), Neilson and Morris (1964), Klomp (1966b), Campbell (1967), and Huffaker et al. (1968). The control may be quite complex and inconspicuous, so that at low endemic
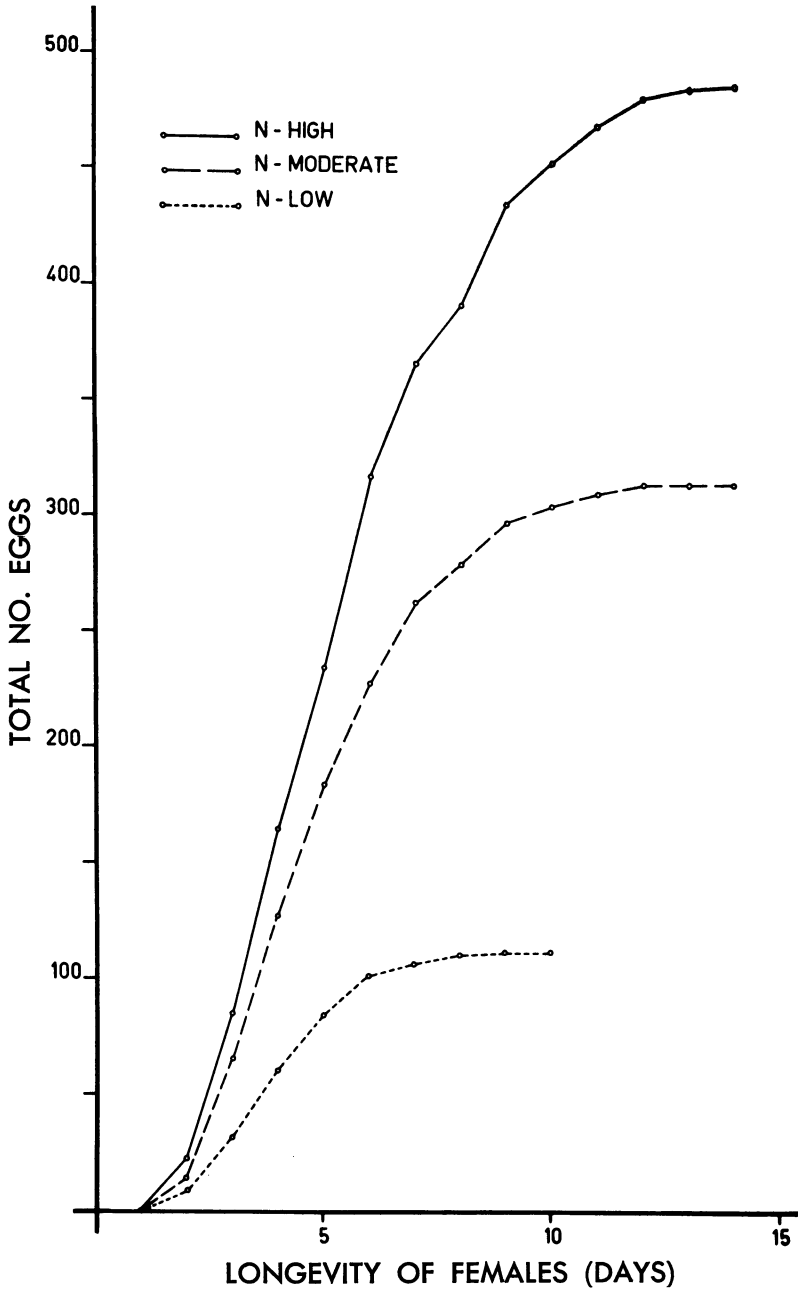
Fig. 1. Egg production and longevity of *Panonychus ulmi* on apple grown under low, moderate, and high levels of nitrogen. (Adapted from van de Vrie and Boersma, 1970.)
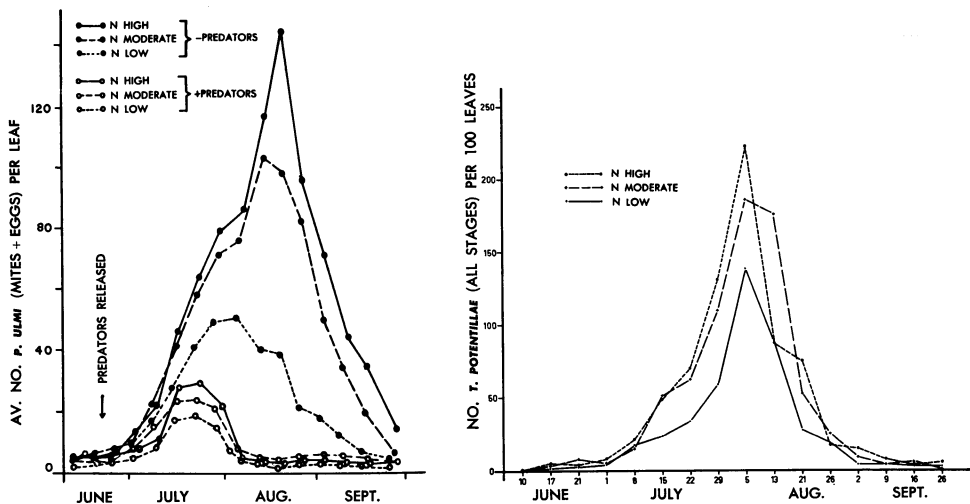
Fig. 2. Left: Populations of *Panonychus ulmi* on apple grown under low, medium, and high levels of nitrogen, with and without the predator *Amblyseius* (= *Typhlodromus*) *potentillae*. Right: Number of *A. potentillae* (all stages) present on apple trees shown at left. The predators present almost completely compensated for the stimulative effect of the high nitrogen level on the fecundity of the prey. (Adapted from van de Vrie and Boersma, 1970.)

densities only the most painstaking methods would reveal true relations. (See Putman and Herne, below, concerning *Panonychus ulmi* on peaches, and Huffaker *et al.* (1968) and Hassell and Huffaker (1969) concerning certain general parameters.)

Observations and studies also indicate that the existing predator complexes have, in many cases, been unable to control tetranychids adequately. A previous disturbance or other imposed factors may, however, have been involved. The fact that certain predators do not achieve control in a particular situation or with a given species does not mean that this applies for other situations or other pest species.

Kremer (1956) concluded, from a two-year study, that an undetermined species of *Typhlodromus*, two anthocorids, *Orius minutus* L. and *Anthocoris nemorum* L., and the coccinellid *Stethorus* (= *Scymnus*) *punctillum* (Weise), all of which avidly fed on *Bryobia arborea* Morgan and Anderson on apple, did not build up in numbers sufficiently early in the year to have a significant influence on the first two generations, but that they had a partial influence on the last (third) generation. Hoyt *et al.* (1967) reported that predation in early season, against *Panonychus ulmi* on apples in Washington, was commonly inadequate, as did Cottier (1934) for this species in New Zealand. Other examples not previously cited that suggest certain inherent or imposed inadequacies of predators in particular situations include the work of Andersen (1947), Roesler (1954), Anderson and Morgan (1958), Chant (1959), Krämer (1961), Dosse (1962b), Post (1962a), and Kuchlein (1967). Some of these are discussed later.

Finally, we note also the view of L. R. Jeppson (personal communication) that increases in phytophagous mites during the past two decades are far from general, being represented mainly by a dozen or so species in the genera *Panonychus* and *Tetranychus;* and that the literature indicates little increase in species of *Oligonychus, Eotetranychus,* and even *Bryobia.* Jeppson questions why a great many more species have not become very troublesome if predators,

which have become seriously reduced, are the primary factor in keeping such populations below injurious levels. Jeppson concludes that the problems and the explanations are more specific than general. We agree that the problem(s) and the explanation(s) are to some extent specific, but we also feel that in the important genera concerned, i.e., *Panonychus* and *Tetranychus*, the phenomenon has had a rather general expression. Moreover, we cannot agree with the gross assumption of Jeppson that since predators have been seriously reduced, plant-feeding mites should have increased much more generally if predators are in fact important in their control. Some species of such mites (e.g., *Bryobia arborea*) seem highly immune to predation by certain predators that are so efficient against certain species of *Panonychus* and *Tetranychus*. Moreover, the pesticides that have been used can be expected to have served to control some phytophagous species, while increases in *Panonychus* and *Tetranychus* may be a factor through competitive suppression of still other species. Jeppson's idea, however, introduces a needed element of caution.

Long-term Studies Indicating Predator Control for Deciduous Fruits and Grapes

As summarized by Collyer (1964a) and presented by her in detail in various earlier papers, the dynamics of *Panonychus ulmi* on apples in England presents one of our clearest indications of effective control of a spider mite by its enemies and of the interference in that control by various pesticides.[3] Of the many insectan and acarine predators of phytophagous mites on apple in England, two are considered of major importance, the phytoseiid *Typhlodromus pyri* and the mirid *Blepharidopterus angulatus* (Fall.).

At first, the mirid appeared to be the major factor (Collyer, 1952), but observations over many years indicated that it was an unreliable control agent, for where it was the sole or main predator, *Panonychus ulmi* fluctuated strikingly, "in almost classical style," being abundant enough to cause economic damage for two to three years and then remaining at low levels for two to three years (Collyer, 1953a, 1960). Muir (1965a,b) further describes this situation. *Blepharidopterus angulatus* hatches four to five weeks later than does *P. ulmi*. In years of very good control, the predation was most effective at the beginning of the second mite generation. Muir estimates that one *B. angulatus* can stabilize a *P. ulmi* population of approximately 2,000, made up of 40 per cent mites and 60 per cent eggs. When the predator:mite ratio became greater than this, the mite population was reduced, but when the ratio was lower, the mite population increased. Egg production of *B. angulatus* was correlated with the density of the prey; egg density was low following seasons in which the mite was scarce because of heavy predation, and higher following seasons of higher mite density. Collyer (1964a) adds, ". . . whereas the phytophagous mite is able to increase from low to very high numbers in one season, the mirid requires a fairly high level of food supply and, being univoltine, requires more than one season to build up again after it has been reduced to low numbers by inadequate food supply. . . . Following these observations it appeared that mites of the family Phytoseiidae were potentially a more useful group of [mite] predators, and subsequent work has confirmed this opinion."

Collyer and Kirby (1959) first ob-

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[3] Huffaker and Kennett (1956) present a well-documented case concerning control by phytoseiids of the tarsonemid *Steneotarsonemus pallidus* (Banks) on strawberries.

tained a strong indication that *Typhlodromus pyri* was a valuable predator when they found that treatments with lime-sulfur were associated with reductions in *T. pyri*, and, initially, some reduction in *Panonychus ulmi*, but were followed by increases in *P. ulmi*, with continued depressed numbers of *T. pyri*. Collyer and Kirby also reported that various insect predators were present, but their numbers varied from tree to tree and did not appear to be correlated with differences in *P. ulmi* densities, a finding that is similar to that reported (Huffaker and Spitzer, 1950) concerning insectan predators of *P. ulmi* and *Tetranychus urticae* on pears in California.

Collyer (1958) conducted insectary experiments with potted *Prunus* seedlings, in which differential numbers of *Typhlodromus pyri* were introduced onto plants that had up to 10 times as many *Panonychus ulmi* as predators (i.e., ratios of 5, 25, or 50, to 5). The action of *T. pyri* (under these limited conditions) was thus tested in the absence of any chemicals or any assistance from other kinds of predators. The predators in each case held the *P. ulmi* populations at levels of less than one mite per leaf (less than 50 per plant) throughout the summer, whereas in the absence of *T. pyri*, rapid increases occurred.

Chant (1959) questioned not only the ability of *Typhlodromus pyri* to control *Panonychus ulmi* on apples, but also the importance of phytoseiids in general as biological control agents. Chant presented two basic points: (1) He considered that *T. pyri* exhibited a distribution, by leaves and by position in the trees, that was too dissimilar to that of *P. ulmi* for it to be an effective predator; and (2) *T. pyri* fed on pollen and other alternative foods, and this was considered, of itself, to be a sufficient criterion of a poor predator.

Regarding Chant's first point, synchronized habitat occupancy would be essential, but concurrent similarity in frequency distributions on the leaves would be found only coincidentally, and only at a particular time, if the predator were a controlling factor and the interaction an oscillating one (see later discussion).

Regarding Chant's second point, Collyer (1964*b*) showed that when *Typhlodromus pyri* was provided alternative prey, *Aculus fockeui* (Nal.), it fed on both phytophagous species but still controlled *Panonychus ulmi*. Acceptance of pollen, honeydew, and other foods may result in maintenance of a better distribution and higher density of predators at low prey density. Predators will not decline to catastrophic levels when prey are absent (or nearly so). If they do nevertheless prefer a particular prey—for example, *Amblyseius aurescens* and *Metaseiulus cucumeris* prefer cyclamen mites (Huffaker and Kennett, 1956)—they survive well distributed in the habitat and can more quickly respond to subsequent increases in prey density. (See later discussion.) Moreover, Dosse (1961*b*) supported Collyer's contention that *T. pyri* can be an effective predator of *P. ulmi* on apple, and showed that it requires mites as food. He found that it can reproduce when feeding on pollen alone, but for only one generation. The dependence on *P. ulmi* is therefore evident, but survival of the predator is cushioned, by feeding on pollen, against the problem of low density occasioned by *P. ulmi* scarcity for one generation.

Collyer (1964*a*) reports continuation of the field study conducted by Chant (1959) in 1953–1956. Chant had also considered that the high winter mortality suffered by *Typhlodromus pyri* contributed to its assumed inefficiency. Collyer considered that, in the absence of additional pesticide-caused reductions, it was nevertheless capable of adequately rebounding in the spring. The reduced densities of phytoseiids in the spring, in contrast to those in the

autumn, has been noted by Dosse (1957), van de Vrie (1965) and Boczek, Dabrowski, and Kapala (1967). Because only females overwinter, a part of the difference depends on the proportion of males in the autumn population. Van de Vrie (1965) also considered that the high winter mortality observed by Chant was partly due to the absence or abrasion of suitable overwintering sites.

Chant (1959) also stated that the fecundity of *Typhlodromus pyri* is low, and the number of generations is less than for *Panonychus ulmi*. As Huffaker and Flaherty (1966), Laing (1968), and Laing and Huffaker (1969) illustrated, such statements can be most misleading. This species' demonstrated capacity to overtake *P. ulmi* and hold it in check over substantial periods of time in both field and laboratory proves that it has sufficient power to increase, relative to *P. ulmi's net effective* power to increase (beyond the number eaten).

Both Chant and Collyer obtained differential numbers of *Typhlodromus pyri* that survived the winter on young apple trees, mainly in bands of sacking used to tie the trees to stakes. In one experiment (Collyer, 1964a), the bands were either covered or not covered before the trees were treated with a non-differential chemical, winter oil.[4] In another experiment (Chant, 1958, 1959), the bands were either removed or left on the trees. During the first season of his study, Chant compared the influence of two different levels of abundance of *T. pyri* on the populations of *Panonychus ulmi*. The trees on which *T. pyri* was abundant had slightly fewer *P. ulmi* during the first year, but these differences were not statistically significant. During the second year, the predators were approximately 15 times as numerous on the sacking-banded

trees, but numbers of *P. ulmi* were again not significantly lower than on plots where the predator was scarce. Collyer (1964a) noted that Chant's data exhibited a consistent, although not significant, difference in the *P. ulmi* populations, the higher populations being on the trees where *T. pyri* had been reduced. Her continued studies with the same trees, for three more years, showed that these differences became much more pronounced from 1957 to 1959. Furthermore, after the initially high densities of *P. ulmi* were reduced, they did not again exceed two mites per leaf in the presence of normal numbers of *T. pyri*, but where *T. pyri* were reduced each winter, the mites reached peaks of 20 to 30 per leaf.

Van de Vrie and Kropczyńska (1965), also working in the field with *Panonychus ulmi*, but with a different phytoseiid, *Amblyseius potentillae* (Garman), obtained different levels in density of prey and predators by adding either prey or predators to small apple trees uniformly treated in all other respects. They found that at initial densities of 30 to 60 *P. ulmi* per predator it took almost two seasons before *A. potentillae* checked the *P. ulmi* populations satisfactorily; when the initial ratios of prey:predators were more favorable to the predator, control was attained more quickly. These results again support Collyer's findings. Collyer (1964a) concludes: "Variation of *P. ulmi* populations from year to year was probably due to such general factors as weather conditions and insect predators which operated throughout the orchard; differences which developed between treatments most probably resulted from the relative numbers of *T. pyri*, the only factor that was deliberately adjusted."

Studies of predation on *P. ulmi* and

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[4] Neither Chaboussou nor other workers has shown any means by which winter oil, when not applied to foliage, produces mite-favoring internal biochemical changes. Anyway, the foliage materials here used were applied to the foliage of both test groups of trees; the difference here lay only in the oil in the sacking bands.

other orchard tetranychids have been conducted over a period of many years in eastern Canada (e.g., Putman, 1937, 1955, 1959, 1962, 1964, 1965*b*; Lord, 1949, 1956; MacPhee, 1953, 1961; Pickett and Patterson, 1953; Lord, Herbert, and MacPhee, 1958; Pickett, Putman and LeRoux, 1958; Putman and Herne, 1958, 1960, 1964, 1966; Pielou, 1960*a, b,* 1962; Lord and Stewart, 1961; LeRoux, 1961; Herbert, 1962*a,* 1965; Patterson, 1966). The net results of these studies (Pickett, Putman, and LeRoux, 1958; Chant, 1963; Putman and Herne, 1966) seem to indicate that, except for the use of pesticides, tetranychids would not be an orchard problem in eastern Canada, and both the major evidence and the researchers' judgments support the hypothesis of pesticide interference with predator action.

