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The Dynamics of Predation of *Stethorus picipes* (Coleoptera: Coccinellidae) and *Typhlodromus floridanus* on the Prey *Oligonychus punicae* (Acarina: Phytoseiidae, Tetranychidae)

Part I. Comparative Life History and Life Table Studies
Part II. Effects of Initial Prey-Predator Ratios and Prey Distribution

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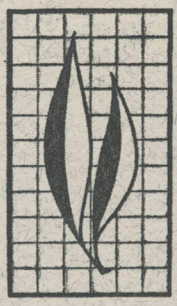

Part I. Comparative Life History and Life Table Studies

Life history studies first were conducted for the prey, the avocado brown mite *Oligonychus punicae* (Hirst), and the predators, the phytoseiid mite *Typhlodromus floridanus* (Muma) and coccinellid *Stethorus picipes* Casey, in an insectary chamber on excised *Persea indica* Spreng leaves. Both mite species developed at a faster mean rate than did *S. picipes.* A life table was constructed for each species from the life history data. Despite a shorter oviposition period than that of either predator, *O. punicae* not only laid more eggs/female per day, but also had a higher mean-age specific fecundity rate. The intrinsic rate of increase, r_m, was highest for *O. punicae* (0.222), followed by *T. floridanus* (0.159) and *S. picipes* (0.121).

In feeding tests, *T. floridanus* females indicated a significant preference for the egg stage of *O. punicae.* In contrast, females of *S. picipes* did not show a significant preference for a particular life stage of *O. punicae.* Assuming no problem whatever in finding prey (an inapplicable assumption for field situations), an arithmetic model was generated from the r_m values, fecundity, and the prey consumption rate of *T. floridanus.* At an initial ratio of 10 prey to 1 predator, this model indicated that *T. floridanus* preying on *O. punicae* eggs could annihilate such a population of *O. punicae* within 13 days.

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The Dynamics of Predation of *Stethorus picipes* (Coleoptera: Coccinellidae) and *Typhlodromus floridanus* on the Prey *Oligonychus punicae* (Acarina: Phytoseiidae, Tetranychidae)[1]

I. Comparative Life History and Life Table Studies

INTRODUCTION

THE FUNDAMENTAL STUDIES reported herein provide a basis for evaluating and comparing the potential for *Typhlodromus floridanus* (Muma) and *Stethorus picipes* Casey to suppress and regulate *Oligonychus punicae* (Hirst) populations.

The avocado brown mite, *O. punicae,* is one of the most ubiquitous arthropod pests infesting avocado in southern California. This tetranychid is restricted in its North American distribution to subtropical southern California (Ebeling, 1959). Pritchard and Baker (1955) suggested that *O. punicae* is tropical Asian in origin and was introduced into California via Central America. Based upon 4 years of field studies on the population dynamics of *O. punicae,* McMurtry and Johnson (1966) reported that peak densities varied considerably in magnitude and time of occurrence from year to year. Peak population infestations usually occurred in late summer, although occasionally the peak was delayed until fall or early winter.

Even though severe bronzing of mature summer foliage can occur under high densities of this spider mite in the field, defoliation and loss of vigor were minimal when compared with the damage induced by the six-spotted mite, *Eotetranychus sexmaculatus* (Riley) and the avocado red mite, *Oligonychus yothersi* (McGregor), (Ebeling, 1959).

The mechanisms responsible for the decline of avocado brown mite populations to low levels in southern California are predation and intraspecific competition, or both acting together (Fleschner, 1958*a,b*; McMurtry, 1970; McMurtry and Johnson, 1966). These researchers found that the most important natural enemies of the avocado brown mite on commercial avocado in California were predaceous species of phytoseiid mites, and the coccinellid, *S. picipes.*

Both field and laboratory work by Fleschner (1958*b*) showed *S. picipes* to be the most effective predator in consistently reducing high spider mite populations in both citrus and avocado ecosystems in southern California south of the Tehachapi Mountains. He attributed the efficiency of this predator to (1) excellent dispersal powers of the adults; (2) high preference for tetranychid mites; (3) functional and numerical responses regulated by their host's density; and (4) relative tolerance to most insecticides then being used. After an extensive ecological study extending over a 4-year period, McMurtry and Johnson (1966) concluded that *S. pici-*

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pes was the key mortality factor effecting abrupt declines of *O. punicae* from peak densities normally occurring sometime between late summer to early winter in avocado agroecosystems. Ebeling (1959) also considered *S. picipes* to be an important predator of plant-feeding mites on both citrus and avocado in California.

Typhlodromus floridanus was originally described by Muma (1955). Of the 10 arthropod predators known to be associated with the six-spotted mite, *T. floridanus* was considered by Muma (1958, 1970, 1971) to be the most important biotic factor regulating its numbers. Our laboratory cultures of *T. floridanus* fed readily on all stages of *Tetranychus pacificus* McGregor, *T. cinnabarinus* (Boisduval) and *O. punicae*. Some field releases were made by the junior author in southern California in an attempt to establish this predator in citrus and avocado groves as a biological control agent for the citrus red mite, *Panonychus citri* (McGregor), and *O. punicae*. Initial recovery attempts indicated that it failed to become established. Because reports have indicated that this predator plays a significant role in control of mites on other subtropical crops, further studies were undertaken to acquire information on its life history, rate of population growth, and predatory behavior.

In addition to comparable studies designed and conducted to measure the predatory behavior and habits of *S. picipes* and *T. floridanus,* further study was done to elucidate the following life history and life table parameters for each species: developmental time, ovipositional rate, longevity, sex ratio, and intrinsic rate of natural increase. Although data obtained from life table studies in the laboratory cannot be applied directly to field populations, they clearly indicate an organism's potential upper limits under ideal situations in the absence of natural enemies and competition, and, in the case of predators, no problem in finding prey.

Using the life table data and predation rates for *T. floridanus,* an arithmetic model was generated similar to that of Laing and Huffaker (1969). Because *S. picipes* did not demonstrate a significant preference for a specific life stage of *O. punicae,* an arithmetic model could not be generated.

MATERIALS AND METHODS

General insectary procedures

All the experiments were conducted in an insectary chamber measuring 1.5 by 2.7 m and 2.1 m high. Light was provided by four Lifeline® Sylvania fluorescent bulbs, 2.5 m in length, programmed to give a 16 h day. The temperature fluctuated from a low of about 22° C, around midnight, to a high of 27° C between 6 and 10 p.m. Relative humidity ranged from 50 to 65 percent.

The stock culture of *Oligonychus punicae* was started with mites obtained from the "Hass" variety of avocado in the vicinity of Fallbrook, California, in the summer of 1970. During the 2-yr period of the study, the stock mites were maintained in the insectary on detached leaves of a noncommercial species of avocado, *Persea indica* Spreng.

The original stock culture of *Typhlodromus floridanus* was obtained from M. H. Muma at the Lake Alfred Citrus Experimental Station, Lake Alfred, Florida. The rearing method study was similar to that described for *Typhlodromus rickeri* Chant by McMurtry and Scriven (1964*a*).

The stock culture of *Stethorus picipes* originated from a population on black nightshade, *Solanum* sp., heavily infested with *Tetranychus evansi* (McGregor), located on the campus of the University of California, Riverside. The adults were maintained in the insectary

in a wooden sleeve cage fitted with a glass top. They were provided with an abundant supply of all stages of *T. pacificus* and *T. cinnabarinus*. The method described by McMurtry *et al.* (1974) was used for confining individual females in oviposition cells for 2 to 3 days, followed by the transfer of each female to a newly prepared cell and the removal of its eggs to a ventilated plastic rearing tube until completion of the imaginal molt.

General experimental procedures

Biology of *Oligonychus punicae.* Sixty adult *O. punicae* females were selected randomly from the stock culture and isolated individually for 8 h in the small cells described above. Then the female and all but one of its eggs were removed from each cell. Observations were made daily at approximately 8 a.m., 4 p.m. and 12 midnight until all individuals reached sexual maturity.

This experiment was conducted on excised *Persea indica* leaves which were dark green, mature, and unbronzed. The leaves were fairly uniform in size, ranging from 5 to 8 cm wide, and were about 13 cm long. They were placed in pairs in stainless steel trays 20 cm square and 4.5 cm deep, with their lower surfaces down on a water-saturated 15 × 15 cm polyurethane pad 1 cm thick. A water-saturated barrier of cellucotton, 1 cm wide, was placed along the periphery of each leaf in order to form a rectangular surface (McMurtry and Scriven, 1964*b*, 1965). This area was then subdivided with Tree Tanglefoot® into 16 smaller cells per leaf, measuring 1 cm^2 each. Tree Tanglefoot®, dispensed from a syringe, provided an excellent barrier because it did not spread outward from its original line of application under the conditions of this study. It remained sticky when wet, was harmless to the leaf, and nontoxic to the mites. Some mortality resulted from mites becoming trapped in the Tanglefoot® barrier; however, this mortality was restricted mainly to senescent and weakened individuals.

Soon after molting from the quiescent deutonymph stage, these virgins were confined with a mature male for a 24 h period. Subsequent to the preoviposition period, each female was observed every morning for egg production and then was transferred to a new individual cell. The sex ratio of each day's progeny was determined for each female after the progeny reached maturity.

