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An Ecological Study of the Spider Mite *Oligonychus punicae* (Hirst) and Its Natural Enemies

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The population dynamics of the avocado brown mite, *Oligonychus punicae* (Hirst), and its natural enemies was studied over a four-year period in six avocado orchards located in two different climatic areas in southern California. Annual peak levels of abundance of *O. punicae* ranged from 4 to 84 adult females per leaf. The seasonal increase usually began in early summer, with a peak in late summer, followed by an abrupt decline. The increase was sometimes delayed until late summer, with the peak in fall or early winter. Abrupt declines were commonly associated with biotic factors: predation, intraspecific competition, or both. The most abundant natural enemies were a lady beetle, *Stethorus picipes* Casey, and two phytoseiid mites, *Amblyseius hibisci* (Chant) and *A. limonicus* Garman and McGregor. The beetle appeared to be the key predator. When it responded numerically to population increases of spider mites before they reached high numbers, control resulted before serious leaf damage occurred. *A. hibisci* usually failed to show a numerical response soon enough to overtake an increasing population of *O. punicae*. Possible factors limiting the effectiveness of *A. hibisci* were a relatively low reproductive rate when feeding on spider mites, failure to congregate and oviposit on infested leaves, and inability to gain access to prey that was well protected beneath silken webbing. *A. limonicus* was found to be a more effective predator than *A. hibisci*, since it could suppress relatively high populations of *O. punicae*, but it occurred only in orchards near the ocean. Other insect predators reported, in larval or adult form, are the six-spotted thrips, *Scolothrips sexmaculatus* (Per-gande); a cecidomyid fly, *Arthrocnodax occidentalis* Felt; a staphylinid beetle, *Oligota oviformis* (Casey); the green lacewing, *Chrysopa carnea* Stephens; and dusty-wings (Coniopterygidae). None of these was observed to keep pace with rapid increases of the prey, even though some species were present early in the season, when the prey density was still extremely low.

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An Ecological Study of the Spider Mite *Oligonychus punicae* (Hirst) and Its Natural Enemies¹

INTRODUCTION

THE AVOCADO BROWN MITE, *Oligonychus punicae* (Hirst), is a pest on certain varieties of avocados in southern California. It was apparently first noticed in the Carlsbad region of San Diego County in the late 1920's (McGregor, 1941; Ebeling, 1959).² The mite presently can be found in nearly all avocado-growing areas of southern California, but reaches high numbers only in the coastal and intermediate climatic areas. In interior areas, such as Riverside, it has been observed only in small numbers, severe summer weather possibly being the limiting factor.

Pritchard and Baker (1955) also record *O. punicae* from tropical Asia and Central America, and suggest that it may have been introduced into California from the latter area. These authors list collection records from pomegranate and grape as well as from avocado.

Feeding is confined to the upper surface of the avocado leaf, except during severe infestations, and it causes a brownish discoloration or "bronzing." In extremely heavy infestations, the entire upper surface and a portion of the lower surface become bronzed, and partial defoliation of the tree may result.

There is an extensive complex of predators that feed on tetranychid mites on the avocado, Fleschner (1958) listing twenty-one species. Fleschner *et al.* (1955) excluded all predators by hand removal from one limb of an avocado tree for an eighty-four-day period. Extremely high populations of both avocado brown mite and six-spotted mite, *Eotetranychus sexmaculatus* (Riley), subsequently developed and severely damaged the limb, demonstrating the importance of predators in the control of avocado mites. They observed that the most important predators in this experiment were several species of predaceous mites of the family Phytoseiidae, and the coccinellid *Stethorus picipes* Casey.

In addition to mites, there are also many species of insect pests found on the avocado, but because of the control exerted by natural enemies they do not often cause economic damage (Fleschner, 1954).

The fact that the level of infestation of *Oligonychus punicae* varies considerably from year to year and from place to place, though sprays are seldom applied, prompted a detailed study of the

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² See "Literature Cited" for citations, referred to in the text by author and date.

population dynamics of this mite. The present paper summarizes the results of a four-year study in unsprayed orchards in two climatic areas. The major objectives were to determine the principal factors affecting the abundance of *O. punicae* and its predators, and to obtain information on the relative impor-

tance of various predator species under different conditions. It is hoped that this study will contribute to the general knowledge of mite and predator ecology, as well as provide a background of information to aid in efficient utilization of predators in the control of mites on avocado and other subtropical crops.

POPULATION TRENDS IN FIELD PLOTS

The study plots were located in untreated avocado orchards in Fallbrook, Santa Paula, Vista, Morro Hills (also in the Fallbrook region), Carpinteria, and Encinitas. The first four locations are in the climatic zone classified as "Coastal Valley" (Kimball and Brooks, 1959), whereas the latter two are in the "Direct Ocean" area. The avocado varieties were Fuerte at Vista, Wurtz at Encinitas, and Hass in all other plots.

A group of four sample trees was selected in each orchard. Populations of *Oligonychus punicae* and predaceous phytoseiid mites were estimated by taking leaf samples from these trees at one- to two-week intervals. This leaf-sampling procedure is described by McMurtry and Johnson (1965). A changeover from old to new leaves was necessary in late spring or early summer, when the foliage became composed predominantly of new leaves. The change was made when the new leaves were mature and a dark green color, at which time they apparently became favorable for feeding by *O. punicae*.

The mites were counted in the laboratory under a binocular microscope. Counts of adult female *Oligonychus punicae* were found to give a reliable index of the population trends (McMurtry and Johnson, 1965), and during the first two years of the study only this stage was counted, with the exception of the Vista orchard. All the major graphs showing seasonal population trends in the other orchards show only adult female spider mites. During the final two years, all active stages were counted,

because records of total mites were used for other parts of the investigation, such as distribution studies.

All stages of phytoseiid mites were counted, but eggs are not shown in the graphs. For the most part, only two species of phytoseiids, *Amblyseius hibisci* (Chant) and *Amblyseius limonicus* Garman and McGregor, were abundant. Although these species could be recognized during counting, samples of several dozen mites were taken periodically and mounted on slides to confirm their identity. The biologies of *A. hibisci* and *A. limonicus* were studied by McMurtry and Scriven (1964, 1965). Both species are known to prey on *Oligonychus punicae* in the field, but *A. hibisci* shows a striking tendency to increase to high numbers in the virtual absence of mite prey. These increases were correlated with the presence of pollen, the source of pollen usually being the avocado trees themselves (McMurtry and Johnson, 1965). Phytoseiids feeding on *O. punicae* acquire a brown coloration in the gut; the number of predaceous mites having this coloration was recorded in order to estimate the intensity of such feeding.

Populations of insect predators were estimated by walking around each sample tree for five minutes and counting all the predators seen; this was similar to the method used by DeBach *et al.* (1950). One disadvantage of this method is that it is impossible to obtain absolute ratios of predators to mites. However, the relative ratios obtained (e.g., predators per 5-minute count to mites

Fig. 1. Population trends of mites and predators on avocado trees in the Fallbrook orchard in 1961 and 1962. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

per 10 leaves) were an adequate index for most purposes. During periods of heavy mite infestations, larvae of insect predators sometimes appeared in the leaf samples. The only insect predator usually represented in the graphs is *Stethorus picipes*, since it was the only species to become numerous. (Fig. 12 shows data for various insect predators.) The abundance of other species was inconsistent, and was usually not high enough to be of significant importance. Such secondary predators are referred to in the text where they seem to be pertinent.

Fallbrook Orchard

1961 (fig. 1). The population of *Oligonychus punicae* began to increase rapidly early in July, and reached a peak of 370 adult females per 10 leaves in mid-August, after which an abrupt decline of the population occurred. This degree of mite infestation caused some bronzing on the upper sides of many leaves, but the trees remained vigorous and no defoliation occurred. Therefore, the damage was considered to be non-economic.

As the average density of *O. punicae* increased beyond 100 adult females per 10 leaves, *Stethorus picipes* began to increase rapidly. At the population peak of mites, most of the heavily infested leaves contained one or more *Stethorus*, which appeared to be a major factor in causing the abrupt decline of the mite population.

Phytoseiid mites (virtually all *Amblyseius hibisci* except during August, when a few *Typhlodromus occidentalis* Nesbitt were present) were more abundant than the spider mites in the spring, when sampling was started. Beginning in July, they showed a marked numerical response to the increase of *O. punicae*. That they began concentrating their feeding on the spider mites is shown by the increase in the percentage of individuals with a brown coloration in the gut. About 50 per cent of the

phytoseiid population acquired this coloration when *O. punicae* reached a level of only about 30 adult females per 10 leaves. *A. hibisci* increased to a peak of nearly 100 per 10 leaves, at which time all the individuals had a brown coloration, and undoubtedly had contributed significantly to the mortality of *O. punicae*.

1962 (fig. 1). *Oligonychus punicae* was not recovered in the leaf samples until mid-August, and remained low except for a minor increase at the end of the year. Phytoseiids (virtually all *Amblyseius hibisci*) were also scarce early in the year, but began to increase in the late spring before *O. punicae* increased. In early October, they reached a level of about 20 per 10 leaves as *O. punicae* began to increase. Before the latter increased to 30 per 10 leaves, over 50 per cent of the *A. hibisci* had a brown coloration, indicative of feeding on *O. punicae*. Thus, a functional response, e.g., increased prey consumption with increasing prey density, was again evident at a relatively low prey density. It is possible that the phytoseiids were an important factor in preventing *O. punicae* from reaching high numbers, but one cannot rule out the possibility that environmental conditions simply were not favorable for an extensive build-up of the tetranychids.

1963 (fig. 2). *Oligonychus punicae* steadily declined in January and February, a rather typical trend for winter populations. However, the species never became extremely scarce, since some individuals were recovered in all the periodic samples. Close examination of the trees in early spring revealed that certain leaves had unusually large numbers of spider mites for that time of year. During late winter and early spring, there is apparently little dispersal of the mites, and populations may build up on single leaves while adjacent leaves remain uninfested. A marked increase was already evident from the leaf samples in early June. The apparent

Fig. 2. Population trends of mites and predators on avocado trees in the Fallbrook orchard in 1963. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

temporary decline during the same month was due, at least in part, to a necessary change in sampling from old to new leaves.