Based on experience in peach orchards at Vineland Station, Ontario, extending over about 25 years, Putman and Herne (1966) stated: "Earlier in these studies the usual scarcity of predators in orchards where *Panonychus ulmi* was also scarce led us to doubt whether endemic densities of the mite were actually regulated by these agents (Putman and Herne, 1958). Further consideration based on later work, however, has removed these doubts." These authors add, however, ". . . we have not in any sense 'proved' the effectiveness of predaceous species either individually or collectively."

As is usual in such studies, Putman and Herne were unable to determine what proportions of prey were destroyed by given predator species or by collective predation, in any given period. They add, "Nor do we know, except in a very general way, the extent of mortality from predation that is needed to augment the mortality from abiotic sources in order to prevent *P. ulmi* from increasing."

Putman and Herne (1966) continued:

The operation of predators at very low endemic densities of *P. ulmi*, sometimes less than one egg or mite per 100 leaves at the seasonal peak, must differ from that at higher densities; the predators cannot survive on this prey alone but must supplement it with other species of mites or insects, or with vegetable nutriment. Under these conditions the dominant predator is *Typhlodromus caudiglans* Schuster. Also, *Haplothrips faurei* Hood, various minor predators, and especially chrysopid larvae may in the aggregate aid substantially at low densities of *P. ulmi*. [This seems to presuppose that vegetable nutriment and/or the aggregate abundance of all prey are sufficient to sustain *T. caudiglans* and the larger, more voracious predators—or else they move in from other places where they have been sustained.]

In summary, endemic densities of *P. ulmi* are maintained in that state by predators, chiefly *T. caudiglans*, that subsist to a considerable extent on other sources of food, whereas epidemics are reduced largely by other predators, chiefly *H. faurei* and *Stethorus punctillum* Weise, that increase by feeding on the mite during its period of rapid population growth but exert their greatest effect through later destruction of winter eggs. We have also seen incipient outbreaks dwindle, apparently through predation, before the foliage was appreciably injured; indeed this may be the usual course of naturally occurring outbreaks, for nearly all of our detailed studies of epidemics have been of those induced by pesticides.

Many other studies, some very important, others less so, have been conducted concerning spider mites and their predators in deciduous fruit orchards, but most of them extended over shorter periods of time than the studies cited for England, Nova Scotia, and Ontario.

For five successive years Dosse (1960) studied the influence of *Typhlodromus pyri* on *Panonychus ulmi* on apples in Germany. Before the start of the tests the trees were under regular commercial treatments. *P. ulmi* was

then abundant. Within two years the population on an isolated, cloth-covered and unsprayed tree was reduced to nearly zero by *T. pyri*, which was the only predator present. On another unsprayed but uncovered tree, *P. ulmi* was also practically eliminated by this predator, but only after five years. Dosse considered that the delay was caused by abiotic factors that impeded progress of the predators in the uncovered tree. This seems doubtful unless the climatic region is one in which the predator can barely exist unless afforded additional advantage by the cloth covering. Dispersal losses or biotic factors not present in the covered tree may have inhibited responsiveness. In cloth-covered and uncovered, DDT-treated trees, *T. pyri* was reduced and *P. ulmi* increased, but after the DDT had deteriorated, *T. pyri* increased, and reduced the *P. ulmi* population.

Dosse (1960) also found that *Typhlodromus zwoelferi* Dosse was less effective on *Panonychus ulmi* than was *T. pyri* under the same conditions in northern Germany. *T. pyri* reduced the red mite population to low levels. Begljarov (1957) considered that phytoseiid predators, notably *Typhlodromus aberrans* Ouds., were primarily responsible for holding in check the two principal phytophagous mites, *Bryobia redikorzevi* and *Tetranychus crataegi*, on apple in the Krasnodar territory, North Caucasus, U.S.S.R. Although normally held by their predators at "practically insignificant" levels, use of DDT was found to markedly reduce the predator populations and to induce increases in the phytophagous species.

Niemczyk and Wiackowski (1965) studied the influence of predatory mites in the field on the population development of *Panonychus ulmi* on plum in southern Poland. On unsprayed trees they found low densities of both prey and predators, and predator regulation seemed to occur at low densities. Of the four species present on these trees— *Phytoseius macropilis* (Banks), *Typhlodromus tiliarum* Ouds., *T. finlandicus* Ouds., and *T. soleiger* (Ribaga)—*P. macropilis* was considered the most important. Sprays of dinitrocresol almost annihilated the predatory mites, resulting in a strong increase in *Panonychus ulmi*. The judgment that *Phytoseius macropilis* was the most important species was based on the fact that *P. macropilis* was the most numerous of the various species found. This judgment needs more critical analysis in view of the findings of Collyer (1958) that this species was ineffective against *P. ulmi* in insectary experiments. Perhaps behavioristically different genotypes are involved. On apple, after addition of high numbers of *P. ulmi* to trees on which it and the predators *A. potentillae* and *T. pyri* both occurred in low numbers, van de Vrie and Kropczńska (1965) found that it took almost two seasons before the artificially increased high densities of *P. ulmi* were reduced by *T. pyri* or *A. potentillae* to noneconomic levels, with each predatory species demonstrating the capacity to do so.

Mathys (1956, 1958) in Switzerland and Flaherty (1967) in California have conducted studies on the role of predators and other factors in the population dynamics of spider mites on grape. Mathys studied the impact of the dominant *Typholodromus pyri* on the development of *Panonychus ulmi*. He found that it can hold its prey to economically unimportant levels provided no pesticides detrimental to these predators are applied. Flaherty demonstrated several points: (1) *Metaseiulus occidentalis* is the most important mite predator on grape in the lower San Joaquin Valley of California. (2) When unhampered by harmful pesticides it maintains both *Eotetranychus*

willamettei McGregor and *Tetranychus pacificus* McGregor at noneconomic levels. (3) Following any substantial pesticide disturbance, three years or more of delicate management may be required to re-establish a balance. (4) During that period, *M. occidentalis* is less effective against *E. willamettei,* but more quickly responds to increases in *T. pacificus* and may then effectively

reduce *E. willamettei* as well. (5) *E. willamettei* is not a real pest of grape even at substantial densities. (6) The presence of some weedy grasses (e.g., johnsongrass) in the vineyard, harboring *T. urticae* which move over to grape but never become established, maintains a more effective year-round continuity of *M. occidentalis* and better control of the two spider mite species on grape.

Role of Predators on Citrus and Avocado in Southern California

Citrus

DeBach, Fleschner, and Dietrick (1950) studied the citrus red mite, *Metatetranychus citri* (McGregor), and its predators in unsprayed orange groves in Orange County, California. They found that the mite remained below economic levels in most cases, and indicated that predators were generally responsible for this. They considered certain coniopterygids, *Stethorus picipes* Casey, and *Chrysopa* as the most important predators. Higher mite populations and lower predator populations on trees treated with DDT were given as supporting evidence of the importance of these predators.

Subsequently, an extensive study was made of the interactions among the citrus red mite, predators, and the citrus plant (Fleschner, 1952). Experiments were conducted in several orchards, and by constant surveillance during daylight hours Fleschner was able to remove all mite predators, by hand, from a single tree in each orchard. Adult female mites were counted daily on all leaves of eight terminals on the "experimental tree" and also on a neighboring tree from which no natural enemies were removed. One orchard showed an increase and then a striking reduction of the citrus red mite populations on the undisturbed trees, while on the tree from which predators were removed, the mites continued to in-

crease and there was serious leaf-drop from mite damage. This demonstrated the effectiveness of the predators which, in this particular case, were almost exclusively *Stethorus picipes*.

In a neighboring orchard, however, there was little difference in the population growth of the citrus red mite on the predator-free tree and that on the undisturbed ones, and there was considerable damage in both cases, indicating that predators were not sufficiently abundant to prevent heavy infestation.

In a third orchard, even when predators were removed, the citrus red mite populations remained extremely low during a 47-day period. Artificial inducement to increase was attempted by adding mites to the terminals, but no significant populations developed even though meteorological conditions were favorable. Fleschner (1952) attributed this phenomenon to "host-plant resistance." He found that the degree of resistance could be altered by various factors, including chemicals, difference in soils or irrigation water, and climatic conditions (Fleschner, 1958*a*).

Fleschner (1958*a*) concluded that predation is the most important factor in the natural control of the citrus red mite in California citrus, and stated (1958*b*): "...if it were not for the use of insecticides to control other citrus insects, increased predator efficiency

would greatly reduce the status of the citrus red mite as a pest of citrus in southern California." His work also demonstrates the important fact that low populations of mites under favorable meteorological conditions cannot automatically be attributed to action of predators. (See also discussion of Chaboussou's work and that of Post in earlier section on "Field Evidence for the Hypothesis of Physiological Inducement.")

Avocado

In another experiment involving hand-removal of predators, Fleschner, Hall, and Ricker (1955) removed all beneficial species from an avocado tree limb containing about 200 leaves, for a period of 84 days. The avocado brown mite, *Oligonychus punicae* (Hirst), on this limb increased to high numbers and caused leaf-drop, whereas the populations remained considerably lower and caused no defoliation on other parts of the tree or on adjacent check trees. *Stethorus picipes* Casey was rated as the most important predator, and the phytoseiid mites, mainly *Amblyseius limonicus* Garman and McGregor, as second. In another case, the six-spotted mite, *Eotetranychus sexmaculatus* (Riley), on a predator-free limb increased to sufficient numbers to cause leaf-drop, but remained at low numbers in all other places. Relatively low populations of this mite were found to cause considerable damage to the foliage, and it was thus demonstrated that predators, in this case mainly phytoseiid mites, were responsible for maintaining the potentially dangerous species at low densities.

McMurtry and Johnson (1966) made a long-term study of *Oligonychus punicae* and its natural enemies in several unsprayed avocado orchards in two climatic areas of southern California. From data totaling 16 grove-years of study, they reported only two cases of considerable leaf-drop caused by this mite, four of rather severe bronzing but little or no leaf-drop, and ten of only medium to very light bronzing. Predation was considered a major factor in suppressing the mite populations, which showed periods of increase every summer. The data strongly suggested that *Stethorus picipes* was the most important factor accounting for a reversal of the upward surge each summer. These results and more recent unpublished data indicate that short-term predictions can be made, relative to the severity of the infestation, based on the average number of *Stethorus* present at a given density of mites during the early phase of the upward surge of population. Avocado tolerates substantial feeding injury.

Of two species of phytoseiid mites present, *Amblyseius limonicus,* a strictly coastal species on avocado, seemed sometimes to suppress *Oligonychus punicae* populations in the virtual absence of other predators. The dominant species of phytoseiid in all areas except near the ocean, however, was *Amblyseius hibisci* (Chant), and the study indicated that, although this predator outnumbers the spider mites in the spring, it generally does not increase fast enough to overtake the rapidly increasing summer populations of the spider mite. This predator probably plays a major role, however, in greatly reducing the population after the decline has started. Greenhouse and laboratory studies have helped to interpret the field data on these two species of phytoseiids (McMurtry and Scriven, 1966c; and in preparation).

ROLE OF PREDATORS IN GLASSHOUSE
AND LABORATORY STUDIES

Stethorus punctillum, Metaseiulus longipilus (Nesbitt), and *Phytoseiulus persimilis* (= *P. riegeli*)[5] have all been shown to be important in the control of *Tetranychus urticae* in greenhouses (Bravenboer, 1959; Dosse, 1959; Bravenboer and Dosse, 1962; Hussey, 1965; Hussey, Parr, and Gould, 1965; Vogel, 1965; Böhm, 1966; Langenscheidt, 1966; and Begljarov, 1967). Under those conditions the situation seems to be less complicated than it is in the field. Bravenboer (1959) showed that the predators *S. punctillum* and *M. longipilus* can be very important in regulating the numbers of *T. urticae* in the greenhouse. Both predators are well adapted to the prevailing meteorological conditions in greenhouses, and remain present for many years.

Phytoseiulus persimilis has been shown to be very effective in controlling *Tetranychus urticae* in greenhouses when artificially introduced (Bravenboer and Theune, 1960; Bravenboer and Dosse, 1962; Bravenboer, 1963, 1965; Vogel, 1963, 1965; Hussey, 1964, 1965; and Hussey, Parr, and Gould, 1965). Bravenboer (1963) showed that several factors are involved in the use of this predator. (1) The life cycle of the predator is shorter than that of its host. (2) The predator is very active, and covers a great leaf area in a short time. (3) An outbreak of phytophagous mites usually starts on a few plants, on which high densities of *P. persimilis* can be bred by introducing stock artificially. (4) No pesticides harmful to *P. persimilis* need be applied. Because this species is not adapted to the climatic conditions of western Europe, it cannot overwinter; it must be reintroduced at least every year. Moreover,

this predator has such high feeding and intensive searching capacities that it can almost eliminate its prey. The predator's high food requirements often result in the prey becoming so scarce that the predator itself dies out completely and the host plants become reinfested by phytophagous mites. In this respect, Laing (1968) and Laing and Huffaker (1969) found *P. persimilis* somewhat less reliable as a self-perpetuating predator than *Metaseiulus occidentalis* when used against *T. urticae* on strawberries in a growth-chamber experiment in California. *M. occidentalis* was better able to survive the very low prey densities resulting from its own overexploitative predation than was *P. persimilis*, under the conditions of this experiment. *P. persimilis*, however, excelled in more quickly overtaking and subduing a high prey population.

Collyer's (1958) insectary studies indicated a potential for control of *Panonychus ulmi* on small prune trees by *Typhlodromus pyri* and *T. finlandicus*, but *T. umbraticus* Chant, *T. tiliarum*, and *Phytoseiulus macropolis* exerted little effect. In laboratory trials in the Netherlands, van de Vrie and Kropczyńska (1965) showed that *T. pyri* can keep *P. ulmi* below damaging levels; in tests in which *T. pyri* was absent, high densities soon developed. Van de Vrie (1963, 1964b, and unpublished data) demonstrated that the predators showed a strong preference for the juvenile stages of the prey. The ratios of females to summer eggs in the cultures, in the presence and absence of the predatory mites, were almost identical; differences in the numbers of juvenile stages in the corresponding

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[5] Kennett and Caltagirone (1968) have recently established, through cross-breeding and other tests, that forms known as *P. persimilis, P. riegeli,* and *P. tardi* are conspecific.

series were great. The same phenomenon was observed in field trials. Furthermore, Collyer (1958) found that similar numbers of eggs were laid by two groups of 25 *P. ulmi* females each, in the presence and absence of *T. pyri*, during the first two weeks of insectary experiments. Only after that time did the high mortality due to *T. pyri* become apparent, and the differential in numbers of egg-laying females then resulted in different egg populations.

EVALUATION OF PREDATOR ACTION AND OF COMPETITIVE FEATURES

Several significant questions related to predator action and natural control of mite populations, as yet inadequately considered, include: direct competition; comparative rates of increase of prey and predators; the predator's powers of prey consumption and its food requirements; functional and numerical responses, both singly and combined; searching capacity and movements; dispersion features; specialized vs. general predators; the prey stage attacked; possible alternate foods; and the problems of sampling and studying populations. These factors are not isolated features, but are interrelated, and affect the performance of predators even if masked by apparently contrary forces. For example, searching efficiency of predators as a population, at a given time, is a function not only of basic searching power (of the individual) but also of numbers searching, and, except in the unreal steady state (see below), numbers searching may be quite dependent on the power of increase established at a previous time.

The phytoseiid-type predator, on average, appears to be a better mite-control agent at low density than does the insectan-type predator. Theoretical analyses indicate this, and empirical evidence suggests it. We do not claim, however, that phytoseiids in nature may necessarily be expected always to excel over the larger, more voracious, and often more general, insectan predators. For many reasons, phytoseiids may prove ineffective in many situations where one or more insectan predators are effective. In the discussion that follows, we are not implying any broad rules without exception. The good predator is the one that does the job in the case at hand.

Intra- and Interspecific Competition

All animals are limited by their food supply if they are not limited in some other way before they become that numerous. While it is clear that food used by one species is not available to another at the same trophic level, different kinds of phytophagous arthropods often obtain their nourishment from a plant in such different ways that the most acute and direct competition is often avoided. Different species of mites attacking the same tree may require different biochemical composition in their food (Chaboussou, 1965), and that biochemical composition may vary naturally with the season, favoring first one species and then another, or it may vary in relation to changes induced by pesticide applications or fertilizers.

Ripper (1956) stated, "In contrast to the fruitful investigations made into interspecies competition between pests of stored products, there is little information on the extent to which phytophagous insects and mites compete for their food supply...." This statement is still essentially true. The use-

ful studies that are being made have not been conducted in the context of interspecific competition.