Biology of *Typhlodromus floridanus.* By random selection, 50 adult *T. floridanus* females were individually isolated in cells 2 cm^2 in size formed by Tanglefoot® barriers. They were provided with oviposition sites consisting of several strands of cotton placed beneath a 15-mm glass coverslip. After 8 h, the female and all but one egg were removed from each cell. Observations were made daily at 8 h intervals. Soon after maturity, each young female was isolated with one mature male for a period of 24 h. Upon removal of these males, the females were observed daily to establish the length of the preoviposition period, prey egg consumption, and oviposition. *Oligonychus punicae* eggs were provided daily at a rate of 25 per cell. These eggs were obtained by placing approximately 15 mature *O. punicae* females into new cells prepared about 1 day before the subsequent introduction of females and males of *T. floridanus*. All eggs in excess of 25 were removed. This unwieldy method was used because the avocado brown mite eggs adhere so tenaciously to the waxy cuticle of *P. indica* leaves. The procedure was continued daily throughout the adult life of both females and males. The F_1 progeny was isolated in similar cells containing a mixed population of avocado brown mites and were observed every 2 days until they completed development. The sex ratio of these F_1 progeny was then ascertained.

Biology of *Stethorus picipes.* Thirty

adult *S. picipes* females were isolated individually for 12 h in the Plexiglass® cells described above. The females were then removed, as well as all but one egg per cell; however, each of only 23 of the females chosen at random from the stock culture laid at least one viable egg. The eggs were observed daily at approximately 8 h intervals until embryogenesis was completed. Soon thereafter, the newly hatched first instar larvae were transferred to individual cells on excised *P. indica* leaves well infested with all stages of *O. punicae*. The *P. indica* substrate was prepared similarly to that described for the *O. punicae* and *T. floridanus* life history studies. Each leaf was subdivided, however, by use of water-saturated cellucotton strips 0.5 cm wide, into six cells measuring about 1 × 5 cm. This water-saturated barrier had no apparent adverse effects on this cohort of larvae, as all of them emerged as adults. The developing immature beetles were always provided with an abundance of prey by being transferred, when necessary, to cells on another leaf well infested with *O. punicae*.

The newly emerged adults were transferred to individual oviposition cells containing an abundance of food and allowed to "harden" for 24 to 36 h. Of the 23 adults, 12 were females. Each of these was then exposed to a mature male. After 24 h, and when copulation had been observed at least once, the males were removed. Each of the newly mated females was then transferred to an individual cage designed for measuring the parameters outlined above. These cages consisted of acrylic tubing with an inside diameter of 3 cm cut into cylinders 1 cm long. The lower half of each cylinder was immersed in hot Parowax® and transferred immediately onto the upper surface of a *P. indica* leaf. This established an effective seal between the wax and the cuticle of the leaf. All mite refuges were eliminated by dipping a Number 0 brush into the hot wax and then brushing it along the inside interface between the leaf and cage floor. Thus, a feeding surface of about 3 cm^2 was available for *O. punicae* provided as prey for *S. picipes*. The top of the cage consisted of a 0.5 cm thick Plexiglass® plate 4 cm^2. Each unit was vented by a hole 0.5 cm in diameter cut into the middle of the lid. This opening was covered by a 100-mesh stainless steel screen. The top of each cage was carefully ground down using 200-grain garnet sandpaper to insure a mite-tight fit between this surface and the Plexiglass® lid.

Every 24 h, a new set of cages was prepared for the surviving female beetles. Just prior to the transfer of the females, 75 adult female *O. punicae* were placed in each cell. As the female spider mites laid some eggs, an undetermined amount of additional food was thus available to the predators. However, the prey eggs consumed probably represented only a minute proportion of the total food intake of the predators. This transferring procedure was repeated daily for each female in the cohort until she began ovipositing nonviable, shrivelled eggs. These individuals were then transferred to 40-dram plastic vials fitted with a plastic mesh lid and periodically provided with sections of *P. indica* leaves infested with all stages of *O. punicae* until they died.

By making daily observations of a cohort of *S. picipes* females, biological parameters of preoviposition period, daily prey consumption, daily oviposition, progeny sex ratio, adult female longevity, and postoviposition period were determined.

Life table analysis

The life table model, which was initially applied to human populations by Lotka (1925, 1945), summarizes the survival and mortality of a population according to age. This model combines both fecundity and survivorship data and is used to predict the rate of change

in the size of a population on a per individual basis. This intrinsic rate of natural increase, denoted by r_m, assumes that fecundity and survivorship remain constant, and that environmental conditions remain stable from generation to generation. Also, it seems that migration does not occur and that individuals are born, live and die in that same population (Birch, 1948; Leslie and Park, 1949; Andrewartha and Birch, 1954), and that resources such as food and space are unlimited and mortality of individuals is physiological and not attributable to interspecific competition or to parasites, predators or disease (Birch, 1948; Laing, 1968, 1969*a,b*). The intrinsic rate of natural increase is, therefore, a specific parameter measuring the physiologically possible rate of increase of a population under specific physical environmental conditions, with all other conditions ideal. This model also assumes that there are enough males within the population to adequately fertilize all the females. The intrinsic rate of natural increase is based only upon the production of female progeny, not total progeny. Therefore, organisms capable of producing large numbers of female offspring, and this early in their life cycles, and coupled with short developmental times, will possess a larger r_m. An r_m of zero implies that the population is neither increasing nor decreasing. If a population increases under these very unrealistic assumptions, it will grow at a steady instantaneous rate (per individual) until it eventually reaches a stable age distribution (Lotka, 1925; Birch, 1948; Leslie and Park, 1949).

If we assume *Oligonychus punicae* to breed the year round in a constant environment, with overlapping generations, and without repeating cycles of uneven age distribution among its progeny and given the unreal assumption of the ideal in the above conditions, the rate at which its population would increase per unit of time would obey the instantaneous exponential growth equation, $\frac{dN}{dt} = r_m N$ (Birch, 1948; Leslie and Park, 1949; Mertz, 1970). The assumed conditions were met by the design of the experiment and the model was reasonably represented by *O. punicae* performance. In nature, however, the conditions for a stable age distribution are probably never realized, nor are various other assumptions of the ideal in favorability. In the field, *O. punicae* populations, starting from a female cohort of the same age and under favorable environmental conditions, will quickly produce successive generations which overlap. Repeating cycles of age distribution are possible with individuals of all life stages present in the population at the same time. The intrinsic rate of natural increase, r_m, may be calculated from the formula derived by Birch (1948).

$$\sum_{x=o}^{\infty} e^{-r_m x} l_x m_x = 1 \qquad 1$$

e is the base of natural logarithms (2.718)

x is the age of individuals in days

$l_{(x)}$ is the survival rate or probability at birth that an individual will survive to age x or longer

$m_{(x)}$ is the age-specific fecundity rate or average number of female offspring born to a female animal of age x during the interval $(x - \frac{1}{2})$ to $(x + \frac{1}{2})$.

The sum of the $m_{(x)}$ column is the gross reproductive rate and represents the rate at which the population would increase per individual per generation if none of the females died before the end of the reproductive period (Leslie and Park, 1949). The sum of the $l_{(x)}m_{(x)}$ column is R_o, called the net reproductive rate, or the replacement rate. It represents the number of female de-

scendants that an average female leaves in one generation. The intrinsic rate of natural increase of this population on a per individual basis can be derived by substituting trial values of r_m into Formula 1 until the sum is approximately 1.0. A Fortran IV program written after Birch's (1948) paper, was utilized, however, to derive both r_m and the net reproductive rate. The mean generation time (T) represents the time from birth to weighted mean reproductive age in the adult female (Messenger, 1964) and can be calculated from the formula,

$$T = \frac{log_e R_o}{r_m} \qquad (2)$$

This formula was derived from the integrated form of the exponential growth equation, $N_t = N_o e^{rmt}$. The studies of Cardona and Oatman (1975) clearly emphasized the fact that the magnitude of r_m varies only as the natural logarithm of R_o. Differences among values of r_m are mainly due, therefore, to differences among developmental times and not to higher reproductive capacities. The shorter the developmental time, the larger the value of r_m. The inverse relationship is also applicable for r_m and the mean generation time (Formula 2).

RESULTS

Life histories

Oligonychus punicae. The contents of the egg of *O. punicae* were milky white when the egg was first deposited but became progressively more granular and opaquely yellow-amber as embryogenesis proceeded. Pigmented paired eye spots became visible just before hatching. The egg bears a stalk at its apex and is globose in shape. The flattened base of the egg adheres tenaciously to the leaf surface. Eggs were also commonly found on the upper surface of the webbing as the leaf began to bronze with an increase in density of the mite population. Duration of the incubation period under these conditions averaged 4.65 days for the females and 4.87 days for the males (Table 1). McMurtry and Johnson (1966) reported an incubation time for this species of about 8 days at 22±2° C.