The phytoseiid population (*Amblyseius hibisci*) began increasing rapidly in the spring as heavy blossoming occurred, indicating a response to the presence of avocado pollen (McMurtry and Johnson, 1965). In spite of these high predator populations, colonies of *O. punicae* remained, and the tetranychids began rapidly increasing in June. Instead of showing a positive numerical response to increasing prey populations at this point, *A. hibisci* declined con-

siderably, and did not again increase until after *O. punicae* averaged over 100 adult females per 10 leaves. In 1961, when predator:prey ratios were more favorable, a numerical response was evident by the time the spider mites reached an average of 30 adult females per 10 leaves. At the relatively low peak of *O. punicae* in 1961 (370), the phytoseiid count was 92, whereas it was only 46 at the high spider mite peak (740) in 1963.

The response of *Stethorus picipes* was also delayed, as this species had not even reached a level of 10 per 5-minute sample when *O. punicae* reached its

highest peak. Thus, there was a striking difference between natural enemy levels at given levels of *O. punicae* in 1961, when adequate control occurred, and 1963, when control was inadequate. Because there was little predation pressure when the tetranychids approached their peak, they remained at over 500 females per 10 leaves for a three-week period, rather than quickly declining after the peak, as in 1961. Nearly all leaves became severely bronzed, and approximately 20 per cent loss of leaves was estimated by the grower.

Both *Stethorus* and phytoseiids subsequently built up to high numbers, but by this time the foliage in general was evidently becoming unfavorable for further population increases of the spider mites. Large numbers of adult females were observed drifting from the trees, a characteristic phenomenon of heavy infestations (Fleschner *et al.*, 1956). Thus, extreme exploitation of the food supply (intraspecific competition) may have been the principal cause of the decline, although the large predator population which subsequently developed must have hastened the decline and prevented additional tree damage. Fleschner *et al.* (1955) noted that heavy infestations of *O. punicae* produced a change in the leaves, so that they became unfavorable for further increase of the mites.

During the high densities of *O. punicae*, a few other species of insect predators were attracted to this source of abundant prey. The six-spotted thrips, *Scolothrips sexmaculatus* (Pergande), reached a maximum number of twenty-three larvae in a forty-leaf sample, but their distribution was erratic, and it is doubtful if they contributed materially to the population reduction. Larvae and pupae of *Arthrocnodax occidentalis* Felt, a cecidomyid known to feed on mites (Fleschner, 1958), were quite numerous on some leaves, but were not widely distributed. Staphylinid beetles, *Oligota oviformis* (Casey); green lace-

wings, *Chrysopa carnea* Stephens (= *C. californica* Coquillett); and coniopterygids (dusty-wings) were present, but only in small numbers.

1964 (fig. 3). In spite of low spring and midsummer populations of *Oligonychus punicae*, a heavy infestation developed in September that caused considerable bronzing and a small amount of leaf drop in the sample area. However, the peak was lower and the damage much less severe than in 1963. As in 1963, the tetranychids remained at a high level, with some irregular fluctuations, for several weeks before an abrupt decline followed. The temporary decline and return to the peak were reflected only in the adult females counted, and were possibly related to dispersal. The immature population counts remained relatively stable during this time (a similar tendency was evident in 1963).

After the spring increase, phytoseiids (*Amblyseius hibisci*) declined sharply in August to a very low level. A numerical response to *O. punicae* was evident in early September, quite soon after a marked increase of the prey was reflected in the samples. However, the predators started their increase from a very low level, and by the time that *O. punicae* was approaching a density of 400 females per 10 leaves, *A. hibisci* had increased to only about 30 per 10 leaves, compared with 90 at the same prey density in 1961. The phytoseiids were, however, the predator species that inflicted the highest mortality, at least until the spider mites began to decline, and possibly during the entire cycle. The response of *Stethorus* was considerably delayed, and the coccinellids probably did not have much effect on the mites before the population peak. Once again, intraspecific competition was probably the major factor causing a leveling-off of the tetranychid population, whereas the two main predator species must have greatly accelerated the rate of decline.

The numbers of *A. hibisci* declined quite gradually after the tetranychid

Fig. 3. Population trends of mites and predators on avocado trees in the Fallbrook orchard in 1964. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

decline (compared with 1961 and 1963). A possible reason for this is that relatively cool fall temperatures prevailed, allowing longer survival after food became scarce. In 1961 and 1963, the numbers of spider mites declined earlier, creating a shortage of food when high temperatures still prevailed.

Santa Paula Orchard

Except for an occasional individual of *Amblyseius similoides* Buchelos and Pritchard, *A. hibisci* was the only species of phytoseiid encountered in this orchard. In all four seasons, *Oligonychus punicae* infestations were well below the level that would cause severe bronzing of the leaves.

1961 (fig. 4). A typical spring increase and summer decrease of *A. hibisci* occurred, and virtually no numerical response was observed when *O. punicae* increased in late summer. However, *Stethorus* quickly increased to high numbers, and was apparently able to overtake the tetranychid population even before it reached an average of 200 adult females per 10 leaves.

1962 (fig. 4). In this season, *Stethorus* did not reach high numbers, but *A. hibisci* responded to the late summer increase of *O. punicae*, and it is probable that in this case the phytoseiids caused a greater mortality than did *Stethorus*. Whether the decline at the end of the year was caused mainly by

Fig. 4. Population trends of mites and predators on avocado trees in the Santa Paula orchard in 1961 and 1962. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

predation or by cool late-season weather could not be determined, but both factors may have been involved.

1963 (fig. 5). *Amblyseius hibisci* was relatively abundant throughout most of the winter, probably because of the presence of mite prey until early January. From a low of about 5 per 10 leaves in February, it increased to high numbers during the spring blossoming period, but then declined to an extremely low level in the fall, even though *Oligonychus punicae* was reaching medium densities at that time. This predator did not show a significant numerical response until after the peak level of spider mites was reached.

A rapid response by *Stethorus* apparently reversed the upward trend in *O. punicae*, but the coccinellids did not reach numbers as high as in 1961, nor did they completely suppress the prey, since a secondary increase occurred beginning in late October. Possibly, the cooler late-season weather slowed the activity of *Stethorus* to a point where its predation pressure on *O. punicae* was reduced. The mean temperature from mid-September to mid-October, when *Stethorus* was rapidly increasing, was 72° F. (maximum 84°, minimum 60°), whereas from mid-October to mid-November, when *Stethorus* was decreasing but *O. punicae* was again increasing, the mean temperature was 61° F. (maximum 71°, minimum 51°). Fleschner (in a personal communication) observed that oviposition of *Stethorus picipes* decreases rapidly as temperatures fall below 70° F.

1964 (fig. 5). *Amblyseius hibisci* was again present in relatively large numbers through the winter, and then increased to nearly 100 per 10 leaves during the flowering period. *Oligonychus punicae* declined to extremely low numbers by the end of January, and was greatly outnumbered by the phytoseiids. The spider mites showed a tendency to increase in September, but then leveled off. Minor increases were

also detected in late October and in December, but, as is usually the case late in the year, these increases did not lead to a heavy infestation.

Vista Orchard

The data from a two-year study in this orchard are of interest because of an apparent controlling effect exerted by *Amblyseius hibisci* throughout the summer of 1962. To better illustrate the numbers of phytoseiids relative to tetranychids, figure 6 shows all active stages of *Oligonychus punicae* rather than adult females only, as in the preceding graphs.

1962. *A. hibisci* was present at about 20 per 10 leaves when the samples first reflected an increase of the spider mites. The brown gut coloration indicated feeding on *O. punicae* as soon as the latter species was recovered in the samples. From late July to mid-August, there was a downward trend of *A. hibisci*, but at the same time the percentage of individuals with brown coloration increased, so that the actual rate of predation probably did not decline during this time.

O. punicae showed a general upward trend to a peak in October. *A. hibisci* also showed corresponding increases, and a possible factor of extreme importance is that the final surge of the tetranychid population was attended by a marked numerical response of predaceous mites. Such a quick response by *A. hibisci* to increasing prey density was not observed in other cases. Thus, the ratio of tetranychids to phytoseiids did not become very high (unfavorable).

The spider mite peak was accompanied by a functional as well as a numerical response of *A. hibisci*, since the percentage of mites acquiring a brown coloration increased from 73 to 85 per cent, the highest for the season. Putman (1962) determined that *Typhlodromus caudiglans* Schuster had to consume at least one larva or nymph of European red mite every other day in order to

Fig. 5. Population trends of mites and predators on avocado trees in the Santa Paula orchard in 1963 and 1964. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

Fig. 6. Population trends of mites and predators on avocado trees in the Vista orchard in 1962 and 1963. Population indices represent all active stages of both spider mites and phytoseiids.

Fig. 7. Population trends of mites and predators on avocado trees in the Morro Hills orchard in 1964. Population indices represent only adult female *Oligonychus punicae*.

maintain a red gut coloration. From this information, Putman and Herne (1964) calculated, on the basis of orchard counts of colored and uncolored individuals, that *T. caudiglans* consumed daily an average of at least 6.6 per cent of the young *Panonychus ulmi* (Koch) population. Assuming that the individuals of *Amblyseius hibisci* which had a brown coloration were consuming one mite every other day at the population peak of *Oligonychus punicae*, this predator would have destroyed daily an estimated 15 per cent of the prey population. However, the actual amount could have been considerably higher, since in the laboratory, at approximately 70° F., at least one adult or large immature *O. punicae* is required daily to maintain a dark brown coloration, which many individuals in the field possessed at this time. Other aspects of this predator-prey interaction are discussed in another section. (See pages 386–390.) *Stethorus* was considered to be only a minor factor in this case, since it was neither common nor very generally distributed.