Spider mites characteristically feed on foliage, causing chlorosis or otherwise damaging the leaves, and when they occur on the same plant they are in more or less direct competition, even if they do not occur at the same time. Such competition is lessened to some degree, however, if the mites are not concurrent or if one species feeds primarily on the upper surface of the leaf (e.g., *Oligonychus punicae* on avocado) and another on the lower (e.g., *Eotetranychus sexmaculatus*), or if one is characteristically more widely dispersed (e.g., *E. willamettei* on grape) while the other (e.g., *Tetranychus pacificus*) breeds in closely aggregated colonies (Flaherty, 1967). The degree to which such competition is lessened in this manner may be only temporary unless the numbers are kept down by enemies or other stress, because general leaf burn, defoliation, and loss of vigor or adequate nutritive qualities of the foliage as a whole would impinge directly as a competitive feature, even into a later period of time.

We do not have good detailed data bearing on the effects of such interspecific competition among tetranychids, but there are indications that it may account for greater or lesser abundance of a given species at a particular time, and correlations of the abundance with some particular factor of real importance can thereby be negated or lessened. This area needs intensive investigation.

Rodriguez (1958) found that populations of the two-spotted mite developed more rapidly in the greenhouse than did those of *Panonychus ulmi*. Foott (1962, 1963) found that greenhouse populations of the two-spotted mite were able to suppress *P. ulmi* because of their production of webbing, greater fecundity, faster rate of development, and greater ability to thrive

on foliage injured by feeding. There was no evidence, however, that this occurred in the orchards. Chaboussou's (1965) findings may have a bearing here (see above).

Webster (1948) indicated that *Panonychus ulmi* and *Tetranychus pacificus* were rarely found on the same leaves, suggesting the possibility of displacement competition between the two species. Flaherty (1967) presented evidence that on grapevines on which *T. pacificus* is able to build up, *E. willamettei* will be correspondingly reduced.

Gonzales (1961) presented data indicating replacement of *Bryobia arborea* M. and A. [= *B. rubrioculus* (Scheuten)] by *Panonychus ulmi* in early summer; *B. arborea* was shown to continue unabated through the normal period of *P. ulmi* abundance when the latter was relatively low in numbers. Gonzales also considered *P. ulmi* to be hindered at times by competition from *Tetranychus urticae* or by the scale insect, *Quadraspidiotus perniciosus* (Comst.).

Lienk and Chapman (1951) suggested that competition between the European red mite and the two-spotted mite in New York apple orchards may be an important factor in their respective seasonal occurrences, although there was no direct evidence to establish such a relationship. Oatman (1965) felt that the seasonal occurrence was most likely due to movement of *T. urticae* from the ground into the trees at a time when *Panonychus ulmi* was seasonally declining, so that the two species were probably not in actual competition. Chaboussou's (1965) explanation of this is given above.

Kuenen and Post (1958) pointed out that, among other effects, sprays can upset the numerical regulation of arthropods on crops by killing certain of the competing members of the community. This reduced competition can lead to more rapid increases in spider mites. These workers demonstrated some

aspects of competition between *Bryobia rubrioculus* and *Panonychus ulmi* on small apple trees.

Cone (1963) found that treatment of alfalfa plots with dieldrin resulted in no significant change in the tetranychid population, but did increase the phytoseiids. He suggested that this lowered the competition of the phytoseiids for their food (the tetranychids) because competing insectan predators were greatly reduced. Lord, Herbert, and MacPhee (1958), Sanford and Lord (1962), and McMurtry and Johnson (1966) indicated other examples of such compensating replacement in predator numbers when other species are absent.

Intraspecific competition for food is inherently more direct than competition between different species. The way in which a population uses, or is allowed to use, its food supply may markedly affect its subsequent population dynamics. If such species as *Panonychus ulmi* are suppressed early in the season, the conserved food is available later, and thus higher late-season and overwintering populations may result (Venables, 1944; Kuenen, 1946; Austin and Massee, 1947; Morgan and Anderson, 1958; Oatman, 1959, 1965; Cutright, 1963).

Extensive feeding obviously results in a less favorable food supply. However, leaves may recover sufficiently to support a later increase in a mite population even though their appearance does not markedly change. McMurtry and Scriven (1966c) observed development of two distinct subsequent population fluctuations of *Oligonychus punicae* on heavily damaged leaves of avocado seedlings in the greenhouse. Of the three observed fluctuations, the peak density per leaf was higher in the third than the second, because of interim production of new leaves. If only the original leaves were considered, however, the third peak was lower than the second.

Henderson and Holloway (1942) found that citrus red mites confined on leaves previously damaged by feeding had reduced reproduction and slightly higher mortality in comparison with mites confined on undamaged leaves. This was also true of the avocado brown mite, *Oligonychus punicae*, on damaged avocado leaves (McMurtry and Johnson, 1966). Fleschner, Hall, and Ricker (1955) observed declines of *O. punicae* on damaged leaves in the field while the population was increasing on new, undamaged leaves on the same trees.

Huffaker and Kennett (1956) observed fluctuations of decreasing amplitude in cyclamen mite populations on strawberry plants in the absence of predation. This was the result of progressive, intense utilization and weakening of the plants.

Huffaker (1966) found that as the physical complexity of an artificial ecosystem was increased, the adverse effect of regulative food depletion on six-spotted mite populations came into play at lower densities because of greater hazards involved in movement from depleted to undepleted arenas.

Davis (1952) noted various changes occurring during a population cycle of *Tetranychus* sp. on banana squash in the absence of predation: (1) a reduction in the number of eggs per female when the total population was still increasing; (2) an increase in the percentage of nonviable eggs after the population peak (this apparently associated with nutrition of the parents); and (3) mortality of immature mites (eggs were left in "fed-out" areas and larvae died before they found less-damaged areas).

Migration can also be a factor in population decline. As the leaves become damaged, large numbers of adult females of some species lower themselves on silken threads and are carried away by air currents (Fleschner, 1958a; Fleschner *et al.*, 1956), or they

wander off the plants. Since "ballooning" apparently does not occur with male tetranychids, this may at least partly account for a decided shift to a predominantly male sex ratio where high populations begin to level off or decline, as has been observed with *Oligonychus punicae* on avocado (McMurtry, unpublished results).

Effects of host-plant conditioning may take place before average density becomes very high if the nutritional level is already low (Huffaker and Kennett, 1956; McMurtry and Johnson, 1966). Foliage fed on by even a few mites may be less favorable for a future population (Cutright, 1963).

The Question of Comparative Rates of Increase

The late H. S. Smith once said that almost any specific natural enemy of a pest insect possesses sufficient reproductive capacity to control the pest species if conditions were ideal in other respects. He thus emphasized searching capacity (Smith, 1935). That remark was based on the assumption of a hypothetical steady state (Nicholson, 1933) in which, for example, a solitary entomophagous parasite, perfectly discriminatory, unisexual, and having one generation to one of the host, can use, on the average, only *one* egg. All the rest of its reproductive capacity is surplus and wasted. Sufficient numbers of such parasites would exist, in relation to the numbers of female hosts surviving to reproduce, to match the total fecundity of the host, save the one. That is, if the host has a fecundity of 100 (again assuming unisexuality), 99 per cent of the progeny in each generation would be parasitized, i.e., there would be 99 adult parasites, and only the one of each 100 hosts would reach adulthood. Thus, such an enemy species at equilibrium can make up in numbers what it lacks in comparative reproductive potential, and the crucial features are then its searching capacity and the favorability of the environment otherwise.

Smith knew, however, that all such parasites must and do possess a considerably greater fecundity than 1. Thus, if other conditions permit (e.g., density of hosts permits ease of finding; lack of mortality factors) and if

we now remove the stricture of the steady state, permitting a temporary imbalance, the enemy would require and could then use that fecundity greater than 1 toward correcting the imbalance in the ratio of hosts to parasites.

Furthermore, even if the difference in reproductive capacities between the host and parasite were so great that the latter could never catch up without assistance (formulas of Thompson, 1924, 1939), such assistance is quite assured. In its seemingly parasite-unlimited and "boundless" increase, the host invariably does increase to the point at which, as Thompson clearly states, the environment cannot sustain it. As soon as the host reaches such densities (at point of starvation, for example), the added mortality then decreases its effective ability to multiply to a point at which the parasite's numbers can catch up, and unless other disruptive features came into play the parasite could regain control and hold it. We know also that such assistance is often afforded in local patches where prey densities press on their food supply even before general densities reach such levels (Huffaker, Shea, and Herman, 1963; McMurtry and Johnson, 1966). In any real situation, however, the enemy would need surplus fecundity to check the host in the increase phases of the oscillations. This hypothetical picture has been presented to illustrate the fact that an enemy species does not by any means require as high

an intrinsic rate of increase as that of the host or prey species, in order to control it.

It should be obvious, too, that fecundity is only one aspect in rate of increase. The importance of an enemy's ability to find the host or prey, and the way in which this is affected at different densities and density dispersion patterns or by the physical environment, seem far more important than reproductive potential. Yet the host and prey species certainly do escape from enemy action, and the speed with which the relative numerical imbalance can be corrected in a single generation or so may mean the difference between economic damage or lack of it (Huffaker *et al.*, 1968). Thus, power of increase in the enemy relative to the net power of increase in the host or prey species (i.e., as reduced by the amount of the parasitism or predation) is still very important in the actual picture (McMurtry and Johnson, 1966; Huffaker and Flaherty, 1966).

As a great variety of environmental conditions can affect actual rate of increase, so may differential climatic effects on predator and prey greatly affect the degree of control (see first paper in this series).

Oviposition of *Stethorus picipes* declines rapidly below 70° F (Fleschner, unpublished data), but that of the citrus red mite is still substantial even at 60° (Munger, 1963). *Amblyseius limonicus* is found only near the coast in southern California, where humidities in summer are not so severe (low). Its eggs do not hatch at relative humidities below 60 per cent (McMurtry and Scriven, 1965). Its prey species occur rather more inland. Chant (unpublished data) found that *Phytoseiulus persimilis* could not control *Tetranychus urticae* at very low temperatures. Force (1967) found differences in temperature to have marked effects on the population control of *T. urticae* by both *P. persimilis* and

Metaseiulus occidentalis in growth chambers. Yet at a low to intermediate mean temperature (68.5° F) Laing (1968) and Laing and Huffaker (1969) found that both species could rapidly overtake *T. urticae* on strawberries, with *P. persimilis* excelling in this regard (but see later discussion).

Mori and Chant (1966b) found that *Phytoseiulus persimilis* and *Tetranychus urticae* reacted differently to certain humidities; the prey avoided high humidity, but the predator did not. *P. persimilis* consumed more prey at high than at low humidity (Mori and Chant, 1966a). However, Begljarov (1967) found that lower consumption was accompanied by a *higher* rate of oviposition at high humidities. Such seemingly paradoxical effects illustrate the point that conclusions regarding the outcome of such an interaction may apply only under very specific situations.

We are just beginning to obtain quantitative data on the comparative intrinsic rates of increase of spider mites and certain of their enemies. Huffaker and Flaherty (1966) used a simple arithmetic scheme and actual data on fecundity, rate of development, prey consumption, and longevity to show that the phytoseiid *Metaseiulus occidentalis* may overtake either the two-spotted mite or the six-spotted mite in population increase even though the prey species produces several times as many eggs per day of oviposition, due partly to the amount of the prey's fecundity that is negated by predation. (See also McMurtry and Johnson, 1966.) Outcomes of extensive population interactions were cited in further support.

We have relatively little information on the intrinsic rates of increase of tetranychids, and still less on their predators. Precise statistics were determined by Nickel (1960) for *Tetranychus desertorum* Banks, and Watson (1964) for *T. urticae*. Laing (1968)

determined similar values for *T. urticae* and two of its predators, *Phytoseiulus persimilis* and *Metaseiulus occidentalis,* under simulated coastal California conditions in a growth chamber. Laing found that, under these conditions, both predatory species had intrinsic rates of increase considerably higher than that of the two-spotted mite, largely because of their more rapid development. When the predators' consumption of prey is also taken into account, the lesser ability of the prey to increase in the presence of active predation is even more pronounced in contrast to that of either predator. While *P. persimilis* possesses the capacity to correct a state of imbalance more quickly, it requires more prey to survive, and *M. occidentalis* appears to have a better chance of survival at low endemic densities in a very small interacting system. In the absence of precise statistics we can only attempt comparisons along lines suggested by the method of Huffaker and Flaherty (1966). (See later section on "Functional, Numerical, and Total Responses of Predators.")

In addition to the negating of prey fecundity by the enemy action itself, if conditions of the host plant or the environment permit only a limited fecundity or only a limited percentage of the hosts or prey to survive for very long, a rather small, though lagging, increase in predator numbers (or percentage kill) may be all that is required for regulation (Fleschner, 1952; Huffaker, Shea, and Herman, 1963; Putman and Herne, 1964). Under such below-optimum conditions for the prey,

the predator may more readily overtake and suppress the prey population (McMurtry and Scriven, 1968).

In the absence of more critical data on comparative intrinsic rates of increase, the following remarks may be of some value, but should be viewed with caution.

In general, spider mites have higher peak rates of egg production during oviposition than do phytoseiids—sometimes much higher—but the latter develop faster to the point of egg production, commonly have greater longevity, and spend longer total time in oviposition. Consequently they may have greater fecundity although their rates of peak production per day are lower. To time of its complete development, a single phytoseiid may destroy one fourth to one half or more of the total progeny of a single spider mite. The earlier first egg deposition of the phytoseiids is an advantage in power of increase, as is the greater number of eggs laid early, in the spider mites. Eggs laid very late add little to power of increase; thus the extended longevity and egg deposition of the phytoseiids mean little in this respect. It may mean much, however, relative to survival of the population at very low prey densities.

Most insectan predators have longer life cycles than spider mites, but if there is an abundance of food they may produce eggs at a faster rate than their tetranychid prey, e.g., *Stethorus* spp. may produce 6 to 12 eggs per day (Putman, 1955) and *Chrysopa* spp. over 10 per day (Hagen, 1950).

Power of Prey Consumption or Appetite

Nicholson (1933), H. S. Smith (1937), Kuenen (1947), and Huffaker and Flaherty (1966) present the view that, *other things being equal* (which they never are), a predator that requires and therefore consumes less prey is better able to survive as an

effectively searching population at low prey density and therefore better able to maintain the prey at a lower density. A greater food requirement obviously may result in annihilation of the predator in localized areas. To depend on its reestablishment seems a less re-

liable prospect for control than does the persistent presence of the predator. Huffaker and Flaherty emphasized, however, that the more voracious predator might possess a sufficiently superior searching capacity to offset its need for a greater food intake. (See Laing and Huffaker, 1969.)

General observations and findings of Kuenen (1947), Fleschner (1950), and Laing and Huffaker (1969), however, indicate that, in general, larger, more voracious enemies of spider mites do not commonly have superior searching power in proportion to their greater food requirements. For example, Fleschner found that hungry last-instar larvae of *Chrysopa californica* Coquillet could traverse 107 square inches in an hour, and that about 1,750 citrus red mites were required to complete development of the stage. Hungry last-instar larvae of the much smaller coccinellid, *Stethorus picipes*, traversed 15.5 square inches in an hour and required about 67 red mites to complete the stage. J. E. Laing (unpublished data) found that hungry adult females of the still smaller predatory mite, *Metaseiulus occidentalis*, traversed 2.1 square inches in an hour and that last-stage nymphs required 7 red mite eggs to complete development. On the basis of his data, we can roughly estimate that feeding last-stage nymphs could "cover" 1.5 square inches in an hour, and would require three or four separate new "finds" of red mites to complete development. It is noted that *Chrysopa* killed every prey contacted, and the area traversed and the area "covered" were identical. *Stethorus* and *Metaseiulus* are not usually this perfect in captures vs. contacts. The prey densities to which these predators are exposed would also modify these values. Very roughly, the ratios of searching success per hour to food requirements of the last-stage young are: *M. occidentalis*, one-half; *Stethorus*, one-fourth; and *Chrysopa*, one-sixteenth. (See also

section, "Searching Capacity and Features of Dispersion.") Contrasting these examples, then, the greater food requirements of the larger species are not offset by correspondingly greater searching capacities of their immature stages. We have other data relative to the food requirements of insectan and phytoseiid predators (e.g., Chant, 1959, 1961b; Herbert, 1961), but relatively little concerning their powers of searching. What we do have on the latter is of dubious value in rating searching under field conditions.

Kuenen (1947) presented an interesting model of the control potential inherent in predation (fig. 3). He used it to contrast the performance potentials of *Scymnus minimus* (Rossi) and of a species of *Typhlodromus,* and on this basis, and as a result of field population studies, he concluded that the less voracious phytoseiid is the better able to hold spider mites at low densities.

