6-30-1972

Prey stage distribution, a factor affecting the numerical response of *Typhlodromus occidentalis* to *Tetranychus mcdanieli* and *Tetranychus pacificus*

B. A. Croft
Michigan State University, East Lansing

Follow this and additional works at: https://scholarsarchive.byu.edu/gbn

PREY STAGE DISTRIBUTION, A FACTOR AFFECTING THE NUMERICAL RESPONSE OF *TYPHLODROMUS OCCIDENTALIS* TO *TETRANYCHUS MCDANIELI* AND *TETRANYCHUS PACIFICUS*[1]

B. A. Croft[2]

ABSTRACT.— The ability of *Typhlodromus occidentalis* to oviposit and numerically increase when consuming various life stage distributions of *Tetranychus mcdanieli* and *Tetranychus pacificus* were studied at several interaction levels. On field-collected apple leaves and 6x6 cm artificial substrates, oviposition rates and rates of increase (*r*) were higher when predators were fed populations of spider mites with high proportions of eggs and larvae as compared to prey colonies composed mainly of deutonymphs-male adults and female adults. Feeding studies indicated that reproductive differences were mainly due to increased predation and food intake when predators were offered eggs and larvae of *Tet. pacificus* and a decreased capture and food consumption when only provided with the larger prey stages. Samples taken throughout a growing season in apple trees and an orchard suggested that during early-season, prey stage distributions were most favorable to predator increases and would undoubtedly contribute to a rapid numerical response by predators. The affect of less favorable stage distributions was much less apparent as these stage proportions occurred during short intervals in early season, at intermediate prey levels, and were most unfavorable at high densities or late season after spider mites overexploited their host plant.

A predator's reproductive rate is greatly influenced by the density, nutritional suitability, and behavioral acceptability of its prey. For example, Chant (1961) reported that the rate of oviposition of the phytoseiid mite, *Typhlodromus occidentalis* Nesbitt, was closely correlated with the number of Pacific spider mites (*Tetranychus pacificus* McGregor) it consumed. Burrell and McCormick (1964) reported differential oviposition rates for *T. occidentalis* when feeding on various tetranychid prey; and *Amblyseius potentillae* (Garman) consumes fewer prey/day per equivalent rate of egg production when feeding on *Panonychus ulmi* (Koch) reared on leaves having a high nitrogen level, as compared to *P. ulmi* reared on leaves with low nitrogen content (van de Vrie and Boersma, 1971).

Many phytoseiid mites prefer feeding on a particular stage or stages of certain tetranychid mites (Chant, 1959; Putnam,

1962; Croft and Jorgensen, 1969; van de Vrie and Boersma, 1971).
Croft and McMurtry (1972a) reported that *T. occidentalis* preferred
feeding on the egg, larval, and protonymphal stages of *Tet. pacificus*,
rather than on late nymphal-male adult or female adult mites.
When provided with different stage groups of *Tet. pacificus* [(a)
eggs, (b) unfed larvae, (c) deutonymphs-male adults, (d) female
adults], predators exhibited marked differences in oviposition rates.
Estimates were twofold greater when *T. occidentalis* females were
fed prey eggs or larvae as compared to deutonymphs—male adults
and female adults. The relationship between the prey stage con-
sumed and the oviposition rate of predators suggested that the
stage distribution of the prey mites might affect the ability of *T. occi-
dentalis* to numerically increase and control *Tet. pacificus* and
Tetranychus mcdanieli McGregor in the field. The investigations
reported herein were conducted to test this hypothesis. This rela-
tionship was studied at several interaction levels; in the laboratory
on confined 6 x 6 cm paper substrates, apple leaves, and 2.5 cm di-
ameter apple-leaf disks and in the field on apple leaves, in apple
trees, and in an apple orchard throughout a growing season.

GENERAL METHODS

Rearing methods for the predator and prey populations have
been described elsewhere (Croft, 1970). Stock colonies of *T. occi-
dentalis* originally were collected from an apple orchard at Wenat-
chee, Washington. *Tetranychus pacificus* was started from a colony
maintained by L. R. Jeppson at the University of California, River-
side. All laboratory experiments were conducted, unless specified
otherwise, at $75 \pm 3°F$ and $50 \pm 10\%$ RH in the insectary at the
University of California, Riverside. Field experiments, samples and
populations of *Tet. mcdanieli* were all taken in apple orchards at
Oak Glen, near Yucaipa, California. With respect to taxonomy,
morphology, and behavior, *Tet. pacificus* and *Tet. mcdanieli* are
closely related species, and *T. occidentalis* is well adapted to either
prey (Flaherty, 1967;[3] Hoyt 1969).