1963. After a typical spring increase, *Amblyseius hibisci* declined to a low level by early August, after which *Oligonychus punicae* began to increase rapidly. The phytoseiids did not show a distinct numerical response as in 1962, and an unfavorable predator:prey ratio developed (about 1:17 at the *O. punicae* peak). It appeared inevitable that the increase would continue, but a period of unusually hot, dry weather followed, with temperatures of 102°, 105°, and 103° F, on three consecutive days, with the relative humidity ranging between 8 and 30 per cent during that period. A sharp decline of the spider mite population occurred immediately thereafter, indicating that in this case weather was the main cause. McGregor (1941) found that a constant temperature of 91° F. killed all stages of *O. punicae* in the laboratory.

Morro Hills Orchard (Fallbrook region)

1964 (fig. 7). Data from this orchard, taken only in 1964, are shown because of the absence of phytoseiid mites and

the high populations of *Stethorus* in relation to the density of *Oligonychus punicae*. *Stethorus* was first noted when the mites reached an average of only 30 adults per 10 leaves. When they exceeded 60 (still a low level), *Stethorus* increased rapidly to high numbers, and seemingly overwhelmed the prey before the latter reached a high level. This serves as an excellent example of the predaceous potential of *Stethorus*. The orchard was located only a few miles from the Fallbrook orchard, where climatic conditions are quite similar. It seems significant that in the latter orchard, where *Stethorus* was slow to build up during this season, an extremely heavy infestation of *O. punicae* developed (fig. 3). It is also noteworthy that *O. punicae* began to increase at approximately the same time in both orchards, although the Fallbrook orchard had moderate populations of phytoseiids during June and July and the Morro Hills orchard had virtually none.

Carpinteria Orchard

Data from this and the Encinitas orchard, both located near the ocean, are pertinent mainly because the phytoseiid population was composed almost entirely of *Amblyseius limonicus* rather than *A. hibisci*. A predaceous mite resembling *Typhlodromus longipilus* Nesbitt was found occasionally, but was not included in the counts on which the graphs were based. This species often had no brown coloration, even during heavy infestations of *Oligonychus punicae*, suggesting that it did not feed readily on the latter. A few *Amblyseius largoensis* Muma were found in the spring, but not later in the year when the *O. punicae* infestations occurred.

1961 (fig. 8). After reaching a peak of 330 adult females per 10 leaves in early August, *O. punicae* rapidly declined before the leaves showed extensive bronzing. Both *Stethorus* and *A. limonicus* responded rapidly to the prey increase, and it is probable that the com-

bined impact of both species brought about control of the tetranychids. When the latter reached their peak, the density of *A. limonicus* was approximately 120 per 10 leaves, and 100 per cent of the individuals in the sample contained a brown coloration indicative of feeding on *O. punicae*. Such numbers must have had a considerable impact on the prey population. This species was found to consume more mites than *A. hibisci* (McMurtry and Scriven, 1965). Since the counts of *O. punicae* represent only adult females, the predator:prey ratios cannot be determined, but on the basis of later observations on percentages of adult females in the populations, it is probable that the observed ratio of over 1 predator to 3 adult female prey, during the latter's peak density, represented a ratio of 1 predator to not more than 10 total active stages of prey.

1962 (fig. 8). Following a slight increase at the end of 1961, *Oligonychus punicae* declined to low levels, and showed no sustained increases until October. The highest level for the season was only somewhat more than 100 adult females per 10 leaves in December. It is not known whether predation was the factor responsible for maintaining the prey at such a low level. However, *Amblyseius limonicus* was definitely causing mortality at low densities, as evidenced by the percentage of individuals containing a brown coloration, and conceivably could have been the key factor. Other predators were present only in small numbers, and were never widely distributed during the season.

1963 (fig. 9). Because tree 1 showed important differences in population trends, the counts for it are shown separately in comparison with the averages of the other sample trees. In January, temperatures dropped well below freezing, and this resulted in partial killing of the foliage and some dieback of twigs. Apparently, this delayed the emergence of new foliage in the spring by several

Fig. 8. Population trends of mites and predators on avocado trees in the Carpinteria orchard in 1961 and 1962. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

weeks, and the leaves did not become hardened (and favorable for mite reproduction) until quite late. This may have partially accounted for the fact that almost no *Oligonychus punicae* were found until September.

A spring peak of predaceous mites in the near absence of mite prey coincided with the flowering period of the trees. In a sample of phytoseiids taken on May 28, 24 per cent were *Amblyseius largoensis* and the rest were *A. limonicus*. On July 6, only 6 per cent of the individuals collected were *A. largoensis*, whereas later, when the spider mites became abundant, only *A. limonicus* were found. The phytoseiids declined to their lowest level of the season in September,

approximately the same time that *O. punicae* began increasing. Before this time, mite population trends were quite similar on all sample trees.

On tree 1, the peak of *O. punicae* was reached on October 15, nearly three weeks earlier than on the other three trees. During the next week, a remarkable increase of *A. limonicus* to 200 active stages per 10 leaves occurred, and the spider mites were reduced to only about half the level of the previous count. There was a notable difference between the rapid decline of *O. punicae* from the peak on this tree and the relatively long leveling-off period before the decline on trees 2, 3, and 4. It was concluded that predation by *A. limon-*

Fig. 9. Population trends of prey and predators on avocado trees in the Carpinteria orchard in 1963. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*. Tree 1 (fine lines) is shown separately from the other three sample trees because of important differences in the population trends.

icus was the main cause of the decline of spider mites on tree 1. Only a moderate amount of leaf bronzing occurred; therefore, overexploitation of the food supply was not considered the major factor which caused the population decline on this tree. Moreover, while this population was in the declining phase, populations on the other three trees were rapidly increasing, demonstrating that unfavorable weather could not have been responsible for the decline on the first tree.

Populations of *O. punicae* on trees 2, 3, and 4 peaked at an average of 545 adult females per 10 leaves, and remained above 400 for about four weeks. As a result of this extended period of high populations, most of the leaves on these trees became heavily bronzed (although no defoliation occurred), and probably became unfavorable for further increase of the mites. *A. limonicus* reached 100 per 10 leaves at the same time the peak of *O. punicae* was attained, but the predaceous mites did not continue to increase during the following four weeks, even though the prey remained near the peak level. Instead, they actually declined during part of that period. The reasons for this decline notwithstanding an abundance of prey were not definitely determined. They did not stop reproducing, since the egg counts during this period averaged 40 to 50 per 10 leaves. It is possible that periods of low humidity (unusually low for this coastal area), associated with east wind conditions, may have had an adverse effect on eggs or immature stages. McMurtry and Scriven (1965) report that eggs of *Amblyseius limonicus* cannot survive low humidities. During the twenty-five-day interval when the counts on trees 2, 3, and 4 indicated a decline of the phytoseiids, there were eight days during which the relative humidity fell below 30 per cent. In contrast, through the period of the most rapid rate of increase of the predaceous mites on tree

1 (the entire month of October), there was almost continual coastal fog, nearly 100 per cent relative humidity, and relatively constant temperatures ranging from about 58° to 64° F.

The eventual decline of the mite populations on trees 2, 3, and 4 appeared to be brought about by a combination of intraspecific competition and predation by *A. limonicus*. Other predators were never present in large numbers during the infestation. As on tree 1, it was observed that other trees in the orchard also had much less damage and higher populations of phytoseiids than the other three sample trees, indicating that variation among trees was of general occurrence, and that small differences in timing or rate of build-up of either the prey or predator populations could have affected the degree of control by the predaceous mites. Although the infestation in this orchard was generally quite heavy, there were no indications that subsequent tree growth and/or fruit yield were affected.

Encinitas Orchard

1962 (fig. 10). Although *Oligonychus punicae* persisted in low numbers during the first half of the year, *Amblyseius limonicus* was extremely scarce during this time. Observations made during the preceding year indicated that the phytoseiids were abundant during the summer, but almost disappeared in the fall after a period of dry east winds and low humidity, and failed to respond numerically to a secondary increase of *O. punicae* during late fall and early winter. In 1962, extensive searches for *A. limonicus* were made throughout the orchard in March, April, May, and June; at least 200 leaves were examined each time. No phytoseiids were found, and it was therefore surprising that an increase was detected in the samples in July before *O. punicae* had reached high numbers. As the tetranychids started building up rapidly in September, the phytoseiids showed a corresponding nu-

Fig. 10. Population trends of mites and predators on avocado trees in the Encinitas orchard in 1962. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

merical increase to a maximum of 140 per 10 leaves, and appeared to be the major factor causing the abrupt decline in numbers of *O. punicae*. Because some of the leaves showed rather severe bronzing at the peak spider mite population, the reproductive potential of *O. punicae* was probably somewhat lowered before it was overtaken by the predator. However, the mites were controlled before they caused serious damage. No other predators were abundant.

1963 (fig. 11). As in the Carpinteria orchard, cold winter temperatures apparently retarded the emergence of new leaves in the spring, and *Oligonychus punicae* remained at a very low population level. However, as soon as the new leaves matured, an extremely rapid surge of the spider mites occurred. They

numbered over 200 adult females per 10 leaves before *Amblyseius limonicus* showed any marked numerical response. When their count first exceeded 500 adult females per 10 leaves, the phytoseiids had reached only 20, compared with nearly 100 at comparable prey levels in 1962.

Stethorus was also scarce, and in this case it was clear that predators were not able to control the infestation. The mites remained at over 450 adult females per 10 leaves (with a peak of 843) for over four weeks, causing severe bronzing with considerable leaf drop. It was not until this time that *A. limonicus* reached high numbers. This serves as an example of the severity an infestation of *O. punicae* can attain in the absence of significant predation pressure.

Fig. 11. Population trends of mites and predators on avocado trees in the Encinitas orchard in 1963. Population indices represent all active stages of phytoseiids, but only adult female *Oligonychus punicae*.