Chant (1961b) and Herbert (1961) found that *Metaseiulus occidentalis* and *Typhlodromus pyri*, respectively, can produce eggs when feeding on only one or two immature mites per day. With reference to Kuenen's (1947) model (fig. 3), Chant determined the critical parameters for *Metaseiulus occidentalis* feeding on *Tetranychus urticae* (protonymphs). He found the maximum number of prey that can be consumed to be 11; the prey density at which the maximum can be found and consumed, 25 per square inch; the minimum number of prey required to stay alive, 1; and the density at which this minimum number can be found, 1 per square inch. The limits imposed by this functional response (a within-generation function), thus fall between densities of 1 and 25 prey per square inch. In this connection, however, Flaherty (1967) concluded that although the average prey density on grape foliage can be well below 1 per square inch, pockets of mites may occur, in micro-
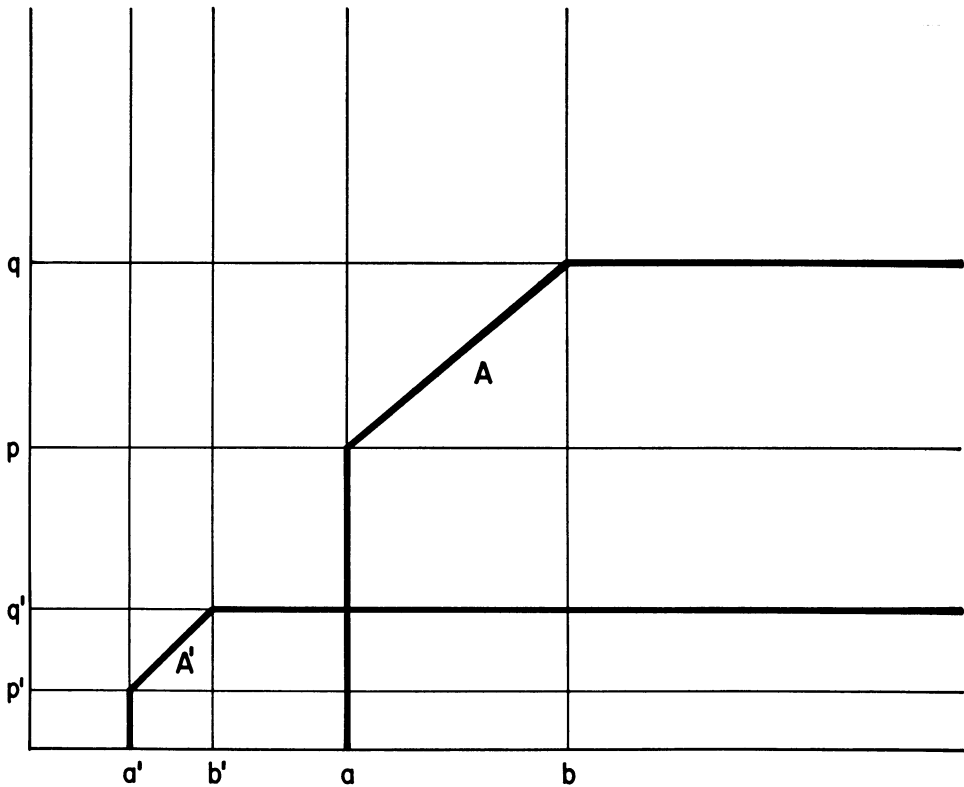
Fig. 3. Limits of prey density for predator survival and reproduction. A and A' represent data for predators; a and a' are prey densities necessary for the minimum number of prey required for survival (p and p') to be found; b and b' are densities at which the maximum number of prey that can be consumed (q and q') are found and consumed. (Redrawn from Kuenen, 1947.)

areas or on certain leaves, which well exceed that density, and he found *M. occidentalis* persisting and effective at general average densities of less than that. Putman and Herne (1964, 1966) also reported *Typhlodromus caudiglans* instrumental in maintaining *Panonychus ulmi* population peak seasonal densities as low as or lower than 1 per 100 leaves, but stated that the predator was obviously obtaining other nourishment.

From their field studies and observations, a number of workers have independently concluded that phytoseiids were better control agents in their situations than were the larger insectan competitors, although better synchrony with the early-season increases in the spider mites, or ability to subsist on alternate foods (Putman and Herne, 1964)— rather than lower food requirements—has often been cited as the cause. This better synchrony, however, may be the result of the lower food requirements. Supporting opinions, based on extensive experience (but not specific data) by Garman and Townsend (1938) and Bailey (1939) were cited in the first paper of this series—*Metaseiulus pomi* (Parrott) is superior to *Scolothrips sexmaculatus* Pergande. Specific support is found in the work of Clancy and McAlister (1958) in West Virginia, by Collyer (1964d) in New Zealand, and Putman and Herne (1964, 1966) in Ontario. The latter found *Stethorus punctillum* active in early spring when the mites were clustered in pockets, but ineffective later

when the infestation became more dispersed. *Typhlodromus caudiglans* was considered effective at very low densities, but was probably being maintained by other foods. Suncova (1963) showed that when releases of the more effective phytoseiids were made in fruit trees in the U.S.S.R., *Stethorus* sp. was unable to compete. Flaherty (1967) and Flaherty and Huffaker (1970a) reported that insectan predators of *Eotetranychus williamettei* and *Tetranychus pacificus* on grapes in California never become active unless relatively high mite densities have developed, whereas under favorable conditions *Metaseiulus occidentalis* keeps high densities from developing. Dosse (1967) reported similar results for *Stethorus gilvifrons* (Mulsant) in Lebanon, in contrast to *Phytoseiulus persimilis,* in areas where the latter survives the winter. Huffaker (unpublished data) showed that although the green lacewing, *Chrysopa californica* Coquillett, when limited primarily to *Panonychus ulmi* on field pears in California, consumed large numbers of the mites, it could not control them, nor complete development even among very high infestations. Plaut (1965) demonstrated the value of *Stethorus punctillum* against *Tetranychus cinnabarinus* (Boisduval) in Israel, but only when densities became high. He indicated no superior performance of any phytoseiid. Rymasevskaja (1964) found that the phytoseiids *Typhlodromus rhenanus* Ouds. and *T. soleiger* and the coccinellid *Stethorus* sp. were very important in control of mites on fruit trees in Tambow, U.S.S.R. He emphasized the fact that the phytoseiids become active in spring, at a time when densities are perhaps low for *Stethorus,* before the phytophagous mites become abundant. The phytoseiids continue their activities until late autumn.

Phytoseiids possibly can be more "active" in early spring not only because many accept alternate foods, but also because they do not require much food. *Stethorus* spp., on the other hand, require large numbers of prey and thus do not commonly increase sufficiently until late in the season because their prey are too scarce until then. An exceptional situation reported by Putman and Herne (1966) supports this general view. These authors found that *Stethorus* may be more effective on *Panonychus ulmi* early in the season when the mite is more aggregated, and locally more abundant, than later on when the population is more dispersed. Some phytoseiids continue to reproduce and replace some of their loss in numbers, where strict diapause does not apply, by feeding on the overwintering stages of the tetranychids themselves or on tarsonemids, eriophyids, or tydeids, for example, beneath the crevices of bark or leaf-bud scales, during warmer periods in winter. Thus they can survive at very low tetranychid densities. Kennett (unpublished data) found that the leaf-inhabiting *Metaseiulus occidentalis* overwintered under the bud scales of grape in California, and when brought into the laboratory all individuals readily fed, but only a portion would immediately respond reproductively.

In Europe, the leaf-inhabiting phytoseiids (e.g., *Typhlodromus pyri, T. tiliarum, T. finlandicus*) enter some form of diapause in autumn; during overwintering (which in these species mainly occurs on the branches and twigs) they are able to move around, but it is doubtful whether they feed on prey. Experiments in progress (by van de Vrie) provisionally show that predators collected from branches and twigs of apple between December and early March did not feed and reproduce when brought into the laboratory and provided with all stages of *Tetranychus urticae* as food. Some lived for two weeks (at 20°C under a long photoperiod), but all eventually died without reproducing. If specimens were collected

after the end of March, the picture completely changed; the predators then readily resumed reproduction. In winter, these phytoseiids certainly do not feed on winter eggs of *Panonychus ulmi.* With the bark-inhabiting species (e.g., *Typhlodromus masseei* Nesbitt, *T. bakeri* (Garman), *T. barkeri* (Hughes), and *T. rhenanus*), the picture is different; these species resume reproduction much earlier in the season. Yet they apparently are of minor importance in the control of tetranychid mites, as they are rarely found on the leaves. The examples cited show that *Stethorus* is not known to be effective at really low prey densities, whereas phytoseiids are.

On the other hand, it should also be noted that some phytoseiids may not become very effective until a given prey density reaches fairly high levels. This may be due to the fact that the predator concerned does not feed primarily on that prey species, but perhaps on some other mite, such as an eriophyid, or on plant materials. Or it may be relatively ineffective against a species that has a dispersed distribution. Furthermore, although *Stethorus* does seem to require a higher prey density for effective numerical response, that level may still be sufficiently low that response is effective before economic injury occurs, particularly if the plant species in the given situation is tolerant of moderate densities (e.g., McMurtry and Johnson, 1966). Moreover, as discussed previously, several cases of effective economic control of spider mites have been credited primarily to *Stethorus* spp.

Functional, Numerical, and Total Responses of Predators

A number of recent papers shed needed light on one aspect of performance of phytoseiid predators that has been quite surprising and contrary to what has been generally assumed. This valuable and stimulating research has, however, overemphasized the functional response in the process of regulation by predation, to the exclusion of the numerical or the total response. Chant (1961*b*), Mori and Chant (1966*a*), Kuchlein (1965, 1966, 1967), and Mori (1969) infer from their data that several species of phytoseiids are unable to serve as regulators of the densities of their prey once such densities have reached rather high levels. It is also significant that Mori and Chant (1966*a*) and Mori (1969) use their data to evaluate species as superior or inferior predators, *ipso facto*. We feel that such laboratory studies are concerned with too limited an aspect of performance to permit such comparative generalizations.

While Chant (1961*b*) noted that reproductive increase in numbers of predators would have to be considered, his conclusions, based on the functional response alone, seemed sufficient to him for the above interpretations. Chant stated: "This experiment shows conclusively that reproduction (oviposition) in *T.* (*T.*) *occidentalis* [= *M. occidentalis*] can vary in response to fluctuations in the density of the prey *T. telarius* [= *T. urticae*]. This density-dependent reaction, however, could operate only until the predator reached its capacity for oviposition [5 prey per square inch] and would then cease to operate. The implications of this, if supported by field observations, are obvious; at prey densities greater than those permitting maximum predator oviposition, the prey would be freed from the density-dependent check imposed by the predator unless the immature predators that hatched from the eggs could mature and start to reproduce at a rate faster than that of the prey. This will be discussed in later papers." The "unless the immature predators," and so forth, is of vital importance. In the presence of the adequate available food, these young pred-

ators would normally assure that the average rate of development of the predator population would exceed that of the prey because those prey that are preyed upon do not mature. Contrary to Chant's inference, time of physiological development is not the main feature in the effective achievement of maturity in adequate numbers for the whole population. Possibly Chant's prospective "later papers" could have forestalled misconceptions. Mori and Chant (1966a) and Mori (1969) likewise rate the efficiency of the predators concerned as if the numerical response were of little consequence.

It seems clear from the above studies that while the kill by a single phytoseiid predator normally increases with prey density only up to a point (which may be at satiation of need), the number killed at densities higher than that may remain the same (Chant, 1961b; Herbert, 1961; Kuchlein, 1965; Bravenboer and Dosse, 1962) or decline (Mori and Chant, 1966a; Mori, 1969). The levelling-off in kill is of the same form as that described by Holling's (1959) disc equation, although degree of satiation of appetite is more likely the explanation here than waste of time in handling prey. Such performance, however, does not mean inability of such a predator to control and regulate its prey species in a realistic population-interaction situation. Even if the functional-response curve turns down (see below) this, too, can be offset through numerical increase by multiplication, and since the young predators get into the act very quickly indeed, even if with some lag, this is a realistic feature.

Kuchlein (1965), however, concluded, from consideration of certain field data (Collyer, 1958; van de Vrie, 1964b) and his own experiments, that numerical responses of phytoseiids are quite restricted: "Based on data in the literature [on *Typhlodromus pyri*] and our own experiments it is presumed that the predacious *Typhlodromus*

mites would be able to regulate the numbers of their prey only in a range of the lowest prey-densities if at all." This statement is both unfortunate and unwarranted, and depends entirely on the assumption that the numerical response applies only within a range of lowest prey densities. It also means that every species of the group must have such a limitation, and it overlooks other ecological aspects. The data of van de Vrie and Collyer cited by Kuchlein in support of the conclusion do not, in fact, support it. Collyer's data showed that the predator was able to bring the population down even at the highest prey density initially employed, and then to maintain control throughout the course of the experiment. Subsequent experiments by Collyer (1964b) also showed a marked and unlimited over-all numerical response in this species, again to the point that the prey species was subdued. It is difficult to determine just what data of van de Vrie (1964b) were used by Kuchlein in the preparation of his illustration. Changes at the same spot must be followed as a sequence in time, and the dynamics properly interpreted, instead of merely plotting densities at a given time, or taking the sum of several counts. Unless that is done, the fact that densities of the predator reach a plateau (in the curves), or even decline with increasing prey density, does not mean that there is no true numerical response. The data were not obtained nor tabulated in a manner to indicate such response. Kropczyńska and van de Vrie (1965) showed why such a plateau or decline in such a curve would automatically be associated with an effective numerical response and a controlling effect. Thus, more predatory mites occur on leaves having low or medium densities. Leaves with high prey density generally have reached that condition because predators have been absent or have just become established. Kropczyńska and van de Vrie presented an ex-

planation which "... shows why it is seldom found that high numbers of both prey and predators occur simultaneously on the same leaves." They remarked, "If this was found it would show that the predator mites have almost no regulatory influence on the population density of their prey."

We believe that even if the numerical response of *M. occidentalis*[6] were somewhat restricted at extremely high prey or predator densities, this in itself, combined with the fact of a limited functional response, does not mean that, under favorable conditions, a well-adapted phytoseiid would be unable to reduce high-density prey populations and regain control at low density. This may seem paradoxical but it is based on a broad perspective of the total ecology. We have seen too many instances of high mite densities brought down by phytoseiids, and economic control reinstated, to accept the inference, based on laboratory studies or improperly interpreted results, that this will not occur once high densities have been attained (e.g., Huffaker and Kennett, 1956; Collyer, 1958, 1964*b;* Bravenboer and Dosse, 1962; Bravenboer, 1965; Flaherty, 1967; Laing, 1968; Flaherty and Huffaker, 1970*a,b;* and many others).

We do not believe that phytoseiids are generally restricted in their numerical response to the low-density range. Furthermore, even if a given species did have a restricted numerical response above some high-density level, its activities on leaves where densities were lower would tend to keep infestations low, and the overexploited condition of the leaves where densities were highest would soon eliminate the population on these older leaves anyway. Moreover, if the phytoseiids are established on leaves before the pest species reaches high densities, the predator's efficiency keeps high densities

from developing. For example, Huffaker and Kennett (1956), working with cyclamen mites, indicated that even if the phytoseiids had such restrictions in numerical response (no evidence suggests this), they would still have been able to bring a high infestation under control because new leaf shoots, which represent the future crop, harbor only low infestations of mites at first. Thus, if one or more predators were present on about one third of such leaflets, it could be reliably predicted that control would be achieved within two weeks. Even if present at very high density on leaflets of intermediate age, the prey population could not sustain itself if it could not gain successful access to the very young shoots.

Returning to the dome-shaped functional response reported by Mori (1969), we are not sure that the decline was the result of disturbance by the prey, since really hungry individuals are more tenacious in their attacks. Furthermore, the numbers of abandoned attacks were related to density only over a very limited range; at high densities they were constant; at low densities no attacks were abandoned. We wonder if ease in finding prey and the energy thus saved are not part of the reason why fewer attacks are made and more attempts abandoned as prey density goes very high. It would be important to determine if oviposition also decreased in each case; in work reported by Chant (1961*b*) it did not. Both Kuchlein and Mori refer to cases of effective suppression of prey populations by the respective phytoseiids. Mori (1969) refers to examples in which continued suppression occurred (Collyer, 1958, 1964*a;* McMurtry and Scriven, 1966*c*), and seems to imply that this was only possible because densities never did go high enough for the described functional inefficiency to become a factor.

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[6] "*T. longipilus*" of Kuchlein and *Metaseiulus occidentalis* have been shown by C. E. Kennett and Junji Hamai (research in progress) to be conspecific, but further study of Canadian stocks of *M. longipilus* (Nesbitt) is necessary to establish their taxonomic status.

Does this not suggest something else in the actual performance of the population of predators, i.e., the numerical response, may have been the very factor that kept densities from generally going that high, and resulted in reduction of high-density pockets when they did occur?

In Mori's results, it is clear that *Amblyseius longispinosus* (Evans) ate far more of the eggs laid by the adult prey used in the experiment than of the adults themselves, and that had the experiments continued long enough, the young hatching from the predator eggs (not indicated) would soon have added markedly to that destruction (Huffaker and Flaherty, 1966). Even comparisons of intrinsic rates of increase (Laing, 1968) between predator and prey species are of no value unless some means is at hand for reducing the value for increase in the prey by the amount of predation by the developing predator population. In no sense can we make a realistic comparison of the value of any predator if we ignore its numerical responses and searching capacities, and certain other factors as well.