The larvae were amber-colored at emergence. Their opisthosoma possessed numerous orange-pigmented spots which were most numerous along the periphery of the dorsum. Upon feeding, the opisthosoma quickly became progressively darker green and granular appearing. Also, the larvae became significantly larger in size as they neared the quiescent period. Average length of the larval stage of the female was 1.04 days and for the male 0.87 day (Table 1). A quiescent period lasting 0.75 day and 0.80 day was observed for the females and males, respectively (Table 1). Development of the fourth pair of legs occurred during this stage. In the initial phase of each quiescent stage, the integument took on a very shiny sheen. Just before emergence, the original integument became dull white as the newly developed stage matured beneath it. Also, two pairs of red-pigmented eye spots were conspicuous in all active states of *O. punicae.*

The eight-legged protonymphs were pale yellow upon emerging through a dorsal split in the old larval skin. As feeding resumed, this stage assumed a light green body coloration. The females averaged only 0.73 day in this stage and 0.57 day in a quiescent state. The males spent 0.66 and 0.47 day in the protonymph and quiescent stages, respectively (Table 1).

As noted by Laing (1969*a*) for *Tetranychus urticae* Koch, sex could be

TABLE 1

DEVELOPMENTAL TIMES OF THE IMMATURE STAGES OF *OLIGONYCHUS PUNICAE* AT 22–26° C

Sex	No. obs.	Number of days			
		Max.	Min.	$\bar{X}$	SD
			Egg		
Female	50	5.00	3.6	4.65	0.29
Male	7	5.30	4.6	4.87	0.28
			Larva		
Female	50	1.50	0.66	1.04	0.25
Male	7	1.20	0.66	0.87	0.32
			Quiescent larva		
Female	50	1.00	0.33	0.75	0.19
Male	7	1.33	0.66	0.80	0.26
			Protonymph		
Female	50	1.00	0.33	0.73	0.24
Male	7	1.00	0.33	0.66	0.20
			Quiescent protonymph		
Female	50	0.66	0.33	0.57	0.15
Male	7	0.66	0.33	0.47	0.18
			Deutonymph		
Female	50	1.33	0.83	1.05	0.19
Male	7	1.00	0.83	0.90	0.09
			Quiescent deutonymph		
Female	50	1.33	0.66	0.94	0.19
Male	7	1.00	0.83	0.88	0.08
			All stages combined		
Female	50	11.82	7.74	9.73	
Male	7	11.49	8.24	9.45	

determined after the deutonymphs had fed and became a deep green color. The precursor of the adult female developed a robustly rounded opisthosoma and a larger body size, whereas the body of the eventual male was smaller and more tapered in outline. Duration of this stage averaged 1.05 days for the females and 0.90 day for the males. The subsequent quiescent stage lasted 0.94 and 0.88 day for the females and males, respectively (Table 1).

Based upon observations of 50 females and 7 males, the average total developmental time for oviposition to adulthood was slightly shorter for the males (9.45 days) than for the females (9.73 days).

The final molt, like the preceding ones, resulted in a transverse splitting of the cuticle of the idiosoma behind the second pair of legs. The newly emerged adults then freed themselves by backing out of their old integument. The mating process and the tendency of the adult males to remain in the vicinity of a quiescent female deutonymph has been observed in many tetranychid species (Ewing, 1914; Boudreaux, 1963). Penman and Cone (1972) have demonstrated that the behavior of adult male *T. urticae* was further influenced by female deutonymph web. The process of sex determination, as commonly found in the Tetranychinae, is arrhenotokus (Boudreaux, 1963; Huffaker *et al.*, 1969).

The preovipositional periods for unmated and mated females were not significantly different. The average for 49 combined was 1.26 days (Table 2), compared to a 2-day period reported by McMurtry and Johnson (1966). The average time required to complete one generation, from egg to egg, was about 11 days for the females. Ebeling (1959)

TABLE 2
DURATION OF PREOVIPOSITIONAL AND OVIPOSITIONAL PERIODS OF *OLIGONYCHUS PUNICAE* AT 22–26° C

Period	No. obs.	Number of days			
		Max.	Min.	$\bar{X}$	SD
Preoviposition	49	2.00	0.66	1.26	0.27
Oviposition	49	20.00	3.00	13.28	4.37

TABLE 3
NUMBER OF EGGS LAID BY 49 *OLIGONYCHUS PUNICAE* AT 22–26° C

Parameter	Number of eggs			
	Max.	Min.	$\bar{X}$	SD
Total no. eggs/female	96.00	14.00	59.14	
No./female/day	5.60	2.80	4.35	0.70

and McMurtry and Johnson (1966) found that *O. punicae* can complete one generation in 7 days at 25° C, and in 15 to 16 days at 22±2° C. At about 33° C, mortality occurred in all stages (McGregor, 1941; Ebeling, 1959).

Body coloration of newly emerged young males and females became more intense, especially in the area of the hysterosoma, as they resumed feeding. As the cuticle hardened, the gnathosoma, the anterior area of the propodosoma, the tapered tip of the male opisthosoma, the first pair of legs, and, to some degree, the second pair, all became orange-red. The rest of the body remained off-white. Ovipositing females developed a whitish, oblong-shaped area occupying one-third to one-half of the dark purple or blackish-brown hysterosoma. Senescent adults were easily recognized by the marked loss of sheen and the wrinkling and shrivelling of the integument.

The average ovipositional period for 49 *O. punicae* females was 13.28 days, with a range of 3 to 20 days (Table 2). These females averaged 59.14 eggs during this period (Table 3). The overall egg deposition rate averaged 4.35 eggs/female per day (Table 3). An oviposition rate of 3.40 eggs/female per day was reported by McMurtry and Johnson (1966) for field-collected females reared in the laboratory on matured and undamaged avocado leaves for a 7-day period. Comparative studies by McMurtry (1970) on greenhouse-reared female *O. punicae* placed on *P. indica* leaves revealed oviposition rates averaging 2.02 and 4.67 eggs/female per day on bronzed and unbronzed leaves, respectively.

The higher mean ovipositional rate observed in this study, compared with that reported by McMurtry and Johnson (1966), may reflect temperature differences. Of the 49 females used, all but two were fertilized when confined with an individual male for 24 hours. These unmated females produced only male offspring. The mean numbers of female and male progeny produced per inseminated female were 44.85 and 14.27, respectively. Therefore, the sex ratio observed for inseminated females under these conditions approximated 3.1 females to 1 male. This compares to the sex ratios of 2.7:1 and 3.2:1 found by McMurtry (1970) on bronzed and unbronzed avocado foliage, respectively. Because of the arrhenotokus mechanism of sex determination in the Tetranychinae and the numerous variables influencing the sex ratio, Boudreaux (1963) cautioned against assuming that a normal sex ratio exists in nature.

Typhlodromus floridanus. The eggs of *T. floridanus* are slightly tapered from one pole to the other. When observed microscopically, they are glossy

TABLE 4
DEVELOPMENTAL TIMES FOR THE IMMATURE STAGES OF *TYPHLODROMUS FLORIDANUS* AT 22–26° C

Sex	No. obs.	Number of days			
		Max.	Min.	$\bar{X}$	SD
			Egg		
Female	16	3.66	1.50	2.90	0.18
Male	18	3.33	1.50	2.66	0.19
			Larva		
Female	16	1.66	1.00	1.27	0.18
Male	17	2.00	0.66	1.21	0.24
			Protonymph		
Female	16	2.66	1.66	2.20	0.13
Male	17	4.33	1.00	2.59	0.30
			Deutonymph		
Female	16	2.33	0.66	1.98	0.20
Male	17	3.00	1.66	1.94	0.24
			All stages combined		
Female	16	10.11	4.72	8.35	
Male	17	12.66	4.82	8.40	

and transparent when freshly laid. As incubation proceeds, the eggs turn whitish, opaque and granular. The ovipositing females of *T. floridanus* have a strong tendency to aggregate and lay their eggs in clusters on the cotton strands or on webbing within the prey colony. This predator appears to be well adapted in regard to feeding, moving and ovipositing within the highly webbed and aggregated colonies of *O. punicae* (Muma, 1961). Duration of the egg stage was 2.90 days for females and 2.66 days for males (Table 4).

The six-legged translucent-white larvae remained relatively quiet and close to their egg cases or the egg clusters. This stage lasted an average of 1.27 days for females and 1.21 days for males (Table 4). As with the majority of phytoseiids (McMurtry *et al.*, 1970; Croft and Jorgensen, 1969; Knisley and Swift, 1971), the larvae of *T. floridanus* do not feed.

The eight-legged protonymph began feeding on *O. punicae* eggs soon after emerging from the larval exuviae. This stage had no difficulty in penetrating the chorion with its chelicerae. All that remained of the egg after feeding was the transparent chorion. As reported by Laing (1969*b*) for *Metaseiulus occidentalis* (Nesbitt), the protonymph was quiescent for only a few minutes before molting. It was not a completely inactive stage, however, as observed for spider mites, as the protonymphs move if disturbed. The developmental time for protonymphs averaged 2.20 days for females and 2.59 days for males (Table 4), during which time they consumed 9.06 and 9.53 *O. punicae* eggs, respectively (Table 5). Average duration of the female and male deutonymphal stages was 1.98 and 1.94 days, respectively (Table 4), during which time they ate an average of 9.25 and 7.80 prey eggs, respectively (Table 5). Deutonymphs also had a short quiescent period prior to transformation to the adult stage.

Developmental time, from egg to adult, of 16 females averaged 8.35 days, and for 17 males 8.40 days (Table 4). Muma (1970) reported that female and male *T. floridanus* averaged 7.8 and 6.5 days, respectively, to develop from egg to adult at 26.7° C when fed *E. sexmaculatus*.