PREDATORS REARED ON PAPER SUBSTRATES

METHODS.— The potential of *T. occidentalis* to numerically in-
crease when fed four life stage groups of *Tet. pacificus* was tested
on waterproofed construction paper units (6 x 6 cm). These arenas
were placed on a water-saturated, plastic foam base and were con-
tained in a 15 x 15 x 3 cm stainless steel pan. Cellucotton strips bor-
dered each unit and were saturated with water to insure the iso-
lation of each predator-prey population. Life stage groups of *Tet.
pacificus*: (a) eggs-larvae, (b) larvae-protonymphs, (c) deuto-
nymphs-male adults, and (d) female adults were collected by the
method described by Scriven and McMurtry (1971). An abundance

---

[3]FLAHERTY, D. 1967. The ecology and importance of spider mites on grape vines in the
southern San Joaquin Valley with emphasis on the role of *Metaseiulus occidentalis* (Nesbitt).
Doctoral Dissertation, Univ. of Calif., Berkeley.

of each prey group was added three times weekly to units where 30 newly oviposited eggs of the predator previously had been placed. A single pan contained four replicates of each treatment. After female predators had developed to maturity, morality (1_x) and oviposition (m_x) measurements were collected daily during the entire oviposition period (16-29 days). Six parameters, including (1) mean eggs produced/female, (2) mean egg production per female/day, (3) mean length of the oviposition period, (4) mean generation time (T), (5) net reproductive rate per female/generation (R_o), and (6) instrinsic rate of increase (r), were measured. A previously reported sex ratio (Croft, 1970) of 1:1.7 ($\male : \female$) for *T. occidentalis* was used in all calculations.

RESULTS.— Table 1 contains the six respective parameters for adult females of *T. occidentalis* when fed on each stage group of *Tet. pacificus*. The mean total egg production for females fed on each prey group were similar. Mean egg production per female/day and the mean length of the oviposition period were inversely correlated; high oviposition rates were associated with short oviposition periods and vice versa. If similar mortality (l_x) values had been obtained for each stage type, mean generation time (T) would have positively correlated with the length of the oviposition period. However, a greater mortality occurred among predators when feeding on deutonymphs-male adults and female adults as compared with those predators feedings on eggs-larvae or larvae-protonymphs. It is not known if these mortality differences are also associated with the consumption of the larger prey stages as occurs in the field. The lower mortality (l_x) values also caused the mean generation time (T) for predators fed on deutonymphs-male adults and female adults to be similar to those values obtained for mites fed on eggs-larvae and larvae-protonymphs. The number of progeny produced per female (R_o) in each generation (T) was greater among mites feeding on eggs-larvae and larvae-protonymphs as compared to those feeding on the larger prey stages. Intrinsic rates of increase (r) were positively correlated with the mean estimates for egg production per female/day.

TABLE 1. Oviposition and rate of increase parameters for *Typhlodromus occidentalis* when fed each of four life stage groups of *Tetranychus pacificus*.

Life Stage type	Mean Total Eggs/Female	Mean Eggs/ Day/Female	Mean Length of Oviposition (Days)	T	R_0	r
Egg-larvae	36.8	2.3	16.0	14.4	21.6	0.213
Larvae-proto-nymph	35.7	1.9	19.0	16.4	21.3	0.186
Deutonymphs-male adult	38.0	1.7	23.0	15.4	15.0	0.176
Female adult	37.7	1.3	29.0	16.7	16.8	0.169

PREDATOR OVIPOSITION RESPONSES ON APPLE LEAVES

METHODS.— The oviposition response of *T. occidentalis* when fed *Tet. mcdanieli* was tested on field-collected apple leaves. Leaves with densities of *ca.* 60 and 200 prey mites/leaf were selected to insure that searching for prey was not a factor affecting predator egg production. These prey also provided sufficient food to allow the predators to oviposit for four to six days. Leaves were placed on foam plastic pads in pans of water. Cellucotton strips bordered individual leaves to discourage predator or prey migrations from the unit. The initial stage distribution of the prey population was noted for each leaf and then recounted on successive days during the experiments. A mean stage distribution value, as the percentage of all preferred stages (i.e., eggs, larvae, and protonymphs) present during the interaction period was estimated from the running percentage means of the preferred stages present each day. Sufficient female predators were added to each leaf to insure the destruction of the prey populations before six days had elapsed. Leaves with lower prey densities (60 mites/leaf) received 1-3 female predators; those with higher levels (200 mites/leaf) received 6-14. Oviposition rates per female/day were calculated, and mean oviposition rate for the entire period was estimated from the daily means, excluding data from the first day of oviposition and all days after prey density was lower than predator density. Prior to test termination, predator populations were largely composed of eggs, larvae, and nymphs which had a low prey-consumption rate. Searching for prey was not a significant factor affecting oviposition during the testing period. Although these experiments were helpful in relating prey stage distribution to the numerical increase of the predators, the limitations of a detached leaf and the methods of estimating the stage distribution values are emphasized.

RESULTS.— When first introduced to a leaf, predators initially fed on the smaller, more preferred prey stages of *Tet. mcdanieli*. Predators consumed over 90 percent of the adult female prey and oviposition was 44 percent less during the latter half of the test periods as the more preferred stages were not available. Figure 1 presents a linear regression fit for the relationship between prey stage distribution and predator oviposition rates for 20 leaf interactions at each density level. A positive regression slope was found at both density levels, and the sample regression coefficients (b) for both density treatments were not significantly different. Predator oviposition rates were high when the mean percent of preferred prey was high and, conversely, were low when prey populations had a low proportion of the preferred stages. Estimated oviposition rates (Y) also were not significantly different between the two prey density levels.

