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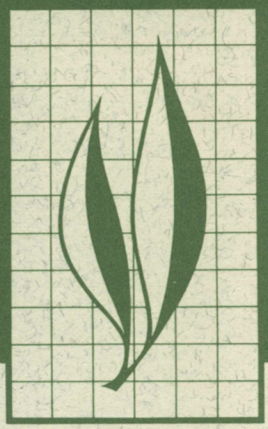

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Biology of *Amblyseius citrifolius* (Denmark and Muma) (Acarina – Phytoseiidae)

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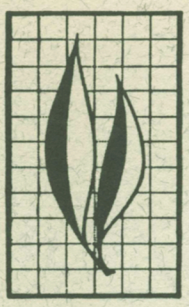

Descriptions of the morphological changes within each stage, of the molting and hatching processes and of the quiescent states of *Amblyseius citrifolius* (Denmark & Muma) were given. The larva emerged, posterior first, from the narrow end of the egg. Hatching took ca. 8 min. The duration of the ecdysis (ca. 20 to 30 min) was approximately the same for all the stages. Quiescent states were characterized by the extended, apposed palpi, by the protruded gnathosoma, by the pale, shiny coloration of the body and by a typical response to a contact stimulus. Duration of the quiescent state ranged from ca. 9.7 to 11.3 hours.

Continuous observations of behavior indicated that more than 80 percent of the time in the postembryonic stages was spent resting. Number of prey (eggs and larvae) consumed by each individual in the larval, protonymphal, and deutonymphal stages were 6.3, 17.2, and 12.0, respectively. Protonymphs averaged 3.2 minutes feeding on each prey; deutonymphs, 4.7 minutes; and larvae, 8.0 minutes.

At a given temperature, different relative humidities did not seem to affect the duration of the egg stage. The eclosion rates of *A. citrifolius* were shown in relation to saturation deficit at 16, 20, 24, 28, and 32 ° C.

Development from egg to adult was completed in 19.7, 7.7, 5.0, and 3.6 days at 15, 20, 25, and 30 °C, respectively. Egg, larval, protonymphal and deutonymphal stages required 27.3, 10.7, 14.1, and 15.8 degree days, respectively, to be completed.

Preoviposition, oviposition, and postoviposition periods and longevity were observed at 15, 20, 25, and 30 °C. Fecundity averaged 31.3, 40.9, 49.7, and 41.3 eggs per female at 15, 20, 25, and 30 °C, respectively. Average daily egg production at 15, 20, 25, and 30 °C was .75, 1.25, 2.11, and 2.51 eggs, respectively, per female. Pollens of *Pyrus kawakamii, Malephora crocea* (Jacq.), and avocado, a combination of *Tetranychus pacificus* McGregor (eggs + larvae) plus *M. crocea* pollen, and *T. pacificus* (all stages) were the best food for oviposition and survival of *A. citrifolius. Tetranychus pacificus* (eggs + larvae) also was one of the best for survivorship of the predator.

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Biology of *Amblyseius citrifolius* (Denmark and Muma) (Acarina—Phytoseiidae)[1,2]

INTRODUCTION

THE FAMILY Phytoseiidae contains some of the more important predators of phytophagous mites. Certain phytoseiids are responsible for the control of population levels of mites which otherwise would be important pests (McMurtry et al., 1970).

Importation of phytoseiid mites from other countries to California has been made to attempt to improve the biological control of phytophagous mites on several crops (McMurtry, 1978). The objective of this research was to study the biology and behavior of *Amblyseius citrifolius* (Denmark & Muma), foreseeing its possible utilization as a biological control agent in southern California. *Amblyseius citrifolius* used in this work originated from material collected by the junior author in 1975 from citrus groves in Tatui-SP Brazil.

Amblyseius citrifolius belongs to the *finlandicus* group of *Amblyseius* Berlese, as characterized by Chant (1959). The genus *Euseius* Wainstein is used by some authors for this group of species (De Leon, 1966; Muma, Denmark, and De Leon, 1970). The generic concepts of Chant (1965) are followed here. Denmark and Muma (1970) stated that there were about 40 described species in the *finlandicus* group, and that the group is worldwide in distribution on trees and shrubs. At present, there are more than 70 described species.

Denmark and Muma (1970) described *Euseius citrifolius, E. paraguayensis,* and *E. flechtmanni* from species collected on citrus in Paraguay. According to their key, *citrifolius* differs from *paraguayensis* by having L_4 (s_4) more than one-half as long as L_8 (S_5), and from *flechtmanni* by having macrosetae of genu III and of genu, tibia, and tarsus IV, blunt setaceous instead of knobbed bacillate, and by having the dorsal scutum reticulate instead of smooth.

METHODS AND MATERIALS

Maintenance of stock cultures

Amblyseius citrifolius was reared by the method described by McMurtry and Scriven (1975) using a standard unit of a 20 × 20-cm stainless steel cake pan, containing a 12-mm thick polyurethane foam mat and a metallic tile resting on the foam mat. Egg masses of *Tetranychus pacificus* McGregor, extracted from glasshouse-grown lima bean plants by the method described by Scriven and McMurtry (1971) and pollen of *Malephora*

[1]Accepted for publication April 7, 1980.

[2]From a thesis submitted by the senior author, in June 1978, to the Graduate Division, University of California, Riverside, in partial fulfillment of the requirements for the degree of Master of Science in Entomology.

crocea (Jacq.), extracted by the method described by McMurtry and Scriven (1965b), were supplied every third day to the rearing units. Water was added daily and the trays were kept in ventilated wood boxes in an insectary room of the University of California, Riverside, at 25 ± 3 °C and 50 ± 10 percent relative humidity.

Arenas of lemon leaves

Arenas were placed on foam mats in stainless steel pans with water. Each arena consisted of a 4-cm-square piece of lemon leaf surrounded by 1-cm wide strip of Cellucotton®. Except for the arenas used for the life cycle and behavior studies, the strips of Cellucotton were surrounded on the inner edge with a layer of tanglefoot as an additional deterrent to escape of the mites.

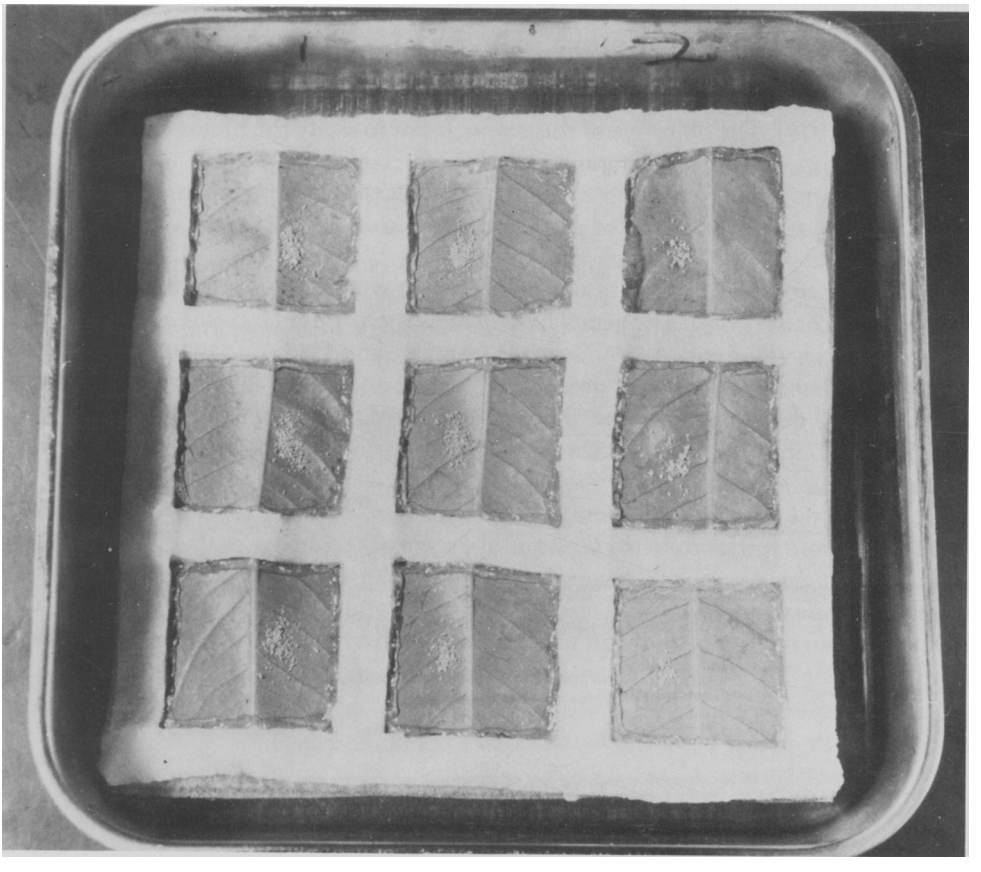

Fig. 1. Arenas of lemon leaves utilized in the studies of the biology of *A. citrifolius*.

Temperature cabinets

Temperature cabinets were modified compact refrigerators (Platner, Scriven, and Braniger, 1973) in which temperature, humidity, and photoperiod could be controlled.

Life cycle and behavior

Observations of the various life stages were made with a dissecting microscope and magnifications up to 120 × . Individuals in each stage were isolated in arenas of lemon leaves and held in a room maintained at 25 ± 3 °C and 50 ± 10 percent relative humidity.

Eggs were observed once every 4 hours, while larvae, protonymphs, and deutonymphs were observed continuously, starting when the desired stage was achieved and finishing when the individuals molted to the next stage. Only three individuals were observed concomitantly. Two sets of three were observed for each stage. In the adult stage, the individuals were taken randomly from the stock culture and observed continuously for 6 hours. Nine individual adults were observed (three sets of three individuals each). The time each individual spent resting, walking, feeding, and drinking was noted. The time a predator spent cleaning itself was considered as "time resting." Walking included the motion when the predator was either searching for food, water, and shelter for resting or oviposition, or when the predator was disturbed by prey.

The duration of the quiescent state was considered as the period of time from the last spontaneous movement to the beginning of the molting process. Movements incited by external factors, such as prey running into a predator, were not considered spontaneous. Different individuals were used in observations of the different stages since it was impossible to make continuous observations from the egg to the adult stage due to the duration of the life cycle.

Active stages were fed a mixture of eggs and larvae of *Tetranychus pacificus*. During the course of the experiment, 20 to 30 prey larvae were maintained per arena by frequently replacing the larvae that had been fed upon or that had become stuck in the water barrier. No attempt was made to count the number of prey eggs in the piles added to each arena.

All individuals to be observed on a certain day were acclimatized to the test conditions for 24 hours before the test started.

Development, oviposition, and longevity at different temperatures

For developmental studies, eggs of *A. citrifolius* were obtained as follows: clumps of eggs of *Tetranychus pacificus* were placed on tiles of rearing units of the stock culture. Three hours later, the clumps were examined and eggs of *A citrifolius* that had been oviposited there were collected and isolated in arenas of lemon leaves. For reproduction and longevity studies, eggs of *A. citrifolius* from the stock culture were isolated on leaf arenas at the respective test conditions. When the mites matured, a male was taken at random from the stock culture and placed in each arena containing a recently molted female. Males were replaced whenever they appeared unhealthy or weakened. Whenever a leaf began to deteriorate, mites thereon were transferred to a new leaf. Predators were fed an abundance of eggs and larvae of *T. pacificus* every fourth day. Clumps of prey eggs were scattered on the leaf surfaces. Thus, eggs also probably functioned as obstacles to the rapid movements of the females, preventing them from getting stuck in the tanglefoot barrier, mainly when avoiding mating.