POPULATION STUDIES ON INDIVIDUAL TERMINAL SHOOTS

The conventional leaf sampling noted in the preceding section does not adequately reflect the dynamics of the spider mite populations early in the season, when they are present in extremely low numbers and in only a few small isolated areas of a tree. In order to afford better study of a population at low densities, field counts were made on in-

dividual terminal shoots in the Fallbrook orchard in the summer of 1964.

Beginning in May, four trees in the orchard were carefully examined for *Oligonychus punicae* during a total searching period of one hour. The trees could be quite thoroughly examined in this length of time, since feeding by even one or two mites produces a small

Fig. 12. Average population trends of mites and predators on eight study terminals (total of 122 leaves) in the Fallbrook orchard in 1964. Dotted line indicates trend reflected in conventional leaf samples (plot average). Upper portion of graph shows percentage of leaves infested with *Oligonychus punicae* and percentage of leaves having increasing and decreasing populations of *O. punicae*.

brown area on the leaf. These feeding areas are particularly conspicuous on the new growth in early summer. When an infested leaf was found, the terminal on which it was observed was marked for continuing observation. Populations were followed on the first eight terminal shoots on which infested leaves were found. Time limitation precluded detailed observation on additional terminals, although general examination of the trees was continued, to determine when new infested areas appeared. The number of leaves on the eight terminals under observation varied from 12 to 28, with a total of 122.

By tying numbered tags to the pet-

ioles of all leaves on the terminals, population records were maintained for individual leaves. During most of the study, the leaves were examined twice weekly, and mites and predators were counted with a $2\frac{1}{2}\times$ binocular head lens and a flashlight. The actual numbers of *O. punicae* were somewhat higher than the counts indicated because larvae could not be counted with low magnification, and probably some small protonymphs were also overlooked.

The first two infested leaves, each in a different part of one tree, were found on June 18. Infested leaves were found on two more terminals on July 2, and on four more on July 15. These termi-

nals first contained only a few individual mites on one or two leaves, but the infestations gradually spread to other leaves of the terminal and also to adjacent terminals. Observations indicated that these widely separated microareas of infestation, which in some cases might have been initiated by single females, were the main foci from which the general infestation progressed. Thus, it appeared that only a small number of mites per tree gave rise to the heavy infestation which subsequently developed.

Figure 12 shows average numbers of mites per leaf and insect predators per 100 leaves for the eight observation terminals, in comparison with the numbers of *Oligonychus punicae* in the conventional leaf samples. The mites on the terminals were counted only until October 6, and thus the declining phase of the cycle is not shown. During the gradual increase of *O. punicae* on the observation terminals during July, there were still many uninfested leaves as well as considerable population fluctuation on individual leaves, as evidenced by the percentages of leaves having increasing or decreasing populations (upper portion of fig. 12). *Amblyseius hibisci* outnumbered *O. punicae* for a time in July, and may have been important in reducing its numbers during this time. Most leaves had one or more phytoseiids, some of which had brown coloration indicative of feeding on *O. punicae*.

At the beginning of August, a rapid increase of *O. punicae* was evident, with many additional leaves becoming infested. However, it was not until late August, after considerable dispersal was evident on the observation terminals, that a decided increase was reflected in the conventional leaf sample. Thereafter, the values obtained from both types of samples closely paralleled each other.

In spite of increased numbers of spider mites on the observation termi-

TABLE 1
PREDATOR:PREY RATIOS OF
AMBLYSEIUS HIBISCI TO
OLIGONYCHUS PUNICAE OBTAINED
FROM CONVENTIONAL LEAF SAMPLES
IN COMPARISON WITH RATIOS ON
OBSERVATION TERMINALS

Date	Ratios based on leaf samples*	Ratios on study terminals†
	Predators: Prey	Predators: Prey
July 15.....	19: 0	2: 1.0
July 28.....	23: 0.	1: 1.1
August 4.....	3: 1.0	1: 4.6
August 11.....	1: 1.8	1: 56.4
August 18.....	1: 1.0	1: 166.4
August 25.....	1: 1.0	1: 287.4
September 1.....	1: 21.3	1: 469.5
September 9.....	1: 14.9	1: 113.2
September 15.....	1: 15.0	1: 168.1
September 22.....	1: 18.2	1: 60.6
September 29.....	1: 21.2	1: 26.3
October 6.....	1: 19.9	1: 21.6

* Average of four sample trees.
† Average of eight observation terminals which became infested early in the season.

nals in August, phytoseiids in these areas declined to very low numbers, during which time they obviously could not have been an important controlling factor because there were too few present compared with the number of prey. This fact would not have been apparent when examining only the averages of mites per leaf obtained from regular leaf samples (fig. 3), since average counts of *A. hibisci* were actually higher than those of *O. punicae* until late August. This point is illustrated in table 1, which shows ratios of *A. hibisci* to *O. punicae* from conventional leaf samples compared with the ratios obtained on observation terminals. The extreme differences indicate that average predator:prey ratios may sometimes be misleading.

It would have been expected that as *O. punicae* started to increase in August, there would have been higher numbers of *A. hibisci* on the infested terminals, where prey density was highest, than on the trees in general, where the average prey density was still low.

However, figures 3 and 12 show that this was not the case. A numerical response of the phytoseiids to *O. punicae* did not occur on the observation terminals until September, which was no sooner than an increase was reflected in the general sample. *A. hibisci* started increasing quite rapidly on the observation terminals at the end of September, and on one terminal reached 16 per leaf on October 13. However, this terminal also yielded the highest count of spider mites on the same date (222 per leaf); consequently, the predators did not prevent them from reaching high numbers.

The numbers of insect predators shown in figure 12 were composed of *Stethorus*, *Oligota*, *Scolothrips*, and *Chrysopa*. Trends of all species were extremely erratic during the period shown, exhibiting what Solomon (1949) termed an inverse density-dependent relationship; e.g., the predators showed little change in density while the prey was increasing, and therefore were killing a progressively lower percentage of the prey as the latter increased. A significant point established from the observations was that all of the major predators associated with *Oligonychus punicae* were found very early, when only a few scattered spider mites were seen.

The predator observed earliest was *Stethorus*. Two adults were seen in a general search of the orchard on June 3, before any *O. punicae* were found. On July 2, when a total of only eight infested leaves (on four different terminals) had been found on the four observation trees, single adult *Stethorus* were observed on two of the terminals, and two eggs were noted on a third terminal. However, no colonies became established from these early arrivals; the coccinellids were not found consistently on the study terminals until September. However, it must be emphasized that, in this particular case, *Ste-*

thorus was unusually slow in building up in the orchard.

A marked reduction of spider mites on one of the terminals in early August (from about 1 to 0.3 per leaf) was associated with the appearance of several larval six-spotted thrips, which apparently had hatched from eggs laid on one or more of the infested leaves. Brown coloration could be seen through the semitransparent integument, indicating that the larvae had been feeding on the spider mites. They were all found among the mite colonies along the midribs of the leaves, and were present on three successive observations up to August 11; but no thrips were seen at the time of the next count, when *O. punicae* again started increasing on this terminal. Another generation of thrips was evident on September 15, when 10 larvae were observed on the same terminal. By this time, however, *O. punicae* had increased to such high numbers that the effect of the thrips could not have been significant.

A decrease of mites on another terminal between August 11 and 21 was associated with the presence of a *Chrysopa* larva which hatched from an egg laid on the same terminal. The larva was seen during three successive counts, each time on a different leaf, and was nearly full-grown when last seen. It is quite conceivable that a single larva could have consumed sufficient mites to account for the observed temporary decrease from 2.5 to 0.9 mites per leaf. Fleschner (1950) demonstrated the high capacity for mite consumption of *Chrysopa*. When the predator disappeared, the number of mites on this terminal again increased.

Small spiders of the family Micryphantidae were found consistently from July 31 to the end of the study. They showed essentially no change in density on the observation terminals between mid-August and mid-September, averaging about 0.5 per terminal. On two different occasions, a spider was ob-

served feeding on a mite, but even though they were sometimes found on the same infested leaf during successive counts, no decided decline in number of mites on any of the leaves was associated with their presence.

It was concluded from the observations that in this particular case a higher percentage of predation occurred early in the year, at low prey densities, than at high densities (until just before the peak, when *Amblyseius hibisci* and *Stethorus* started showing a numerical response to the high densities of prey). Certain insect predators, which were generally assumed to be a factor only at relatively high prey densities, were observed to cause some mortality at extremely low densities. Different predator species were important on different terminals, the cause of predation on a given terminal apparently being the result of chance factors, depending on what species of

predator happened to find the particular localized infestation. This suggests that a wide variety of general predators early in the season can be beneficial.

In no case was a small early infestation on an observation terminal eliminated by predators, even when the population was confined to a few leaves of a terminal and was relatively isolated from other populations. Local extermination on a terminal might almost have happened in one or two instances, but larvae or protonymphs were always found on subsequent counts, indicating that at least some eggs escaped predation.

The terminals on which the mites first started increasing were not necessarily the ones which developed the highest numbers. For example, the one on which the mites increased most slowly in August ultimately developed the highest population (222 per leaf on October 13).

SOME FACTORS POSSIBLY INFLUENCING PREDATION BY PHYTOSEIIDS

Reproductive rates

There has been considerable discussion on whether phytoseiids can reproduce at a sufficiently high rate to overtake and control a rapidly increasing population of tetranychid mites. Chant (1959) indicated that *Typhlodromus pyri* Scheut. on apples in England laid only one egg every three or four days, whereas the European red mite, *Panonychus ulmi* (Koch), laid one egg per day and had more generations than the predators. However, Collyer (1964) contended that *T. pyri* could maintain adequate control of the prey despite its lower apparent reproductive capacity. On the other hand, *Phytoseiulus persimilis* Athias-Henriot has an extremely high reproductive capacity and a very short developmental time (Bravenboer and Dosse, 1962). Greenhouse experiments have demonstrated that this spe-

cies can rapidly overtake a prey population (Bravenboer and Dosse, 1962; Chant, 1961). Its high reproductive capacity is apparently one of its most notable attributes as an effective predator.