FEEDING RESPONSES OF PREDATORS AFTER PERIODS OF STARVATION

Several factors may contribute to the differential oviposition responses of *T. occidentalis* females to differing stage distributions of
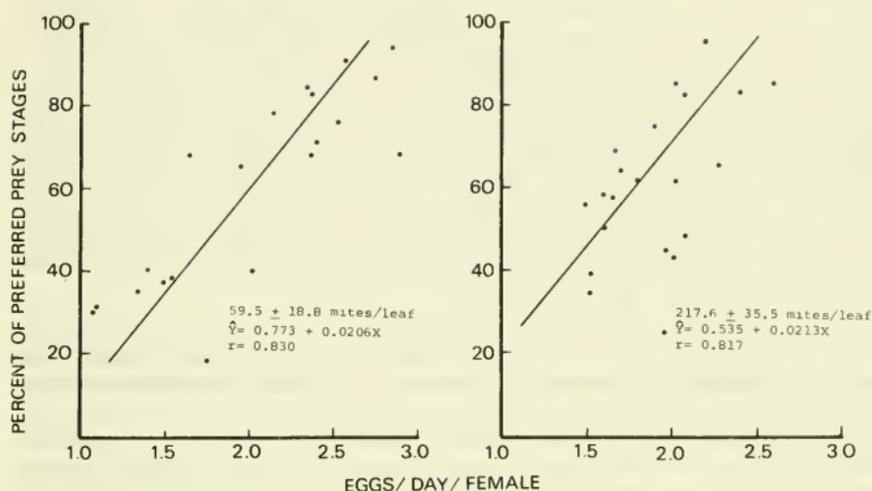
Fig. 1. Regression relationships between the combined percentage of eggs, larvae, and protonymphs (preferred prey stages) available for food and the oviposition rates of *Typhlodromus occidentalis* for 20 predator-prey interactions on apple leaves at two prey density levels.

Tet. pacificus and *Tet. mcdanieli*: Croft and McMurtry (1972a) esti-mated that *T. occidentalis* females after feeding on *Tet. pacificus* eggs produced five times more eggs than did predators fed on an equiva-lent weight of adult female prey. On the basis of equivalent number of prey, predators oviposited only 41 percent as many eggs when fed eggs as compared to feeding on adult female prey. Unfed larvae were 1.9 times and 16 percent for the same respective parameters. Also, comparisons of oviposition and prey consumption rates for *T. occi-dentalis* fed on prey eggs v. larvae (Croft and McMurtry, 1972a) in-dicated that an increased feeding response occurred as predators con-sumed about 2.5 times as many larvae as eggs, yet maintained a similar level of egg production (2.3 eggs per female/day). When preying on adult female prey, predator oviposition rates were lower (1.3 eggs per female/day) even though an abundance of food was provided. Data suggested that eggs and larvae were more ac-ceptable stages to the predator females than were the larger prey stages.

METHODS.— To test the above hypothesis, standard-sized (2.5 cm in diameter) leaf disks without prey were placed on water-saturated, foam plastic pads. A uniform starvation schedule prior to the initiation of the experiments provided female adult preda-tors in a similar hunger state. These mites were placed singly on each disk, and at logarithmically-spaced time intervals they were offered a particular prey stage (eggs, larvae, or female adults). All tests were made concurrently; 20 predators per replicate and three replicates (60 total mites) were tested for each stage group at each time interval. Predators which had been offered a particular

prey stage (e.g., eggs only) in previous tests were given a different type (e.g., larvae or female adult mites) at the next time period to insure that treatment conditioning did not occur. The percentage of predators effecting a successful capture after two contacts with a particular prey stage was recorded at each test period. Direct frontal approaches to adult female prey nearly always resulted in an avoidance response by the predators at all starvation times. These contacts were not counted. After a predator had captured a particular prey stage and had assumed the feeding position, the prey was withdrawn. Predators obtained little, if any, food and were further starved until the next test period.