The transformation of the deutonymph to the adult stage was similar

TABLE 5
EGGS OF *OLIGONYCHUS PUNICAE** CONSUMED DURING DEVELOPMENT OF THE IMMATURE STAGES OF *TYPHLODROMUS FLORIDANUS*

Sex	No. obs.	Number of eggs		
		Max.	Min.	$\bar{X}$
			Larva	
Female	16	0.0	0.0	0.0
Male	18	0.0	0.0	0.0
			Protonymph	
Female	16	20.0	6.0	9.06
Male	17	21.0	5.0	9.53
			Deutonymph	
Female	16	15.0	1.0	9.25
Male	17	12.0	3.0	7.80
			All stages combined	
Female	16	30.0	6.0	18.31
Male	17	32.0	12.0	17.33

* 25 eggs of *O. punicae*/cell/predator/day.

to that described for the metamorphosis of the pre-adult stages. Adult males are markedly smaller, but are more active than the females. As the female feeds and becomes gravid, sexual dimorphism becomes more apparent. Observations on eight females revealed that mating usually took place immediately after the deutonymph molted to an adult. Copulatory time ranged from 42 to 210 min. All of these females mated more than one time. The significance of single versus multiple matings of adult females during their complete lifetime was not ascertained.

The preoviposition period for 13 female *T. floridanus* averaged 3.23 days, during which time they consumed an average of 5.29 *O. punicae* eggs/female per day (Table 6). Laing (1969*b*) also reported a preoviposition period of 3.2 days for *M. occidentalis,* but he observed a consumption rate of about 3.8 *T. urticae* eggs per day. A preoviposition period of 2 to 3 days appears to be common for many species; however, temperature and seasonal variations will affect its duration, as summarized by McMurtry *et al.* (1970).

The laboratory-reared females of *T. floridanus* laid an average of 1.97 eggs/female per day, with a mean total of 41.14 eggs (Table 7) during an oviposition period averaging 22.53 days (Table 6). When given an abundance of prey eggs, these females consumed an average of 12.19 eggs/female per day during the oviposition period and lived for an average of 4.62 days after oviposition ceased (Table 6). Unmated females did not oviposit. The natural mortality of these F_1 progeny during development was essentially negligible. Six F_1 males observed throughout their lifetimes each ate about three *O. punicae* eggs per day.

Muma (1970) reported that laboratory-reared *T. floridanus* females laid from 16 to 45 eggs, and a mean total of 26.2 eggs, during their oviposition pe-

TABLE 6
DURATION OF VARIOUS PERIODS AND NUMBER OF PREY EGGS CONSUMED BY ADULT FEMALE *TYPHLODROMUS FLORIDANUS* AT 22–26° C

Period	No. obs.	Duration (days)	Eggs eaten per day
Preoviposition	13	3.23±0.59	5.29±1.42
Oviposition	13	22.53±8.40	12.19±1.28
Postoviposition	8	4.62±1.76	2.72±0.76

TABLE 7

NUMBER OF EGGS LAID BY *TYPHLODROMUS FLORIDANUS* AT 22–26° C

No. of females, 13	Number of eggs			
	Max.	Min.	$\bar{X}$	SD
Total no. eggs/female	52.00	7.00	41.15	
No./female/day	2.66	1.62	1.97	0.26

riod of 1 to 2 weeks. Detailed studies by Sandness and McMurtry (1970), designed to describe the functional response curve for *T. floridanus,* revealed an ovipositional rate slightly above two eggs/female per day on arenas containing five to 300 female *O. punicae* each. Laing (1969*b*) reported that *M. occitentalis* ate 8.5 *T. urticae* eggs per day during their ovipositional period. Prey consumption by *Phytoseiulus persimilis* Athias-Henriot averaged 14.3 and 34.0 *T. urticae* eggs per day in studies by Laing (1968) and Bravenboer and Dosse (1962), respectively.

The sex ratio of 529 progeny produced by the 13 females used for the life table studies was 1.8 females to one male. This ratio was similar to those reported for *Typhlodromus pyri* (= *T. tiliae*) (Chant, 1959), *T. rickeri* (McMurtry and Scriven, 1964*a*), and *T. mcgregori* (Croft and Jorgensen, 1969).

Stethorus picipes. The newly laid egg of *S. picipes* was creamish-white, oval in shape, and about 0.30 to 0.35 mm in length. As embryogenesis proceeded, the egg gradually became pinkish-white, the pink appearing after about the second day of incubation. Two red eye spots at the animal pole became evident by the third day. Soon thereafter, the egg took on an increasingly grey coloration until hatching occurred. The numerous pits observed on the surface of the chorion appeared to elongate and interconnect to form a mosaic pattern prior to hatching. The eggs were laid at random and were commonly attached to the side of the plastic ovipositional cell. Apparently, the chorion possesses an adhesive-like substance which anchors the egg to any substrate with which it comes in contact. The incubation period averaged 3.85 days for the females and 4.00 days for the males (Table 8).

Stethorus picipes has four larval instars, the last including a prepupal period of about one day. Morphologically, all four instars appeared similar, except for a progressive increase in size and a gradual darkening of the integument from a light pinkish-brown to a very dark grey. Newcomer and Yothers (1929) described the larval stages as having a pair of irregular black-pigmented spots on the dorsal surface of each thoracic segment. Long setae cover the head, thorax, and abdomen. In addition, the nine segments of the abdomen, except the last, possess six whorls of setae emanating from a raised tubercle-like base.

Observations on feeding behavior within the ovipositional cells and on the *P. indica* leaf surfaces revealed that little difficulty was experienced by any of the stages of *S. picipes* in penetrating the webbing of *O. punicae.* The larvae fed by sucking out the fluid contents of the eggs and various active stages of *O. punicae,* and subsequently regurgitating and sucking these contents without ingestion until completely liquified. This feeding process was first described by Newcomer and Yothers (1929) for *S. picipes* and later was reported by Cottier (1934), Fleschner (1950), Collyer (1953), Robinson (1953), Putman (1955) and Kaylani (1967).

Average developmental time for the larval instars of *S. picipes* was 9.5 and 9.55 days for female and male, respectively (Table 8). About 1 day before pupation, the larva enters the quiescent prepupal period. It attaches itself to the

TABLE 8
DEVELOPMENTAL TIMES OF THE IMMATURE STAGES OF *STETHORUS PICIPES* AT 22–26° C

Sex	No. obs.	Number of days			
		Max.	Min.	$\bar{X}$	SD
			Egg		
Female	14	4.00	2.00	3.85	0.52
Male	9	4.00	4.00	4.00	0.00
			1st instar		
Female	14	4.67	2.00	2.59	0.69
Male	9	3.00	2.00	2.53	0.53
			2nd instar		
Female	14	3.00	0.33	1.66	0.56
Male	9	2.00	1.00	1.66	0.42
			3rd instar		
Female	14	2.00	1.00	1.65	0.30
Male	9	2.00	1.16	1.53	0.24
			4th instar		
Female	14	3.67	1.50	2.28	0.64
Male	9	3.50	2.00	2.74	0.45
			Pre-pupa		
Female	14	2.00	0.50	0.97	0.38
Male	9	1.50	0.83	1.09	0.22
			Pupa		
Female	14	4.50	3.33	3.83	0.40
Male	9	4.00	3.00	3.66	0.33
			All stages combined		
Female	14	19.00	15.82	16.86*	0.87
Male	9	18.33	16.00	17.24*	0.72

* no significant difference at 5% level ("t" test of difference).

substrate by everting its caudal anal area. The prepupa takes on a yellowish-brown coloration during this period.

Pupal metamorphosis is preceded by the shedding of the fourth instar larval skin and its attachment on the substrate surface near the secreted organ of attachment. Within 12 h, the pupa changes from a yellowish-brown to a dark brown. The dorsal surface of the pupa is covered with moderately long and uniformly shaped setae. The pupal period lasted 3.83 and 3.66 days for the females and males, respectively (Table 8).

The newly formed adult emerges through a dorsal weakening in the head and thoracic region of the pupal skin. The cuticle is yellowish-cream in color until it "hardens" and turns black several hours after emerging. There is little sexual dimorphism. Only by examining the sixth abdominal sternite under at least 20× magnification can the sexes be differentiated. The sixth or terminal sternite of the male is emarginated in the middle of the posterior margin, whereas that of the female is rounded (McMurtry *et al.*, 1974).

A premating period of about 1 day was assumed. This was based on observations of newly emerged females exposed to mature males. Copulation, or the mere interest of the male in the virgin female, did not occur until her cuticle had "hardened." The act of copulation consisted of the male excitedly mounting the back of the female and bending the tip of his abdomen under the tip of hers in order to insert his aedeagus into her ventrally located genital opening. The female either became quiescent, or she continued to walk about with the male still mounted on her back.