The trays were kept in temperature cabinets at a photoperiod of 12L:12D. Temperatures and relative humidities were 15 ± 3 °C and 80 ± 10 percent, 20 ± 1 °C and 80 ± 10 percent, 25 ± 1 °C and 85 ± 10 percent and 30 ± 1 °C and 85 ± 10 percent. Variable numbers of individuals were utilized in each set of conditions. To determine the dura-

tion of each stage, observations were made every 4 to 6 hours. To determine the several parameters related to reproduction and the longevity of the adults, observations were made daily.

Influence of different levels of humidity on egg hatching at different temperatures

Eclosion rates of *A. citrifolius* were observed at 16, 20, 24, 28, and 32 °C, at 20, 30 40, 50, 60, 70, 80, and 90 percent relative humidity. Humidity chambers consisted of 1-liter polystyrene plastic containers containing sulfuric acid solutions at different concentrations to maintain the desired relative humidities (McMurtry and Scriven, 1965a). After adding the solutions, the containers were closed and placed in constant temperature cabinets at the desired temperature and the photoperiod of 12L:12D, and then held for 24 hr to allow conditions to stabilize before starting the tests.

Ten eggs of *A. citrifolius* were placed inside 2-cm-diam.-Syracuse watch-glasses held over the solution by a polyurethane, perforated, circular support fitted tightly into the container at some distance from the solution surface (McMurtry, Mahr, and Johnson, 1976). Three replicates of 10 eggs were utilized at each combination of temperature and relative humidity, each replicate corresponding to a watchglass and the eggs therein.

Watchglasses were removed from the container and the eggs examined under a dissecting microscope once daily until hatching or shrivelling occurred. Lids of the containers were opened only partially, and the eggs were observed as quickly as possible and returned to the cabinets.

Suitability of different kinds of food

Experiments were conducted in temperature cabinets at approximately 25 °C and 75 percent relative humidity. There were four replicates per each kind of food, and 10 females, taken randomly from the stock culture, per replicate. Counts of the number of eggs and live females in each arena were made at approximately the same time each day for 11 days. The first count was discarded because of the possible influence of previous kinds of food ingested.

Females of each replicate were placed in a lemon leaf arena to test *Tetranychus pacificus* (eggs + larvae), *Panonychus citri* (McGregor), pollens, and *Hemiberlesia lataniae* (Signoret) as food. Arenas of lima bean leaves (10-16 cm^2) were used to test *T. pacificus* (all stages) as food. In each arena, a transparent coverslip was placed on two threads, providing the females with a place to oviposit and rest.

Foods were supplied as follows: 1) *Tetranychus pacificus* (eggs + larvae)—eggs plus larvae were extracted from lima bean leaves and replaced daily in the arenas; 2) *T. pacificus* (all stages)—leaves heavily infested with all the stages of the prey were utilized. On the fifth and eighth days, additional eggs and larvae were supplied as the prey became scarce in the arenas; 3) *T. cinnabarinus* (Boisduval)—all stages on small pieces of leaves of wild tobacco, *Nicotiana glauca* Grah., collected in the field and changed every third day; 4) *P. citri*—all stages transferred daily to the arenas from a laboratory culture; 5) *Malephora crocea* pollen-extracted by the method used by McMurtry and Scriven (1965b) and added to the arenas every other day; 6) *T. pacificus* + *M. crocea* pollen—eggs plus larvae changed daily and pollen added every other day; 7) *Pyrus*

kawakamii, Eucalyptus, Pinus, citrus and avocado pollen—anthers changed every other day. *Pinus* pollen was tested in an early (*Pinus* (early)) and in a late (*Pinus* (late)) stage of maturation. Grains in early stage were obtained from anthers which were almost open, while grains in late stage were obtained from anthers which were already open in the field; 8) *Hemiberlesia lataniae*—all instars, with an excess of crawlers, were daily transferred from a laboratory culture on small pieces of potatoes onto the arenas.

RESULTS AND DISCUSSION
Life Cycle and Behavior

Life cycle

Egg stage. A sticky substance on the surface of the egg of *Amblyseius citrifolius* adheres it to the substratum. Similar observations were reported by Ballard (1954) for *A. fallacis,* Knisley and Swift (1971) for *A. umbraticus* (Chant), and Lee and Davis (1968) for *Typhlodromus occidentalis.* The sticky substance is a relatively thick layer of transparent material deposited on the egg surface in contact with the inner side of the genital flap as the egg leaves the body of the female. The female then holds the egg by the opposite side with her first pair of legs and deposits it on the substratum.

Soon after oviposition, the egg is colorless and translucent. Prasad (1967) observed a variation in the colors of the eggs of *Phytoseiulus macropilis* depending upon the kind of food consumed by the female. He noted that eggs laid by females reared on *Tetranychus tumidus* Banks (a red species of spider mite) were light to deep orange, but those laid by females reared on *Eotetranychus lewisi* McGregor (a green spider mite) were pale yellow.

Internally, the presence of small globular structures (yolk particles?) evenly distributed in the egg give it a crystalline appearance. A few hours after oviposition, the egg becomes more translucent. Eight hours after oviposition, some faint, oblique lines corresponding to the rudiments of the appendages were visible. Four hours later, a longitudinal line was apparent, extending from the center of the more expanded end to a point at the opposite end, passing between the oblique lines which were then more conspicuous.

Approximately 16 hours after oviposition, the globular structures were mostly concentrated at the narrow end and at one side of the egg, corresponding to the posterior end and to the dorsum of the larva respectively. A few hours later, some pulsating movements of the region with globular structures occurred. The globular structures were yellowish-brown, whereas the rest of the egg was light-yellow when viewed against a green leaf.

Thirty hours after oviposition, the darker area showed a rotational movement around the surface of the egg (blastokinesis?). This movement lasted for a short time, as movement was not observed when the eggs were observed 4 hours later.

Edney (1977) referred to blastokinesis as a process whereby the developing embryo undergoes devious turnings and migrations, usually amounting to a movement up and around the yolk to a dorsal position and a subsequent return.

One to 2 hours before eclosion, movements of the appendages of the larva within the egg were observed. A microscopic examination of eggs of *Typhlodromus occidentalis* showed that the embryonic appendages were developed late in the stage (Lee and Davis, 1968).

The Z_4 setae were the first structures to penetrate the chorion, immediately becoming straight. At this time, the egg shrivelled suddenly like a balloon punctured by a pin. Then, back and forth movements of the appendages were observed through the chorion, and the larva started eclosion, posterior first, from the narrow end of the egg. The legs and the gnathosoma were the last structures to leave the egg. Eclosion lasted approximately 3 minutes.

Ballard (1954) found eclosion of *A. fallacis* required 5 to 15 minutes and that the egg chorion appeared to split transversely as the larva backed out of the shell. Prasad (1967) reported that larvae of *Phytoseiulus macropilis* required only 1.5 to 2 minutes to free themselves completely from the egg shell, and that they ruptured the chorion at the broad end of the egg, using the palpi and the front legs. Lee and Davis (1968) stated that the lapse of time from the initial splitting of the egg of *Typhlodromus occidentalis* to the completion of the hatching process was about 10 minutes. They also reported that during eclosion, a rupture first appeared in the anterior portion of the chorion and then the first pair of legs of the larva emerged and stretched forward.

Larval stage. The body of the larval *A. citrifolius* is approximately rectangular just after emergence, and the posterior margin, between the 2 long, terminal setae (Z_4), is almost a straight line. During the first hours, the larva is almost transparent, except in the area of the digestive tract, that is visible externally as 3 longitudinal carinae, corresponding to the regions of the midgut and of the diverticula.

The legs are relatively strong. The third legs extend almost perpendicularly to the lateral surfaces of the body. When walking, the mite moves alternately from side to side to maintain equilibrium. The body is supported mainly on the last two pairs of legs, the first pair of legs being used mostly as sensory structures, moving actively when the mite walks. Lee and Davis (1968) stated that the larvae of *Typhlodromus occidentalis* used their first pair of legs for walking and also in what appeared to be a sensory manner, not unlike the antennal movement of an insect.

Near the end of the larval stage, the posterior portion of the body expands and the digestive tract increases greatly in volume in relation to the total volume of the body, reducing the clear areas to a small region behind the gnathosoma and another in the opisthosoma.

Although it was not determined whether or not the larvae of *A. citrifolius* required food to pass to the protonymphal stage, feeding was observed. Some species have been reported to feed in the larval stage (Waters, 1955; Lee and Davis, 1968; Swirski, Amitai, and Dorzia, 1967a, b; Swirski and Dorzia, 1968; Takafuji and Chant, 1976). Occasionally, however, individuals of certain species may molt to the protonymphal stage without feeding (Ballard, 1954; Smith and Newsom, 1970b; Burnett, 1971; Amano and Chant, 1977). Other species do not seem to feed in the larval stage (Dosse, 1955, 1958; Laing, 1968, 1969; Takafuji and Chant, 1976; Amano and Chant, 1977, Smith and Summers, 1949; Prasad, 1967; McMurtry and Scriven, 1964a; Blommers, 1976; Croft and Jorgensen, 1969; Charlet and McMurtry, 1977). McMurtry, Huffaker, and Van de Vrie, (1970) suggested it may be advantageous if the larva does not have to find food, assuming that it has a lower searching ability than the 8-legged protonymph.

Apparently *A. citrifolius* grasps the prey *(Tetranychus pacificus)* by any part of the body. Burrell and McCormick (1964) reported that *A. cucumeris* seizes *Bryobia* by the leg but seizes other tetranychid species in the more usual manner of piercing the body. Referring to this observation, McMurtry, Huffaker, and Van de Vrie (1970) suggested that the large size and long legs of *Bryobia* may be an important factor in the different mode of attack.

In capturing the prey, *A citrifolius* uses the palpi and the first and second pairs of legs. Later, the first pair of legs is usually positioned over the body of the prey. After feeding, the predator cleans its mouthparts, palpi and first pair of legs while resting near the dead prey. As with other stages, the larva usually rests close to obstacles in the arena, such as clumps of prey eggs or pieces of Cellucotton. Putman (1962) concluded that *Typhlodromus caudiglans* Schuster presented a behavior classified as low thigmokinesis.

All immature stages appear to drink free water, as they were frequently observed with the gnathosoma in the water film barrier. Adult females were never seen drinking free water, although in the stock culture they frequently were observed near the water saturated foam, apparently drinking. The dependence on free water has been reported for some species of Phytoseiidae (Mori and Chant, 1966b; Blommers and Van Etten, 1975). Burnett (1971) stated it was unlikely free water was necessary for the survival and reproduction of *A. fallacis*.

Protonymphal stage. Soon after molting, the protonymphs of *A. citrifolius* are approximately oval and have three carinae on the dorsum. The presence of a fourth pair of legs permits the protonymphs to walk more easily and rapidly, without the lateral body movement of larvae.

Occasionally, protonymphs appeared to detect the prey before actually touching it. This detection may have been through contact with the silk produced by the prey.