With the exception of some observations made by McGregor (1941), there was little information available on the reproductive rate of *Oligonychus punicae* on avocado leaves. A series of laboratory tests was conducted to determine the rate of development and oviposition at $72^{\circ}\text{F} \pm 2^{\circ}$ and 40 to 50 per cent relative humidity. Avocado leaves of the Hass variety were collected at the Fallbrook orchard in August of 1963, when *O. punicae* was starting to increase rapidly. The leaves were placed lower side down on foam plastic pads in pans of water. Strips of Cellucotton® were placed around the periphery of

the leaves.³ Further details of this arrangement are described by McMurtry and Scriven (1964).

Tests for determining rate of development were begun by placing large numbers of field-collected adult female *O. punicae* on four excised leaves which were mature, dark green, and free of mite feeding damage. The females were left on the leaves to oviposit for 16 hours and then removed. A total of 134 eggs was deposited. These progeny were observed daily through hatching, immature development, and preoviposition. The number of progeny completing development was 126; 83 females and 43 males. The duration of the egg stage was approximately 8 days; the combined larval and nymphal stages, 6 days; and the preoviposition period, 2 days. A generation, from egg to egg, was completed in 15 to 16 days.

Tests for determining the rate of oviposition were conducted, using four replicates each of three different physiological types of leaves: mature, dark green, undamaged leaves; young, light green, undamaged leaves; and mature leaves, severely bronzed from mite feeding. Thirty-two adult female *O. punicae*, also collected from the Fallbrook orchard, were placed on each leaf, resulting in 128 mites for each leaf category. Counts of adults and eggs were recorded daily for 7 days, removing the eggs each day. At the end of this period there was a 51 per cent loss of females (probably mainly from escape) on the young leaves, a 47 per cent loss on the damaged leaves, but only a 23 per cent loss on the mature, undamaged leaves. The mean production of eggs per female per day, based on the number of live females present each day, was 3.40 on the mature, undamaged leaves, 1.33 on the young leaves, and 1.65 on the

heavily bronzed leaves. An analysis of variance indicated highly significant differences between oviposition rates on the mature, undamaged leaves and on the other two types.

The results illustrate the importance of the physiological condition of the host leaf in influencing the reproduction rate of the mites. The use of excised leaves is open to criticism, since it can be argued that the leaves may change, resulting in a rate of reproduction of the mites different from that occurring on intact leaves. However, there are also serious problems involved in conducting controlled experiments on intact leaves. There was no indication that the excised leaves were becoming less favorable as the tests progressed, since there was no marked decrease in reproduction toward the final days.

In comparison with the development and oviposition rates obtained for *Oligonychus punicae*, the average values obtained for the two most common phytoseiid species under the same temperature and humidity conditions (with an abundance of tetranychid mite prey) were as follows: *Amblyseius hibisci*, 12.5 days to complete a generation, and an oviposition rate of 1.3 eggs per female per day; *A. limonicus*, 8.5 days to complete a generation, and an oviposition rate of 2.3 eggs per female per day (McMurtry and Scriven, 1964; 1965). Consequently, both species completed a generation in a shorter time, but had a lower rate of oviposition than *O. punicae* when the latter was feeding on mature, undamaged leaves. However, when the tetranychids were on immature or severely bronzed leaves, their rate of oviposition was lower than that of *A. limonicus* and nearly the same as for *A. hibisci*, indicating that under some conditions, the reproductive potential of the phytoseiids may be higher than that

³ In order to make the information in our publications fully intelligible, it is sometimes necessary to use trade names of products. No endorsement of a named product is intended, nor is criticism implied of similar materials which are not mentioned.

of the tetranychids. McMurtry and Scriven (1964) point out that the presence of other foods, such as pollen or honeydew, may also influence the reproductive rate of the phytoseiids.

It becomes clear that erroneous conclusions can be drawn from comparing the maximum reproductive rates. Both prey and predators may seldom reproduce near their maximum rates at the same time. For example, early in the season, the density of the prey may be very low, but as soon as leaf condition, weather, and other factors become favorable, the prey may begin reproducing near its maximum rate. At this point, the average reproductive rate of the predators will probably be very low (unless suitable nonanimal food is abundant), since, in general, prey will still be relatively scarce. A considerable period of time may elapse before the prey density is high enough for the predators to find sufficient food for a high average rate of reproduction. Depending on distribution of the prey, this point may be reached relatively soon in small areas of a tree, but probably only much later (when average prey densities are quite high) on the tree in general. By this time, as a result of intraspecific competition, the reproductive rate of the prey may have declined below that of the predator, allowing the latter to overtake the prey. As Holling (1961) and Huffaker and Messenger (1964, p. 107) have pointed out, a natural enemy may have a lower inherent reproductive capacity than the host and yet be effective if the fecundity of the host is reduced by other factors.

The reproduction of the prey can, of course, also be partially nullified by the predator. For example, if the prey is reproducing at a rate twice as high as the predator, but the latter is consuming 50 per cent of the prey's progeny, the net result may be equal reproduction of both predator and prey. Consequently, the number of eggs laid by the prey may give little indication of its

rate of increase. Obviously, other factors, such as searching efficiency of the predator, can be of great importance in such an interaction.

Distribution

Chant (1959) found that interleaf distribution of *Typhlodromus pyri* on apple trees in England was dissimilar to that of the European red mite. Frequency distribution curves indicated that until late summer there was a high percentage of leaves on which no predators were present, but a much lower percentage on which no prey occurred. The data also indicated that there was a differential preference between predator and prey for leaves of different ages. Chant concluded that it was doubtful whether a predator with such a distribution could control the European red mite. Van de Vrie (1964), working with the same two species in the Netherlands, indicated that on the basis of total leaf area, the predators were equally distributed on all leaves of the shoots, but the prey showed a preference for basal leaves. Contrary to Chant's findings in England, his frequency distribution curves were similar for both predator and prey. Chant and Fleschner (1960), considering phytoseiids in general on citrus and avocado in southern California, concluded that the distribution of the predators was similar to that of the prey, *Oligonychus punicae* (Hirst) and *Panonychus citri* (McGregor). Their data also suggested that sometimes the phytoseiids were found more frequently on mite-infested than on noninfested leaves.

The data accumulated in the present four-year study enabled the authors to examine in detail the distributional patterns of *Amblyseius hibisci*. Several aspects of distribution which could conceivably have a bearing on the potential effectiveness of phytoseiids were investigated. Insufficient data were available for a similar analysis on the distribution of *A. limonicus*.

Tendency to congregate on infested leaves. This aspect of distribution was investigated by determining whether there were any cases in which there were significantly more *A. hibisci* on infested than on noninfested leaves. Data obtained from weekly population samples in the Vista and Fallbrook orchards were used. Only the data taken during periods of medium prey densities during the increase phase of the population cycle could be used, because at low densities there were insufficient numbers of infested leaves to make valid comparisons, and at high densities there were too few uninfested ones. The average numbers of *A. hibisci* per leaf on infested and noninfested leaves were compared for five to seven weekly samples per season for both orchards, and "t"-test analyses were performed on the paired averages. In the Vista orchard in both 1962 and 1963, the analyses indicated that there were significantly more *A. hibisci* on leaves infested by *O. punicae* ($P = < .01$). However, there were no significant differences or even indications of differences in the Fallbrook orchard. Other general observations on the Hass variety likewise failed to reveal any definite tendency of *A. hibisci* to congregate on infested leaves. The significant differences found in the Vista orchard may have been owing in part to variety and orchard conditions. (See discussion on p. 396.)

Percentages of leaves containing predators and prey at different times during the season. It was of interest to determine if there was a critical time during the season when a large percentage of the leaves contained prey but no predators, and if this situation was correlated with a rapid increase in numbers of spider mites. Data from the Vista orchard for 1962 and 1963 were used. Figure 13 shows percentages of leaves having *Amblyseius hibisci* (with or without prey), percentages having *Oligonychus punicae* (with or without predators), and percentages having *O.*

punicae with no predators (*O. punicae* only).

In 1962, when *A. hibisci* apparently controlled *O. punicae*, there was only one occasion (August 23) when the percentage of leaves containing prey was noticeably higher than that containing predators. At that time, 26 per cent of the infested leaves had no predators. However, this percentage subsequently decreased, and at the peak density of spider mites on October 11, there were predators on nearly 100 per cent of the infested leaves. Such a distribution suggests that it would be possible for the predator to maintain control of the population.

In 1963, when *A. hibisci* clearly was not able to control *O. punicae*, the distribution trends were considerably different. Although nearly 100 per cent of the leaves contained predators in early July, there was a decrease to 50 per cent or lower as the percentage of leaves containing prey began to increase rapidly. There was not a corresponding increase in the number of leaves occupied by *A. hibisci*, as in the previous year, and the number of leaves with prey but no predators increased to 30 per cent. When *O. punicae* attained its maximum density on September 25, over 25 per cent of the infested leaves contained no predators.

In the Fallbrook orchard in 1963 and 1964, the trends were quite similar to those in Vista in 1963, except that the number of leaves containing *A. hibisci* fell to an even lower level (15 per cent) at the time when the percentage containing *O. punicae* began to increase.

Relationships between density and distribution. The percentage of leaves occupied by *A. hibisci* appeared to be related more closely to density than to other factors, such as prey distribution. This is illustrated in figure 14, which shows the percentage of infested leaves plotted against the average number of mites per leaf for both *A. hibisci* and *O. punicae*. Data were taken from popula-

Fig. 13. Percentage of leaves infested with tetranychids (*Oligonychus punicae*) and phytoseiids (*Amblyseius hibisci*) in the Vista orchard in 1962 and 1963. Based on periodic mite population sample records.

tion sample records at the Fallbrook orchard (A) and the Vista orchard (B) in 1962 and 1963. Each point represents the average number of mites per leaf and the percentage of the sample leaves infested at a given sampling date during the spring and early summer for the two years. Since no spider mites occurred in many of the samples in the spring, the points shown for them are fewer than for the predaceous mites. The curves are quite similar for both orchards. The points for *A. hibisci* indicate a very consistent relationship between density and percentage of leaves infested, an average of 1 mite per leaf corresponding to about 50 per cent of the leaves infested, 2 mites per leaf to

75 or 80 per cent infested, 3 mites per leaf to about 90 per cent infested, etc.