The preovipositional period for nine females that copulated 24 to 36 h after pupal emergence averaged 5.6 days,

TABLE 9
DATA FOR SEVEN *STETHORUS PICIPES* (EMERGED ON THE SAME DAY) AND OVIPOSITING VIABLE EGGS AT 22–26° C

Female No.	Days of* oviposition	Total no. eggs† per Female	Average no.‡ laid per day
1	104	353	3.4
2	64	359	5.6
3	61	220	3.6
4	27	60	2.2
5	4	12	3.0
6	95	391	4.1
7	37	151	4.1

* $\bar{X}$ = 56.0 days.
† $\bar{X}$ = 221.0 eggs.
‡ $\bar{X}$ = 3.7 eggs per day.

with a range of about 4.0 to 6.0 days. Putman (1955) found that the duration of this period for *Stethorus punctillum* Wiese was influenced by the age of the female at copulation.

The ovipositional period determined for a cohort of seven females averaged 56 days (Table 9) and ranged from 4 to 104 days. Total number of fertile eggs laid per female and the daily oviposition rate averaged 221 eggs and 3.7 eggs/female per day, respectively. Eleven eggs was the maximum number laid by any one female in 1 day. McMurtry *et al.* (1974) reported a longer ovipositional period (130 days) and higher fecundity (4.33 eggs/female per day) for *S. picipes* when fed an abundance of eggs and larvae of the Pacific spider mite than those observed in this study. Experimental conditions were comparable in both studies. Our beetles were provided with adult *O. punicae,* however, and those of McMurtry *et al.* (1974) were given primarily an abuntance of eggs and larvae. The latter workers also observed marked declines in oviposition when *S. picipes* were fed larger immatures or adults, and they suggested that the artificial conditions of a plastic cell were probably unfavorable for capture and handling of active spider mite stages.

In the larval feeding studies (Table 10) the average number of prey consumed per female during development was 361, with a maximum of 379. Fourth instar larvae averaged nearly a 10-fold increase in prey consumed over that of the first instars. Second instars consumed twice the number of prey consumed by first instars, while third larval instars consumed four times as many. In feeding studies by Fleschner (1950), in which the larvae of *S. picipes* preyed upon adult *Panonychus citri,* a maximum of 190 was consumed by a single fourth instar *Stethorus* and a maximum of 486 was consumed during the entire larval period. Newcomer and Yothers (1929) reported that the larvae of *S. picipes* in Washington State prefer the eggs of *Panonychus ulmi* and that one predator consumed 372 mites and eggs during its developmental period which ranged from 13 to 15 days.

Predation data from the life table studies (Table 11) indicated that during their ovipositional period, *S. picipes* adults are capable of consuming 32 to 44 adult *O. punicae* per day. This rate compares favorably with that summarized by McMurtry *et al.* (1970) for three different species of *Stethorus* females recorded in the literature. The adults were observed to masticate and ingest the chorion and exoskeletons of all stages of their prey. A number of prey killed, however, were only partially consumed.

It is probable that *S. picipes* would complete development on considerably fewer prey. Fleschner (1950) found large differences between maximum consumption of *P. citri* by *S. picipes* larvae

TABLE 10

PREY CONSUMPTION BY THE IMMATURE STAGES OF *STETHORUS PICIPES* AT 22–26° C

Larva no.	1st instar*			2nd instar*			3rd instar*			4th instar†			Total No. of mites eaten
	Days	No. mites eaten	$\bar{X}$	Days	No. mites eaten	$\bar{X}$	Days	No. mites eaten	$\bar{X}$	Days	No. mites eaten	$\bar{X}$	
1	3	34	11.3	2	59	29.5	2	86	43.0	2	198	99.0	377
2	2	21	10.5	2	54	27.0	2	88	44.0	2	212	106.0	375
3	2	18	9.0	2	52	26.0	2	88	44.0	2	175	87.5	333
4	2	24	12.0	2	42	21.0	2	83	41.5	2	216	108.0	365
5	3	36	12.0	2	48	24.0	2	91	45.5	2	196	98.0	371
6	2	19	9.5	2	46	23.0	2	86	43.0	2	218	109.0	369
7	2	24	12.0	2	55	27.5	2	93	46.5	2	200	100.0	372
8	2	17	8.5	2	48	24.0	2	89	44.5	2	171	85.5	325
9	2	24	12.0	2	48	24.0	2	87	43.5	2	182	91.0	341
10	3	36	12.0	2	53	26.5	2	89	44.5	2	201	100.5	379
		$\bar{X} = 10.8$			$\bar{X} = 25.3$			$\bar{X} = 44.0$			$\bar{X} = 98.5$		$\bar{X} = 360.7$

* Each larva given 50 proto-deutonymphs of *O. punicae* per day.
† Each larva given 130 proto-deutonymphs of *O. punicae* per day.

TABLE 11

ADULT FEMALES OF *OLIGONYCHUS PUNICAE* CONSUMED BY OVIPOSITING *STETHORUS PICIPES FEMALES* AT 22–26° C

Female no.	Days obs.	Total no. eaten	Average no. eaten/day
1	108	4652	33.1
2	67	2937	43.8
3	67	2330	34.8
4	33	1098	33.3
5	9	343	38.1
6	101	3295	32.6
7	43	1529	35.6

and the minimum consumption needed to complete development.

Near the end of the ovipositional period, the oviposition rate of these females became very irregular or sporadic, with egg-laying sometimes ceasing and then being resumed. After the respective ovipositional period of viable eggs for each female, however, all females subsequently laid only shrivelled eggs. One female laid shrivelled eggs for 69 days after ovipositing her last viable one. Apparently, the effective ovipositional period for these long-lived females is determined largely by the frequency of mating subsequent to the initial one(s). As these females were individually exposed to males for a single 24 h period, duration of their ovipositional period is probably dependent upon the frequency of copulation, quantity of sperm stored within the spermatheca, and age of the male (Putman, 1955). Kaylani (1967) and Putman (1955) reported similar observations for *Stethorus gilvifrons* Muls. and *S. punctillum,* respectively.

From a total of 1546 progeny produced by seven females, 701 were males and 845 females, giving a sex ratio of 1:1.2.

TABLE 12

LIFE TABLE AND FECUNDITY TABLE FOR 49 *OLIGONYCHUS PUNICAE* AT 22–26° C

Age in days (x)	Survival rate l(x)	Number of offspring (♀)	Fecundity rate m(x)	l(x)m(x)
0–11	1.000	0	0.00	0.00
12	1.000	91	1.86	1.86
13	1.000	158	3.22	3.22
14	1.000	174	3.55	3.55
15	0.980	160	3.33	3.26
16	0.940	161	3.50	3.29
17	0.920	171	3.80	3.49
18	0.900	181	4.11	3.69
19	0.900	169	3.84	3.45
20	0.818	164	4.10	3.35
21	0.736	116	3.22	2.37
22	0.675	137	4.15	2.80
23	0.593	97	3.34	1.99
24	0.573	81	2.89	1.66
25	0.369	71	3.94	1.46
26	0.328	59	3.68	1.22
27	0.287	43	3.07	0.89
28	0.205	29	2.90	0.61
29	0.185	22	2.44	0.46
30	0.124	21	3.50	0.45
31	0.002	5	0.00	0.00

GRR = 64.49 R_o = 43.07

Life table studies

Oligonychus punicae. The intrinsic rate of natural increase for *O. punicae,* under the specified laboratory conditions, was 0.222 per female per day. The mean generation time (T) was 17.10 days. During this time, the net reproductive rate (R_o), or replacement rate, was 43.07 female offspring per female in one generation (Table 12). Caution should be exercised when comparing R_o values for two or more populations (Birch, 1948; Leslie and Park, 1949). Unless the mean generation times for two or more populations are identical, a valid comparison of their respective R_o values cannot be made. Two similar R_o values will not be associated with the same r_m value if their mean generation times are different.

Typhlodromus floridanus. Population equations derived from the basic instantaneous exponential growth formula indicated that the mean generation time for *T. floridanus* was 19.60 days. During this time, and under the given laboratory conditions, a cohort of females will increase by 22.60 times (R_o) (Table 13). The intrinsic rate of natural increase (r_m) of the population/individual female per day was 0.159. Life table studies of two other phytoseiid predators, *M. occidentalis*

TABLE 13

LIFE TABLE AND FECUNDITY TABLE FOR 15 *TYPHLODROMUS FLORIDANUS* AT 22–26° C

Age in days (x)	Survival rate l(x)	Number of offspring (♀)	Fecundity rate m(x)	l(x)m(x)
0–10	1.000	0	0.00	0.00
11	1.000	2	0.13	0.13
12	0.867	12	0.92	0.80
13	0.867	17	1.31	1.14
14	0.867	18	1.38	1.20
15	0.867	19	1.46	1.26
16	0.801	16	1.33	1.06
17	0.735	14	1.27	0.93
18	0.735	15	1.36	0.99
19	0.735	16	1.45	1.06
20	0.735	13	1.18	0.86
21	0.735	11	1.00	0.74
22	0.735	15	1.36	0.99
23	0.735	15	1.36	0.99
24	0.735	12	1.09	0.80
25	0.735	15	1.36	0.99
26	0.735	15	1.36	0.99
27	0.735	15	1.36	0.99
28	0.735	13	1.18	0.86
29	0.735	10	0.91	0.66
30	0.735	10	0.91	0.66
31	0.735	8	0.73	0.54
32	0.735	8	0.73	0.54
33	0.735	9	0.82	0.60
34	0.669	11	1.10	0.74
35	0.669	11	1.10	0.74
36	0.536	10	1.25	0.67
37	0.536	7	0.88	0.47
38	0.536	3	0.38	0.20
39	0.536	0	0.00	0.00
40	0.536	0	0.00	0.00
41	0.470	0	0.00	0.00
42	0.337	0	0.00	0.00
43	0.271	0	0.00	0.00
44	0.205	0	0.00	0.00
45	0.005	0	0.00	0.00

GRR = 30.67 R_o = 22.60

and *P. persimilis,* by Laing (1968, 1969*b*) and Laing and Huffaker (1969), under physical conditions similar to those of this study, produced intrinsic rates of natural increase of 0.183 and 0.219, respectively. Their higher rates, compared to those of *T. floridanus,* were due to the fact that *M. occidentalis* and *P. persimilis* had shorter respective mean generation times, i.e., values of 17.4 and 17.3 days, and larger net reproductive rates, i.e., R_o values of 24.3 and 44.4 in one generation. However, as suggested by Leslie and Park (1949) and demonstrated by Laing and Huffaker (1969), a direct comparison of these various parameters for different species may be misleading, especially when considering natural predator/prey interactions in a changing universe.