Similar to the larvae, the protonymphs grasp prey by any part of the body, or even the legs. The functions and positions of the palpi and legs in pursuing, capturing, and consuming prey are the same as in the larval stage. Ballard (1954) observed that, while feeding, protonymphs of *A. fallacis* manipulated and held the spider mite prey with the first pair of legs and that, similar to what was observed for *A. citrifolius* in this experiment, once the prey had become subdued, the first pair of legs were raised above its body.

Deutonymphal stage. As with most phytoseiid species, the deutonymphal stage is present in both male and female *A. citrifolius*. Males of *A. fallacis* reportedly have no deutonymphal stage (Ballard, 1954).

In the capturing and feeding processes, the function and position of the palpi and first and second pair of legs is the same as in the earlier stages.

Adult stage. Soon after emergence, the adults are shiny and almost transparent. Females can be distinguished from males by their more elongate body and the straight rear margin between the two long terminal dorsal setae (Z_5). With age, the body of the female enlarges much more than that of the male and acquires a pear-like shape. A few days before death, the female becomes light colored, almost transparent. Similar characteristics were reported by Ballard (1954). In many cases, the females become swollen during the last few days of the postoviposition period and then become slender shortly before death.

The capturing and feeding processes are similar to those of other stages. Mating is required for oviposition. Normally, some minutes before ovipositing, the female pierces several prey without sucking much fluid from them, as if testing the suitability of the prey around the oviposition site. Depending upon the level of hunger, each stage of the predator shows one of the following types of behavior when touching a prey: avoidance with evasive movement, indifference, casual chase, and emphatic chase. The first three types were observed soon after the predators had fed. Similar observations were reported by Sandness & McMurtry (1972).

Molting. The steps and duration of the molting process are approximately the same in the larval, protonymphal or deutonymphal stages. At the beginning of the process, the mite raises its body from the leaf surface and rolls from side to side. At each turning

movement, the front legs are raised and, like the palpi, moved up and down for a few seconds. These steps proceed for 10 to 15 minutes. Later, the mite raises and lowers the body at constant intervals for approximately 5 minutes. At each lowering movement, the chelicerae are rubbed together by alternate protraction and retraction movements. Then, the individual contracts, twists, and arches the body dorsally from time to time for 2 to 3 minutes. Finally, the mite raises the opisthosoma and begins to free itself from the old exuvium, posterior first. In molting to the protonymphal stage, the fourth pair of legs, apposed to the metapodosoma, are unfolded. The posterior part of the body moves up and down, and, at each downward movement, the mite partially withdraws the first and second pairs of legs and the palpi. With each upward movement it appears to partially withdraw the third pair of legs (and the fourth pair of legs in the case of a protonymph molting to a deutonymph or of a deutonymph molting to an adult). Molting (after splitting of the cuticle) lasts for 2 to 3 minutes.

When the mite is completely out of and on the old skin, it rubs the palpi together for a few seconds and then pushes itself forward and arranges the arched legs equidistantly around the exuviae. It rubs the palpi together again and walks away from the old skin to the leaf surface, where it cleans the front legs and the palpi for a few seconds. These steps require 1 to 2 minutes. Finally, it raises and swings the legs as if expanding and drying them, alternately. The molting process takes 20 to 30 minutes. Ecdysis for *A. fallacis* required 10 to 30 minutes (Ballard, 1954), and that for *Typhlodromus occidentalis* (Lee and Davis, 1968), 10 to 20 minutes.

After molting, *A. citrifolius* remained inactive for 20 minutes to over 1 hour before starting to move around in search for food. The resting period after molting varies with species. Ballard (1954) reported it to last for 5 to 10 minutes for *A. fallacis*. Practically no resting period was observed for *Phytoseiulus macropilis* (Prasad, 1967), *P. persimilis* (Laing, 1968) and *A. umbraticus* (Knisley and Swift, 1971). Conversely, Lee and Davis (1968) reported that *Typhlodromus occidentalis* moves very little during the first several hours after molting.

Quiescent state. When *A. citrifolius* is in the quiescent state, the palpi are fairly extended and apposed, the gnathosoma is protruded, the body is pale and shiny and a typical response to a stimulus such as contact with a prey occurs. The longer the individual is in the quiescent state, the less responsive it is to contact stimuli. The response is an evasive movement of relatively short duration in the beginning of the quiescent state or a simple, momentary contraction of the appendage touched by the prey later in the state.

Lee and Davis (1968) observed that quiescent larvae of *Typhlodromus occidentalis* remain in small depressions in the rearing cage walls, usually motionless and not feeding during this time. *Phytoseiulus persimilis* has no distinctive quiescent periods in any of the stages (Laing, 1968). Ballard (1954) reported short quiescent states for *A. fallacis*. *P. macropilis* has distinctive quiescent states. Its larval stage is almost completely quiescent (Smith and Summers, 1949; Prasad, 1967). Quiescent states have also been observed for *Phytoseius plumifer* (Canestrini and Fanzago) (Zaher et al., 1969).

Duration of each activity in each stage

Percentages of time spent by each stage in each activity are shown in Table 1. The protonymphs spent proportionately less time resting than did deutonymphs and adult females. In all postembryonic stages, *A. citrifolius* spent more than 80 percent of its

TABLE 1

PERCENTAGE OF TIME SPENT BY EACH ACTIVE STAGE OF *A. CITRIFOLIUS* IN EACH ACTIVITY*

	Activity			
	Resting	Walking	Feeding	Drinking
Stage	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Larva	88.93ab ± 3.6	6.71b ± 2.7	3.95a ± 1.4	0.41a ± 0.25
Protonymph	82.27b ± 5.0	13.90a ± 4.5	3.40a ± 1.0	0.44a ± 0.32
Deutonymph	89.11a ± 4.3	6.57b ± 3.8	3.88a ± 1.3	0.45a ± 0.29
Adult female	92.25a ± 3.5	2.64c ± 2.3	5.11a ± 2.5	0.00b ± 0.00
Total mean	88.14 ± 4.2	7.46 ± 4.7	4.09 ± 0.7	0.33 ± 0.22

*Different letters in a vertical row indicate significant differences at the 5% level.

time in resting. The longest and the shortest percentage of time in walking were spent by the protonymphs and the adults, respectively. Sandness and McMurtry (1972) and Blommers et al. (1977) reported that females of *A. largoensis* and *A. bibens* Blommers, respectively, spent a relatively long time in searching. In some cases, however, this involved searching for a suitable place in which to oviposit.

In general, adult females of *A. citrifolius* moved only when searching for food or a place to oviposit or when disturbed by a prey, whereas the young stages frequently moved even when satiated and undisturbed by the prey. Furthermore, the females always had suitable and abundant places for oviposition on the prey egg masses. This could explain the low percentage of time spent in walking by the females. No significant evidence was found for differences among stages in the percentage of time spent in feeding. All the immature stages spent a similar low, less than 1 percent proportion of time in drinking.

Variation in the percentage of time spent in each activity in the course of each immature stage is shown in Figure 2. The quiescent state (100 percent resting) lasted for approximately 35 percent of the total larval and deutonymphal stages, and approximately 25 percent of the total protonymphal stage. However, the average absolute durations of the quiescent states in each stage did not differ significantly from each other (Table 2).

The values obtained for these parameters may vary with environmental conditions.

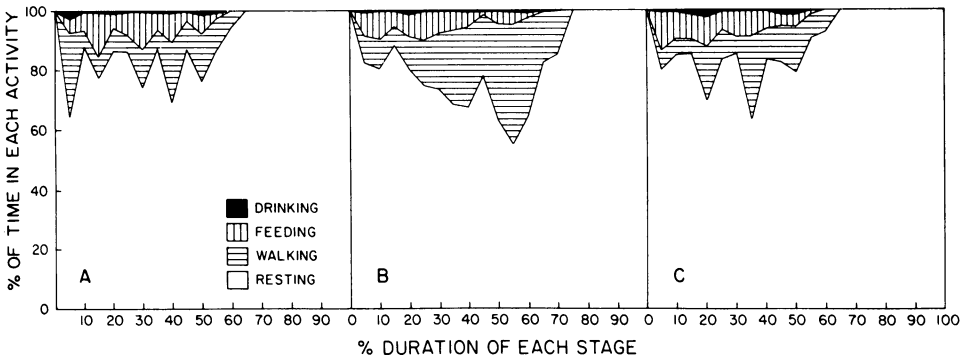

Fig. 2. Variation in the percentage of time spent in each activity by larvae (A), protonymphs (B) and deutonymphs (C) of *A. citrifolius*. The total duration of each stage is 100 percent.

TABLE 2

DURATION OF THE QUIESCENT STATE (IN HR) IN EACH STAGE OF *A. CITRIFOLIUS*

Stage	Replicate 1	2	3	4	5	6	Mean* ± SD
Larva	9.78	8.48	8.40	10.97	10.18	10.13	9.66a ± 1.02
Protonymph	13.83	9.12	8.97	9.13	9.25	9.92	10.04a ± 1.89
Deutonymph	9.07	10.00	12.68	12.03	12.23	11.68	11.28a ± 1.42

*Same letters in a vertical row indicate no significant differences at the 5% level.

In a less favorable situation, the time spent in walking, in search of food, water, shelter, or oviposition sites presumably would be greater, and the total duration of each stage longer (Takafuji and Chant, 1976). Prey density influences the time required to locate a prey and, consequently, the number of prey consumed by a predator per unit of time.

Prey consumption

Initially, only prey eggs were fed to the predator to determine prey consumption. However, it was observed that the predators did not feed well on eggs. Moreover, when the eggs started hatching, it appeared that the predator larvae preferred prey larvae to eggs.

Young stages of *A. citrifolius* apparently had difficulty in perforating the eggs. Frequently, predators stroked the egg shell with the palpi and finally left the egg without feeding on it, although feeding occurred on eggs when prey larvae were not promptly available. Eggs in advanced stage of development seemed to be preferred to the freshly oviposited ones. Opposite behavior was observed by Croft and McMurtry (1972) for *Typhlodromus occidentalis* feeding on the same prey.

Several phytoseiid species reportedly prefer the larval or the early nymphal stages to eggs of tetranychids (Burrell and McCormick, 1964; McMurtry and Scriven, 1964a; Elbadry et al., 1968a; Zaher, Wafa, and Shehata, 1969; Croft and McMurtry, 1972; Takafuji and Chant, 1976). Other species, however, apparently show some preference for the egg stage (Smith and Summers, 1949; Prasad, 1967; Burnett, 1971; Blommers and Van Etten, 1975; Blommers, 1976; Takafuji and Chant, 1976).

The number of prey (larvae + eggs) consumed by the immature stages of *A. citrifolius* is shown in Table 3. Although the analysis did not show significant differences between the average number of prey consumed by the larvae and the deutonymphs, there was a

TABLE 3

NUMBER OF PREY (EGGS + LARVAE) CONSUMED BY THE IMMATURE STAGES OF *A. CITRIFOLIUS*

Stage	Replicate 1	2	3	4	5	6	Mean* ± SD
Larva	5	10	6	5	8	4	6.33a ± 2.25
Protynymph	12	10	13	18	29	21	17.17b ± 7.08
Deutonymph	9	8	9	10	20	16	12.00ab ± 4.86
Total	26	28	28	33	57	41	35.50 ± 11.84

*Means followed by different letters are significantly different at the 5% level.

trend of higher to lower prey consumption by the protonymphs (17.2) deutonymphs (12.00) and larvae (6.3).