RESULTS AND DISCUSSION.— Figure 2 shows the feeding response curves of *T. occidentalis* females to each prey stage after varying periods of starvation. Successful capture and acceptance of prey larvae were extremely high at all starvation periods, reaching 98 percent at 48 hours after the initiation of the tests. Eggs were slightly less acceptable than larvae at most test periods. Adult female prey were almost unacceptable during the early periods of the tests (3-6 hr), increasing to 65 percent successful captures at the most responsive period (48 hr). In the initial tests (3-6 hr), predators often made normal feeding approaches to adult female prey, holding
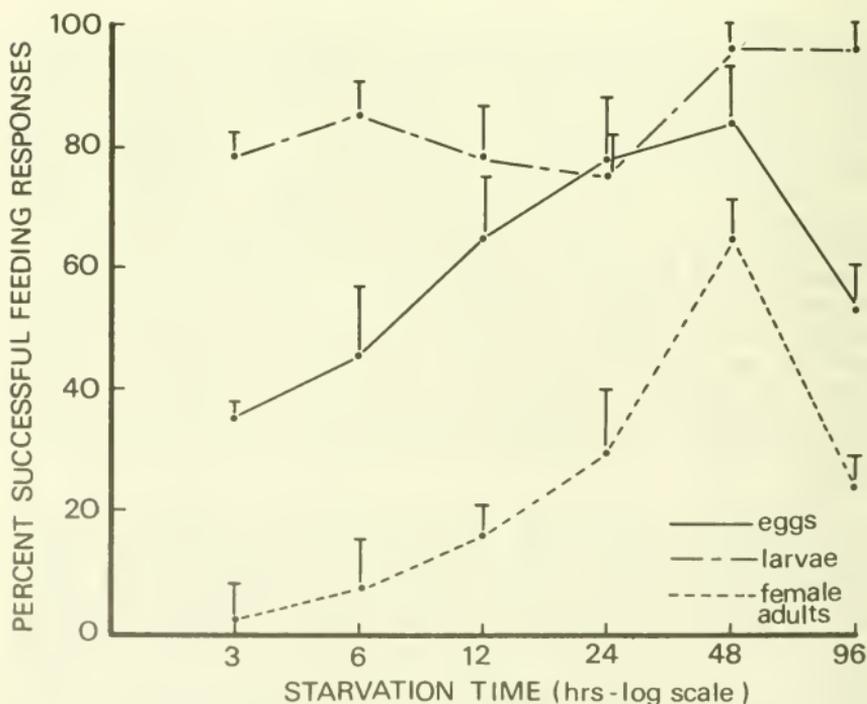

Fig. 2. Feeding response curves for *Typhlodromus occidentalis* to 3 prey stages of *Tetranychus pacificus* after varying periods of starvation.

them with their front pair of legs; however, they usually released
the larger mites and did not feed.

During the late stages of starvation (48-96 hr), many predators
ceased searching and remained still until a prey encountered them
or until they died. If a prey larva contacted a starving predator, the
predator would immediately respond and a high percent of successful
captures (95 percent at 96 hr) was effected. Few eggs were en-
countered by predators in this condition. The decline in adult female
consumption at 96 hr resulted from the inability of the starved
predators to overcome and feed on the larger prey stages.

Although these tests were helpful in comparing the hunger
thresholds of *T. occidentalis* to each prey stage, the interpretation
of these data in terms of field populations should be qualified. Preda-
tors were never 100 percent successful in obtaining prey at any test
period. However, under field conditions, these mites may contact the
prey mites more than twice during each time interval or more than
12 times in 96 hours of searching. We may interpret these data in
terms of field populations by suggesting that when prey densities
are sufficiently high, and a high proportion of the preferred prey
stages are present, predators feed mainly on eggs and larvae. Adult
prey consumption mainly occurs when the density of the preferred
stages is reduced and the hunger level of the predators becomes
high enough to elicit a feeding response on the larger prey stages.

COLONIZATION PATTERN AND CHANGES IN PREY DISTRIBUTION

The data discussed previously in this paper have dealt with the
numerical response of *T. occidentalis* to different stage distribution
of *Tet. pacificus* and *Tet. mcdanieli* on a paper substrate and apple
leaf surfaces. Predator-prey interactions at tree and orchard levels
are of greater interest if spider mite control is to be attained. Subse-
quent portions of this paper deal with the effect the previously de-
scribed response on individual leaves may have, in toto, on the larger
sample units in the field.

In southern California, adult females of *Tet. mcdanieli* overwin-
ter at the base of apple trees and under bark scales in the trunk
region. During April and May, females move up the trunk onto
leaves on water-sprout growth and to leaves on the inner branches
of the scaffold limbs. The initial distribution of prey mites during
this period is typically confined to a low percentage of leaves (1-5
percent) in the lower central portion of the tree. Progeny of the
first generation complete their development on this foliage. At ma-
turity, many of the newly molted females migrate to noninfested
leaves in the upper central portions of the tree and a lateral spread
occurs in subsequent generations. By 1 July, from 20-60 percent of
the leaves in a tree are infested by prey mites (Croft and Barnes,
1971; Croft and McMurtry, 1972b).

The colonization habits of the predator, *T. occidentalis* are
adapted to those of *Tet. mcdanieli*. Adult females overwinter in the
debris at the base of trees and under bark scales on the trunk and

scaffold branches (Hoyt, 1969; Leetham and Jorgensen, 1969). Female predators move from these hibernacula during the same period as do the prey mites and initially disperse to the lower, central region of the tree where the prey population also occurs.

The initial density and distributional relationships between prey and predator populations vary. On occasion, these relationships favor the predators, which reduce the initial prey populations to a low density level (Croft and Barnes, 1972). When no alternate prey species is present, the early prey reduction results in a starvation decline in predator populations, a later increase in prey levels, and a second numerical response by the predators.

Occasionally an equilibrium ratio of prey:predators is present, and a less fluctuating interaction develops with the predator population maintaining a reduced density just sufficient to maintain the prey at a low equilibrium level. The author has observed this condition in naturally developing populations (Croft and Barnes, 1972) and during minimum release tests (Croft and McMurtry, 1972b).

