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

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ABSTRACT

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. The 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. The duration of the quiescent state ranged from ca. 9.7 hr to 11.3 hr.

Continuous observations on behavior indicated that more than 80% of the time in the postembryonic stages was spent resting. The 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.

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. The 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. The 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 foods for oviposition and survival of A. citrifolius. T. pacificus (eggs + larvae) also was one of the best for survivorship of the predator.

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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. A. citrifolius used in this work originated from material collected by the junior author in 1975 from citrus groves in Tatui-SP-Brazil.

A. 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 et al., 1970). The generic concepts of Chant (1965) are followed here. Denmark & Muma (1970) stated that there were about 40 described species in the finlandicus group, and that the group is world-wide in distribution on trees and shrubs. At present, there are more than 70 described species.

Denmark & 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

A. citrifolius was reared by the method described by McMurtry & Scriven (1975) using a standard unit of a 20x20-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 & McMurtry (1971) and pollen of *Malephora crocea* (Jacq.), extracted by the method described by McMurtry & 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% relative humidity.

Arenas of Lemon Leaves

The 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 (Figure 1).

Temperature Cabinets

The temperature cabinets were modified compact refrigerators (Platner et al., 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 120X. Individuals in each stage were isolated in arenas of lemon leaves and held in a room maintained at 25±3°C and 50+10% 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 3 individuals were observed concomitantly. Two sets of 3 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 (3 sets of 3 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, 20-30 prey larvae were main-

tained 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 the 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 the 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. The predators were fed an abundance of eggs and larvae of T. pacificus every fourth day. The clumps of prey eggs were scattered on the leaf surfaces. Thus, the 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%, 20±1°C and 80±10%, 25±1°C and 85±10% and 30±1°C and 85±10%. Variable numbers of individuals were utilized in each set of conditions. To determine the duration of each stage, observations were made every 4-6 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

The 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% 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 & 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 watchglasses held over the solution by a polyurethane, perforated, circular support fitted tightly into the container at some distance from the solution surface (McMurtry et al., 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.

The watchglasses were removed from the container and the eggs examined under a dissecting microscope once daily until hatching or shrivelling occurred. The 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% relative humidity. There were 4 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 the 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 Hemiberlesea 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 2 threads, providing the females with a place to oviposit and rest.

Foods were supplied as follows: 1) T. 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 & 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) H. 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 & Swift (1971) for A. umbraticus (Chant), and Lee & Davis (1968) for T. 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 P. 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 T. occidentalis showed that the embryonic appendages were developed late in the stage (Lee & Davis, 1968).

The Z_5 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 P. 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 & Davis (1968) stated that the lapse of time from the initial splitting of the egg of T. 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_5), 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 2 pairs of legs, the first pair of legs being used mostly as sensory structures, moving actively when the mite walks. Lee & Davis (1968) stated that the larvae of T. 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 & Davis, 1968; Swirski et al., 1967a; Swirski et al., 1967b; Swirski & Dorzia, 1968; Takafuji & Chant, 1976). Occasionally, however, individuals of certain species may molt to the protonymphal stage without feeding (Ballard, 1954; Smith & Newsom, 1970b; Burnett, 1971; Amano & Chant, 1977). Other species do not seem to feed in the larval stage (Dosse, 1955, 1958; Laing, 1968, 1969; Takafuji & Chant, 1976; Amano & Chant, 1977; Smith & Summers, 1949; Prasad, 1967; McMurtry & Scriven, 1964a; Blommers, 1976; Croft & Jorgensen, 1969; Charlet & McMurtry, 1977). McMurtry et al. (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 (T. pacificus) by any part of the body. Burrell & 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 et al. (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 T. caudiglans 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 & Chant, 1966b; Blommers & 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 3 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 2 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 3 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 equi-distantly 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 T. occidentalis (Lee & 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 P. macropilis (Prasad, 1967), P. persimilis (Laing, 1968) and A. umbraticus (Knisley & Swift, 1971). Conversely, Lee & Davis (1968) reported that T. 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 & Davis (1968) observed that quiescent larvae of T. occidentalis remain in small depressions in the rearing cage walls, usually motionless and not feeding during this time. P. 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 & 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

The 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% of its time in resting. The longest and the shortest percentage of time in walking were spent by the protonymphs and the adults, respectively. Sandness & 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.

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 & McMurtry (1972) for T. occidentalis feeding on the same prey.

Several phytoseiid species reportedly prefer the larval or the early nymphal stages to eggs of tetranychids (Burrell & McCormick, 1964; McMurtry & Scriven, 1964a; Elbadry et al., 1968a; Zaher et al., 1969; Croft & McMurtry, 1972; Takafuji & Chant, 1976). Other species, however, apparently show some preference for the egg stage (Smith & Summers, 1949; Prasad, 1967; Burnett, 1971; Blommers & Van Etten, 1975; Blommers, 1976; Takafuji & 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 and between the number of prey consumed by the protonymphs and the deutonymphs, there was a trend of higher to lower prey consumption by the protonymphs (17.2) deutonymphs (12.0) 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 & Davis, 1968; Laing & Huffaker, 1969; Zaher et al., 1969; Knisley & Swift, 1971; Blommers, 1976; Takafuji & 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 den-

sities. Other workers have shown that males of some species may also have a similar trend in prey consumption (Elbadry et al., 1968a; Tanigoshi & 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 & Zaher, 1961), T. pyri (Herbert, 1961) and I. degenerans (Takafuji & 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 2 of the 6 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 & Chant (1966a) studied the number of repeat feedings of females of P. 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 & 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 & Summers, 1949; Ballard, 1954; Bravenboer, 1959; Mori & Chant, 1966a; Prasad, 1967; Lee & Davis, 1968). Sandness & McMurtry (1972) found that the hunger level of A. largoensis directly affects the time spent feeding on individual prey.