For *O. punicae*, the points are more widely scattered, but it is evident that there were not high percentages of leaves infested unless average densities were relatively high, indicating a less random type of distribution than that of *A. hibisci*. The data suggest that the predator does in fact show a type of distributional pattern different from that of the prey. There was no evidence that the distributional pattern of the predator changed as the prey's density increased.

Predator:prey ratios on individual leaves. In situations where most leaves have a relatively high predator:prey

Fig. 14. Relationships between density (mites per leaf) and percentage of leaves infested by *Amblyseius hibisci* (predator) and *Oligonychus punicae* (prey). Based on periodic mite population sample records from the Fallbrook (A) and Vista (B) orchards in 1962 and 1963.

TABLE 2
NUMBERS OF *AMBLYSEIUS HIBISCI* PER LEAF ON DIFFERENT AGED
LEAVES IN THE SANTA PAULA ORCHARD IN EARLY SUMMER OF 1963*

Date	Old leaves†		New leaves‡		Ratio old: new	
	Mites	Eggs	Mites	Eggs	Mites	Eggs
June 18.....	8.1	3.2	7.0	0.8	1.1:1	4.0:1
July 2.....	6.8	2.8	7.9	0.6	1:1.2	4.7:1
July 16.....	3.6	0.8	6.1	0.5	1:1.7	1.6:1

* Numbers based on 40-leaf sample.

† Previous season's growth.

‡ Current season's growth.

ratio, the predator should be better able to maintain control of the prey. This was investigated for the Vista orchard in 1962 (apparent control by *A. hibisci*) and the Fallbrook orchard in 1963 (poor control by *A. hibisci*). In the former case, there were few leaves on which *O. punicae* reached high numbers. From a total of 341 leaves sampled between July 26 and October 18, 69 per cent had a ratio of at least 1 predator to 5 prey, 13 per cent had a ratio of 1 predator to 6–10 prey, and 18 per cent had a ratio of 1 predator to more than 10 prey.

In the Fallbrook orchard between June 12 and August 6, 1963, only 35 per cent of the total leaves had a ratio of at least 1 predator to 5 prey, 16 per cent had 1 predator to 6–10 prey, and 49 per cent had only 1 predator to more than 10 prey. Some of the most heavily infested leaves had few or no predaceous mites, suggesting that on some leaves the spider mites were able to increase almost free of predation from *A. hibisci*.

Influence of leaf age, shape, and position on distribution. Although *Oligonychus punicae* generally does not colonize leaves of the current season's growth until they have matured and hardened considerably (usually in early summer), *Amblyseius hibisci* can be found on the new leaves even before they have completely expanded, and is quite abundant on these leaves by the

time they become favorable for *O. punicae*. This is illustrated in table 2, which shows phytoseiid mites and eggs per leaf on new and old leaves collected from the Santa Paula orchard on three different dates in 1963. The data indicate that active stages of *A. hibisci* were somewhat more abundant on old leaves on June 18, but by July 16 they were considerably more numerous on the new leaves. During this period, *O. punicae* was still confined almost entirely to the old leaves. More phytoseiid eggs were laid on the old leaves in all cases, but especially on the first two dates shown in table 2. This species seems to prefer to lay eggs on the underside on strands of webbing rather than directly on the leaf surface. Such conditions are more likely to be found on old than on new leaves.

With regard to leaf shape, *O. punicae* appears to colonize slightly upturned leaves more readily than those which are flat or curled downward. Sometimes the opposite appears to be the case for *A. hibisci*, but when counts were made on both types of leaves at the Fallbrook orchard during a heavy infestation of spider mites, no differences in abundance of the predators on the two types of leaves mentioned above could be demonstrated.

It is well known that phytoseiids tend to avoid bright light. Fleschner *et al.* (1955) observed that the species in their study orchard⁴ tended to remain

⁴ Collection records indicate that the species present in this orchard was predominantly *Amblyseius limonicus*.

on shaded, protected leaves on warm days, but became generally distributed over all leaves on the trees at night. In the present studies, it was often observed that *A. hibisci* was quite active and roaming the upper surfaces of the leaves even in midday on shaded portions of the trees, especially during the spring or during cool weather. However, the mites could also be found on parts of trees receiving the most sunlight, although they remained on the undersides of the leaves, protected from direct sunlight. Although it sometimes appeared that there were higher numbers of *A. hibisci* in the shadiest portions of the trees, no conclusive evidence to this effect was obtained. On the individual terminal studies, the terminal on which the highest phytoseiid population was counted was heavily shaded, but on some of the other shaded terminals the predators did not reach high numbers, even though prey density was high.

It is concluded that distribution *per se* is not a major factor limiting the effectiveness of *A. hibisci*, since the species becomes thoroughly distributed over virtually all parts of the tree, is found on all types of leaves inhabited by *O. punicae*, and searches over both the upper and lower surfaces. However, this predator does exhibit a type of distribution that differs from that of *O. punicae* (more random). The fact that it does not show a strong tendency to congregate and lay more eggs on heavily infested leaves may be a critical factor in its inability to respond rapidly to prey increases in many cases.

Webbing

Colonization of avocado leaves by *Oligonychus punicae* was almost invariably observed to begin along the midrib or in depressions on the upper side of the leaf. Close examination of these areas under a microscope usually revealed that many fine strands of webbing, produced by the adult female

mites, were suspended above the lower areas, forming a canopy under which the colony developed. In the field, a dead phytoseiid occasionally could be seen suspended in the webbing, or a live individual would be observed moving with apparent difficulty among the silken strands.

The effect of webbing produced by *O. punicae* on the predatory activity of *Amblyseius hibisci* was observed more closely by bringing mite-infested leaves from the Fallbrook orchard into the laboratory and placing them on foam plastic pads in pans of water, as in the tests mentioned under "Reproductive Rates." (See p. 384.) Ten adult females of *A. hibisci* were placed on each of two leaves. These leaves curved upward slightly from the midrib, and a canopy of webbing, produced by the tetranychids in the field, was suspended above the leaf surface at the midrib. When moving over the leaf surface, the predaceous mites sometimes backed away and proceeded in another direction when contacting the webbed-over area, whereas in other cases they walked over it, but were never observed to contact the mites below. The spider mites thus remained protected from predation until they ventured onto the exposed areas of the leaf. When the webbing was removed, the mites were destroyed by *A. hibisci*.

It appears that the degree to which the webbing protects the population from predation will depend on the density of the prey. At low densities, the mite colonies are usually confined to areas along the midrib or in depressions over which a network of webbing can be suspended. During this time, the dispersal rate seems to be relatively low, and thus most mites remain in the protected locations. However, as numbers increase, dispersal likewise increases, and a higher percentage of the population may be exposed to predation by *A. hibisci*, either while seeking other protected areas or attempting to colo-

nize flat areas of the leaf which cannot be protected by webbing. The effects of such "protective refuges" on predation have been demonstrated in the laboratory by Gause (1934), Flanders (1948), and others. Flanders (1947) lists several examples of this phenomenon in natural populations. However, the "refuges" of *O. punicae* do not furnish absolute protection to the individuals within, because a few *A. hibisci* occasionally have been observed beneath the webbing, having gained access to the prey.

Some species of phytoseiids, such as

Typhlodromus occidentalis and *Phytoseiulus persimilis*, are well adapted to preying on spider mites in densely webbed areas. The same experiment conducted with *A. hibisci* was also done with *Amblyseius chilensis* (Dosse), a species introduced from South America. Contrary to the behavior shown by *A. hibisci*, *A. chilensis* almost immediately crawled between the strands of webbing down into the midrib area containing the spider mites. *A. limonicus* was also less hindered by the webbing than was *A. hibisci*.

DISCUSSION AND CONCLUSIONS

Apparently, extreme fluctuations are inherent in the population dynamics of *Oligonychus punicae* in unsprayed avocado orchards in southern California. Population levels can change from possibly one mite per 1,000 leaves to more than 100 mites per leaf (a millionfold increase) in three or four months. The main source of an infestation in most cases appears to be from residual populations within the orchard rather than from migration of individuals into the orchard.

The subtropical climate of southern California permits at least some activity of *O. punicae* all year. Measurable population increases are common as late as November and December, but unusual in January and February. Weather obviously determines the potential rate of increase, and when other conditions are favorable, the reproductive potential is higher in the summer (except during extreme hot weather) than at other times of the year. Population peaks were observed by the authors to vary considerably from year to year, both in magnitude and time of occurrence. Low populations in the spring did not necessarily indicate a low seasonal peak, although the peak usually occurred later than when spring populations were relatively high.

The data here presented are the accu-

mulation of sixteen grove-years, in which there were two cases where considerable defoliation resulted from feeding by *O. punicae* (Encinitas, 1963; Fallbrook, 1963), two cases of severe leaf bronzing but little or no defoliation (Carpinteria, 1963, on some trees; Fallbrook, 1964), and twelve cases of medium to very light leaf bronzing. Thus there were two, or at most four, instances where spraying might have been advantageous, provided that it would not have disrupted the balance of other species in the ecosystem or induced a subsequent outbreak of *O. punicae*. In the remainder of the cases, there would have been no justification for spraying for mite control.

Leaf drop from an infestation of *O. punicae* was generally observed only when the population had become so heavy that even the lower surfaces of the leaves were partially damaged. This usually took place when counts had reached a peak of over 700 adult females per 10 leaves or had persisted for several weeks at over 500. The likelihood of defoliation appears to be less during cool weather than during hot, dry weather. It has not been determined if partial defoliation significantly reduces tree growth and fruit yield, but it appears that the trees always con-

tinue to grow vigorously the following spring.