Most often, the initial numerical and distributional relationships of predators and prey favor the increase of prey populations. Predators contact the prey, increase on a limited number of leaves, and initially have a much lower density and poorer distribution than do the prey mites. However, some time after prey density has surpassed a certain minimal level (*ca.* 2-5 mites/leaf, Croft and McMurtry, 1972b), predator populations numerically respond to the extent of overcoming and reducing the prey to a low level.

In the latter case, the interaction sequence is generally similar on individual leaves and in the entire tree. The overwintering female adult predators disperse to individual leaves in the lower central region of the tree and encounter a prey population of a certain density and stage distribution. Either one or both of these two factors affect the predator's rate of numerical increase during the period of interaction on the leaf. The mean rate of predator increase or decrease on all leaves determines the prey density attained and the length of time a particular prey level persists in the tree.

If prey density on the leaf is sufficiently high and predator searching is not a limiting factor, the stage distribution and the acceptability of these prey to the predators influence the rate of increase on that leaf. The r values in Table 1 give the possible range of effects this factor might have. One might conclude from mean tree estimates that the above conditions occur only at high prey densities; but even at low mean levels (1-5 mites/leaf) the few leaves with prey have many mites present and the majority are without prey. If prey density on a leaf is low or zero, searching for prey is the major factor limiting the rate of numerical increase or decrease among predators. During this period, the effect of a differential stage distribution is not greatly expressed. This also applies to those periods of low prey density on leaves after the predators have numerically increased and reduced the prey to a low level.

The following interaction sequence in early season was observed in repeated studies of the numerical response of *T. occidentalis* to

populations of *Tet. mcdanieli* on leaves where prey initially were
abundant (Croft and Barnes, 1971, 1972; Croft and McMurtry,
1972b): the immature progeny from eggs oviposited by the over-
winter female predators completed development on the originally
colonized leaf. If prey density was still sufficiently high, a second
generation developed on the leaf. Prior to the complete extincting
of all prey, the original female predators and/or gravid females of
subsequent generations migrated to other infested leaves. Further
prey consumption by developing immature predators most often re-
sulted in the complete extinction of prey from the leaves until later
migrations occurred. At maturity the newly molted female predators
were mated and shortly thereafter dispersed to leaves with prey and
the interaction sequence was repeated. As the predator density in-
creased in the tree, population distribution (percentage of leaves
infested) also increased at a proportional rate (Croft and Barnes,
1971; Croft and McMurtry, 1972b). Eventually a predator population
numerically increased and was distributed throughout the tree to the
extent of overcoming further prey increases, and control was at-
tained.

Assuming that the above sequence describes a typical numerical
response of *T. occidentalis* to populations of *Tet. mcdanieli* in an
individual apple tree, tests were conducted to measure changes in the
stage distribution of the prey mites as related to density and time
upon leaves, in trees, and in an apple orchard. These measurements
were taken to suggest the stage distributions that dispersing predator
populations would encounter in enacting control of the pest.

Prey Infestation on Individual Apple Leaves

As the density and distribution of *Tet. mcdanieli* initially in-
creased in the tree, a common development was for a single gravid
female prey to disperse to an uninfested leaf. Later, several females
would disperse to uninfested leaves as density further increased
and intraspecific competition intensified. At high density levels,
large numbers of mites would occupy almost all available leaves,
and the remaining uninfested leaves would soon be colonized by
high densities of migrant female mites. These infestations assume
single migrations by various densities of prey mites, but also an in-
finite number of continuous migrations may occur at any time (i.e.,
a single female colonizes a leaf but is joined by one or more addi-
tional females at day 2, day 3, etc., or any other random time).

METHODS.— To simulate these infestations, leaf spurs without
mites were collected from a single branch of a "Standard Delicious"
apple tree. All leaves except one of uniform size were removed from
each spur. The spurs were placed in leaf cages and maintained in a
greenhouse under long day photoperiods at 70-90 F, and 50-70 per-
cent R.H. At the initiation of the test, a leaf was infested with either
1, 2, 4, or 16 field-collected prey mites (*Tet. mcdanieli*, female
adults) of an unknown age. One treatment contained a leaf on
which 1 adult female was added the first and each successive day.

Prey density and stage distribution were counted every three days until test termination. Each of the five treatments was replicated 10 times and the reported data are mean values for all replicates in each treatment.