In most other reported cases, prey consumption was progressively higher for larvae, protonymphs, and deutonymphs, respectively, (Ballard, 1954; Prasad, 1967; Elbadry et al., 1968a; Laing, 1968; Lee and Davis, 1968; Laing and Huffaker, 1969; Zaher, Wafa, and Shehata, 1969; Knisley and Swift, 1971; Blommers, 1976; Takafuji and Chant, 1976). Similar to the trend shown by *A. citrifolius,* Herbert (1961) obtained higher prey consumption for the larval, deutonymphal, and protonymphal stages of *Typhlodromus pyri* Scheuten, respectively, at several prey densities. Other workers have shown that males of some species may also have a similar trend in prey consumption (Elbadry et al., 1968a; Tanigoshi and McMurtry, 1977).

The average prey consumption of each species of predator varies with the species, stage of the prey, as well as the experimental conditions. Thus, it is difficult to compare consumptions of different species of predators. However, the observed average total prey consumption by the immature stages of *A. citrifolius* (35.5 eggs + larvae) is within the usual range observed for other phytoseiid species. Species consuming noticeably more prey than *A. citrifolius* include *A. cucumeris* (Elbadry and Zaher, 1961), *Typhlodromus pyri* (Herbert, 1961) and *Iphiseius degenerans* (Berlese) (Takafuji and Chant, 1976). *Amblyseius aleyrodis* Elbadry seems to consume fewer prey than *A. citrifolius* (Elbadry, 1968).

The number of repeat feedings by the immature stages of *A. citrifolius* on the same prey is shown in Table 4. Only two of the six larvae returned to feed on the same prey individual. The protonymphal stage which killed the most prey also had the most returns to previously captured prey (Table 3 and 4). Mori and Chant (1966a) studied the number of repeat feedings of females of *Phytoseiulus persimilis* at different combinations of prey densities, relative humidities, and levels of starvation. It was significantly higher in the starved groups than in the non-starved groups. Sandness and McMurtry (1972) noted that *A. largoensis* usually returned more times to the first prey captured than to subsequent prey.

The average time spent by individuals of each stage feeding on the prey they captured is shown in Table 5. Protonymphs fed the shortest time on each prey, and larvae the longest. Stages that consumed greater numbers of prey (Table 3) fed for shorter periods on each prey.

Several authors reported on the time that different species of predators spend feeding on each individual prey captured (Smith and Summers, 1949; Ballard, 1954; Bravenboer, 1959; Mori and Chant, 1966a; Prasad, 1967; Lee and Davis, 1968). Sandness and McMurtry (1972) found that the hunger level of *A. largoensis* directly affects the time spent feeding on individual prey.

TABLE 4

NUMBER OF REPEAT FEEDINGS BY THE IMMATURE STAGES OF *A. CITRIFOLIUS* ON THE SAME PREY

	Replicate						
Stage	**1**	**2**	**3**	**4**	**5**	**6**	**Mean**
Larva	2	0	0	0	1	0	.50
Protonymph	0	1	3	1	1	0	1.00
Deutonymph	2	1	0	0	2	0	.83

TABLE 5
AVERAGE TIME (IN MIN.) REQUIRED FOR EACH PREY TO BE CONSUMED BY *A. CITRIFOLIUS*

Stage	Replicate						Mean* ± SD
	1	2	3	4	5	6	
Larva	8.2	7.3	10.4	8.8	5.9	7.2	7.97c ± 1.55
Protonymph	3.4	3.5	3.7	2.8	3.1	3.0	3.25a ± .34
Deutonymph	4.8	5.6	4.6	4.7	5.0	3.7	4.73b ± .62

*Means followed by different letters are significantly different at 5% level.

Development, Oviposition and Longevity At Different Temperatures

Development

Durations (in days) of the egg, larval, protonymphal and deutonymphal stages of *A. citrifolius* are shown in Table 6. The egg stage was the longest, regardless of temperature. At all temperatures, the larval, protonymphal and deutonymphal stages were of approximately equal duration, and male and female developmental periods were similar. Similar observations were reported for *Typhlodromus occidentalis* (Lee and Davis, 1968; Laing, 1969), *Phytoseiulus persimilis* (Laing, 1968), *A. umbraticus* (Knisley & Swift, 1971) and *A. brazilli* (Elbenhawy, 1975b). Amano and Chant (1977) showed shorter developmental time for males of *P. persimilis* and *A. andersoni* (Chant). They stated that more rapid development of males is advantageous, because searching for mates is mostly dependent on the efforts of males, which in some species are able to recognize female deutonymphs and mate when adults emerge. Females of some species accept copulation only in the 2- or 3-day period after their emergence (Amano and Chant, 1977).

The developmental period decreased with increasing temperatures (Table 6). The development from egg to adult was completed in 19.7, 7.7, 5.0, and 3.6 days at 15, 20, 25 and 30 °C, respectively. Porres-Arreaga (1974) found that the period required to complete the life cycle (from egg to adult) was not significantly different between *A. stipulatus* Athias-Henriot, *A. hibisci* (Chant), and *A. fructicolus* Gonzales & Schuster at temperatures varying from 15.6 °C to 32.2 °C. Nevertheless, those species seem to require longer periods to complete development than *A. citrifolius* at 32.2 °C and 26.6 °C (4.3—4.7 and 4.9—5.5 days, respectively), and shorter periods at 21.6 °C and 15.6 °C (5.4—5.5 and 10.7—11.2 days, respectively).

Charlet and McMurtry (1977) observed that *Typhlodromus validus* has a longer developmental period than *Typhloseiopsis pini* at several temperatures, except at 29 °C. The developmental times of the immature stages of *A. andersoni* did not differ from those of *A. citrifolius* (Amano and Chant, 1977). Other species of the *finlandicus* group showed developmental periods similar to those reported in this paper, with some variations perhaps due to the kind of prey (Elbadry, 1968; Elbadry and Elbenhawy, 1968b; Elbadry et al., 1968b; Elbenhawy, 1975b). However, McMurtry (1977) reported a somewhat longer developmental period for *A. stipulatus* than that observed in this study for *A. citrifolius* on the same prey (*T. pacificus*).

TABLE 6

DURATION (IN DAYS) OF THE IMMATURE STAGES OF *A. CITRIFOLIUS* AT DIFFERENT TEMPERATURES

Temp. (°C)	Female				Male				Female & Male			
	Min	Max	Mean ± SD	N	Min	Max	Mean ± SD	N	Min	Max	Mean ± SD	N
					(Egg)							
15	5.5	7.0	6.1 ± .41	17	6.0	6.7	6.5 ± .33	4	5.5	7.5	6.3 ± .47	48
20	2.8	3.2	2.9 ± .12	36	3.1	3.2	3.2 ± .03	2	2.8	3.2	3.0 ± .13	49
25	1.7	2.1	1.9 ± .10	54	1.8	2.2	2.0 ± .12	18	1.7	2.2	1.9 ± .11	110
30	1.2	1.5	1.4 ± .10	40	1.3	1.6	1.4 ± .08	14	1.2	1.6	1.4 ± .09	64
					(Larva)							
15	2.9	6.6	4.5 ± .96	17	4.2	5.9	4.9 ± .70	4	2.9	6.6	4.5 ± .90	30
20	1.2	1.8	1.5 ± .96	36	1.3	1.5	1.4 ± .10	6	1.2	1.8	1.5 ± .16	46
25	0.8	1.4	1.0 ± .13	54	0.7	1.3	0.9 ± .11	18	0.7	1.4	1.0 ± .14	102
30	0.5	0.8	0.6 ± .08	40	0.5	0.7	0.6 ± .10	14	0.5	0.8	0.6 ± .08	59
					(Protonymph)							
15	2.5	6.6	4.3 ± .92	17	3.6	4.5	4.1 ± .40	4	2.5	6.6	4.3 ± .81	24
20	1.4	2.1	1.6 ± .22	36	1.4	2.0	1.6 ± .26	6	1.4	2.3	1.7 ± .23	46
25	0.9	1.3	1.1 ± .11	54	0.9	1.4	1.1 ± .17	18	0.9	1.4	1.1 ± .12	98
30	0.5	1.0	0.8 ± .09	40	0.6	0.9	0.7 ± .07	14	0.5	1.0	0.8 ± .08	56
					(Deutonymph)							
15	2.9	6.5	4.6 ± .85	17	4.0	5.0	4.6 ± .42	4	2.9	6.5	4.6 ± .78	21
20	1.4	2.1	1.7 ± .20	36	1.3	2.0	1.6 ± .26	6	1.3	2.1	1.6 ± .21	42
25	0.9	1.3	1.1 ± .09	54	0.9	1.1	1.0 ± .06	18	0.9	1.3	1.1 ± .08	96
30	0.6	1.1	0.8 ± .16	40	0.5	1.2	0.9 ± .21	14	0.5	1.2	0.9 ± .17	54
					(Combined Immature Stages)							
15	16.4	24.5	19.6 ± 2.86	17	19.4	21.2	20.0 ± .83	4	16.4	24.5	19.7 ± 1.88	21
20	7.1	8.3	7.7 ± .38	36	7.2	8.7	8.0 ± 1.07	2	7.1	8.7	7.7 ± .41	38
25	4.7	5.5	5.1 ± .15	54	4.7	5.5	5.0 ± .21	18	4.7	5.5	5.0 ± .16	96
30	3.2	3.9	3.6 ± .23	40	3.3	3.9	3.7 ± .22	14	3.2	3.9	3.6 ± .23	54

N: Number of individuals observed.

The relationship between the temperature and the development of the egg, larva, protonymph, deutonymph, and combined immature stages of *A. citrifolius,* respectively, is shown in Figures 3 and 4. The logistic curve, with a sigmoid appearance, relates the velocity of development to the temperature throughout most of the range suitable for the development of a given insect (Davidson, 1944). However, between 15 °C and 30 °C, a straight line approximates the data for *A. citrifolius.* A cubic hyperbola relates satisfactorily the temperature to the developmental time of *A. citrifolius* (Figures 3, 4), since at high temperatures, the developmental period is not shortened proportionally. This temperature-developmental relationship already has been shown with several phytoseiid mites (Putman, 1962; Smith and Newsom, 1970a; Charlet and McMurtry, 1977).

Regression equations of the developmental period and of the velocity of development and its correlation coefficient (r), the calculated threshold temperature of development (t), and the thermal constant (k) corresponding to each stage are shown in Table 7.

The egg stage requires the most degree days, and the larval stage requires the least. Both the protonymphal and deutonymphal stages require similar amounts.