While we do not intend to present a synopsis of the functional and numerical responses of predators in their roles as regulators of prey density in general, certain points should be made. For information on the total relation of the combined functional and numerical responses, the reader is referred especially to work of Holling (1961), Hassell (1966), and Huffaker *et al.* (1968). The latter two add materially to a fuller understanding of these combined roles. Holling (1964, 1965, 1966) has given a remarkably detailed and ingenious analysis of the components of the functional response, but not of the more important numerical response. He has not yet published studies in that area.

The important point here is that even in the area of a decisively declining functional response, enough numerical response (the between-generation variety) may occur (or may have occurred previously) before prey densities became so unfavorable as to offset the reduced performance per predator. Using a method similar to that of Huffaker and Flaherty (1966), Laing and Huffaker (1969) showed that *Metaseiulus occidentalis* can rather quickly achieve control over the two-spotted mite at initially high prey densities in spite of a hypothesized leveling-off, or, by inference, even some decline in its functional response equal to that described by Mori and Chant (1966*a*) and Mori (1969) for other species of phytoseiids. Laing and Huffaker developed a simple, arithmetic total dynamics model (table 1) that can be computerized from realistic and precisely determined parameters on fecundity, intrinsic rates of increase of both the two-spotted mite and the predator, and rates of consumption of the predator. They generated day-by-day performance, taking into account a hypothetical leveling-off in consumption of prey with increasing prey density. The performance was adequate to overtake and subdue initially high prey densities (table 2). For simplicity in these calculations, it was assumed that prey fecundity was always a maximum, i.e., not depressed by intraspecific competition at high densities. Interference, if any, between predators was also not included. These two factors would operate counter to one another.

These results are compatible with observations and experimental results over the past twelve years to the effect that *Metaseiulus occidentalis* in its real over-all performance under otherwise favorable conditions never seems to have any trouble in bringing high tetranychid densities down on oranges (Huffaker, 1958; Huffaker, Shea, and Herman, 1963; Huffaker and Flaherty, 1966), on strawberries (Laing and Huffaker, 1969), on grapes (Flaherty, 1967; Flaherty and Huffaker, 1970*a,b*),

TABLE 1

CONSUMPTION OF PREY EGGS BY VARIOUS STAGES OF *PHYTOSEIULUS PERSIMILIS* PROGENY IN A HYPOTHETICAL INTERACTION*

Days of development	Eggs laid (day)	No. prey eggs eaten by progeny from eggs laid on successive days				Total
		Larvae	Protonymphs	Deutonymphs	Adult¶	
1......................	a	....	....	....	....	0
2......................	b	....	....	....	....	0
3......................	c	....	....	....	....	0
4......................	d	0(a)	....	....	....	53
5......................	e	0(b)	53(a)†	....	....	106
6......................	f	0(c)	53(a) 53(b)	....	....	106
7......................	g	0(d)	53(b) 53(c)	72(a)‡	....	178
8......................	h	0(e)	53(c) 53(d)	72(a) 72(b)	....	250
9......................	i	0(f)	53(d) 53(e)	72(b) 72(c)	175(a)#	425

* Modified from Laing and Huffaker (1969).
† 24 protonymphs consume 24 × 2.2 eggs per day = 53.
‡ 24 deutonymphs consume 24 × 3.0 eggs per day = 72.
¶ Adult in a preovipositional period.
# 24 preoviposition adults consume 24 × 7.3 eggs per day = 175.

TABLE 2

THEORETICAL CONTROL OF *TETRANYCHUS URTICAE* BY *PHYTOSEIULUS PERSIMILIS*,* ASSUMING NO TROUBLE IN FINDING EGGS†

Day	T. urticae (100) No. eggs oviposited	P. persimilis (10)				No. prey remaining each day
		No. eggs oviposited	No. prey eggs consumed by adults	No. prey eggs consumed by progeny‡	Total eggs consumed	
1.........................	240	24	140	0	140	100
2.........................	240	24	140	0	140	200
3.........................	240	24	140	0	140	300
4.........................	240	24	140	0	140	400
5.........................	240	24	140	53	193	447
6.........................	240	24	140	106	246	441
7.........................	240	24	140	178	318	363
8.........................	240	24	140	250	390	213
9.........................	240	24	140	425	565	−112

* Based on an oviposition rate of 2.4 eggs per day for both predator and prey.
† After Laing and Huffaker (1969).
‡ See Table 1.

on celery (Finney, unpublished results; Flaherty, unpublished results), and on apples and peaches (Hoyt and Caltagirone, 1971). (See also section, "Specialized and General Predators and the Use of Alternate Foods.")

Moreover, McMurtry and Scriven (1966c) presented a different sort of example wherein total predation was improved through numerical increase of predators as a result of feeding on a more nutritious non-prey food (i.e., for *Amblyseius hibisci*), even though prey-feeding per predator was much reduced.

An important point in the natural situation is the fact—already alluded to—that when prey densities reach high levels in local arenas or patches (on leaves or branches), food shortage is sure to cause crash declines soon. This means that the predators can go on

acting in their more efficient manner in pockets of moderate density (at least a moderate density is necessary to facilitate finding of prey), and the overall control of the population on the plant can proceed. The ratio of predators to prey can be improved by poor reproduction or starvation of prey in such pockets or by their emigration. The percentage of leaves having even one predator is, in fact, often a better indicator of probable control of a mite population than is the general density of predators, for the distributional pattern may be poor. If, however, the ratio of prey to predators is very high initially, more time may be required for control to occur, and leaf damage may intervene. (See in these connections, Huffaker and Kennett, 1956; Flaherty, 1967; Flaherty and Huffaker, 1970 *a,b*.) Bravenboer (1965) showed that *Phytoseiulus persimilis* can bring down very high densities of *Tetranychus urticae* and correct a poor ratio of predators to prey in spite of either a prospective decline in its functional response or a lack of numerical response due to high prey numbers or interference between predators. However, his data include some examples wherein densities on the leaves were so high (e.g., 1,300 per leaf) that a crash decline may be presumed to have occurred independent of the heavy predation.

Kuchlein (1967) also concluded that the phytoseiid *Metaseiulus longipilus* [= *M. occidentalis*] exhibited an inadequate "combined" functional and numerical response, relative to increase in prey density. In his "curve D" (his fig. 1), however, he did not use a proper means of presenting a combined functional and numerical response. Kuchlein simply combined a hypothetical immediate numerical response with a functional one. He did not attempt to incorporate the far more powerful, meaningful, and real delayed numerical response, such as was done by Laing and Huffaker (1969). His "curve D"

does not, in itself, mean that *M. longipilus* cannot control prey densities exceeding those at the hump of the curve, through a proper combined functional and numerical response.

Kuchlein, however, presents still other data in which *Metaseiulus longipilus* did not respond at all, even numerically, when densities of *Tetranychus urticae* were maintained at high levels artificially. This seems to contradict the performance observed in the same species (i.e., *M. occidentalis*) in many sorts of high-density situations in California. The implications certainly need full investigation. One wonders about the nature of the environment, the species of host plant, the nutritional quality of the prey mites, or a possible state of reproductive diapause that might possibly account for the lack of response, independent of any intrinsic or self-limiting aspects. (The latter seem highly doubtful in this case.) Recently, Hoy and Flaherty (1970) showed that this species in California enters such a state of diapause under short-day photoperiods. Putman and Herne (1964) also reported, however, that *Typhlodromus caudiglans* seems to reach an upper limit in density (numerical response) beyond which no further increase occurs regardless of prey abundance, an effect they attributed to cannibalism.

Kuchlein (1966) reported an interference among *Metaseuilus longipilus* as their numbers were increased from 1 to 10. The method of confinement he used permitted the searching predators to wander into a "moat" of water surrounding a leaf-disc unit, and drown, a fate he considered equivalent to loss of the predator from the population. He ignored the fact that in the absence of a "moat" such "emigrants" would be important as "immigrants" to nearby arenas. Such approaches need further study. Kuchlein's stimulating work is probing new ground.

Again referring to natural situations,

our observations suggest that since leaf units are often relatively small parts of the total plant habitat, it would be an advantage, and assure more efficient and stable exploitation or control at low prey density if the predators *were* stimulated to move away from leaves where too many predator-to-predator contacts were being made. Thus, theoretically, "interference" causing local "emigration" could be conducive to better control. Hassell and Varley (1969) and Huffaker and Stinner (in press) describe how such mutual interference effects can theoretically stabilize a predator-prey interaction. Moreover, specific leaves on which a disproportionate number of contacts occur between predators, in contrast to those between predators and prey, would soon be unproductive for the predator because: (1) being so numerous, the predator would soon deplete the prey and either become cannibalistic or unable to reproduce; or (2) if that did not happen, the prey, being abundant (else the predators could not be abundant), would soon exhaust their food supply and die or move off, leaving the predators to starve. Moving away from really crowded predator or prey situations could well be anticipatory behavior set by natural selection in such a way as to assure a

higher, more efficient level of over-all control—on the whole plant or crop. We are by no means sure, however, that such behavior is exhibited by phytoseiids. As always, density levels presumed sufficient to trigger such movements would vary with the species and conditions. We could not say whether proved behavior of this nature in the laboratory would mean a better or a poorer potential for control in given field situations.

Finally, Huffaker *et al.* (1968) stressed that although the functional and/or numerical responses of a given species to prey density may be limited, the fact that additional species of predators are brought into play, both functionally and numerically, as prey density increases (e.g., Kuenen, 1947; Dosse, 1962*b;* Collyer, 1964*d;* and earlier and subsequent discussions herein) lends a very real density-dependent aspect to the *combined* predation. Putman and Herne (1964) emphasized that because many predators respond functionally, even if they do not respond numerically[7] or quickly enough, their increased attention, per predator, to the specific prey species as the latter's density increases results in an increase in percentage kill, up to a point.

Searching Capacity and Features of Dispersion

Searching capacity and the dispersion patterns exhibited by prey and predator species have already received attention, but additional material is presented here.

Given adaptation to the physical rigors of the environment and a corresponding synchrony with the prey, searching capacity is regarded as the principal attribute of a good predator. Other attributes, although often important, are secondary. A predator that must rely primarily on high power of

increase rather than on its searching capacity is not a "good predator" in terms of being a reliable regulator at low prey density.

In studies on phytoseiids, coniopterygids, chrysopids, and coccinellids *(Stethorus)* the prey appear to be found only by actual contact (Fleschner, 1950; Putman, 1955, 1962). Therefore, the area of perception is apparently little greater than the width of the predator.

The searching capacity of larvae of

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[7] Most efficient entomophagous predators (including parasites) do respond numerically; prey-specific ones must necessarily so respond.

Chrysopa, Stethorus, and *Conwentzia* was studied in detail by Fleschner (1950), and on the basis of speed of travel, width of perception, and number of successful captures in relation to total contacts, *Chrysopa* was shown to possess the highest searching power. Yet Fleschner found that the minimum density of mite prey necessary to complete development was one mite per 26.7 square inches for *Chrysopa,* and only one mite per 14.9 square inches for *Stethorus.* Putman (1955) estimated that the average minimum density of *Panonychus ulmi* necessary to sustain adults of *Stethorus punctillum* was at least one per peach leaf (about 2 to 3 square inches), and that even at densities considerably above that, few larvae reached maturity. This is not a high density, but a high food requirement may nullify a high searching capacity. Immature phytoseiids appear to have a considerably lower basic searching capacity than do larvae of the insect predators studied, but this lower searching power may actually be higher, in comparison with the respective food requirements. (See earlier section, "Power of Prey Consumption or Appetite.") One immature prey per 6 square inches, or slightly less, was sufficient for *Amblyseius limonicus* to complete development (McMurtry, unpublished results). These data suggest, roughly, that when limited to spider mites, *A. limonicus* could survive at one-half the prey density of *Stethorus,* and *Stethorus* at one-half the density of *Chrysopa,* in spite of the fact that their basic searching powers are in reverse order. Moreover, the adult female phytoseiid has a greater searching capacity than the nymphs and probably accomplishes 20 to 30 times as much of the total predation as do the nymphs, considering the time span of the two stages and their respective food intake capacities.

Success in searching, however, is not a simple constant, for predators may interfere with one another, utilize time in handling prey, or be disturbed by contact with prey, and searching does not follow a simple, random pattern. If it did, a given predator, on average, would find just as many prey in a population of 100 mites on 10 leaves, whether they were uniformly spread over the leaves or clustered in a few pockets. Burnett (1958) demonstrated the different degrees of success associated with different patterns of prey dispersion. Fleschner (1950) has also shown that such predators temporarily change their searching behavior and search more intensively, in tighter, torturous bends, when encountering and utilizing aggregations of prey, in contrast to searching without a recent encounter, as when the prey are dispersed singly over the area. A general density that, if "spaced-out," would not support a phytoseiid population may nevertheless do so if it is aggregated to some extent (Flaherty, 1967). Thus, the pattern of dispersion of the prey on the host plant is very important, as are the general searching behavior and the specific searching power of the predator.

The effective predator will, of course, inhabit the plant in similar fashion to that of the prey species (Chant, 1959), but this does not mean that their leaf frequency distributions must coincide (see previous discussion).

A predator that lays its eggs where the prey are located should have a higher effective fecundity than one that lays its eggs at random. This is the case for *Phytoseiulus persimilis* (Chant, 1961a). However, *Amblyseius hibisci* shows little or no tendency to congregate, and readily lays its eggs on leaves uninfested with *Olygonychus punicae;* this may be why its response to increases in this prey species is often poor and delayed (McMurtry and Johnson, 1966). Bakels and van de Vrie (unpublished research) studied the distribution of *A. potentillae* on potted apple trees, in greenhouse and field experiments. The trees were infested artificially with

various densities of *Panonychus ulmi* and uniform densities of the predator. There was no correlation between the subsequent occurrence of prey and predators on identical leaves nor between the presence of prey and of predator eggs on identical leaves, thus indicating that this predator did not respond to the distribution of the prey. *Metaseiulus occidentalis* lays its eggs in the webbing of *Tetranychus urticae* and *Eotetranychus sexmaculatus,* and is not content on bare, unprotected surfaces. *Stethorus punctillum* also lays its eggs in the webbing of tetranychids on fruit trees (Berker, 1958) or on peach leaves where prey are present in glasshouses (Bravenboer, 1959). *S. gilvifrons* also prefers webbing for oviposition (Dosse, 1967). The number of eggs was greatly increased, however, on the trees with the higher prey density. (See also the first paper in this series, phytoseiid section.)

The complexity and nature of the plant habitat may affect dispersion patterns and maintenance of predator-prey balance. Fleschner (unpublished data) observed lower citrus red mite and higher phytoseiid populations in plots of citrus having a covercrop. Muma (1961b) found that groves with minimum cultivation generally had lower populations of citrus red mite and six-spotted mite, but the relation to predator numbers was inconclusive, a situation that might be expected even if the predators were the cause of the lower mite densities. Flaherty (1967, 1969) found that better distribution and control of tetranychids on grape by *Metaseiulus occidentalis* prevailed where johnsongrass occurred in the grape rows as a weed. This was shown to be associated with a source of alternate prey, *Tetranychus urticae,* on the grass. Dispersion patterns may vary according to the specific host plant. Putman and Herne (1966) noted that distribution of both tetranychids and predators was different on peach than on apple, apparently because of the variation in pubescence of the foliage.

Anderson and Morgan (1958) considered *Metaseiulus occidentalis* and *Typhlodromus rhenanus* inefficient in control of *Panonychus ulmi* on apples in British Columbia because they tend to develop only on the under surfaces of the leaves and are more aggregative, whereas *Panonychus ulmi* occurs on both leaf surfaces and is more randomly dispersed. This finding indicates one of the reasons why Chant (1959) considered *T. pyri* a poor predator of *P. ulmi* on apples in England (see earlier discussion). But the poor ability of *M. occidentalis* to use *P. ulmi* as food (Burrell and McCormick, 1964) may be of major pertinence here. The inability of *M. occidentalis* to respond to increases of early-season *P. ulmi* populations on apples in Washington was not explained, but its response to later increases in *Tetranychus mcdanieli* McGregor, a more aggregative species, was attributed by Hoyt *et al.* (1967) and Hoyt and Caltagirone (1971) to the maintenance of better densities and better dispersion of this predator in the trees through use of rust mites in May and June when the population would otherwise have been unable to maintain itself adequately.

Flaherty *et al.* (1966), Flaherty (1967), and Flaherty and Huffaker (1970a) also found *Metaseiulus occidentalis* ineffective during early season against *Eotranychus willamettei,* but quite effective against *Tetranychus pacificus* on grapes in the Central Valley of California. These authors attributed the difference to the lighter densities and more dispersed distribution of the former on the vines, particularly in early season. L. M. Smith and Stafford (1955) had observed the same differences, but attributed them to the unlikely reason that the predators could not *catch* the Willamette mites—perhaps they should have said, "cannot *find* them." Flaherty and Huffaker

(1970*b*) also provide clear evidence that the adequacy of the dispersion of this predator on the vines and in the vineyard, relative to that of the prey species, is as important in effectiveness as is its average density.