RESULTS.— Figure 3 A-F presents the results from the infestation experiments. The following generalizations were made from these data: (1) At the lower density levels after colonization had begun, the percentage of prey in the egg, larval, and protonymphal stages was extremely high and would be optimally favorable for the numerical increase of predator populations (Fig. 3 A-E). (2) As density further increased, the prey population contained a lower percent of preferred stages (Fig. 3 A-E). (3) If 1, 2, 4, or 16 female prey mites dispersed to an uninfested leaf and no other mites moved to that leaf before the first generation was completed, there was a short period of time (3-6 days in the laboratory) at the end of the first generation when the stage distribution of the prey was mostly composed of the large prey stages and would be less favorable for the numerical increase of the predator (Fig. 3 A-D). (4) The periodic introduction of additional females to a previously infested leaf tended to dampen fluctuation (extreme variations in successive sample dates) in stage distribution on the leaf (Fig. 3E). However, the slope of decreasing stage favorability (Fig. 3E) was not markedly different from the other treatments which supported similar densities, but were
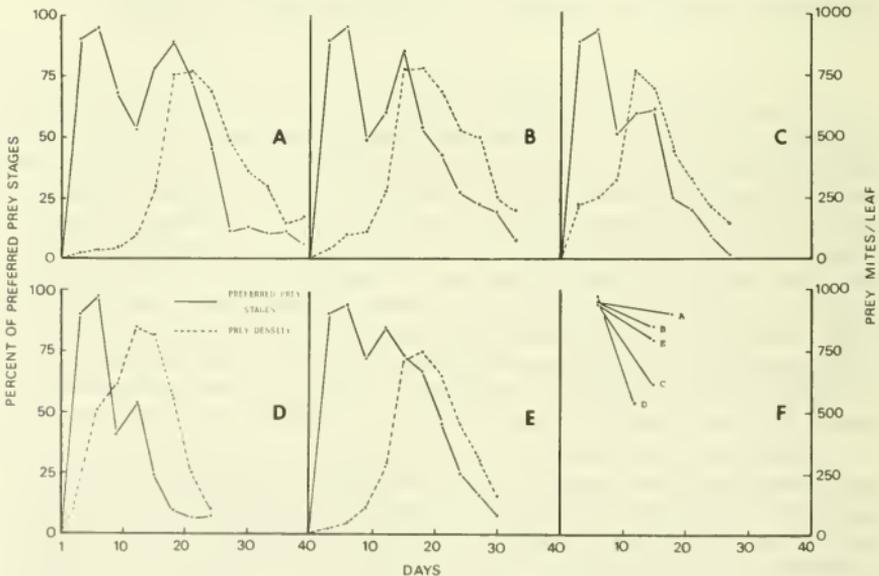

Fig. 3 A-F. Prey stage distribution and density changes for individual leaf infestations of *Tetranychus mcdanieli* originating fro msingle introductions of 1 (3A), 2 (3B), 4 (3C), 16 (3D female mites, one periodic release treatment of 1 adult female mite/day (3E) and a combined slope comparison of all treatments (3F).

started by a single infestation rather than a periodic introduction of prey mites (Fig. 3 A-D). (5) Depending on the number of prey introduced initially, the period of time that preferred stages would be available to predators was lessened and the slope of decreasing stage favorability was steeper as the introduction density of mites was increased (Fig. 3F).

DISCUSSION.— These experiments had implications to the colonization of apple leaves by prey populations under field conditions. Previous population studies in a *T. occidentalis-Tet. mcdanieli* system (Croft, 1970;[4] Croft and Barnes, 1972) indicated that most often the initial contact and subsequent numerical increases of predator populations were begun in early spring as prey populations were beginning to increase and total tree densities were low (<5 prey mites/leaf, but individual leaf densities may be high). During this period, the stage distribution of the prey would be optimally favorable for the numerical response of the predator. This factor undoubtedly contributes to a rapid numerical increase of predators and the remarkable ability of *T. occidentalis* to control *Tet. mcdanieli* populations during early season (Croft and McMurtry, 1972b).

Also, during early season, populations of *Tet. mcdanieli* show considerable developmental synchronization as generations are somewhat discrete. Samples (total tree estimates) taken prior to the maturity of the first generation of prey mites will often include leaves where the proportion of late nymphal newly and molted adult mites is high (Croft, unpublished data). These conditions of less favorable stage distribution only persist for short periods in early spring when temperatures are low.

A comparison of slope differences at each introduction density (Fig. 3 E) indicated that the period of time in which a highly favorable stage distribution was present on a leaf, lessened as the introduction density was increased. Data suggest that as prey increased, the prey stage distribution at the leaf, tree, and orchard levels would also become less favorable to predator increases.

SEASONAL PREY DISTRIBUTION ON APPLE LEAVES

METHODS.— Field samples collected throughout the season were sampled to test the above hypothesis. Leaves were randomly collected from 5 trees at one-month intervals throughout the growing season. A sufficient number of leaves were collected at each sample period to insure that 50 were selected with prey mites present. Mean total tree densities during the summer increased from 0.88-162.3 prey/leaf, but individual leaf densities ranged between 1-1000 prey of all stages.

RESULTS.— Figure 4 represents a plot of the combined percentage of prey in the egg, larval, and protonymphal stages (preferred