Stethorus picipes. Construction of a life table for *S. picipes* followed the procedure described earlier for *O. puni-*

TABLE 14

LIFE TABLE AND FECUNDITY TABLE FOR 7 *STETHORUS PICIPES* AT 22–26° C

Age in days (x)	Survival rate l(x)	Number of offspring (♀)	Fecundity rate m(x)	l(x)m(x)
0–21	1.000	0	0.00	0.00
22	1.000	2	0.29	0.29
23	1.000	16	2.29	2.29
24	1.000	19	2.71	2.71
25	1.000	15	2.14	2.14
26	1.000	13	1.86	1.86
27	1.000	12	1.71	1.71
28	1.000	12	1.71	1.71
29	1.000	17	2.43	2.43
30	1.000	11	1.57	1.57
31	1.000	5	0.71	0.71
32	1.000	8	1.14	1.14
33	1.000	13	1.86	1.86
34	1.000	10	1.43	1.43
35	1.000	8	1.14	1.14
36	1.000	12	1.71	1.71
37	1.000	8	1.14	1.14
38	1.000	8	1.14	1.14
39	1.000	10	1.43	1.43
40	1.000	7	1.00	1.00
41	1.000	11	1.57	1.57
42	1.000	7	1.00	1.00
43	1.000	10	1.43	1.43
44	1.000	10	1.43	1.43
45	1.000	10	1.43	1.43
46	1.000	9	1.29	1.29
47	1.000	9	1.29	1.29
48	1.000	8	1.14	1.14
49	1.000	8	1.14	1.14
50	1.000	9	1.29	1.29
51	1.000	8	1.14	1.14
52	1.000	10	1.43	1.43
53	1.000	13	1.86	1.86
54	1.000	18	2.57	2.57
55	1.000	16	2.29	2.29
56	1.000	11	1.57	1.57
57	1.000	15	2.14	2.14
58	1.000	18	2.57	2.57
59	1.000	16	2.29	2.29
60	1.000	13	1.86	1.86
61	1.000	10	1.43	1.43
62	1.000	10	1.43	1.43
63	1.000	13	1.86	1.86
64	1.000	9	1.29	1.29
65	1.000	7	1.00	1.00
66	1.000	9	1.29	1.29

TABLE 14—Continued

Age in days (x)	Survival rate l(x)	Number of off-spring (♀)	Fecundity rate m(x)	l(x)m(x)
67	1.000	8	1.14	1.14
68	1.000	9	1.29	1.29
69	1.000	8	1.14	1.14
70	1.000	11	1.57	1.57
71	1.000	10	1.43	1.43
72	1.000	9	1.29	1.29
73	1.000	10	1.43	1.43
74	1.000	11	1.57	1.57
75	1.000	6	0.86	0.86
76	1.000	5	0.71	0.71
77	1.000	5	0.71	0.71
78	1.000	8	1.14	1.14
79	1.000	7	1.00	1.00
80	1.000	7	1.00	1.00
81	1.000	3	0.43	0.43
82	1.000	6	0.86	0.86
83	1.000	6	0.86	0.86
84	1.000	2	0.29	0.29
85	1.000	2	0.29	0.29
86	1.000	7	1.00	1.00
87	1.000	3	0.43	0.43
88	1.000	4	0.57	0.57
89	1.000	3	0.43	0.43
90	1.000	4	0.57	0.57
91	1.000	4	0.57	0.57
92	1.000	6	0.86	0.86
93	1.000	3	0.43	0.43
94	1.000	1	0.14	0.14
95	1.000	1	0.14	0.14
96	0.857	5	0.83	0.71
97	0.857	3	0.50	0.43
98	0.857	2	0.33	0.28
99	0.714	1	0.20	0.14
100	0.714	1	0.20	0.14
101	0.714	6	1.20	0.86
102	0.714	2	0.40	0.29
103	0.714	5	1.00	0.71
104	0.714	2	0.40	0.29
105	0.714	7	1.40	1.00
106	0.714	1	0.20	0.14
107	0.714	2	0.40	0.29
108	0.714	1	0.20	0.14
109	0.714	5	1.00	0.71
110	0.714	4	0.80	0.57
111	0.714	3	0.60	0.43
112	0.714	4	0.80	0.57
113	0.714	2	0.40	0.29
114	0.714	2	0.40	0.29
115	0.714	1	0.20	0.14
116	0.714	2	0.40	0.29
117	0.571	0	0.00	0.00
–				
–				
212	0.428	0	0.00	0.00
–				
–				
238	0.285	0	0.00	0.00
–				
–				
259	0.142	0	0.00	0.00
–				
–				
264	0.000	0	0.00	0.00

GRR = 106.50 R_o = 103.26

cae and *T. floridanus*. An intrinsic rate of natural increase (r_m) of 0.121 and a net reproductive rate (R_o) of 103.26 were derived (Table 14). Analysis of the oviposition data revealed that the gross reproductive rate was nearly the same at 106.5. The mean generation time was 38.3 days.

Cannibalism

Typhlodromus floridanus. Cannibalism by *T. floridanus* was uncommon. Tests conducted within individual ovipositional cells indicated that adults and immature stages, in the absence of other food, underwent severe hunger rather than feed upon either the small stages or weakened individuals of their own species. After doing without food for more than 2 days, however, the females did consume their own eggs. McMurtry *et al.* (1970) referred to six other species of adult phytoseiids reported to feed on smaller stages of their own species in the absence of other food.

Stethorus picipes. Cannibalistic tendencies were reported for the larvae of *Stethorus bifidus* Kapur, *S. picipes*, and *S. punctum* LeConte by Cottier (1934), Fleschner (1950) and Robinson (1953), respectively, and for all the active stages of *S. punctillum* by Putman (1955). In this study, tests consisting of confining various stages of *S. picipes* within individual ovipositional cells devoid of spider mites were conducted. It was found that adults are not cannibalistic toward each other but that after a few hours without other food the larger stages fed upon smaller ones (i.e., the egg and early instars). It was also observed in rearing the F_2 progeny that, in the presence of an adequate number of spider mites, larvae of the same size and age all reached maturity when isolated together. Thus, the conclusion that cannibalism by *S. picipes* becomes an important limiting factor only when spider mite prey become scarce is in agreement with that of Putman's (1955) for *S. punctillum*. Nicholson (1933) theorized that "... the efficiency of the average surviving predator is increased by cannibalism, so permitting the steady density of predators to be maintained in a lower density of prey than would otherwise be possible."

Preying of *Stethorus* spp. upon Phytoseiids

Tests were conducted in the isolation cells to determine whether *S. picipes* would feed on *T. floridanus*, or *T. floridanus* on *S. picipes*, when isolated together without normal prey. These tests indicated that the second instar, fourth instar, and adults of *S. picipes* readily preyed upon female *T. floridanus* after 2 or 3 days. Putman (1955) reported *S. punctillum* adults preyed upon the eggs and nymphs of *Amblyseius fallacis* (Garman) and *T. pyri;* and all stages of *P. persimilis* were preyed upon by *S. gilvifrons* when isolated together in Plexiglass® cages (Kaylani, 1967).