In the orchards where these studies were conducted, the rapid declines of *O. punicae* populations could be attributed to biotic factors in nearly all cases. Except in the Vista orchard, where extremely hot weather apparently reversed the upward trend of the population in the late summer of 1963, all abrupt declines were associated with large numbers of natural enemies, or sufficiently high densities of tetranychids to cause depletion of favorable leaf feeding surface (intraspecific competition), or a combination of both factors. However, where populations remained low for the entire season, such as at Fallbrook and Carpinteria in 1963 and Santa Paula in 1964, it could not be determined whether biotic or abiotic factors were more important in preventing the spider mites from reaching high numbers.

The condition of the host leaves is unquestionably a major factor affecting the reproductive potential of *O. punicae*. This was shown experimentally in the laboratory, where considerably fewer eggs were laid on young or mite-damaged leaves than on mature, undamaged leaves. The avocado trees have foliage throughout the year, but during the spring many of the old leaves drop before the new leaves have fully opened. During this period, significant increases of *O. punicae* rarely occur. Residual populations remain on old leaves, and the new leaves are not readily colonized until they become quite hardened and have a dark green color (usually in early summer). From this time onward, a rapid surge of *O. punicae* may occur, reach a peak, and again decline to low numbers. After the leaves have matured, they apparently remain favorable throughout the summer and fall, or until they become bronzed from mite feeding.

If not controlled by other factors, the population ultimately becomes self-lim-

iting. The bronzed areas caused by the feeding of the mites are not favorable for further feeding and reproduction. This phenomenon has long been recognized (Henderson and Holloway, 1942; Kuenen, 1949; Fleschner *et al.*, 1955). As a large percentage of the total leaf area of the tree becomes bronzed, intraspecific competition must become severe; the population levels off and eventually declines.

It is noteworthy that when this apparent self-limitation occurred, and natural enemies were late in building up (Encinitas, 1963; Fallbrook, 1963, 1964; Carpinteria, trees 2, 3, 4, 1963), the populations remained at high levels for several weeks. However, when the population declines were attributed mainly to natural enemies (Fallbrook, Carpinteria, and Santa Paula, 1961; Encinitas, 1962; Morro Hills, 1964; Carpinteria, tree 1, 1963), the trends showed a single peak followed almost immediately by a rapid decline, rather than a prolonged leveling-off period. Thus, the shapes of the population curves where intraspecific competition was considered the main limiting factor were often different from those where predators were considered to be the controlling factor.

It is possible that leaf bronzing may become a factor in reducing the reproductive potential of *O. punicae* considerably before a high percentage of the total leaf surface of the trees is damaged. This may be true, at least in localized areas, of a tree where some leaves are heavily infested, but the tree in general still has only low populations. Perhaps even a slight reduction in the reproductive rate of the prey may allow the predators to "catch up" and bring the population under control before extensive damage occurs. Therefore, in many cases where the predators overtake the *O. punicae* population, the reproductive rate of the latter may already have become somewhat reduced as a result of intraspecific competition.

Fig. 15. Counts of *Stethorus picipes* at various levels of *Oligonychus punicae* in cases where the mites were adequately controlled (circles) and in cases where mites were not controlled before heavy leaf damage resulted (triangles). Based on periodic population sample data from various orchards during the increase phase of the spider mite population fluctuations. Black circles represent data from the Fallbrook orchard in 1961, when predaceous mites increased rapidly in response to the build-up of *O. punicae*. Open circles represent instances where predaceous mites were not numerous enough to be considered a major mortality factor. Regression lines suggest theoretical densities of *Stethorus* required at given densities of spider mites for adequate control to result.

This statement does not detract from the importance of predation, however, since it was clear to the authors that when predators were late in building up or did not build up at all, the populations of spider mites remained at a high level for several weeks, and often caused partial defoliation of the trees. The following statement by Huffaker (1958, p. 377) seems especially applicable to the interaction between *Oligonychus punicae* and *Stethorus*: "Significantly, in the presence of an effective predator, overpopulation by the plant feeding form in one arena is to a marked degree an assurance against such overpopulation in other arenas."

Stethorus picipes must be considered

the key predator in the environment, since it is capable of suppressing relatively high populations of *O. punicae*, sometimes in the near absence of other predator species. Without this predator, it appears that the incidence of effective control of *O. punicae* by natural enemies may be much lower. In every case where heavy bronzing or defoliation occurred, *Stethorus* was either slow in building up or did not build up at all. However, when *Stethorus* showed a marked increase before *O. punicae* reached high levels, the mites were controlled before severe damage occurred.

This relationship is illustrated in figure 15, which shows relative densities of *Stethorus* plotted against the

corresponding densities of *O. punicae* in cases where the mites were controlled before severe leaf damage occurred (circles) and in cases where they were not adequately controlled (triangles). The points shown are based on population sample data from the various orchards during the increase phase of the mite cycles. Although there are insufficient data to demonstrate a precise linear relationship, a general trend is evident. When the mites were not controlled, the numbers of *Stethorus* were low, even at high prey densities. On the other hand, where adequate control occurred, there was a definite increase of *Stethorus* with increase in the density of prey.

It is of interest that *Stethorus* reached higher densities at comparable densities of prey when *Amblyseius hibisci* was not numerous (open circles in fig. 15) than it did when *A. hibisci* also built up rapidly in response to the increase of spider mites (Fallbrook, 1961; black circles). This appeared to hold true also where *A. limonicus* was abundant. The data suggest that lower numbers of *Stethorus* are necessary to suppress the population when phytoseiids are contributing significantly to the mortality of the prey, but when predation pressure from other species is low, *Stethorus* compensates by increasing to higher numbers. Examples of the compensation principle in reference to natural enemies are given by Solomon (1957).

In examining figure 15, it appears possible that in some cases, based on the level of *Stethorus* at certain mite densities, short-term predictions can be made on whether or not the mites will cause severe leaf damage, or will be controlled before this point is reached. For example, if the population of *O. punicae* is approaching a level of 300 adult females per 10 leaves at a population index of only 10 or 15 *Stethorus*, the mites may be expected to keep on increasing to a level where they can cause

considerable leaf damage unless checked by other factors, such as extreme heat or high levels of *A. limonicus*. Conversely, if *O. punicae* is approaching a level of 200 with a corresponding *Stethorus* index of 30 or 40, this may suggest a favorable ratio and adequate control of the mites. Further work is needed to test the reliability of predictions made on this basis.

It is apparent that there are important factors, in addition to the availability of mite prey, which affect the abundance of *Stethorus* in an orchard. If these factors can be determined, it will probably be possible to utilize this predator more efficiently.

Some of the highest observed densities of *Stethorus* have developed where predators were not able to overtake *O. punicae* in time to prevent damage (e.g., Fallbrook, 1963). However, these were cases where *Stethorus* did not begin to increase rapidly until after the mites reached a high peak and had started to level off as a result of intraspecific competition. It is therefore evident that timing is an extremely critical factor.

It has long been recognized that the species of *Stethorus* require relatively high densities of prey for reproduction (Clancy and Pollard, 1952; Fleschner, 1958; Putman, 1955; Putman and Herne, 1958). The lowest mite density at which *S. picipes* was observed to begin reproducing rapidly was somewhat below 100 adult females per 10 leaves at the Morro Hills orchard in 1964 (fig. 7). Both in the latter and in the Santa Paula orchard in 1961, the predator was apparently able to overtake the mite population before it reached 200 adult females (or 500 total mites) per 10 leaves. Sometimes, the upward trend was not reversed until it reached an average of 400 to 500 adult females, but this was still considered adequate control, since the number of spider mites remained at this high level for only a

few days.⁵ By some standards, this may be considered an intolerably high density of mites. With the six-spotted mite, for example, a density as low as 25 to 30 mites per leaf can cause defoliation and killing of twigs (Fleschner *et al.*, 1955). Thus, it is evident that with certain species of mites on certain crops, the "high-density" control exerted by *Stethorus* may be inadequate to protect the crop.

Generally speaking, the authors concluded that phytoseiid mites would have to be rated second to *S. picipes* in importance, though in some specific cases where the latter did not build up, phytoseiids were obviously the most important. *A. limonicus* definitely appeared to be a more effective predator than *A. hibisci*. The field data reported here support the conclusions of McMurtry and Scriven (1965), based on laboratory data, that *A. limonicus* possessed more desirable characteristics as an effective predator than *A. hibisci*. Population data strongly indicated that sometimes *A. limonicus* was able to suppress *O. punicae* in the virtual absence of other predators, but the former did not show indications of overtaking the population of prey until the latter reached high densities (400 to 500 adult females per 10 leaves). Some workers have suggested that phytoseiids are effective at low, but not at high, densities of prey (Collyer, 1958; Lord *et al.*, 1958). It appeared that at Encinitas in 1962, and Carpinteria in 1963, *A. limonicus* had a profound impact on *O. punicae* at high densities, and that a fairly high density of prey was required before a marked numerical response occurred. Unfortunately, the limited geographical distribution of *A. limonicus* reduces its over-all importance as a predator of *O. punicae*. Its relative importance in controlling the six-spotted mite must be much greater, since this

tetranychid is also confined mainly to coastal areas. Fleschner *et al.* (1955) demonstrated conclusively that phytoseiids (composed mainly of *A. limonicus* in their experiment) maintained six-spotted mites at low levels.

An interesting difference observed between the two phytoseiid species was that *Amblyseius limonicus* did not show large numerical increases during the flowering period in the spring, as did *A. hibisci*. It is possible that the former does not feed on pollen in the field as readily as in the laboratory (McMurtry and Scriven, 1965), or possibly that it is not so efficient as *A. hibisci* in perceiving and utilizing pollen present only in small quantities.