Yet, average ratios of predators to prey may be misleading. McMurtry and Johnson (1966) found that *Amblyseius hibisci* may, on average, outnumber *Oligonychus punicae* on avocado in early summer. But the predator density in areas having no *O. punicae* was essentially the same as in "pockets" where the prey species was getting started; in those significant pockets the predator-prey ratios were poor.

Lumping of data from different portions of a habitat where the predator-prey or host-parasite interactions are in different phases may mask any real rela-

tion that exists, and lead to wrong conclusions. The motility of the organisms involved is a prime factor in maintaining an interaction at the same relative phase over a given area. If the predator (including parasitoid) gets about readily as individuals it will tend to synchronize the phase over a greater area than if its motility is very low. Motility in the prey, if unmatched or unsynchronized by motility in the enemy, would also tend to produce a lagging response and varying phases of interaction (see Huffaker and Stinner, in press).

It is only when effective enemy control has been generally disrupted for a time and extensive high density has been reached—thus inducing extensive numerical response in the predator— that the classical rise and fall in the two
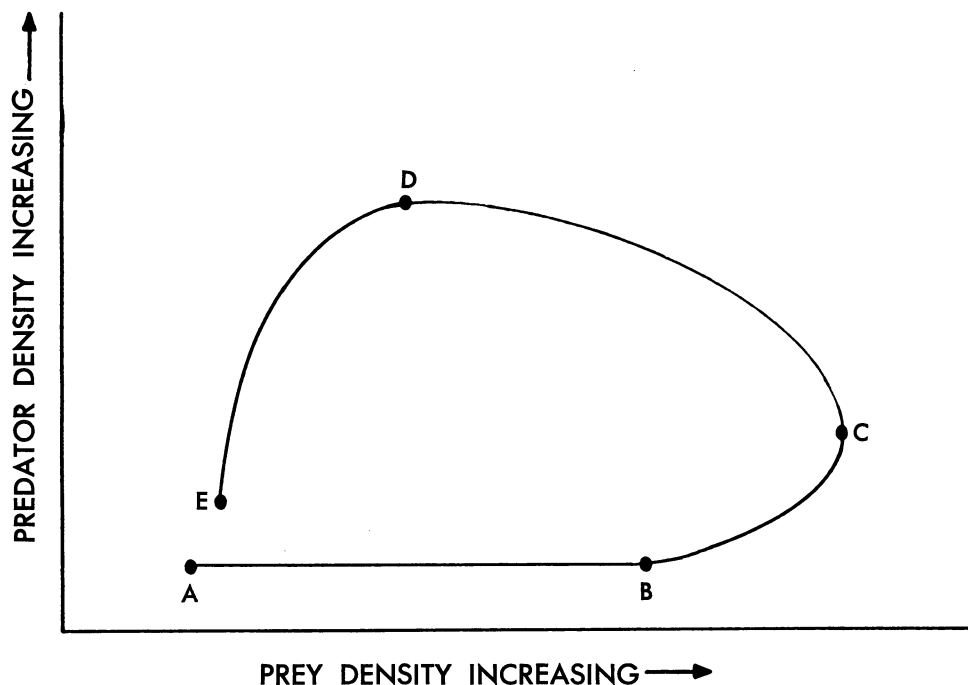

Fig. 4. Diagram illustrates a typical phytoseiid-tetranychid interaction on a leaf. At *A*, a leaf is infested with one female tetranychid, which reproduces and increases. At *B*, one female predator appears. Both species reproduce and increase in numbers until, at *C*, the predation is sufficient to cause a decline in the tetranychids. Then, for a time, there are still enough tetranychids that the predator can continue to increase to *D*, after which, it, too, declines (either from starvation or emigration) to *E*. The scheme is not intended to picture repeated oscillations. (Modified from Kropczyńska and van de Vrie, 1965.)

populations (the enemy lagging behind) become obvious. As Kropczyńska and van de Vrie (1965) stated, when control occurs at low endemic levels, the significant interaction is at the leaf, twig, or branchlet level (in mite populations). Gross correlations encompassing areas of contrary phases of interaction could not reveal the inherent response. In fact, if the pseudo-numerical response so determined did not show a levelling off or a decline in predator numbers with prey density, this would mean that predator numbers are simply related to their food supply, but not in a controlling way. Huffaker and Kennett (1956) used very small plots in their study of predation on cyclamen mite, and emphasized the necessity of not pooling data from areas too distant from one another. This latter practice precludes obtaining of data that permit detection of differences in dispersion or in phases of the predator-prey interaction, locale to locale.

In a related study, Wallace (1957) showed that a collembolan population (the lucerne flea) in each such microarea may pass through similar phases of intraspecifically induced, density-dependent dynamics, and the relation can only be discovered by separate micro-area study in a time-series of censuses. Only by studying the populations on single vines over a period of time were Flaherty (1967) and Flaherty and Huffaker (1970 a,b) able to relate control or lack of it to the percentage of leaves having predators. This was also true in Huffaker and Kennett's study. Oatman and McMurtry (1966) also found marked variations in the numbers of *Tetranychus urticae* between small, adjacent plots of strawberries.

Bravenboer (1959) found that *Metaseiulus longipilus* on peach in greenhouses in the Netherlands almost annihilated its prey in some spots, but left it undisturbed in others at relatively short distances away, in the same greenhouse. This finding was attributed to the poor dispersal abilities of this species, in contrast to that of *Stethorus punctillum* under similar conditions.

Considering the data given here and elsewhere in this paper, certain phytoseiids are apparently much more effective against tetranychids that form aggregative colonies than against those that exhibit greater dispersion, even on the same plants.

The nature of predator-prey oscillations also seems to be affected by the kind of clumping and any disproportionate movements of predators and prey from arena to arena (Huffaker *et al.*, 1968; Huffaker and Stinner, in press). These are subjects we know little about, and we need more study like that of Huffaker and Stinner, directed to illustrating the principle that the effective environment is not a single, homogenous arena wherein predator-prey interactions occur as if instantaneous and complete diffusion is ever-present. Previously, models of such interactions had invariably been built on this unreal assumption. Some thought-provoking evolutionary concepts on the phenomenon of dispersion as related to animal numbers are discussed at length by Wynne-Edwards (1962) and Wellington (1964).

Specialized and General Predators and the Use of Alternate Foods

The question of advantage or disadvantage in effective enemy control posed by a choice or lack of choice in prey or hosts is a fundamental one, and is related to the foregoing topics. Undoubtedly, evolution has maintained broad choice of diets in some taxa while creating increasing selectivity of diets in others.

The value of broad dietary range is obvious, for when one species becomes rare others can be substituted. But a price is exacted in terms of efficiency. Specialization is a deeping rut in evolu-

tion, and once a form settles into it, the tendency is for intensification, for the specialists are more efficient in that role in the ecosystem. By their very nature, such specialists (monophagous or steno-phagous forms) are, in principle, more reliable and intricately attuned enemies of the given prey. The relatively prey-specific ones are more closely synchron-ized in their habits, haunts, phenology, and patterns of dispersion, and are nor-mally more effectively attuned in nutri-tional needs, reproductive potential, and searching capacity than are the more generalized, and usually larger, oligo-phagous or polyphagous predators that attack the same species. Thus the spe-cialists are able to maintain the prey populations at lower densities. Our em-phasis on phytoseiids is not meant to relate to ones that are only incidentally predacious on a given prey species.

For the specialists, natural selection would have operated, logically, to de-velop the above-mentioned traits to greater perfection as loss in dietary range was sacrificed; conversely, the loss in dietary range would not have occurred were it not an advantage to the possessor in competition with other claimants of the general food supply. Theoretically, other things being per-missive, since specialists are the more efficient predators, they are capable of surviving as effective regulating populations at lower prey densities, and will naturally tend to maintain the density of the prey species at the lowest level consistent with their own needs for survival (Nicholson, 1933). And since they are strictly lim-ited to their specific prey species, they may be relied upon to respond numer-ically (except for unfavorable circum-stances) to changes in the density of their prey, although with a lag. Exam-ples of tetranychid specialists are: *Phy-toseiulus persimilis* (Dosse, 1959; Chant, 1961a; Bravenboer and Dosse, 1962; Oatman and McMurtry, 1966); *Blepha-ridopterus angulatus* (Collyer, 1952,

1953a; Muir, 1965b, 1966); and many *Stethorus* spp. (e.g., Bravenboer, 1959; Kuenen, 1947; and first paper in this series). Experience also shows that many of the most efficient predators in the real situation, e.g., *Amblyseius aurescens, Typhlodromus caudiglans, Metaseiulus occidentalis, M. cucumeris,* and *T. pyri,* are not strictly specialists; they have compromised, and accept certain alternate foods (see later dis-cussion).

General predators, on the other hand, are less dependent on the given species of acceptable prey, and may be less re-liable in control because of lower func-tional and numerical responsiveness to changes in density of the given prey species. At the very low prey densities attained by action of efficient specialists, the general predators, being less at-tuned, would normally die out or move away unless sustained by shifting to alternate prey species. This on-and-off action (involving threshold levels) of general predators tends to damp the violence of primary interaction and pro-mote more stable low-density control. There are all degrees of oligophagy, and those truly predacious forms with a very broad dietary range (these are com-monly larger) may be looked upon as ultimate regulators of stability in the general ecosystem, rather than at the single-species level. Species of interme-diate dietary range would serve inter-mediate roles. The nonspecialist preda-tors are thus rear-guard safety devices, with a built-in ability to shift attention from those prey forms that are declining in importance to ones that are increas-ing. They may at times feed more on a primary specialized predator than on its prey, for the former at certain phases of the interaction may constitute the more readily available food. This action would tend to reduce the severity of the primary interaction and cushion its dis-turbing effect on the ecosystem as a whole (Huffaker, Messenger and De-Bach, 1971).

To be sure, size and dietary range in mite predators are not strongly linked. In considering strictly predacious predators, some relationship exists, but when plant host-feeding is coupled with predatory habit, as is common in some species—especially the phytoseiids—the relationship seems remote.

Evolution gives us a crazy-quilt mosaic of forms fitted to the situations at hand. While the patterns described above may roughly characterize basic tendencies, conditions often prevail wherein the strictly monophagous, inherently most efficient regulating predator could not exist at all. We may then find a modification that gives the form maximum efficiency in its specific role consistent with its own survival, needs for food and for outdoing its competitors on a year-round basis. The result presumably would be a form with a marked predilection for a specific prey and geared in that direction in its adaptive traits, but because of seasonal or other severe stress, the prey's numbers may for a time be too few for the predator's survival, and it thus utilizes some other food strictly as an emergency feature. The phytoseiid *Amblyseius aurescens* does not reproduce in the absence of prey mites, but utilizes alternate food substances, such as honeydew or plant exudates, for mere survival (Huffaker and Kennett, 1956). Thus, such a form retains maximum reliability, as a regulator of cyclamen mites, consistent with the situation. Dosse's (1961b) example, cited previously, wherein *Typhlodromus pyri* [= *T. tiliae*] accepts pollen as food and may reproduce on pollen alone (but only for a single generation), illustrates a less close dependency on the specific prey and greater, but limited, reliance on alternate food. Furthermore, McMurtry and Scriven (1964b) found that *A. hibisci* will produce successive generations on pollen alone, and that a given individual fed on pollen more readily than on spider mites. McMurtry and

Scriven (1966a) demonstrated, however, that even in such a case, the predator population increased to high densities and controlled *Oligonychus punicae* when pollen was added, but failed to do so when no pollen was supplied. Thus, feeding on pollen resulted in increased predator efficiency as a population, even though individual predators fed less on mites when pollen was at hand.

This question of dietary range in phytoseiids was discussed in some detail in the first paper in this series. While Chant's (1959) view that acceptance of alternate prey lessens efficiency in the *regulation* of a given prey species (but not necessarily in the *control*, see below) is true in principle, the particular situation may have dictated the habit and may be quite essential to the most efficient predation and control possible under the existing conditions. The examples cited above, of *Typhlodromus caudiglans*, *T. pyri*, and *M. occidentalis* may fit in here. In a given situation, the genotypes of these species may not necessarily be tetranychid specialists, but rather rust mite specialists, for example. Putman and Herne (1964, 1966) gave a good example of the importance of retaining a capacity to utilize more than one kind of prey. They stated that the peak level of *Panonychus ulmi* on peaches in Ontario in some seasons may be only one per 100 leaves. *Typhlodromus caudiglans* is considered the most important factor in maintaining control at such low levels, and obviously, at such times, it must be feeding primarily on other things.

The question of the diets reported for *Metaseiulus occidentalis* and *Typhlodromus cucumeris* or of the identity of different forms considered to be *M. occidentalis* and *T. cucumeris*, respectively, in Washington and California is pertinent here, for seemingly contradictory data may in fact be the result of working either with different species or different genotypes of the same species.

Burrell and McCormick (1964) found *Metaseiulus occidentalis* from Washington to prefer and to develop much faster when feeding on the rust mite, *Aculus schlectendali* (Nal.), than when feeding on tetranychids. Yet Laing (1968) has found a California form to develop quite rapidly and successfully when feeding on two-spotted mite alone, while Huffaker (1958), Huffaker, Shea, and Herman (1963), Flaherty (1967), Laing and Huffaker (1969), and Flaherty and Huffaker (1970a), have found it to thrive and be very effective in control of six-spotted mite, Pacific mite, and two-spotted mite, in laboratory and field situations where eriophyids were either rare or absent. Hoyt *et al.* (1967) and Hoyt and Caltagirone (1971) found that *M. occidentalis* in Washington apple orchards failed to check early-season *Panonychus ulmi* infestations, but did respond to later increases in *Tetranychus mcdanieli,* and often controlled late-season infestations of *P. ulmi* as well, if rust mites were adequately present in May and June as a source of alternate food. (See also section, "Functional, Numerical, and Total Responses of Predators.") Huffaker and Kennett (1956) also found *M. cucumeris* on strawberries in California to feed primarily, if not entirely, on tarsonemids rather than tetranychids, whereas this same species from other areas and situations is apparently rated primarily as a predator of tetranychids (Chant, 1959; Burrell and McCormick, 1964). Klostermeyer (1959) noted that it seemed to thrive on alfalfa whether or not tetranychids were present.

Collyer (1964a) found that *Typhlodromus pyri* increased better and had more effect on *Panonychus ulmi* populations on apples when *Aculus fockeui* was also present than when only *P. ulmi* was present (see also earlier section on predator control for deciduous fruits and grapes). Putman and Herne (1964) also found *T. caudiglans* to build up more readily and to attack *P. ulmi* more effectively when *A. cornutus* (Banks) was abundant. McMurtry and Scriven (1964a) found that *T. rickeri* Chant readily accepts either eriophyids or tetranychids as prey. Thus it is clear that use of alternate foods may be important in the role of a given predator species. Kropczyńska (personal communication) found that *T. finlandicus* bred readily on mildew spores, but the longevity was reduced when that was the only food.

Furthermore, if an alternate food were always available in super-abundance, use of it by a predator population would make possible greater control but not regulation of the specific prey species, possibly nearing or achieving annihilation. But in such a situation, the alternate food would likely have become the preferred and principal nutrition toward which adaptive properties would have been geared, and the high degree of control or preclusion of the given prey species would be largely coincidental and not density-dependent or regulating. Either preference for rust mites or their more ready accessibility may explain the above-suggested lack of attention in *Typhlodromus caudiglans* or *Metaseiulus occidentalis* to *Panonychus ulmi* on occasions. As a predator of tetranychids in California, *Amblyseius hibisci* (McMurtry and Johnson, 1966) may be considered somewhat intermediate between the condition described above from Dosse's work (1961b) and the hypothetical situation presented here. In the absence of prey, use of non-prey foods can serve either to prolong survival (Huffaker and Kennett, 1956) or for reproduction (Dosse, 1961b; McMurtry and Scriven, 1966a, 1966c). Huffaker and Flaherty (1966) concluded, however: "Thus, the view is unrealistic that a given species is a poor predator only because it accepts alternate foods. Only if the preference of

alternate foods results in neglect of the prey is this view necessarily valid."

It would be remiss, however, to leave the reader with the impression that insectan predators (or ones of more generalized feeding habits) are unimportant in control of tetranychids. For example, we saw evidence that certain coniopterygids, *Stethorus picipes*, and *Chrysopa* spp. may be effective against *Metatetranychus citri* on citrus in southern California, and that *S. picipes* may achieve a good degree of control almost alone (see section, "Role of Predators on Citrus"). We saw also that *S. picipes* may, in some situations, be the principal factor in a somewhat less effective level of control of *Oligonychus punicae*—a level that the avocado tree can tolerate. A point of possible value is that avocado in California is far from its native home area and is therefore less likely to have a really effective predator (a phytoseiid) associated with it than might be expected in its endemic region. This point might also apply to citrus and many other crops.