prey stages) as related to the density of the total prey population on
individual leaves. The broken line in Figure 4 represents the mean
percent of preferred prey stages at increasing density levels. A large
variation in stage distribution was present on individual leaves at
all leaf density levels (Fig. 4). The mean curve declined rapidly as
prey density increased from 0-200 mites/leaf, flattened to an almost
horizontal line from 200-700 prey/leaf, and upturned slightly be-
tween 700-1000 prey/leaf. Although a curve decline occurred at in-
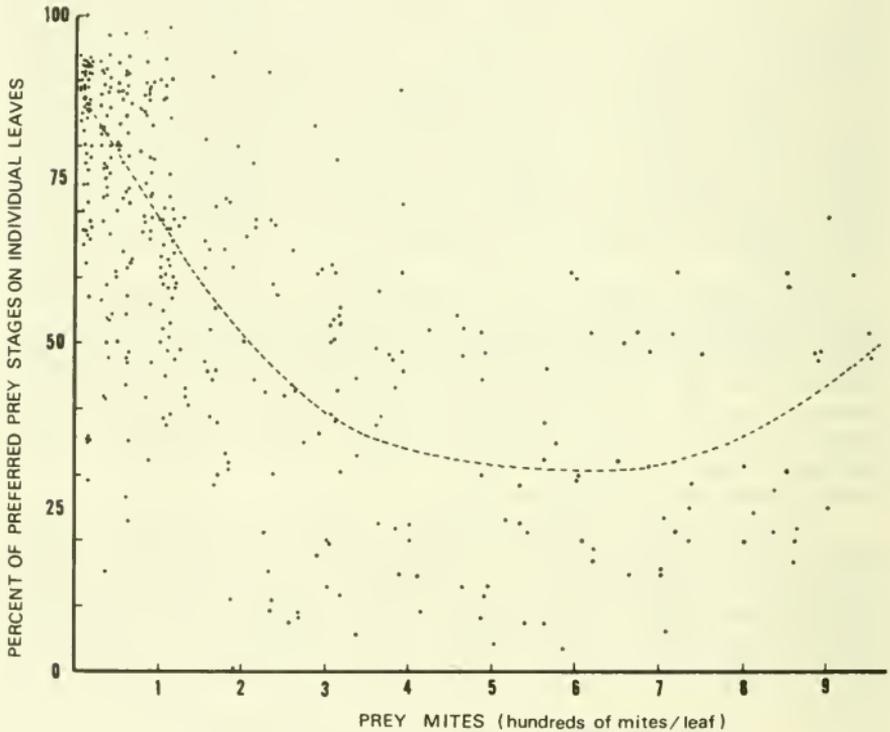creasing prey densities, the mean percentage of preferred prey re-

Fig. 4. A scatter plot of the combined percentage of eggs, larval and proto-
nymphal stages (preferred stages) of *Tetranychus mcdanieli* as related to the
density of spider mite populations on individual apple leaves at Oak Glen, Cali-
fornia (1970).

mained above 25 percent at all levels and did not attain <10 percent
which would result in the magnitude of r differences as were reported
for eggs and female adult prey in Table 1. The slight upturn at high
prey densities (Fig. 4, 700-1000 host/leaf) occurred as the highest
prey densities and the more uniform stage distributions developed
just before the plant was overexploited by *T. mcdanieli*. As leaves
became damaged and were unsuitable food for the spider mites,
their density declined and only the larger mature stages were pres-
ent on the leaves.

SEASONAL PREY DISTRIBUTIONS IN TREES AND AN ORCHARD

METHODS.— Changes in prey distribution also were measured throughout the summer of 1970 in the 5 trees selected for the previous test. Twenty leaves were collected as described by Croft and Barnes (1971) from each tree at two-week intervals throughout the season. The number of each stage type on all leaves were counted at each interval. Density relationships at tree and orchard levels were also estimated.

RESULTS AND DISCUSSION.— Figure 5 presents the combined percentage of eggs, larvae, and protonymphs (preferred prey stages) present in two of the trees where fluctuations in stage distribution were the greatest and a mean measurement for the entire orchard (5 trees). As expected, data for the individual trees were more variable than was the orchard measurement. Individual tree and orchard data did not reflect the extreme stage distribution differences that were observed in the individual leaf samples. This probably was due to the temporal heterogeneity between individual leaf interaction within any given tree and the masking effects of lumping individual leaf counts together. However, individual tree and orchard curves did show a rapid rise to a peak of host favorability during the initial phases of colonization, a slow decline during the midseason, and a rapid decline at the end of the growing season.

From a biological control standpoint, the most favorable time for predators to numerically respond and enact control of the prey would be when prey density had just surpassed the minimum density required to maintain an increasing predator population (Fig. 5). Subsequent increasing predator population would encounter less favorable prey stages and denser populations. Also, *Tet. mcdanieli* populations at Oak Glen in 1970 (Fig. 5) attained a lower density and developed later in the season when compared to the dynamics of this species in 1968 or 1969. In seasons that prey populations attain high densities earlier in the season, less favorable stage distri-
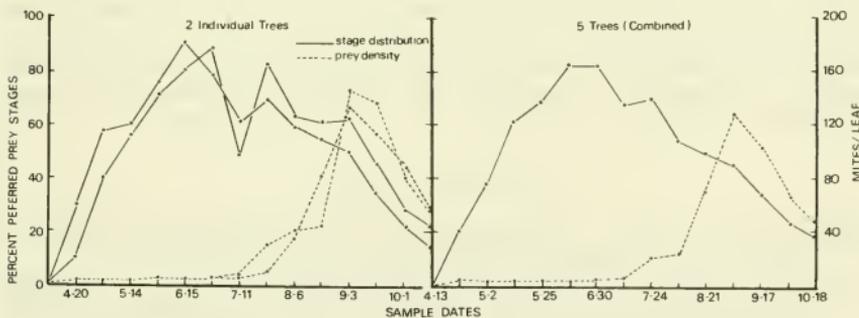

Fig. 5. The combined percentage of eggs, larvae, and protonymphs (preferred prey stages) and total population density of *Tetranychus mcdanieli* in 2 individual apple trees and an apple orchard (mean of 5 trees) at Oak Glen, California (1970).

bution probably would be present earlier and over a greater period
of time.