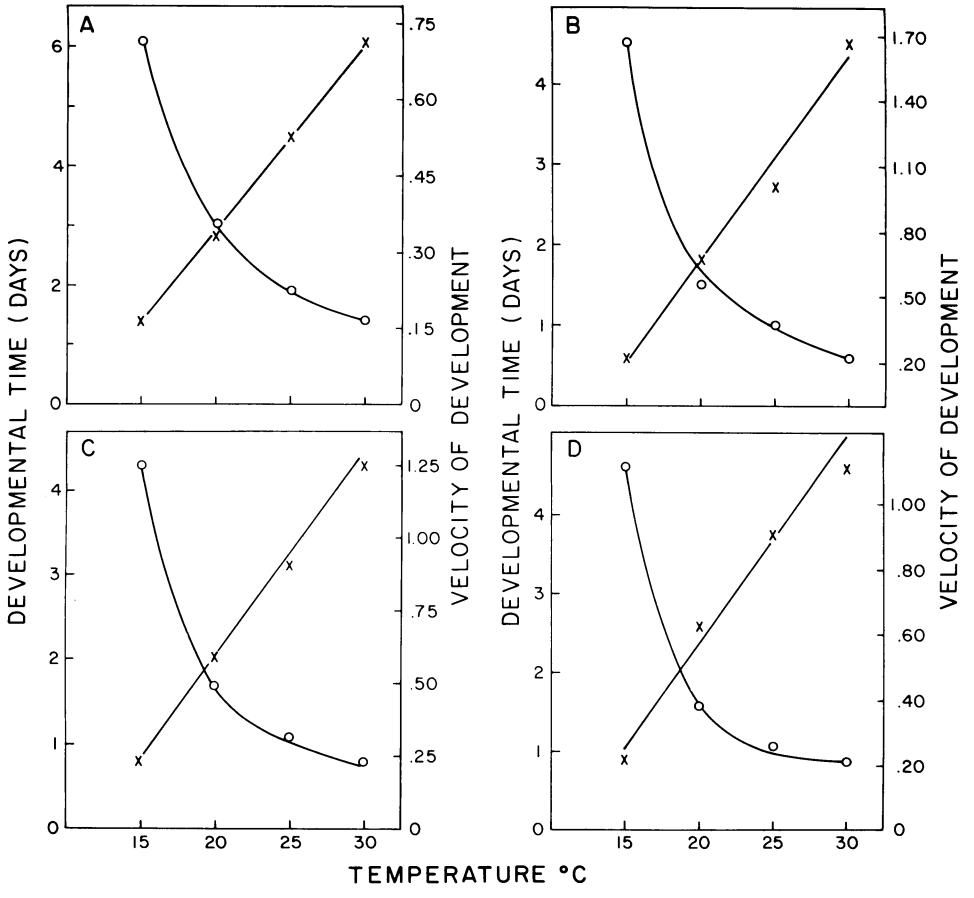

Fig. 3. Relationship between temperature and developmental time (circles) and velocity of development (crosses) of each immature stage of *A. citrifolius*. A: egg; B: larva; C: protonymph; D: deutonymph. Velocity of development = 1/developmental time (in days).

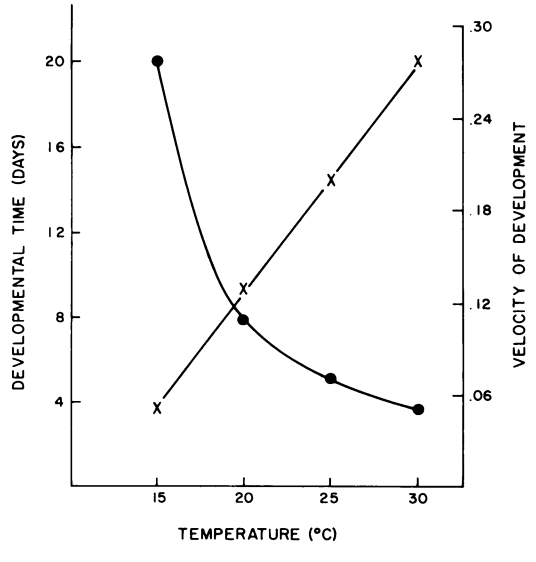

Fig. 4. Relationship between temperature and developmental time (circles) and velocity of development (crosses) of the combined immature stages of *A. citrifolius*. Velocity of development = 1/developmental time (in days).

TABLE 7

REGRESSION EQUATIONS OF DEVELOPMENTAL TIME (IN DAYS) AND VELOCITY OF DEVELOPMENT (1/DEVELOPMENTAL TIME IN DAYS) OF *A. CITRIFOLIUS* IN RELATION TO TEMPERATURE (y); CORRELATION COEFFICIENTS OF THE CURVES OF VELOCITY OF DEVELOPMENT (r); CALCULATED THRESHOLD TEMPERATURE OF DEVELOPMENT (t) AND THERMAL CONSTANT (k)

Stage	Regression equations: Developmental period (in days)	Regression equations: Velocity of development	r	t(°C)*	k** (degree days)
Egg	$y = 45.1036 - 4.7288x + 0.1751x^2 - 0.0022x^3$	$y = 0.03664x - 0.3916$	0.99	10.68	27.66
Larva	$y = 51.8510 - 6.0154x + 0.2372x^2 - 0.00312x^3$	$y = 0.0938x = 1.2050$	0.99	12.85	10.46
Protonymph	$y = 42.2881 - 4.7480x + 0.1832x^2 - 0.00237x^3$	$y = 0.07104x = 0.8284$	0.99	11.66	13.75
Deutonymph	$y = 47.8932 - 5.4023x + 0.2078x^2 - 0.00267x^3$	$y = 0.06392x - 0.7039$	0.98	10.88	14.66
Total immature stages	$y = 191.379 - 21.432x + 0.8258x^2 - 0.01067x^3$	$y = 0.01489x - 0.1712$	0.99	11.50	65.44

x: Temperature in °C.
*: Calculated at y = 0 is the regression equation of the velocity of development.
**: Calculated with the formula k = Developmental time in days (x − t).

Hamamura et al. (1976) presented similar results with *Phytoseiulus persimilis,* reporting thermal constants of 28.65, 36.65, and 65.79 degree days for the egg, motile young stages, and combined immature stages, respectively. From the data of Bravenboer (1959), it appears that *Typhlodromus longipilus* Nesbitt requires higher thermal constants for the egg and motile young stages than *A. citrifolius.* Tanigoshi et al. (1975) and Blommers (1976) presented developmental curves for *T. occidentalis* and *A. bibens,* respectively.

The threshold temperature of development of *A. citrifolius* seems to be between 10.68 °C and 12.85 °C. These values are very close to those determined by Hamamura et al. (1976) for *Phytoseiulus persimilis* (12 °C) and by Bravenboer (1959) for *Typhlodromus longipilus* (10 °C).

Oviposition and longevity

Durations (in days) of the preoviposition, oviposition, and postoviposition periods and longevity of *A. citrifolius* at 15, 20, 25, and 30 °C are shown in Table 8. The durations of these periods decreased with increasing temperatures. The preoviposition period

TABLE 8

DURATION (IN DAYS) OF PREOVIPOSITION, OVIPOSITION AND POSTOVIPOSITION PERIODS AND LONGEVITY OF ADULT FEMALES OF *A. CITRIFOLIUS* AT DIFFERENT TEMPERATURES

Temp. (C°)	N	Preoviposition (days) Min	Max	Mean ± SD	Oviposition (days) Min	Max	Mean ± SD	Postoviposition (days) Min	Max	Mean ± SD	Longevity (days) Min	Max	Mean ±
15	26	3.0	12.0	5.3 ± 2.3	19.0	55.0	40.1 ± 10.2	2.0	52.0	20.7 ± 15.3	37.0	103.0	66.0 ± 16.5
20	27	2.0	10.0	3.0 ± 1.7	15.0	58.0	33.5 ± 10.6	1.0	43.0	18.3 ± 13.4	25.0	86.0	54.8 ± 15.6
25	37	1.0	3.0	1.8 ± 0.6	11.0	34.0	23.68 ± 4.7	1.0	19.0	7.9 ± 4.2	22.0	44.0	33.5 ± 5.9
30	24	1.0	3.0	1.7 ± 0.6	10.0	33.0	16.8 ± 5.5	1.0	27.0	5.3 ± 6.4	13.0	44.0	23.8 ± 8.4

N: Number of individuals observed

varied from a mean of 5.3 days at 15 °C to 1.7 days at 30 °C, while the average oviposition period varied from 40.1 to 16.8 days. The postoviposition period varied greatly with temperature. Premature mortality seemed to be associated with the presence of precipitates, probably of guanine, frequently observed through the transparent cuticle as large white masses in the diverticula. The legs on the side of the body where the precipitate occurred could not move normally at times, and the female apparently died prematurely.

The oviposition period for *Typhlodromus occidentalis,* varying from 17.61 days at 18 °C to 9.47 days at 35 °C, was shorter than that of *A. citrifolius* (Tanigoshi et al., 1975). *Amblyseius brazilli,* another species in the *finlandicus* group, also had a shorter oviposition period than *A. citrifolius* (Elbenhawy, 1975b). At temperatures of 21 °C to 32 °C, the preoviposition and oviposition periods and longevity of *A. fallacis* varied from 2.2 to .75, 35 to 8.6 and 61.5 to 13.5 days, respectively, (Smith and Newsom, 1970a). Considerable variations in the postoviposition period have been reported (Elbadry and Elbenhawy, 1968a; Elbadry et al., 1968b; Amano and Chant, 1977).

Females of *A. citrifolius* were frequently observed mating during the oviposition period. The necessity of periodic mating to prevent premature cessation of oviposition has been shown for some species (Putman, 1962; McMurtry and Scriven, 1964a; Elbadry and Elbenhawy, 1968a; Knisley and Swift, 1971; Elbenhawy, 1974; Hamamura et al., 1976), whereas a single mating seems to be sufficient for continuous oviposition of other species (Lee and Davis, 1968; Laing, 1968, 1969).

Total number of eggs per female of *A. citrifolius* increased from a mean of 31.3 at 15 °C to 49.7 at 25 °C and decreased to a mean of 41.3 at 30 °C (Table 9). The average number of eggs per female of *A. citrifolius* seems to be within the range most commonly observed (Elbadry et al., 1968b; Zaher, Wafa, and Shehata, 1969; McMurtry et al., 1970; Tanigoshi & McMurtry, 1977). McMurtry, Huffaker and van de Vrie, (1970) indicated that the fecundity of species of the genus *Phytoseiulus* was higher than that of other genera, being in the range of 50 to 60 eggs per female. This was corroborated by the findings of Hamamura, Shinkaji, Ashihara (1976) and Amano and Chant (1977). High fecundity was also observed by Blommers (1976) for *A. bibens.* Species showing lower fecundity than *A. citrifolius* include *Typhlodromus occidentalis* (Tanigoshi et al., 1975) and *T. pini* (Charlet and McMurtry, 1977).