The first paper in this series treats the various insectan predators in detail, and many examples are available of contributory action by them, particularly (but not exclusively) when densities have exceeded low levels. Such examples include: *Haplothrips faurei; Conwentzia hageni* Banks; *Blepharidopterus angulatus; Scolothrips sexmaculatus; Chrysopa* spp.; *Stethorus punctillum; S. punctum* Leconte; *S. picipes; S. utilis* Horn; *Saula japonica* Gorham; and others. Putman and Herne (1966) reported effective early-season control of *Panonychus ulmi* on peaches in Canada by *S. punctillum*, and Oatman and McMurtry (1966) and Oatman *et al.* (1967) reported effective outbreak-preventive action of *Scolothrips sexmaculatus* in early season on strawberries in California. McMurtry (personal communication) believes that in some cases adequate predator control of citrus red mite in California is

achieved in the virtual absence of phytoseiids. Some workers have felt that a complex of insectan predators has been more important in the control picture than have the phytoseiids. Indeed, Krämer (1961), supported to a degree by Dosse (1962*a, b*) and Berker (1956, 1958), considers that action of some of these insectan predators on the phytoseiids renders the latter largely ineffective. Some of these results were obtained before we became aware of the role of phytoseiids, however; consequently, the latter may have been neglected.

Also, a form of control in some situations could be achieved by specifically poorly-responsive phytoseiids or other predators (as a single species or complex) if their populations were maintained at densities beyond that possible when dependent solely on the particular mite species itself, i.e., by their feeding on various other prey. This control would presumably be broken at times by the prey's escape to higher densities, and supplemented at such times by the action of more specific mite predators, such as *Stethorus* spp. or certain phytoseiids. All such predators add to the total machinery of control. We do not have adequate data to fully evaluate the real importance of such insectan predators as the coniopterygids, mirids, thrips, anthocorids, staphylinids, etc. that feed as semispecialists on spider mites. *Haplothrips faurei* feeds on eggs of lepidoptera, but it can be important against *Panonychus ulmi* in Canada (MacPhee, 1953; Putman, 1965*b*). *Blepharidopterus angulatus* feeds on plant tissue, but is important in control of *P. ulmi* in England. (See earlier section, "The Worldwide Record.") Dusty wings prey on scale insects, but are often important in control of citrus red mite (DeBach, Fleschner, and Dietrick, 1950; Fleschner and Ricker, 1953). In a number of instances where tetranychids have been observed to be under control for extended pe-

riods, a complex of insectan predators and phytoseiids has been present (e.g., Lord, 1949; Pickett and Patterson, 1953; Fleschner, Hall, and Ricker, 1955; Fleschner, 1958a; Collyer and Kirby, 1959; Putman and Herne, 1964, 1966; Collyer, 1953a, b, c, 1960, 1964a; Muir, 1965 a, b, c).

As a note of interest, ants may interfere with predator control of spider mites. DeBach, Dietrick, and Fleschner (1951) reported heavier incidence of citrus red mite damage and much higher densities of mites on lemons in southern California on ant-infested trees than on ant-free trees. The mean peak seasonal mite density in the ant-free trees was 1,437 mites per 100 leaves, and in the ant-infested trees, only 66.

Pickett and Patterson (1953) stressed the importance of general predators. Putman and Herne (1966) concluded, however, that *Typhlodromus caudiglans* is primarily responsible for control of *Panonychus ulmi* at endemic levels in Ontario, Canada, while other forms become important mainly at higher densities. The combined annihilative pressure from a complex of predators could conceivably be so intense at times as to reduce the chances of effective survival of even the low-density active phytoseiids. McMurtry and Johnson (1966) noted, however, that *Stethorus picipes* on avocado start to disappear when some *Oligonychus punicae* are left, and that the phytoseiid *Amblyseius hibisci*, a heavy pollen feeder, may remain at densities of 8 to 10 per leaf, and will then more severely reduce the tetranychid population. It is to be noted, however, that for two of the most thoroughly studied situations, those in England and Canada (discussed in section, "The Worldwide Record"), the earlier viewpoint that the insectan predators of greater voraciousness and dietary range were of major importance has given place to the view that phytoseiids are the prime force in maintaining low mite densities in orchards.

The Stage of Prey Attacked

Chant (1963), Mori and Chant (1966a), and Mori (1969) felt that the strong preference of *Phytoseiulus persimilis* for adult female prey gives it an advantage over forms that attack primarily the eggs or larvae, for it thus destroys the reproducing unit. This thought is worth examining. Opposing viewpoints are largely conjectural, and they center on whether we are thinking of quick suppressive ability or sustained control at the lowest density.

It seems obvious that parasites of scale insects such as *Aphytis* sp. near *mytilaspidus* Le Baron, that attacks fig scale, *Lepidosaphes ficus* (Signoret), only when the scale is fully mature are less effective than ones that attack before the scale matures, for in the former case many eggs are laid before the reproducing unit succumbs from the attack. Furthermore, if *Phytoseiulus per-* *similis* reluctantly attacks the younger stages, presumably many of the adult females they attack must already have produced progeny. In any event, the predator must leave sufficient progeny to mature so that it is supported as a population even after prior-acting factors have taken their toll. Also, the individual prey is not killed until after it has caused much more feeding injury than would be so had it been destroyed as an egg or larva. Thus the level of economic injury may be greater. Van de Vrie and Kropczyńska (1965) conducted greenhouse and field experiments on the distribution of prey (*Panonychus ulmi*) and predators (*Amblyseius potentillae*), in which they found this predator to prefer the juvenile stages of the prey, leaving the adults almost unattacked. This finding may explain why, under their circum-

stances in the Netherlands, this predator was able to maintain the prey at relatively low densities.

If the predator species can efficiently use the males as well as the early stages of both sexes before much loss of food supply from other causes has occurred, such utilization would seem to assure maximum use by the predator and support of the latter at densities and distribution patterns capable of maintaining the prey species itself at minimum mass or density. Obviously, if larger, more mature individuals are required for the predator species to thrive— that is, if enough energy is wasted in handling the prey, even after contact is made, to offset the amount obtained— then the most efficient utilization would be to avoid the younger stages and concentrate on mature ones. (Huffaker and Spitzer (1950) found *Chrysopa californica* unable to mature in pear trees with high densities of *Panonychus ulmi*, except in those trees where Baker's mealybug, *Pseudococcus maritimus* (Ehrhorn), was present to furnish larger units of food.) Juvenile stages of *Anthocoris nemorum* feed readily on *P. ulmi* on apple in the Netherlands, but the fourth and fifth instars and the adults have a clear preference for larger prey, such as aphids (van de Vrie,

unpublished data). This preference would mean, however, that such a species has sacrificed some of its potential regulatory power, given equal searching capacity, because the other factors act first. Furthermore, they may act in such a way as to short-circuit support of the predator and thus the reliability of its regulatory function. Also, if two such predators have equal searching capacities, the one that attacks the earlier stages would displace the other in a strictly one-niche situation (Nicholson, 1933), except as intraspecific interference features might favor coexistence (Hassell and Varley, 1969).

We have here compared only two hypothetical situations, contrasting the predator's preference for early stages of the prey with a preference for adult females only. Actually, if all stages are accepted when the predator is really hungry, and no contact is wasted, such a condition would apparently provide better control than either of the abovementioned situations. If the predator is not really hungry enough to require a whole adult female for satiation, the expected situation would be one in which the predator tends to select the younger stages and not waste the surplus afforded by the adult.

Some Problems in Sampling and Studying Mite Populations

The study of the ecology and the natural control of tetranychids presents a number of difficulties that have not yet been surmounted. We shall discuss those difficulties in the light of study methods now used, with the hope of encouraging development of better methods. One purpose of the worldwide spider mite project of the International Biological Program (IBP) is to develop more suitable methods and eventually bring them together and summarize them in one publication. This contribution is now in manuscript and is expected to be published soon.

Sampling Techniques and Equipment

Spider mites. Spider mite populations are usually sampled by periodically counting the mites on a certain number of leaves. It is generally recognized that mites are not randomly distributed, and this has influenced the development of sampling techniques (Kuenen, 1946; Hueck, 1953; Stollwerck, 1962; van de Vrie, 1966). Jones and Prendergast (1937) kept separate records of leaves taken from the north and south sides of citrus trees. Jeppson,

Fleschner, and Complin (1957) and Dean (1959) sampled a certain number of leaves from each quadrant of citrus trees. Michelbacher (1959) sampled only those areas of walnut trees that showed evidence of mite feeding. Flaherty (1967) and Flaherty and Huffaker (1970a) segregated leaf samples from the tops and the morning-sun and afternoon-sun sides of grapevines. Putman and Herne (1964) used as sampling units all leaves on a certain number of twigs of peach trees; thus the number of leaves in a sample increased during the season.

A significant proportion of the population of some mites (e.g., *Bryobia rubrioculus*) may be on the wood (Summers and Baker, 1952; Herbert, 1965); thus woody parts must be included in the sampling. Branchlets often suffice. No specific recommendations can be made regarding the number of leaves or branchlets to take, the proper segregation of positions on the plant from which given numbers are taken (or on which mites are counted or removed), and the frequency with which sampling should be done. General guidelines set forth by Southwood (1966) will be helpful in arriving at decisions. Whether variation is greatest within the plant, between plants, between rows, or in a block will need to be determined. A number of workers have found that variation is often greater between trees than within a single tree (between leaves or branchlets); hence sampling from more trees rather than numbers of leaves taken per tree would be indicated (Oakland, 1953; Daum and Dewey, 1960).

A problem encountered here is one always associated with the removal of a part of the population and of the food plant itself. At times of low density, and where frequent sampling is required in order to follow changes in the populations adequately, it may be virtually impossible to remove enough leaves or branchlets from the plants to obtain reliable samples without substantially altering the food plant's capacity to produce the mites or without removing too large a portion of the populations. Huffaker and Kennett (1953, 1956) found it necessary to remove leaflets rather than whole leaves of strawberry plants in order to reduce the disturbance involved, i.e., a thinning and opening up of the plants that in itself was not conducive to survival and reproduction of the cyclamen mites under study. Clipping of branchlets from young peaches, apples, or pears may be quite disturbing if heavy pruning has already been done. The self-evident solution would be to count the mites without removing the leaves or branchlets, were it not for the fact that this is often quite infeasible in the field. Often a compromise must be made between the objective of a fully adequate sampling and the disturbance entailed.

Some methods of sampling mite populations are:

1. Counting all mites directly on the leaves. This method is used by many investigators, and is thought to be essential by many workers when densities are low and predator counts are required (see below).

2. Counting only adult females in the field (Jeppson, 1951).

3. Washing mites from leaves and taking an aliquot while the solution is agitated (Jones and Prendergast, 1937; Newell, 1947; Henderson, 1960).

4. Counting mites only on portions of the leaves (Hoskins, Boyce, and Lamiman, 1938; Baten and Hutson, 1943; Michelbacher, 1959).

5. Leaf-imprint method (Venables and Dennys, 1941).

6. Use of a mite-brushing machine. This machine was developed by Henderson and McBurnie (1943), and the counting plate was modified by Klostermeyer and Rasmussen (1956). By taking photographs of portions of the plate, counts can then be made when-

ever convenient (Asquith, 1965), or the plates may be cold-stored.

7. Counting the mite-free leaves only. Pielou (1960a) found that by comparing plotted values based on actual counts of mites and the number of leaves having no mites it was possible to estimate roughly the densities of *Panonychus ulmi* from the determined proportion of mite-free leaves.

8. Knocking the mites from foliage and branchlets (Summers and Baker, 1952; Boudreaux, 1953).

The value of some of these methods was discussed by Morgan, Chant, and Anderson (1955) and Mathys and van de Vrie (1965), and the brushing machine was rated most efficient. Putman (1966) also studied the efficiency of this method and found that great care is needed to obtain reliable results.

Predators. Predacious mites are usually sampled in the same way as the spider mites they are feeding on (e.g., by leaf samples). However, this method may not always present a complete picture of the populations of some species. Putman and Herne (1964) found that a large portion of the population of *Typhlodromus caudiglans* is found on the twigs. Some species are thought to move back to more sheltering crevices or rough surfaces when not hungry, or during daytime. In studies on predation of *Metaseiulus occidentalis* on *Eotetranychus sexmaculatus* on partially covered oranges in the laboratory, Huffaker (unpublished observations) has noted that large numbers of the eggs of this predator are sometimes laid away from, but near, the exposed orange surfaces along ridges or depressions of the paper folds or wax sealings. This apparently has no adverse effect on their ability to curtail the prey mite's increase. The observations of Bakels and van de Vrie (unpublished research) on the relative dissimilarity in the distribution of prey and that of an effective predator, on apple, support this view. It may simply be a way of

escaping from the "disturbance" presumed to occur when prey are dense (Mori and Chant, 1966a; Kuchlein, 1967) without greatly reducing efficiency. Thus, an adequate sample for such species must include individuals found on plant parts where they may be spending time away from the scene of the prey population.

Many insectan predators of mites may drop from the leaves or fly away when leaves or branchlets are being removed from the plants. Sampling methods other than those used for the phytoseiids are commonly employed to assay their abundance:

1. A "knock-down" spray or dust. The predators are then collected on a sheet or tray (Lord, 1949).

2. Beating or shaking the foliage and branchlets so that the insects fall into a tray or other type of container (Lord, 1949; Steiner, 1956, 1959, 1965b; Post, 1962a; van de Vrie, 1965; van de Vrie and van den Anker, 1967). A mechanical shaker was even used by Lord (1965), but it damaged parts of the tree.

3. Predators collected by suction (Dietrick, Schlinger, and van den Bosch, 1959; Mathys, 1965; Lord, 1965).

4. Visual search over the plant. A major advantage of this method is that neither the predators nor the plants is disturbed. Usually a certain number of plants or trees are searched over for a designated period of time (DeBach, Fleschner, and Dietrick, 1950; Putman and Herne, 1958; McMurtry and Johnson, 1966). Reproducibility (i.e., adequacy) is sometimes good.

5. Trapping in burlap or corrugated bands (Huffaker and Spitzer, 1950).

Lord (1965) commented that there is no ideal method for sampling predators on apple trees because of their non-random distributions, variation in growth of foliage, and the active nature of such predators.

In laboratory studies, it is generally

necessary to confine the test insects in a small area in order to make the necessary observations. Various methods have been used, including the major ones listed below:

1. Confining the mites and predators on an intact leaf by means of a small cage or a sticky barrier (Cagle, 1946; Chant, 1959; Specht, 1963; Watson, 1964; and others).

2. Confining the mites and predators on detached leaves.

Leaf discs floated on water or nutrient solutions were used by Rodriguez (1953) and modified by Foott and Boyce (1966). Other modifications of this general technique have been used by Putman (1962), McMurtry and Scriven (1964*a*, *b*), Helle (1965), and Kuchlein (1966, 1967). Henneberry (1963) found that reproduction of *Tetranychus urticae* varied between detached and intact leaves. In Kuchlein's technique, drowning of predators in moving about is an undesirable feature.

Various types of small cages on detached leaves have been used by Munger (1942), Huffaker (1948), Ballard (1954), Laing (1968), and Kennett and Caltagirone (1968).

3. Population-interaction studies have been conducted by using oranges with various coverings, set up in various dispersal patterns in cabinets or trays sealed with sticky or greasy barriers (Huffaker, Shea, and Herman, 1963; Huffaker, 1958, 1966), or by using strawberries growing in a glasshouse or growth chambers (Huffaker and Kennett, 1956). Others have been carried out in growth chambers (Force, 1967; Laing and Huffaker, 1969) or by using small trees in glasshouses or cages (Collyer, 1958; Herbert, 1962*b;* van de Vrie and Kropczyńska, 1965; McMurtry and Scriven, 1966*c*). Dosse (1960) and Krämer (1961) conducted semifield experiments by covering small trees with sheets. This procedure may be used to exclude insectan predators if detailed studies with phytoseiids are desired.

The objectives in these studies are usually quite different from those involved when small cells or single-leaf units are employed, and the necessary methods and equipment required will vary with the objective and the test insects. Such "ecosystems" are much simpler than orchard ecosystems, but they can be used to study specific processes or details.

Some Problems Posed in the Over-all Appraisal

Several methods have been used to determine if a given predator species feeds on a given tetranychid, direct observations in the field or laboratory being most common. The precipitin test (Hall *et al.*, 1953) and paper chromatography techniques (Putman, 1965) have been used. Some progress has been made in development of the precipitin technique for ascertaining the extent of predation in the field, but in this use the technique is weak, for it is worth little to know whether a predator can or will feed on a given prey species under confinement, or whether it does so in the field, if we cannot relate the *amount* of such feeding to curtailment of the prey population. Techniques concerned with population dynamics are therefore essential.