Conclusions

The studies discussed in this paper demonstrate that prey stage
distribution of *Tet. mcdanieli* and *Tet. pacificus* is an important
factor influencing the numerical increase of *T. occidentalis* in small
interaction arenas (apple leaves, 6 x 6 cm construction paper sub-
strates). The direct effect of this factor at larger interaction levels
(apple trees and orchards) was not obtained. This effect is likely a
complex function of stage distributions, densities, dispersal patterns,
and spatial distributions for both predators and prey and other inter-
acting features of the entire predator-prey-host plant system. How-
ever, measures of prey stage distribution, in the absence of predators,
suggested possible types that *T. occidentalis* would encounter in en-
acting control of *Tet. mcdanieli*.

At low and intermediate densities, prey stage distributions were
optimally and generally favorable for the numerical increase of pred-
ators. During short periods early in the season as prey generations
were synchronized and as prey densities became high or overwinter-
ing conditions approached, the stage distribution became less favor-
able for the numerical increase of predators.

It is likely that the prolonged periods of prey stage favorability
contributes to the ability of *T. occidentalis* to numerically respond
at a rapid rate in early or midseason. However, it is unclear from
these studies if the period of prey stage unfavorability is ever of a
duration or magnitude to have a significant effect on the rate of
numerical response in predator populations. Also, the temporal
asynchrony between leaf interactions may be sufficient to dampen
the effect of these differences on the mean rate of predator increase
at the tree and orchard levels. From an applied biological control
consideration, the effects of unfavorable stage distributions would
most often occur at high densities. Effective control interactions
should have occurred long before these destructive prey levels were
attained. For mass release programs, the most favorable period for
predator release would be shortly after a minimum prey density to
sustain a numerical increase of predators was attained. Not only
would pest density be reduced, but a highly favorable prey stage
distribution would be available to the released predators.

Literature Cited

Burrell, R. W., and W. J. McCormick, 1958. *Typhlodromus* and *Amblyseius*
as predators on orchard mites. Ann. Ent. Soc. Amer. 57:483-87.
Chant, D. A. 1959. Phytoseiid mites (Acarina:Phytoseiidae) Part I. Bionomics
of seven species in southwestern England. Part II. A taxonomic review of
the family Phytoseiidae, with descriptions of 38 new species. Canadian Ent.
91:Suppl. 12, 164 p.
———. 1961. The effect of prey density on prey consumption and oviposition
in adults of *Typhlodromus* (*T.*) *occidentalis* in the laboratory. Canadian J.
Zool. 39:311-5.

CROFT, B. A. 1970. Comparative studies on four strains of *Typhlodromus occidentalis* Nesbit (Acarina:Phytoseiidae). I. Hybridization and reproductive isolation studies. Ann. Ent. Soc. Amer. 63:1558-1563.

CROFT, B. A., AND M. M. BARNES. 1971. Comparative studies of four strains of *Typhlodromus occidentalis*. III. Evaluations of releases of insecticide resistant strains into an apple orchard ecosystem. J. Econ. Ent. 64:845-850.

————. 1972. Comparative studies on four strains of *Typhlodromus occidentalis*. VI. Persistence of insecticide: resistant strains in an apple orchard ecosystem. Ibid. 65:211-216.

CROFT, B. A., AND C. D. JORGENSEN. 1969. Life history of *Typhlodromus mcgregori* (Acarina:Phytoseiidae). Ann. Ent. Soc. Amer. 62(6):1261-1267.

CROFT, B. A., AND J. A. McMURTRY. 1972a. Comparative studies on four strains of *Typhlodromus occidentalis* Nesbitt (Acarina:Phytoseiidae). IV. Life history studies. Acarologia (In press).

————. 1972b. Minimum releases of *Typhlodromus occidentalis* to control *Tetranychus mcdanieli* on apple. J. Econ. Entomol. 65:188-191.

HOYT, S. C. 1969. Population studies of five mite species on apple in Washington. Proc. 2nd Intern. Cong. Acari:117-133.

LEETHAM, J. W., AND C. D. JORGENSEN. 1969. Overwintering phytoseiid mites in central Utah apple orchards. Great Basin Nat. 29:96-104.

PUTMAN, W. L. 1962. Life history and behavior of the predaceous mite *Typhlodromus* (*T.*) *caudiglans* Schuster (Acarina:Phytoseiidae) in Ontario with notes on the prey of related species. Canadian Ent. 94:163-177.

SCRIVEN, G. T., AND J. A. McMURTRY. 1971. Quantitative production and processing of tetranychid mites for large scale testing or predator production. Jour. Econ. Ent. 64:1254-1258.

VAN DE VRIE, M., AND A. BOERSMA. 1970. The influence of the predaceous mite *Typhlodromus* (*A.*) *potentillae* (Garman) on the development of *Panonychus ulmi* (Koch) on apple grown under various nitrogen conditions. Entomophaga 15:291-304.