Arithmetic model

Modifying the model proposed by Huffaker and Flaherty (1966) to measure the effectiveness of *M. occidentalis* on *T. urticae*, Laing and Huffaker (1969) developed a precise arithmetic model, predicated on certain assumptions, to compare the ability of a predator to overtake high and increasing prey populations. This model incorporates both the oviposition and intrinsic rates of natural increase of the predator and prey and the consumption rates by the predator. As emphasized by Huffaker *et al.* (1970), this method not only combines the immediate functional response of the predator but, more importantly, it also incorporates the delayed numerical response. The assumptions necessary to generate this model are: the predator consumes all prey as eggs; searching for prey is negligible; predator and prey fecundities are maximal; and intraspecific competition does

TABLE 15

ARITHMETIC MODEL OF A HYPOTHETICAL INTERACTION BETWEEN THE DEVELOPING PROGENY OF *TYPHLODROMUS FLORIDANUS* AND THEIR RATE OF PREY EGG CONSUMPTION

Day	Stages* of *T. floridanus* on successive days and prey eggs consumed†									No. of prey consumed
1									eggs	0
2									incu	0
3									bating	0
4									a	
									L(0)	0
5								a	b	
								P(93)[1]	L(0)	93
6							a	b	c	
							P(93)	P(93)	L(0)	186
7						a	b	c	d	
						D(86)[2]	P(93)	P(93)	L(0)	272
8					a	b	c	d	e	
					D(86)	D(86)	P(93)	P(93)	L(0)	358
9				a	b	c	d	e	f	
				pA(106)[3]	D(86)	D(86)	P(93)	P(93)	L(0)	464
10			a	b	c	d	e	f	g	
			pA(106)	pA(106)	D(86)	D(86)	P(93)	P(93)	L(0)	570
11		a	b	c	d	e	f	g	h	
		pA(106)	pA(106)	pA(106)	D(86)	P(93)	P(93)	P(93)	L(0)	683
12	a	b	c	d	e	f	g	h	i	
	A(178)[4]	pA(106)	pA(106)	pA(106)	D(86)	D(86)	P(93)	P(93)	L(0)	854
13	a A(178)	b A(178)	c pA(106)	d pA(106)	e D(86)	f D(86)	g D(86)	h P(93)	i P(93)	j L(0)	912

* A = adult, pA = preovipositional adult, D = deutonymph, P = protonymph, L = larva.

† [1]20 protonymphs consume 20 × 4.64 eggs per day = 93; [2]20 deutonymphs consume 20 × 4.32 eggs per day = 86; [3]20 p-adults consume 20 × 5.29 eggs per day = 106; [4]20 adults are composed of 13 females which consume 13 × 12.19 eggs per day = 157 and 7 males which consume 7 × 3.0 eggs per day = 21 for a total adult consumption of 178 eggs per day.

not occur. Obviously, in nature, searching is variable in result, especially when the prey becomes scarce. This model, when generated from laboratory data obtained under optimal conditions for food, space, shelter and the absence of competition, indicates, however, the potential ability of a predator to overtake increasing populations of prey. Tables were constructed for *T. floridanus* similar to those constructed for *P. persimilis* and *M. occidentalis* by Laing and Huffaker (1969). Based upon the life history study, the average oviposition rate of this predator is about two eggs per day. Table 15 was constructed by starting with 10 mature females which collectively lay 20 eggs on Day 1, and projecting the progeny and consumption of these individuals, and the progeny until adulthood is reached on Day 13. The rate of egg consumption was calculated for each stage of development, and those of subsequent progeny, based upon prey consumption studies. After 13 days, this predator population, having a sex ratio of 1.8 females to one male, would theoretically have consumed 4,392 *O. punicae* eggs. If an initial ratio of 100 *O. punicae* adult females to 10 adult *T. floridanus* females is assumed, Table 16 indicates that the immature population of prey would be decimated by Day 13. On that day there would be only 893 prey eggs present for a population of immature and adult predators capable of consuming 912 and 120 prey eggs, respectively. Thus, the food requirements for the predator could not be met.

Even though *O. punicae* has a higher intrinsic rate of natural increase than *T. floridanus*, the latter has the potential of overtaking and suppressing an increasing population of *O. punicae*.

TABLE 16

POTENTIAL FOR THE THEORETICAL CONTROL OF *OLIGONYCHUS PUNICAE* BY *TYPHLODROMUS FLORIDANUS*

	100 female *O. punicae*		10 female *T. floridanus*			
Day	No. of eggs oviposited	No. of prey eggs consumed by adults	No. of eggs oviposited	No. of prey eggs consumed by progeny	Total eggs consumed	No. of prey remaining
1	440	120	20	0	120	320
2	440	120	20	0	120	640
3	440	120	20	0	120	960
4	440	120	20	0	120	1280
5	440	120	20	93	213	1507
6	440	120	20	186	306	1641
7	440	120	20	272	392	1689
8	440	120	20	358	478	1651
9	440	120	20	371	491	1600
10	440	120	20	570	690	1350
11	440	120	20	683	803	987
12	440	120	20	854	974	453
13	440	120	20	912	1032	−139

SUMMARY AND CONCLUSIONS

Separate life history and life table studies were conducted for the prey *Oligonychus punicae* and for the predators *Typhlodromus floridanus* and *Stethorus picipes* under similar controlled conditions. These studies provided a background for subsequent investigations of predator-prey interactions.

The mean developmental time, from egg laying to adult female emergence (Table 17), indicated that both mite species developed faster than did *S. picipes*. The developmental and generation time period for *T. floridanus* was about the same as for *O. punicae*, at 10.50 and 19.60 days, respectively.

Adult female longevity data were derived from the survivorship column (l_x) of the life tables. These data indicated that female longevity for both predators was longer than that of the prey (Table 17) by 13.00 and 84.50 days. The time required for initial individuals of each organism to reach 50 percent mortality was estimated from the survivorship data, which indicated about 24 days for *O. punicae*, 40 to 41 days for *T. floridanus*, and 125 days for *S. picipes*.

TABLE 17

BIOLOGICAL PARAMETERS FOR THE PREY, *OLIGONYCHUS PUNICAE*, AND PREDATORS, *TYPHLODROMUS FLORIDANUS* AND *STETHORUS PICIPES*

Growth †statistics	*O. punicae*	*T. floridanus*	*S. picipes*
♀ developmental time (days)	11.50	10.50	21.50
♀ mean adult longevity (days)	11.50	24.50	96.00
50% adult mortality (days)	24.00	40.50	125.00
Mean eggs per female (total)	59.00	41.00	221.00
Oviposition rate (eggs/♀ per day)	4.35	1.97	3.70
Mean age-specific fecundity*	3.39	1.96	1.12
Sex ratio (♀:♂)	3.1	1.8:1.0	1.2:1.0
GRR (♀/♀)	64.49	30.67	106.50
R_o (♀/♀)	43.07	22.60	103.26
T (days)	17.10	19.60	38.30
r_m (♀/♀ per day)	0.22	0.16	0.12

* ♀progeny/♀ per day.
† GRR = Gross Reproductive Rate; R_o = Net Reproductive Rate; T = Mean Generation Time; r_m = Intrinsic Rate of Natural Increase.

Mean total eggs per female (Table 17) revealed that *S. picipes* produced the largest number of eggs (221 per female) and *T. floridanus* the least (41 per female). Despite a shorter oviposition period than either predator, *O. punicae* adult females not only laid more eggs per female (59) than *T. floridanus* adults, but also laid more eggs/female per day (4.35) than either predator (1.97/day and 3.70/day).

With respect to population growth, however, the ability of a female to produce female progeny is more important than the total number of eggs produced. This is represented by the mean age-specific fecundity rate (m_x) (Table 17), for which *O. punicae* had the highest value, at 3.39, of the three species, the value for *S. picipes* being 1.12, and for *T. floridanus* being 1.96. The peak female progeny production for *O. punicae* occurred between the 7th and the 12th days (Table 12), followed by a gradual reduction which seemed to be correlated with their increasing mortality rate. In contrast, the number of female progeny per day for *T. floridanus* reached its maximum after 5 days and remained at that level for the next 21 days. This was followed by an abrupt cessation for oviposition within 5 days (Table 13). The age-specific fecundity trends for *S. picipes* females averaged over one female progeny/female/day for the first 52 days of their reproductive period. This was followed by an irregular and decreasing pattern of progeny production which indicated that their initial supply of sperm was becoming depleted. Oviposition and the production of female progeny continued, however, for the next 42 days (Table 14).

The average sex ratio (♀ : ♂) for *S. picipes* was 1.2:1.0; whereas, the ratio of *T. floridanus* was 1.8:1.0 and that for the arrhenotokous *O. punicae* approximated 3.0:1.0 (Table 17).

Under conditions which assume unlimited food, space, stable age distribution and the absence of natural enemies, *O. punicae* possessed the highest intrinsic rate of increase ($r_m = 0.222$), followed by *T. floridanus* (0.153) and *S. picipes* (0.121) (Table 17). As was discussed by Birch (1948), Andrewartha and Birch (1954), and Cardona and Oatman (1975), the higher values of r_m resulted from: 1) a high female progeny production during the first days of the reproductive period, 2) a shorter developmental time, and 3) a shorter generation time.

Under natural conditions, the capacity for increase is seldom realized by the prey, because its biotic potential is being reduced by various amounts of predation (Laing and Huffaker, 1969). The biotic potentials of these two predators are also seldom realized in nature. The following combination of factors probably contributed to the ability of each of these predators, as model-generated, to suppress a prey population with a higher potential for increase: 1) shorter developmental time of *T. floridanus,* cancelling of some of the prey increase potential by prey consumption by both predators, with the effect being greater for *S. picipes,* 2) greater longevity of both predators, and 3) a longer oviposition period of both predators.

Caution must be exercised when attempting to utilize laboratory model-generated data (or, for that matter, actual population interaction data in the laboratory) to predict natural population growth rates of *O. punicae* and its predators. These life table and life history data should be useful, however, for estimating the potential population growth rates of the prey and their two predators and for developing more sophisticated population models.

In feeding tests, *T. floridanus* females had a significant preference for the egg stage of *O. punicae.* Parameters of fecundity, rates of prey consumption, and intrinsic rates of natural increase of *T. floridanus* and *O. punicae* were used to

generate an arithmetic model of the type described by Laing and Huffaker (1969). At an initial prey:predator ratio of 10:1, this model indicated that *T. floridanus* could annihilate a population of *O. punicae* within 13 days when feeding only on their eggs.