Amblyseius hibisci has obvious limitations as an effective predator of *Oligonychus punicae*. However, strong indications were noted that in one instance (Vista, 1962) this species was able to maintain control of the spider mites at a relatively low level. It is not entirely clear why it should appear effective in one case and not in others, although in this orchard of the Fuerte variety, certain conditions differed from the other plots: (1) The trees were completely grown together, creating shadier, more humid conditions, which might have been more favorable to the phytoseiids. (2) There was an unusually quick response of *A. hibisci* to increasing prey densities in 1962. A possible significant factor affecting this response was that in the Vista orchard in 1962, there were higher numbers of mealybugs than are usually observed in avocado orchards, and drops of honeydew could be found on many leaves. McMurtry and Scriven (1964) showed that *A. hibisci* reproduced more rapidly on mite prey in the presence of mealybug honeydew than without honeydew. It is possible, therefore, that an abundance of supplemental food in the form of honeydew might

⁵ It is important to point out that avocado leaves are relatively large. McMurtry and Johnson (1965) estimated that leaves of the Hass variety collected at the Santa Paula orchard averaged 15 square inches.

have contributed to a numerical increase at lower densities of mite prey than usual. (3) *O. punicae* on the Fuerte variety was seldom observed to build up to numbers as high as on Hass trees. It is possible that it failed to reach the high reproductive potential attained on the Hass and Wurtz varieties, and that the predator was better able to overtake the prey.

Normally, however, *A. hibisci* does not appear to be capable of maintaining control of *O. punicae*, at least not by itself. It is probable that it usually causes the highest percentage of mortality in *O. punicae* when the latter is still at low densities in the spring (at which time *A. hibisci* reaches high numbers from pollen feeding), and again during the decline phase of the tetranychid population cycle, when the predator again approaches a density comparable to that of the prey or even greater. However, except for the case mentioned above, it usually does not seem to be capable of overtaking a rapidly increasing prey population because it simply does not show a sufficiently quick numerical response.

There are several factors which can conceivably limit the effectiveness of *A. hibisci* and tend to prevent it from responding quickly to increased numbers of prey. This species is not readily able to move through the webbing produced by *O. punicae*; therefore, even though it is very numerous and searching on virtually every leaf in the spring, it may contact only a few of the spider mites, which are well protected beneath a layer of webbing. Although it is distributed over every type of leaf which the prey inhabits, individuals do not tend to congregate on infested leaves or in infested areas of a tree (the Vista orchard appeared to be an exception), or lay more eggs on infested leaves. The latter circumstance would seemingly be a prerequisite for density-dependent action. The inherent failure of *A. hibisci* to show this habit may be due to a lack

of preference for mites, so that it may fail to consume large numbers of them until the trees become quite heavily infested.

A. hibisci does not reproduce very rapidly on mites alone (McMurtry and Scriven, 1964), and is much more difficult to rear in the laboratory on mites than on pollen. Greenhouse studies with small trees have been consistent with the field studies here reported, in that a slow response to increasing densities of *O. punicae* was observed in both cases (McMurtry and Scriven, 1966).

The fact that *A. hibisci* often shows a temporary decrease in numbers rather than an increase in early or midsummer when *O. punicae* begins to display a marked increase, possibly can be partly associated with weather conditions. As warm temperatures become prevalent (usually in early July in the intermediate climatic areas), avocado pollen is no longer available, and mite prey, although starting to increase in density, is usually not yet widely distributed. The warm weather will reduce the amount of time that the predator can survive without food, which may account for a decline in the phytoseiid population. An earlier experiment showed that populations declined during a period of hot weather, even when abundant pollen was artificially added to caged limbs at weekly intervals (McMurtry and Johnson, 1965).

Chant (1959) and Putman and Herne (1964) mentioned winter mortality as a factor limiting the effectiveness of phytoseiids on apple in England and peach in Canada, respectively. On the other hand, Collyer (1964) was of the opinion that winter mortality is inherent in the species and is not a critical factor. Under the conditions of the present study, winter mortality caused by cold weather was of no consequence. Although numbers often decreased during the winter, this was probably brought about by scarcity of food, since sometimes both *A. hibisci* and *A. limon-*

icus remained through the winter in relatively large numbers if late-season populations of *O. punicae* were present. However, when there was little prey or other food available late in the season, usually only a low population of phytoseiids was noted at the beginning of the following spring. Both species of phytoseiids remained active on the avocado leaves during the entire winter, and showed no tendency to hibernate.

None of the other species of predators encountered in this study appeared to be of great importance. They often appeared to inflict their highest percentage of mortality early in the season, when densities of *O. punicae* were still low, but usually failed to show a marked numerical response. The studies on individual terminals revealed that nearly all species observed during heavy infestations were also present early, when only an occasional mite-infested leaf could be found. These individuals could be considered "transients," since they came to a tree, sometimes left a few progeny, but did not establish permanent colonies until the infestation became heavy.

The results of this study suggest several possible avenues of approach in attempting to reduce the incidence of heavy infestations of *O. punicae*. There is little doubt that *Stethorus picipes* can be extremely effective under some conditions. Therefore, finding ways of encouraging it to build up rapidly is a logical possibility, although extensive ecological studies will be necessary to proceed intelligently with such

an approach. It is especially important to determine whether rapid build-ups of *Stethorus* (sufficiently rapid to overtake the mite population) are brought about largely by immigration of large numbers of adults from areas outside the orchard, or whether such build-ups can occur merely from reproduction of individuals which have been present in the orchard. If the former applies, the degree of control exerted can be greatly influenced by factors affecting migration of adults from other areas or from other mite-infested plants. If the latter applies, it will logically suggest that the failure of the predators to increase adequately has been the result of unfavorable conditions within the orchard.

In an attempt to improve the degree of control by phytoseiids, one possibility for investigation could be to supply a supplemental food (e.g., carbohydrate or protein) with the intent of preventing the decline of *A. hibisci* which usually occurs in early summer when the pollen supply is depleted and mite prey is not yet abundant. This could also be beneficial to *A. limonicus* or to some of the insect predators. Possibly more promising would be the establishment in the environment of new species more effective than *A. hibisci*. As McMurtry and Scriven (1965) pointed out, the establishment of a species adapted to the intermediate climatic areas which is as effective as *A. limonicus* would be a significant addition to the predator complex.

SUMMARY

The population dynamics of the avocado brown mite, *Oligonychus punicae* (Hirst), and its natural enemies was studied over a four-year period in six avocado orchards located in two different climatic areas in southern California. Populations were sampled at one- to two-week intervals. A special study was conducted one season in one of the

orchards, observing the populations twice weekly on individual terminal shoots which became infested early in the season.

A single annual major peak of abundance of *O. punicae* occurred, with considerable variation in magnitude, ranging from 4 to 84 adult females per leaf. The typical seasonal trend was an in-

crease beginning in early summer with a peak in late summer, followed by an abrupt decline. Occasionally, the increase did not start until late summer, with the peak being delayed until fall or early winter. Abrupt declines from peak numbers were nearly always associated with biotic factors; either predation, intraspecific competition, or a combination of both. Without effective predation, the spider mites usually remained at peak densities for several weeks before declining. However, when the declines were attributed mainly to predation, populations remained at or near their peak for only a few days.

From the total of sixteen grove-years of study, there were two cases in which *O. punicae* caused considerable defoliation, two of severe leaf bronzing but little or no defoliation, and twelve of medium to light bronzing.

The most abundant natural enemies were *Stethorus picipes* Casey, *Amblyseius hibisci* (Chant), and *A. limonicus* Garman and McGregor. *S. picipes* was considered the key predator. When this species showed a marked numerical response to increases of *O. punicae* while the latter was still at low to medium densities (10 to 20 adult females per leaf), mite control resulted before severe leaf bronzing ensued. Conversely, when severe bronzing occurred, *Stethorus* was either slow to increase or did not increase at all. The data indicated the possibility of making short-term predictions on whether or not *O. punicae* would cause severe leaf damage, based on the abundance of *Stethorus* at given mite densities.

Phytoseiid mites were rated second in importance as predators. *A. hibisci* usually had two seasonal peaks of abundance: one in the spring, correlated with the presence of pollen during the blossoming period; and another in the summer or fall, correlated with the presence of *O. punicae*. In one instance, *A. hibisci* showed unusually quick numerical response to increases of prey,

and apparently maintained control of the spider mites throughout the season. Normally, this predator failed to respond soon enough to overtake an increasing prey population, although data indicated that it caused a high percentage of mortality after the prey had reached its peak.

Some factors possibly limiting the effectiveness of *A. hibisci* were investigated. The phytoseiid had a relatively low reproductive capacity when feeding on mites. The rate of oviposition was considerably lower than that of *O. punicae*, except when the latter was confined on immature leaves or those heavily bronzed from previous feeding. *A. hibisci* was found on all types of leaves inhabited by the prey, but the two species exhibited different types of distribution. That of *A. hibisci* was more random, since at comparable densities it was found on a considerably larger percentage of leaves than was *O. punicae*. This predator usually did not show any tendency to congregate, or lay more eggs, on leaves or parts of the tree most heavily infested with the prey. This was a probable reason why the predator failed to show marked density-dependent action. Colonies of *O. punicae* developing along the midribs of slightly up-turned leaves were partially protected from *A. hibisci*, owing to a network of webbing spun by adult female spider mites. Even though the predator often outnumbered the prey early in the season, the prey in well-protected locations apparently increased relatively free from predation.

A. limonicus was found to be a more effective predator of *O. punicae* than *A. hibisci*, confirming conclusions based on laboratory data. This species usually showed a greater numerical response to increases of spider mites, often reaching levels of 15 to 20 per leaf, and suppressed relatively high populations of *O. punicae* in the virtual absence of other predators. The over-all importance of this species was found to be

limited because it occurred only near the ocean.

Observations on terminal shoots infested with *O. punicae* early in the season revealed that most insect predators usually associated mainly with high densities of spider mites were also present at extremely low densities of prey.

These early-arriving predators were considered "transients" because there was no establishment or reproduction in response to increases of prey until much later in the season.

Possibilities of reducing the incidence of heavy infestations of *O. punicae* by the use of predators are discussed.

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