TABLE 9

FECUNDITY OF *A. CITRIFOLIUS* AT DIFFERENT TEMPERATURES

Temp. (°C)	No. females	Fecundity (Eggs/♀)		
		Min	Max	Mean ± SD
15	26	9.0	52.0	31.3 ± 11.8
20	27	21.0	69.0	40.9 ± 12.9
25	37	19.0	73.0	49.7 ± 12.1
30	24	20.0	62.0	41.3 ± 13.7

Average daily oviposition rates of *A. citrifolius* were 0.75, 1.25, 2.11, and 2.51 eggs per female at 15, 20, 25, and 30 °C, respectively. As a first approximation, a straight line of equation $y = 0.11 \times - 1.087$ satisfactorily relates temperature and daily rate of oviposition (Figure 5). However, the relationship may be more nearly represented by a sigmoid curve, as proposed by Blommers (1976) and as suggested by the data of Porres

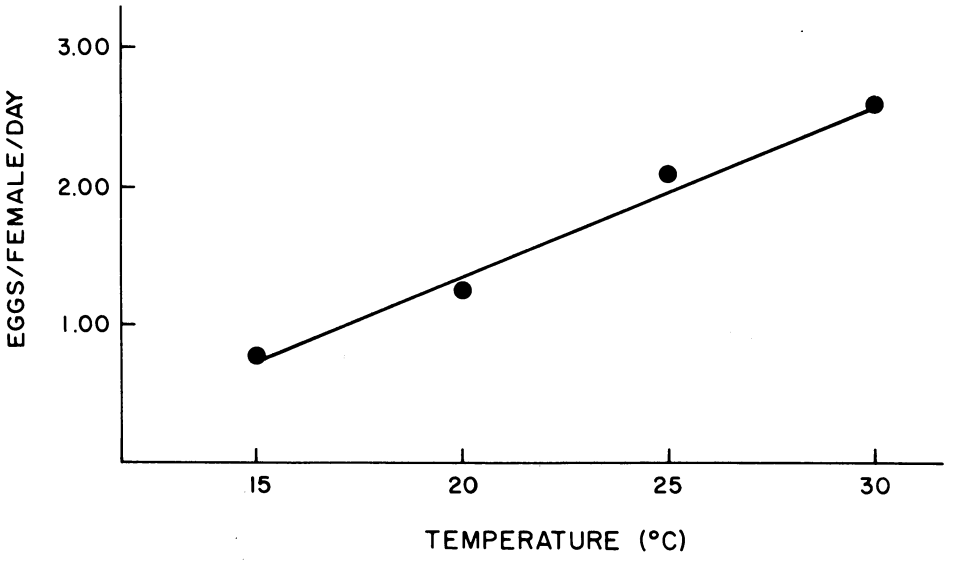

Fig. 5. Relationship between the average daily rate of oviposition of *A. citrifolius* and temperature. y = .122x − 1.087 r = .9912

Arreaga (1974). Apparently, there is considerable variation in oviposition rates between species of the *finlandicus* group. Rates recorded for *A. aleyrodis* (Elbadry, 1968) and *A. gossipi* (Elbadry and Elbenhawy, 1968a; Elbadry et al., 1968b) were similar to that of *A. citrifolius*. The oviposition rates for *A. rubini* (Swirski et al., 1967a), *A. hibisci* (Swirski et al., 1970; Porres Arreaga, 1974), *A. fructicolus* (Porres Arreaga, 1974), *A. brazilli* (Elbenhawy, 1975b), and *A. stipulatus* (Porres Arreaga, 1975; McMurtry, 1977) generally were lower.

Variation of the average daily oviposition rate of *A. citrifolius* in the course of the oviposition period is shown in Figure 6. The higher the temperature, the higher and

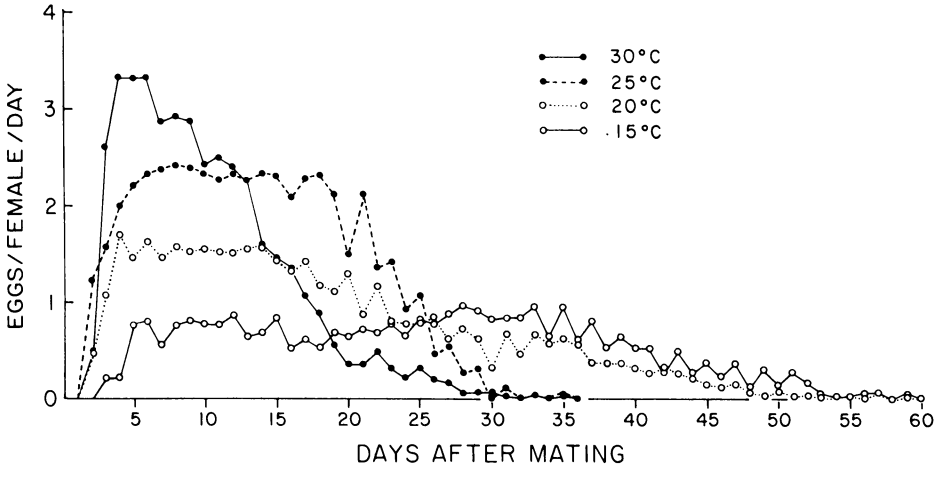

Fig. 6. Daily oviposition rate of *A. citrifolius*. Day zero = day of mating. Rate calculated on the basis of number of females at the beginning of the experiment.

sharper was the peak in the oviposition rate. Therefore, although at low temperatures the predator had lower daily oviposition rates, oviposition was maintained for longer periods. Similar results were obtained by McClanahan (1968) for *Phytoseiulus persimilis.*

Amblyseius citrifolius had longer oviposition periods and more gradual declines in oviposition rates than were reported for *Phytoseiulus persimilis* (McClanahan, 1968; Takafuji and Chant, 1976; Amano and Chant, 1977), and *A. fallacis* (McClanahan, 1968) at corresponding temperatures. Hamamura, Shinkaji, and Ashihara (1976) observed a slow decline of the oviposition rate of *P. persimilis* from a maximum of approximately five eggs per female per day on the 4th day to zero on the 22nd day. However, after reintroduction of males into the arenas, the oviposition rate increased again to more than 2 eggs per female per day on the 41st day, decreasing thereafter to zero on the 50th day. Insufficient periodic matings may account for the short oviposition period and the slow decline of the daily oviposition rate in some cases.

The percentage of survivorship of *A. citrifolius* from the mating time is shown in Figure 7. Mortality increased after most of the females stopped ovipositing; therefore, the daily oviposition rates obtained in considering the total number of females instead of the number of live females are practically the same, except during the last few days. Consequently, comparison of the data obtained for *A. citrifolius* with those for *Phytoseiulus persimilis* and *A. fallacis* can be made.

In the field, the physical conditions in the microenvironment affecting the biology of a mite species may not be the same as those of the macroenvironment. Wellington (1950) showed that the temperature of a leaf in relation to the temperature of the environment varied greatly, depending on various factors, including position of the leaf on the plant, season, cloudiness, wind and rain. Moreover, phytoseiid species usually oviposit in protected places where the danger of the egg being negatively influenced by harsh conditions is diminished. Lee and Davis (1968) reported that 82 percent of the eggs of *Typhlodromus occidentalis* were in protected areas along the central leaf rib and large subsidiary veins. McMurtry and Scriven (1965a) stated that *A. limonicus,* when confined on excised leaves, often laid eggs very close to the water-saturated Cellu-

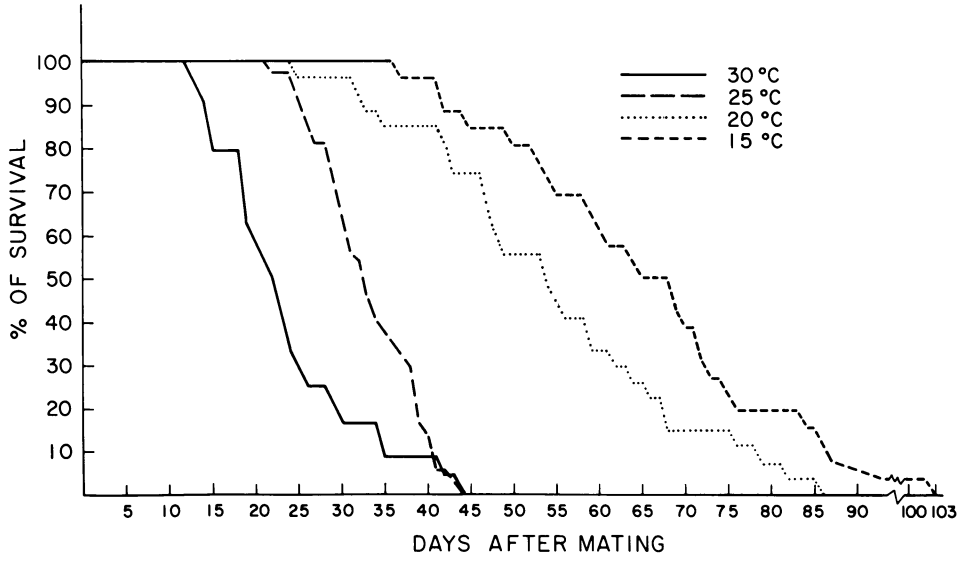

Fig. 7. Survivorship of *A. citrifolius* at four temperatures. Day zero = day of mating.

cotton barrier where the humidity probably approached the saturation point. The eggs of *Phytoseiulus macropilis* were deposited singly on the webs of *Tetranychus tumidus* or in the grooves formed by the veins of the leaves (Prasad, 1967). *Amblyseius umbraticus* generally oviposit near leaf veins or in the webbing of *Tetranychus urticae* Koch (Knisley and Swift, 1971). *Amblyseius citrifolius* was also observed to search for protected places to oviposit. Presumably this behavior would increase the survival of the eggs under adverse field conditions.

Influence of Different Levels of Humidity on Egg Hatching at Different Temperatures

Eggs of *A. citrifolius* that did not hatch became shrivelled, as observed with other species of Phytoseiidae (McMurtry and Scriven, 1965a; McMurtry, Mahr, and Johnson, 1976).

The daily percentage of eclosion from the day of oviposition to the day when all the eggs were hatched or shrivelled, at each temperature and relative humidity, is shown in Figure 8. No hatching occurred at 20 percent RH.

The higher the temperature, the shorter was the period of time from oviposition to

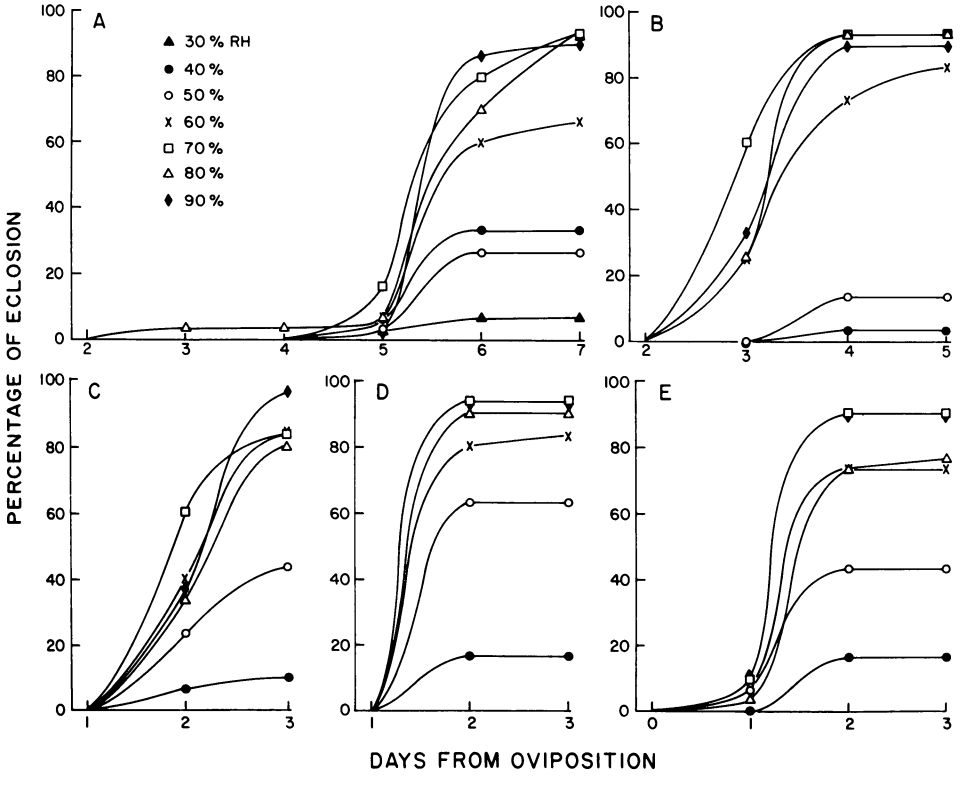

Fig. 8. Daily percentage of eclosion of *A. citrifolius* at each temperature and relative humidity. A: 16 °C; B: 20 °C; C: 24 °C; D: 28 °C; E: 32 °C.

maximum eclosion, regardless of the relative humidity tested. At a given temperature, relative humidity had little effect on the duration of the egg stage. Similar results were reported by Johnson (1940a) and Howe (1956) with insect species. Hatching occurred 6 to 7, 3 to 5, 2 to 3, 2 to 3, and 1 to 3 days after oviposition at 16, 20, 24, 28, and 32 °C, respectively.