Data from food preference tests indicated that the larvae and adults of *S. picipes* preyed upon all stages of the avocado brown mite, with large variations between replicates being the rule for both individual and total stages. Life table studies indicated that the larvae were capable of consuming between 32 and 44 adult *O. punicae* per day. Because *S. picipes* did not demonstrate a significant preference for a particular life stage of the prey, the arithmetic model used to simulate the interaction between *T. floridanus* and *S. picipes* could not be generated. These data showed, however, that both the larval and adult stages of *S. picipes* possess a greater consumption capacity than the females of *T. floridanus* and *S. picipes* also has a comparable intrinsic rate of increase. It should be capable, therefore, of annihilating a comparable *O. punicae* population in less than 13 days.

LITERATURE CITED

ANDREWARTHA, H. G., and L. L. BIRCH
1954. The distribution and abundance of animals. Chicago: University of Chicago Press, 782 pp.

BIRCH, L. L.
1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17:15–26.

BOUDREAUX, H. B.
1963. Biological aspects of some phytophagous mites. Annu. Rev. Entomol. 8:137–54.

BRAVENBOER, L., and G. DOSSE
1962. *Phytoseiulus riegeli* Dosse als Prädator einiger Schadmilben aus der *Tetranychus urticae*-Gruppe. Entomologia Exp. Appl. 5:291–304.

CARDONA, C., and E. R. OATMAN
1975. Biology and physical ecology of *Apanteles subandinus* Blanchard (Hymenoptera: Braconidae), with notes on the temperature responses of *Apanteles scutellaris* Muesebeck and its host, the potato tuberworm. Hilgardia 43(1):1–51.

CHANT, D. A.
1959. Phytoseiid mites (Acarina: Phytoseiidae). Part I. Bionomics of seven species in south-east England. Part II. A taxonomic review of the family Phytoseiidae with descriptions of thirty-eight new species. Can. Entomol. 91, Suppl. 12, 166 pp.

COLLYER, E.
1953. The biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-east England. II. Some important predators of the mite. J. Hort. Sci. 28:85–97.

COTTIER, W.
1934. The natural enemies of the European red mite in New Zealand. N. Z. J. Sci. Tech. 16:68–80.

CROFT, B. A., and C. D. JORGENSEN
1969. Life history of *Typhlodromus mcgregori* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Amer. 62:1261–67.

EBELING, W.
1959. Subtropical fruit pests. Univ. of California, Div. Agr. Sci. 436 pp.

EWING, H. E.
1914. The common red spider or spider mite. Oregon Agr. Exp. Sta. Bull. 121, 95 pp.

FLESCHNER, C. A.
1950. Studies on searching capacity of three predators of the citrus red mite. Hilgardia 20(13):233–65.
1958*a*. Field approach to population studies of tetranychid mites on citrus and avocado in California. Proc. 10th Int. Congr. Entomol., Montreal (1956)2:669–74.
1958*b*. Natural enemies of tetranychid mites on citrus and avocado in southern California. Proc. 10th Int. Congr. Entomol., Montreal (1956)4:627–31.

HUFFAKER, C. B., and D. L. FLAHERTY
1966. Potential of biological control of two-spotted spider mite on strawberries in California. J. Econ. Entomol. **59**:786–92.

HUFFAKER, C. B., M. VAN DE VRIE, and J. A. MCMURTRY
1969. The ecology of tetranychid mites and their natural control. Annu. Rev. Entomol. **14**: 125–74.
1970. Ecology of tetranychid mites and their natural enemies: a review. II. Tetranychid populations and their possible control by predators: an evaluation. Hilgardia **40**(11):391–458.

KAYLANI, S.
1967. Biology and life history of *Stethorus gilvifrons* Mulsant in Lebanon. Magon. Inst. de Rech. Agr. Liban, Pub. No. **11**, 24 pp.

KNISLEY, C. B., and F. C. SWIFT
1971. Biological studies of *Amblyseius umbraticus* (Acarina: *Phytoseiidae*). Ann. Entomol. Soc. Amer. **64**:813–22.

LAING, J. E.
1968. Life history and life table of *Phytoseiulus persimilis* Athias-Henriot. Acarologia **10**: 578–88.
1969*a*. Life history and life table of *Tetranychus urticae* Koch. Acarologia **11**:32–42.
1969*b*. Life history and life table of *Metaseiulus occidentalis*. Ann. Entomol. Soc. Amer. **62**: 978–82.

LAING, J. E., and C. B. HUFFAKER
1969. Comparative studies of predation by *Phytoseiulus persimilis* Athias-Henriot and *Metaseiulus occidentalis* (Nesbitt) (Acarina: Phytoseiidae) on populations of *Tetranychus urticae* Koch (Acarina: Tetranychidae). Res. Popul. Ecol. **11**:105–26.

LESLIE, P. H., and T. PARK
1949. The intrinsic rate of natural increase of *Tribolium castaneum* Herbst. Ecol. **30**:469–77.

LOTKA, A. J.
1925. Elements of physical biology. Baltimore: Williams and Wilkins.
1945. Populations analysis as a chapter in the mathematical theory of evolution: a contribution to "Essays on growth and form presented by D'Arcy Wentworth Thompson," (W. E. Le Gros Clark and P. B. Medawar, eds.). Oxford: Clarendon Press.

MCGREGOR, E. A.
1941. The avocado mite of California, a new species. Entomol. Soc. Wash. Proc. **43**:85–88.

MCMURTRY, J. A.
1970. Some factors of foliage condition limiting population growth of *Oligonychus punicae* (Acarina: Tetranychidae). Ann. Entomol. Soc. Amer. **63**:406–12.

MCMURTRY, J. A., C. B. HUFFAKER, and M. VAN DE VRIE
1970. Ecology of tetranychid mites and their natural enemies: a review. I. Tetranychid enemies: their biological characters and the impact of spray practices. Hilgardia **40**(11): 331–90.

MCMURTRY, J. A., and H. G. JOHNSON
1966. An ecological study of the spider mite *Oligonychus punicae* (Hirst) and its natural enemies. Hilgardia **37**(11):363–402.

MCMURTRY, J. A., and G. T. SCRIVEN
1964*a*. Biology of the predaceous mite *Typhlodromus rickeri* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Amer. **57**:362–67.
1964*b*. Studies on the feeding, reproduction, and development of *Amblyseius hibisci* (Acarina: Phytoseiidae) on various food substances. Ann. Entomol. Soc. Amer. **57**:649–55.
1965. Life-history studies of *Amblyseius limonicus*, with comparative studies on *Amblyseius hibisci* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Amer. **58**:106–11.

MCMURTRY, J. A., G. T. SCRIVEN, and R. S. MALONE
1974. Factors affecting oviposition of *Stethorus picipes* (Coleoptera: Coccinellidae), with special reference to photoperiod. Environ. Entomol. **3**:123–27.

MESSENGER, P. S.
1964. Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. Ecol. **45**:119–31.

MERTZ, D. B.
1970. Notes on methods used in life-history studies. *In:* Readings in ecology and ecological genetics (J. H. Connell, D. B. Mertz, and W. W. Murdoch, Eds.). New York: Harper and Row, 397 pp.

MUMA, M. H.
1955. Phytoseiidae (Acarina) associated with citrus in Florida. Ann. Entomol. Soc. Amer. **48**:262–72.
1958. Predators and parasites of citrus mites in Florida. Proc. 10th Int. Congr. Entomol., Montreal (1956)**4**:633–47.
1961. Mites associated with citrus in Florida. Florida Agr. Exp. Sta. Tech. Bull. **640**, 39 pp.
1970. Natural control potential of *Galendromus floridanus* (Acarina: Phytoseiidae) on Tetranychidae on Florida citrus trees. Florida Entomol. **53**:79–88.
1971. Food habits of Phytoseiidae (Acarina: Mesostigmata) including common species on Florida citrus. Florida Entomol. **54**:21–34.
NEWCOMER, E. J., and M. A. YOTHERS
1929. Biology of the European red mite in the Pacific Northwest. U. S. Dept. Agr. Tech. Bull. **89**, 70 pp.
NICHOLSON, A. J.
1933. The balance of animal populations. J. Anim. Ecol. **2**:132–78.
PENMAN, D. R., and W. W. CONE
1972. Behavior of male two-spotted spider mites in response to quiescent female deutonymphs and to web. Ann. Entomol. Soc. Amer. **65**:1289–93.
PRITCHARD, A. E., and E. W. BAKER
1955. A revision of the spider mite family Tetranychidae. Pac. Coast Entomol. Soc. Mem. Ser. **2**, 472 pp.
PUTMAN, W. L.
1955. The bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. Can. Entomol. **87**:9–33.
ROBINSON, A. G.
1953. Notes on *Stethorus punctum* (Lec.) (Coleoptera: Coccinellidae), a predator of tetranychid mites in Manitoba. 83rd Annu. Rep. Entomol. Soc. Ontario **1952**:24–26.
SANDNESS, J. N., and J. A. MCMURTRY
1970. Functional response of three species of Phytoseiidae (Acarina) to prey density. Can. Entomol. **102**:692–704.