Mites pose many problems of analysis that make methods that are useful with many insect populations inherently unsuitable (e.g., Morris, 1963*a, b;* Varley and Gradwell, 1963; Neilson and Morris, 1964; Huffaker *et al.*, 1968; Bateman, 1968). (1) Mites are so small, so delicate-bodied, and can reproduce so fast that mark-and-recapture techniques, or simply marking or tabbing of individuals, is impracticable. (2) They have such short life cycles that although the peaks of different generations in cool climates can sometimes be identified, this cannot be done in others. The indistinctness of the generations makes most difficult the tabulating of causes of mortality by genera-

tions or the rates of increase that prevail from one generation to the next, and are thereby relatable to the density of the generations. (3) After death, mites shrivel and dry up, so that it is impossible to determine the cause of death. (4) The complexity of factors that may make for natality, mortality, or movements is often subtle, and many compensating features may come into play. (5) Even if the causes of mortality or higher or lower rates of natality and movements into or away from the area could be tabbed, the interactions when two or more independent variables are related, either positively or negatively, can hinder the effort to develop fully understandable and predictive formulas for estimating abundance (Tukey, 1954; Goldberger, 1964; Mott, 1966; Huffaker *et al.*, 1968; Luck, in press). The latter three papers show some progress in identifying and understanding certain of these interactions. (6) Predation, death from weather stress, emigration to other habitats induced by crowding, and perhaps disease are the main causes of loss in numbers. Yet the numbers of individuals affected by each of these causes cannot be even estimated except very roughly in some cases. (7) Estimates of losses and correlations with predator numbers suffer because a large complex of predators (and sometimes disease) attacks the population, and we do not know how to assign proportions of the losses to the various species of predators. To do so, we should need to know which ones feed exclusively on the mites and on what stages; which ones feed on other animal or non-animal matter, in what proportions on each; and the numbers of prey and other food required to maintain them and to sustain given levels of reproduction. (8) Finally, most of the spider mite infestations in which we are interested are those of cultivated crops, many of them annual row crops, subject to chem-

ical and cultural disturbances that further complicate the picture.

Facing these problems, it is perhaps surprising that we have learned as much as we have, and it is understandable that spider mite ecologists have resorted to two main lines of approach: (1) experimental study of environmental and nutritional features as related to fecundity of the mites; and (2) study, by experimental means, of the role of enemies, by use of adjacent comparison plots, in both instances so as to minimize any meteorological differences.

Huffaker *et al.* (1968) discussed the value of the check method of analysis of the role of enemies and contrasted the meaning of the results with those obtained by nonexperimental techniques of Morris (1963*a*), Varley and Gradwell (1963), and Neilson and Morris (1964), in which correlations are used. While it may be desirable to use both correlations in long-term data from nonexperimental plots and check methods in analysis of the same situation (Huffaker and Kennett, 1966; Huffaker *et al.*, 1968), the circumstances in many studies on mites do not permit meaningful research over the long number of generations required by correlation methods. Disturbances caused by varying the crop from year to year on a particular plot of ground preclude such studies. Also, Varley and Gradwell (1963), Mott (1966), Southwood (1967), Hassell and Huffaker (1969) and Luck (in press) point to shortcomings in the key-factor approach of Morris (1963*a*). Mott emphasized that where two independent variables are themselves correlated, the variance cannot be segregated among them, while Southwood showed that if a cycle consists of five or fewer generations, the slope of the regression is not, as postulated, a measure of the density-dependence in the system, and he, as well as Hassell and Huffaker, and Luck, showed that delayed density-dependence is not in any event so measured validly.

While the methods of Morris (1963 *a, b*) and of Neilson and Morris (1964) may be used with some success in ascertaining the causes of some of the variance and may suffice for prediction of population trends, changes in slope of the regressions associated with their treatment of entomophagous parasitism do not have the significance claimed. That is, the changes in slope do not indicate the delayed density-dependent, and therefore regulating, action by the parasites (or predators). Hassell and Huffaker (1969) explored this possibility, using parasites having one, two, and three generations, respectively, in a single host generation. One might expect that where two or more parasite generations are exhibited, to one of the host, the effect of the parasitism within the generation would be similar to that of a prompt or direct-acting, density-dependent factor, since numerical response is generated within the generation. Hassell and Huffaker found, however, that in their instance this was not shown statistically. Huffaker and Stinner (in press), however, present examples wherein this is suggested statistically.

In any event, it is important to note that we do not have a statistical method for appraising the intensity of the density-dependent action of entomophagous or acarophagous parasitoids or predators in all of which reproductive numerical response is delayed. The method of Varley and Gradwell (1963) can be used to detect the presence of such meaningful delayed density-dependent action, but not to appraise its intensity.

Most important, such correlation methods are no replacement for check methods, for they give no measure of the degree of *control* exerted. One does not know how high densities would go in the absence of the factor judged to be regulating, for the data do not tell whether or not some other compensat-

ing factor would come into play and stop the increase at some level perhaps only slightly above that of the peak population levels observed.

On the other hand, while the check method is the only means known of learning the degree of control a given enemy species can exert, it has limitations. It is designed only to test such action by an enemy. Its use may induce other changes in the environment important to the mite species under study (e.g., Fleschner, 1958*b;* Chant, 1963; Putman and Herne, 1964). It does not define nor indicate the intensity of any density-dependent action by the enemy or enemies, nor actually show that the effect is in fact a density-dependent one. This is often assumed, however, from the nature of the proved action by such enemies, in many instances, and on theoretical grounds. The chemical check method was used with considerable success by DeBach (1947), DeBach, Fleschner, and Dietrick (1950), Huffaker and Kennett (1956), and Lord (1956) for evaluation of the action of certain mite predators. While this method has been criticized largely on theoretical grounds, it is a most valuable technique if used collaterally with other means of removing or excluding the predators (Fleschner, 1952, 1958*c;* Huffaker and Kennett, 1953; Fleschner, Hall, and Ricker, 1955; Chant, 1963) and if each method used gives a comparable result. (See DeBach, 1964.)

The other approach to understanding has involved experimental determination of the influence of cultural practices and the specific nutrition of the spider mites on their fecundity and rate of increase (see first paper in this series). Field studies have been conducted to determine the influence on mite fecundity of pruning, manuring, and use of chemical fertilizers. The application of various agricultural sprays in other studies has involved use of similar techniques under more refined,

hydroponic culture situations; and still other studies have been directed at determining a chemically-defined proper diet. (See also sections, "Field Evidence for the Hypothesis of Physiological Inducement," and "Field Evidence for the Hypothesis of Predator Inhibition.")

Such studies will help greatly to ascertain whether or not the rates of increase observed under particular well-studied situations may have been instrumental in causing sudden outbreaks in mites. Yet such information on fecundity or power of increase does not, in itself, explain why an outbreak occurs in a situation conducive to a particularly high power of increase while in others, equally favorable in all known respects, populations remain low. Further studies like those of van de Vrie and Boersma (see figs. 1 and 2) are suggested to evaluate the power of suitable enemies to prevent increases in spite of physiologically-induced, maximum potential powers of increase in the prey.

Theoretically, under proper situations, a good regulating enemy might be able to maintain a higher degree of stable control at a low level when the prey has a high rather than low power of increase, for at low points in the prey-enemy fluctuations the predator would then be better able to maintain itself in a good distributional pattern in the environment, and thus be able to check subsequent increases before they get going very far. Processes giving an opposite result are also conceivable.

Certainly, some kinds of enemies can and do check population increases in their hosts or prey species regardless of whether the latter's powers of increase are high or low. With respect to mite infestations, we do not know to what extent reported increases have been due to physiologically-improved powers of increase in the mites in the orchards, for example, or to lack of efficient predators or inhibition of their action. At any rate, population abundance is not regulated in any sense by power of increase, although if nutritional potential of the host plants is improved, regulation through competition for the food could then take place at much higher densities than before. Moreover, in orchards nutritionally marginal for spider mites, general enemies not closely geared as regulators of mite populations may have marked supplemental controlling influences, but if conditions are made highly favorable nutritionally, these same predators may be poorly attuned to respond to the mite increase, and outbreaks may ensue. In conclusion, the complexities of each situation need to be fully explored in order to uncover the explanations for mite increases, and both nutritional studies and check methods of analysis of predator action are prime tools. We can, however, make greater use of correlation analysis by comparing rates of increase over short-term intervals as related to density and other factors. The methods of Hughes (1962), Tanner (1966), and Salt (1967) may prove useful.

POTENTIALS FOR GREATER USE
OF BIOLOGICAL CONTROL

The general aspects of biological control have been covered by DeBach (1964), and the problems associated with conserving and augmenting such enemies as are found in given crops and areas are outlined therein. The material in the first paper of this series, and in the third, to follow, on the effects of chemicals and other cultural practices on mite enemies and on the pest mites themselves, indicate proper methods to explore in obtaining the most effective control by enemies, consistent with profitable production. This,

of course, involves both the practicality as well as the potential of an integrated control approach (R. F. Smith, 1962; Bartlett, 1964; R. F. Smith and Reynolds, 1966; Huffaker, 1970). The relation between mite density and damage to the host plant, with the ensuing impact on crop losses, needs more elucidation. The work of Parr and Hussey (1962), Hussey (1965), and Hussey and Parr (1963) with cucumbers grown in greenhouses in England indicates that a considerable amount of damage can be tolerated before economic losses occur, and the integrated control approach is feasible. This would certainly depend on the species and the crop plant.

Hoyt *et al.* (1967) and Hoyt and Caltagirone (1971) present the outlines for a practical program of integrated control of pests of apple in Washington state, and peaches in California, including spider mites. The prolonged successful program in Nova Scotia (Lord, 1949; Pickett, Putman, and LeRoux, 1958; MacPhee and Sanford, 1961; MacPhee and MacLellan, 1971) is of world renown. Unfortunately, the application of integrated controls is limited at present because we lack both the adequate basic information concerning all the elements involved and the sufficiently trained personnel to carry out such programs "on the ground." (See Huffaker, 1970.)

In general, it seems justified to consider that specifically responsive phytoseiid predators have the most potential for use in spider mite control, although other predators or complexes of such predators may serve as useful components, or perhaps at times be adequate in the absence of effective action by phytoseiids. In general, however, phytoseiids have relatively lower powers of reproduction than do certain insectan predators. These characteristics restrict the speed with which the predators may come in, multiply, and correct explosive situations, particularly in row

crops or annual plantings. However, their capabilities as responsive, persisting, and reliable regulating agents at low prey densities in continuing favorable situations make them prime agents in programs of biological control in the more stable situations. Their use in temporary situations, as in greenhouses or annual crops, seems promising where methods are developed to introduce them economically in adequate numbers early in the growing season of each crop. The potentials for this type of program have been shown for greenhouse cucumbers (Hussey, Parr, and Gould, 1965; Begljarov, 1967; Hussey and Bravenboer, 1971) and for field strawberries (Oatman and McMurtry, 1966; Oatman *et al.*, 1967; Oatman, McMurtry, and Voth, 1968).

We have not progressed very far in economic mass production of mite predators. In some cases they have been produced in quantities of some tens of thousands over a period of several months (Scriven and Fleschner, 1960; McMurtry and Scriven, 1965; Begljarov, 1967). The more specific mite predators have been reared only on spider mites, but some of the more general feeders can be reared on synthetic foods or plant products, such as pollen (Hagen, 1950; McMurtry and Scriven, 1966*a*). However, millions rather than thousands, may be necessary if an entire area is to be properly managed by repeated releases. This would require drastic modifications of present methods, but the difficulties may not be insurmountable. Discovery and use of phytoseiids that can thrive under suitable conditions in the absence of repeated stocking would be ideal.

If it is determined that existing predators of mites are inadequate even when maximum favorability in conditions is maintained, or if those present have too little tolerance for chemicals essential in the pest-control program, then consideration should be given to introductions of new species from else-

where. There seems little use in introducing new ones if perfectly capable ones are present and if the necesssary measures of pest control would be as harmful to the new species as to the ones already present. We know, however, from wide experience in the general field of biological control, that the best enemy is not by any means always the one at hand. Furthermore, certain species or forms found elsewhere may have greater tolerance for the chemicals required in the particular situation.

Efforts in establishing new spider mite enemies have been disappointing. McMurtry (unpublished paper presented at I.B.P. meeting, Sutton-Bonnington, England, July, 1967) pointed out that, in California, attempts over the past 15 years to establish a conioptergid, four or more species of *Stethorus,* and 11 species of phytoseiids have resulted in only one establishment (for four seasons in the coastal locations). This species, *Typhlodromus rickeri,* has exhibited no substantial spread nor promising potentials in other respects. That it was the only phytoseiid established may have been due to its having been colonized in much greater numbers (500,000 or more). Phytoseiids appear to be poor dispersers, and are subject to periodic extreme shortages of tetranychids either after decimating them or during periods when they experience catastrophic crashes from other causes. It may therefore be necessary to colonize such predators in very large numbers and on a rather extensive basis. If we knew more about their seasonal activities—including diapause —alternate prey or other foods utilized, kinds of vegetation accepted, climatic requirements, and the like, we should perhaps be in a better position to establish new, promising species. *Phytoseiulus persimilis* was obtained by Dosse from Chile, and cultures were sent to Europe and later to Canada and the United States where it has been used mainly in greenhouses, but field trials have not resulted in establishment.

CONCLUSIONS

Spider mites have become a major problem largely since World War II. The effects of pesticides on predators and on host-plant nutrition, the development of resistance to pesticides, and altered or improved management practices have all played a part. We need greater understanding of this complex of causes. For example, how, precisely, do pesticides lead to outbreaks of spider mites in specific instances?

Basic studies on such things as behavior, physiology, nutrition, and diapause are notably lacking or inadequate for both spider mites and predators. For example, we know little about the factors attracting predators to their prey or to certain host plants, or about what conditions are conducive for spider mites to colonize a leaf or migrate to another one. We know little about why certain predators (e.g., some phytoseiids) thrive on a given prey species on one plant host but not on another. We know little about why, in one situation, they survive well from autumn to spring, but largely die out in another, although recent studies in Poland and the United States offer some explanations.

The condition of the host plant is a major factor affecting success and abundance of spider mites. Weather, the seasonal growth cycle, soil, water, soil nutrients, and pesticides can alter the physiology of the plant, thereby affecting its nutritional quality for mites. Better understanding of these factors could be rewarding: it might lead to possibilities of altering the plant growth so as to lower the reproduction of the mites feeding on it.

Although favorable host-plant nutrition and weather are prerequisites to

spider mite increase and abundance, these pests were of much less importance before World War II than they soon became with the advent of new, synthetic pesticides. Destruction of predators has been shown, in many instances, to cause increase of mites to high densities whether or not any stimulus to mite fecundity could be demonstrated. Thus endemic predators certainly hold much promise. We need, therefore, to investigate their roles in spider mite suppression more thoroughly, and to test their abilities to keep high densities from developing, even when the prey species' fecundities are at maximum levels. We need to explore the possibilities of altering management practices to favor such predators.

Although much information strongly suggests that native predators are important in controlling tetranychid populations, we have been largely unable to measure directly the actual effect of a given predator or a complex of them. We have not been able to determine how much mortality from predation is necessary for regulation. In some cases a complex of predators may act either in a density-dependent way or simply as density-unrelated mortality factors, to control a population.

Some idea of the potential capacity of a predatory species can be gained from population studies in the insectary, greenhouse or in growth chambers, and significant results have been so obtained.

Yet our methods of appraisal need much improvement. The lack of discreteness in mite generations, the impracticability of marking techniques, and our inability to assign causes of death by predators are troubling. Improvements in sampling are needed. In particular, area-by-area sampling should be done in such a way as to follow population changes frequently, in small

areas; otherwise, a meaningful action by enemies could not be detected.

Several important factors in interpreting predation caution against appraisals based on a limited perspective. Component parameters, intrinsic rate of increase, searching power, functional, numerical, and total response, voraciousness, use of alternate foods, variety and stage of prey attacked, dispersal potentials, and dispersion patterns are all important aspects. The importance of each may vary with the circumstances. Generalities condemning predators as groups are quite open to question, as are generalities implying that other factors are of no importance.

Many attempts have been made to introduce new predators of spider mites from foreign areas, but these have met with nearly complete failure. Either they cannot subsist in the new area, or we have not tried suitable species, or the conditions and methods of establishment have been unfavorable. These possibilities need to be explored much more intensively. It is most unlikely that, in every situation, we already have the best predator available. Great opportunity for control should open up if we can learn how to establish new species of mite predators.

Timely, or mass releases of predators may have considerable value in control of spider mites on high-value crops, such as strawberries and flowers, or on vegetables grown in greenhouses, such as cucumbers and tomatoes.

We have also just begun to investigate pathogens of tetranychids, and we need to know much more about them before we can say that particular ones are inadequate in any instance; it may be that rather subtle manipulations in our practices can improve their utility. So far, their use has met with little practical success.

On many crops, tetranychids would pose no real problem, apparently, if sprays could be avoided. But this solu-

tion is not possible if the crop has other pests which, uncontrolled, would make the crop unprofitable. But in some cases, by judicious use of selective materials, mites may be reduced to minor importance (Pickett, Putman and Le-Roux, 1958; Bravenboer, 1959, 1963; LeRoux, 1961; Vogel, 1965; Patterson, 1966). Some chemicals, e.g., lead arsenate and ryania for codling moth, and glyodin as a fungicide, are rather innocuous to many mite predators. However, it is not likely that we can obtain control of every important pest by using selective compounds. For example, Putman and Herne (1959) indicated that since DDT and parathion give the best control of oriental fruit moth, use of these materials is likely to continue even if orchard mites remain a problem. But certainly we should learn to use both chemical and biological methods of pest control to maximum long-term advantage, rather than in piecemeal fashion to solve an immediate problem regardless of later consequences.

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