The maximum rates of egg shrivelling tended to occur earlier at the higher temperatures. At 20 percent relative humidity and at 16, 20, 24, 28, and 32 °C, maximum rates of egg shrivelling occured 6, 3, 3, 3, and 2 days after oviposition, respectively.

The maximum percentages of eclosion at the different combinations of temperature and relative humidity are shown in Figure 9. At 30 percent relative humidity, egg hatching occurred only at 16 °C, which agrees with the fact that 30 percent relative humidity at higher temperatures corresponds to greater saturation deficits. The highest rates of eclosion were attained at the highest relative humidities (up to 90 percent relative humidity). High humidities also are more favorable for eggs of other phytoseiid mites (McMurtry and Scriven, 1965a; Knisley and Swift, 1971; McMurtry et al., 1976).

Apparently, *A. citrifolius* requires higher relative humidity for egg hatching than *A. hibisci* but tolerates lower relative humidities than *A. limonicus* and the Netherlands stock of *A. potentillae* (Garman). The Italy stock of *A. potentillae* showed responses most similar to *A. citrifolius* (McMurtry and Scriven, 1965a; McMurtry, Mahr, and Johnson, 1976).

Saturation deficit seems to be a more appropriate index than relative humidity in estimating the effect of atmospheric moisture on insects (Birch, 1944). Wellington (1949), however, discussed the drawback in utilizing saturation deficit as compared to using the "rate of evaporation." Bursell (1974) suggested that easily measurable properties of the environment such as saturation deficit often proves to be perfectly satisfactory, at least as a first approximation to explain the effect of moisture.

The saturation deficit is the difference between the saturated vapor pressure and the actual vapor pressure at a given temperature (Mellanby, 1935; Bursell, 1974). Silveria Neto et al. (1976) commented on saturation deficit (s.d.) and gave the following equa-

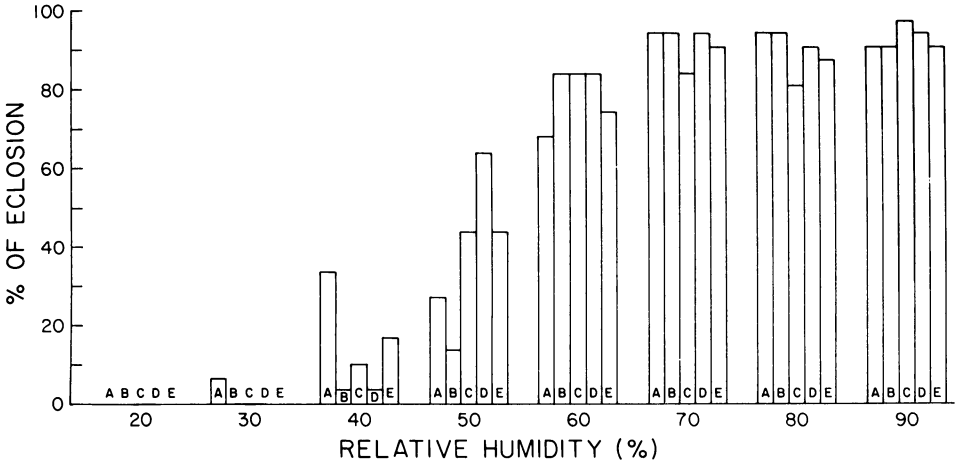

Fig. 9. Maximum percentage of eclosion of *A. citrifolius* at each temperature and relative humidity. A: 16 °C; B: 20 °C; C: 24 °C; D: 28 °C; E: 32 °C.

tions for its calculation.

$s.d. = es - ea$

where *es* represents the saturated vapor pressure (directly related to the temperature), *ea*, the actual vapor pressure, and *RH*, the relative humidity.

$$ea = \frac{(RH)\ (es)}{100}$$

By these two equations, it can be deduced that:

$$s.d. = es\ (1 - \frac{RH}{100})$$

An example of the relationship between relative humidity and saturation deficit at two temperatures is shown in Figure 10. At 0 percent relative humidity, the saturation deficit is maximum and equal to the saturated vapor pressure. The higher the temperature, the greater the rate of decrease of the saturation deficit with increasing relative humidity. Thus, the higher the relative humidity, the closer are the values of saturation deficit at different temperatures. The extreme is reached at 100 percent relative humidity, where the saturation deficit is minimum and equal to zero, regardless of the temperature.

The eclosion rates of the larvae of *A. citrifolius* in relation to saturation deficit at the five different temperatures are shown in Figure 11. The eclosion curves are quite close to each other in the "low" range of saturation deficit (up to 4 to 8 mm Hg), i.e., at the highest values of relative humidity. However, the eclosion curves diverge at higher saturation deficits (over 4 to 8 mm Hg) and, at a given saturation deficit, the percentage of eclosion is higher at higher temperatures.

These data suggest that high temperatures become more favorable for egg hatching than low temperatures, as the saturation deficit increases.

Evans (1934) observed a linear relationship between the amount of water lost by the eggs of *Lucilia sericata* Meig. (Diptera) and the saturation deficit. Similar evidence was

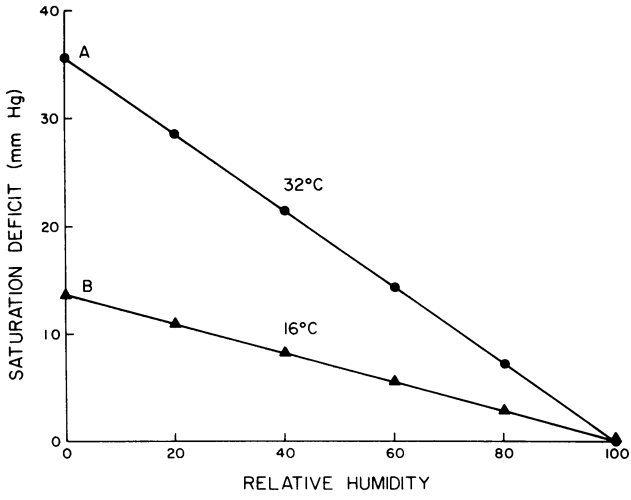

Fig. 10. Relationship between relative humidity and saturation deficit at 2 temperatures. A: saturated vapor pressure at 32 °C. B: saturated vapor pressure at 16 °C.

presented by Mellanby (1935) and Johnson (1940b) for adult insects. Evans (1934) has also shown that the rate of loss of water by the eggs increased with increased temperature, at constant levels of saturation deficit. Assuming that the same phenomena occur with *A. citrifolius* and considering the results shown in Figure 8, the following hypothesis is suggested: at higher saturation deficits, the net amount of water loss in the egg stage is less at higher temperatures, because the duration of the stage is shorter. Therefore, the eclosion rate is higher. However, at the lower saturation deficits (4 to 8 mm Hg) the water loss is not critical at any of the temperatures tested and temperature has little or no effect on eclosion in the range of 16 °C to 32 °C (Fig. 11).

Evans (1934) and Birch (1944) observed that for any particular value of saturation deficit multiplied by time, the mortality rate of insect eggs increased with temperature.

Figure 12 shows the relationship between the percentage of egg shrivelling of *A citrifolius* and the product of the saturation deficit and the average duration (in days) of the egg stage at the respective saturation deficit at each temperature. The positions of the curves for 16, 20, and 24 °C seem to agree with the results of Evans (1934) and Birch (1944). The curves for 28 °C and 32 °C are not in the expected positions, possibly because the average duration of the egg stage was overestimated because the number of eggs hatched or shrivelled was observed just once a day.

A possible explanation for the higher mortality observed at higher temperatures at

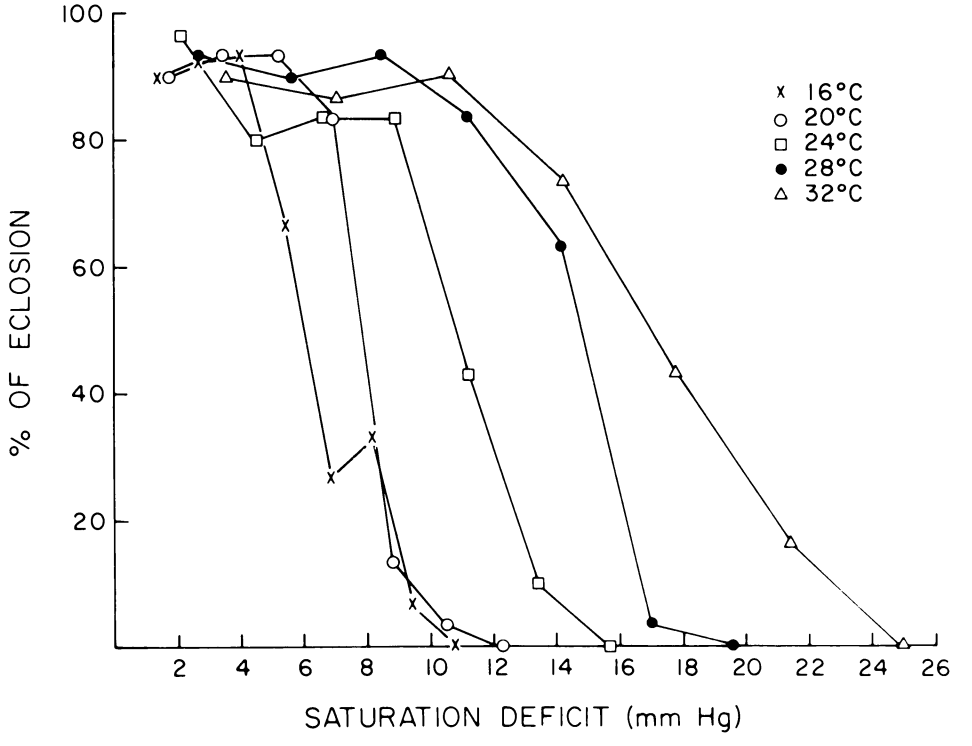

Fig. 11. Percentage of eclosion of the larvae of *A. citrifolius* at 16, 20, 24, 28, and 30 ° at different saturation deficits.

any particular value of saturation deficit X time could be as follows:

If

$te_1 < te_2$

where te = temperature, then

$s.d._1 < s.d._2$, $ti_1 > ti_2$ and $r_1 < r_2$, where

$s.d.$ = saturation deficit

ti = developmental time

r = rate of water loss (water lost/unit of time)

If, however,

$\frac{r_2}{r_1} > \frac{ti_1}{ti_2}$ then $r_2 ti_2 > r_1 ti_1$, or in other words,

the total amount of water lost at the same value of saturation deficit X time is higher at higher temperatures. However, it is possible that the depletion of other components could occur in the egg before the depletion of water at higher temperatures. Chapman (1971) stated that, in the pupae of *Glossina* sp. (Diptera), less fat was utilized at 22 to 24°C than at other temperatures. At higher temperatures the consumption of fat increased without any corresponding reduction in the pupal period, while at lower temperatures, the pupal period lengthened considerably with no corresponding decrease in fat consumption.

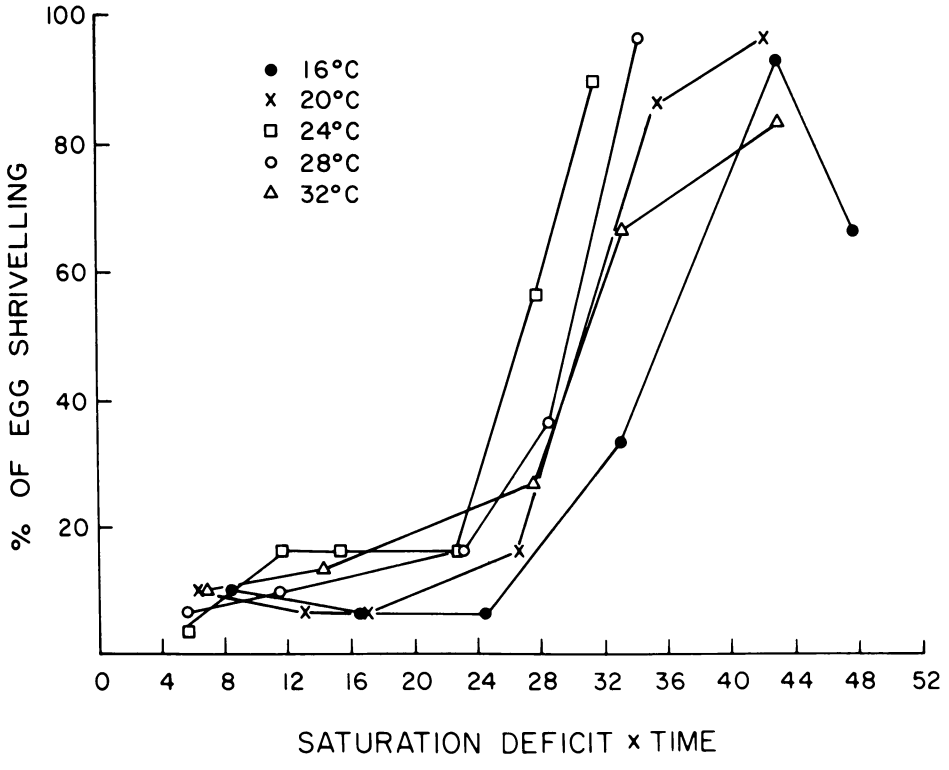

Fig. 12. Egg shrivelling of *A. citrifolius* at different values of saturation deficit X time (in days) at various temperatures.

Suitability of Different Kinds of Food

The purpose of this part of the study was to evaluate the suitability of three species of phytophagous mites, viz., *Tetranychus pacificus, T. cinnabarinus* and *Panonychus citri,* six kinds of pollen and a species of diaspidid scale insect, *Hemiberlesea latiniae,* as food for *A. citrifolius,* using the oviposition rate and the level of survival as indexes.

The average oviposition rate (eggs/female/day) for *A. citrifolius* reared on each kind of food is shown in Figure 13. The daily oviposition rate was calculated by dividing the number of eggs deposited in each arena by 10, regardless of the actual number of females in the arena at a given day.

Rate of survivorship of *A. citrifolius* on each kind of food, on the fourth, eighth, and eleventh days is shown in Table 10.

Five categories of foods can be identified in relation to their decreasing suitability for oviposition of *A. citrifolius:* 1) *Pyrus kawakamii, Malephora crocea* and avocado pollen, *Tetranychus pacificus* (eggs + larvae) + *M. crocea* and *T. pacificus* (all stages); 2) *T. pacificus* (eggs + larvae); 3) *Panonychus citri* and *T. cinnabarinus*; 4) *Hemiberlesia lataniae*; and 5) citrus, *Eucalyptus* and *Pinus* (early) and (late) pollen (Fig. 13).

Three categories of foods can be identified in relation to decreasing survivorship of *A. citrifolius:* 1) *Tetranychus pacificus* (all stages), *T. pacificus* (eggs + larvae) + *Malephora crocea* pollen, *M. crocea, Pyrus kawakamii,* and avocado pollens, and *T. pacificus* (eggs + larvae); 2) *P. citri, T. cinnabarinus, H. lataniae* and citrus pollen; and 3) *Eucalyptus* and *Pinus* (early) and (late) pollen (Table 10).

Pollen of *Pyrus kawakamii, Malephora crocea,* and avocado were the best foods. These observations agree with the statement that species in the *finlandicus* group are pollen feeders (McMurtry, 1977).

McMurtry and Scriven (1964b) observed that the oviposition rate of *A. hibisci* was significantly lower on spider mites than on pollen. Other authors have also shown the superiority of pollen as food (Swirski, Amitai, and Dorzia, 1967a, b; Elbadry and Elbenhawy, 1968b; Swirski and Dorzia, 1968; Knisley and Swift, 1971, Porres Arreaga, 1974; Elbenhawy, 1975b; McMurtry, 1977). However, spider mites are more favorable than

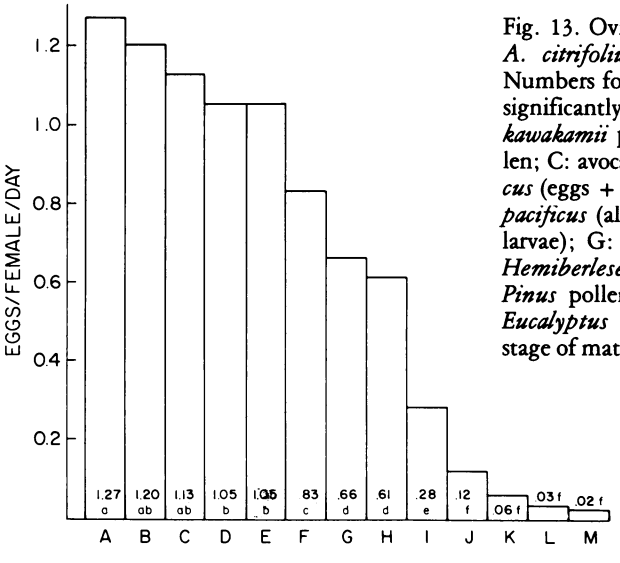

Fig. 13. Ovipositon rate (egg/female/day) of *A. citrifolius* fed different kinds of food. Numbers followed by the same letter are not significantly different at 5% level. A: *Pyrus kawakamii* pollen; B: *Malephora crocea* pollen; C: avocado pollen; D: *Tetranychus pacificus* (eggs + larvae) + *M. crocea* pollen; E: *T. pacificus* (all stages); F: *T. pacificus* (eggs + larvae); G: *P. citri;* H: *T. cinnabarinus;* I: *Hemiberlesea lataniae,* J: citrus pollen; K: *Pinus* pollen (late stage of maturation); L: *Eucalyptus* pollen; M: *Pinus* pollen (early stage of maturation).

TABLE 10

PERCENT (± SD) SURVIVAL OF *A. CITRIFOLIUS* ON THE FOURTH, EIGHTH AND ELEVENTH DAYS FED DIFFERENT KINDS OF FOOD

Source of Food	Days from beginning of the test		
	4	8	11
T. pacificus (all stages)	97.50 ± 5.00	95.00 ± 5.77	*a95.00 ± 5.77
T. pacificus (eggs + larvae) + *M. crocea* pollen	97.50 ± 5.00	95.00 ± 5.77	a90.00 ± 8.16
M. crocea pollen	95.00 ± 10.00	90.00 ± 14.14	a90.00 ± 14.14
P. kawakamii pollen	95.00 ± 5.77	92.50 ± 9.57	a90.00 ± 8.16
Avocado pollen	95.00 ± 5.77	92.50 ± 5.00	a87.50 ± 5.00
T. pacificus (eggs & larvae)	92.50 ± 9.57	85.00 ± 10.00	ab82.50 ± 15.00
P. citri (all stages)	82.50 ± 5.00	75.00 ± 12.91	bc65.00 ± 10.00
T. cinnabarinus (all stages)	90.00 ± 8.16	75.00 ± 5.77	c60.00 ± 8.16
H. lataniae (all stages)	92.50 ± 9.57	77.50 ± 12.58	c60.00 ± 14.14
Citrus pollen	87.50 ± 5.00	67.50 ± 5.00	c45.00 ± 17.32
Pinus pollen (**)	52.50 ± 17.08	20.00 ± 16.33	d 5.00 ± 5.77
Eucalyptus pollen	32.50 ± 12.58	2.50 ± 5.00	d 2.50 ± 5.00
Pinus pollen (***)	32.50 ± 9.57	5.00 ± 5.77	d 0.00 ± 0.00

(*) Numbers preceded by the same letter are not significantly different at 5% level.
(**) Late stage pollen from anthers open in the field.
(***) Pollen in early stage of maturation from anthers almost open.

pollen for some species (Chant, 1959; McMurtry and Scriven, 1964a; Zaher, Wafa, and Shehata, 1969; McMurtry et al., 1970; McMurtry, 1977). Putman (1962) considered that the longer developmental time of *Typhlodromus caudiglans* on pollen could be caused by the greater amount of time and energy expended in feeding on the minute pollen grains of peach, *Chenopodium,* or *Setaria,* that were pierced individually and the contents sucked out.

Amblyseius citrifolius apparently was not hindered by the heavey webbing produced by *Tetranychus pacificus* on lima bean leaves. *Amblyseius hibisci* and *A. limonicus* were hindered by the webbing produced by *T. cinnabarinus* (McMurtry and Scriven, 1964b, 1965a). McMurtry, Huffaker, and van de Vrie, (1970) presented other examples of phytoseiids hindered by webbing, as well as of those favored by it.

Although *Hemiberlesia lataniae* crawlers and citrus pollen were relatively poor sources of food for reproduction, they were reasonably good survival foods for *A. citrifolius* (45 and 60 percent respectively, after 11 days from the beginning of the experiment). *Eucalyptus* and *Pinus* (early) and (late) pollen were not good foods for either reproduction or survival of *A. citrifolius.*

Several phytoseiids have been reported to feed on species of other arthropod groups, mainly Homoptera and Lepidoptera (McMurtry and Scriven, 1964a; McMurtry and Johnson, 1965; McMurtry, 1963, 1977; Teich, 1966; Swirski, Amitai, and Dorzia, 1967a, b, 1970; Elbadry et al., 1968a; Swirski and Dorzia, 1968; Knisley and Swift, 1971). Of seven different sources of food offered to *A. aleyrodis,* nymphs of *Bemisia tabaci* (Gennadius) were the best (Elbadry, 1968). In general, the availability of a secondary source of food enhances the ability of a predator to survive during periods when the population of its primary prey is at an unfavorably low level. This makes it possible for the predator population to increase early in the season, before the prey population

reaches high levels (McMurtry and Johnson, 1965). Sometimes, the presence of a secondary source of food results in more effective control of the prey (Collyer, 1964; McMurtry and Scriven, 1966a, 1966b, 1968). On the other hand, Putman and Herne (1964) suggested that an increasing population of the eriophyid mite, *Aculus cornutus* (Banks) resulted in an increase in the population of *Panonychus ulmi* by releasing the predation pressure of *Typhlodromus caudiglans* on the latter.

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