Development, Oviposition and Longevity At Different Temperatures

Development. The 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 & Davis, 1968; Laing, 1969), Phytoseiulus persimilis (Laing, 1968), Amblyseius umbraticus (Knisley & Swift, 1971) and A. brazilli (Elbenhawy, 1975b). Amano & 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 & 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 Amblyseius 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 & 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).

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 tem-

perature-developmental relationship already has been shown with several phytoseiid mites (Putman, 1962; Smith & Newsom, 1970a; Charlet & McMurtry, 1977).

The 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.

Hamamura et al. (1976) presented similar results with P. 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 Amblyseius 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 P. persimilis (12°C) and by Bravenboer (1959) for T. longipilus (10°C).

Oviposition and Longevity

The 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 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 T. 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). A. 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 Amblyseius fallacis varied from 2.2 to .75, 35 to 8.6 and 61.5 to 13.5 days, respectively, (Smith & Newsom, 1970a). Considerable variations in the postoviposition period have been reported (Elbadry & Elbenhawy, 1968a; Elbadry et al., 1968b; Amano & 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 & Scriven, 1964a; Elbadry & Elbenhawy, 1968a; Knisley & Swift, 1971; Elbenhawy, 1974; Hamamura et al., 1976) whereas a single mating seems to be sufficient for continuous oviposition of other species (Lee & Davis, 1968; Laing, 1968, 1969).

The 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 et al., 1969; McMurtry et al., 1970; Tanigoshi & McMurtry, 1977). McMurtry et al. (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 et al. (1976) and Amano & Chant (1977). High fecundity was also observed by Blommers (1976) for A. bibens. Species showing lower fecundity than A. citrifolius include T. occidentalis (Tanigoshi et al., 1975) and T. pini (Charlet & McMurtry, 1977).

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 $y = 0.11 x - 1.087$ 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 Arreaga (1974). Apparently, there is considerable variation in oviposition rates between species of the finlandicus group. Rates recorded for Amblyseius aleyrodis (Elbadry, 1968) and A. gossipi (Elbadry & Elbenhawy, 1968a; Elbadry et al., 1968b) were similar to that of A. citrifolius. The oviposition rates for Amblyseius 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.

The 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 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 McClanhan (1968) for P. persimilis.

A. citrifolius had longer oviposition periods and more gradual declines in oviposition rates than were reported for P. persimilis (McClanhan, 1968; Takafuji & Chant, 1976; Amano & Chant, 1977) and A. fallacis (McClanhan, 1968) at corresponding temperatures. Hamamura et al. (1976) observed a slow decline of the oviposition rate of P. persimilis from a maximum of approximately 5 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 P. 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 & Davis (1968) reported that 82% of the eggs of Typhlodromus occidentalis were in protected areas along the central leaf rib and large subsidiary veins. McMurtry & Scriven (1965a) stated that Amblyseius limonicus, when confined on excised leaves, often laid eggs very close to the water-saturated cellucotton® 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 & Swift, 1971). A. 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.

The 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 & Scriven, 1965a; McMurtry et al., 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% RH.

The higher the temperature, the shorter was the period of time from oviposition to 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 in 6-7, 3-5, 2-3, 2-3, and 1-3 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% relative humidity and at 16, 20, 24, 28, and 32°C, maximum rates of egg shrivelling occurred 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% relative humidity, egg hatching occurred only at 16°C, which agrees with the fact that 30% 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% relative humidity). High humidities also are more favorable for eggs of other phytoseiid mites (McMurtry & Scriven, 1965a; Knisley & Swift, 1971; McMurtry et al., 1976).

Apparently, A. citrifolius requires higher relative humidity for egg hatching than A. hibisci but tolerates lower relative himidities than A. limonicus and the Netherlands stock of Amblyseius potentillae (Garman). The Italy stock of A. potentillae showed responses most similar to A. citrifolius (McMurtry and Scriven, 1965a; McMurtry et al., 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). Silveira Neto et al. (1976) commented on saturation deficit (s.d.) and gave the following equations 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 2 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 2 temperatures is shown in Figure 10. At 0% 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% 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 5 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 4-8 mm Hg), i.e., at the highest values of relative humidity. However, the eclosion curves diverge at higher saturation deficits (over 4-8 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 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 (4-8 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 (Figure 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 over-estimated 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 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 $r_1 \leq r_2$, where

s.d. = saturation deficit

ti = developmental time

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

If, however,

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

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 22-24°C than at other temperatures. At higher temperatures the consumption of fat increased without any corresponding reduction in the pupal period, while at lower tempertures the pupal period lengthened considerably with no corresponding decrease in fat consumption.

Suitability of Different Kinds of Food

The purpose of this part of the study was to evaluate the suitability of 3 species of phytophagous mites, viz., Tetranychus pacificus, T. cinnabarinus and Panonychus citri, 6 kinds of pollen and a species of diaspidid scale insect, Hemiberlesea lataniae, 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.

The 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) P. kawakamii, M. crocea and avocado pollen, T. pacificus (eggs + larvae) + M. crocea and T. pacificus (all stages); 2) T. pacificus (eggs + larvae); 3) P. citri and T. cinnabarinus; 4) H. lataniae; and 5) citrus, Eucalyptus and Pinus (early) and (late) pollen (Figure 13).

Three categories of foods can be identified in relation to decreasing survivorship of A. citrifolius: 1) T. pacificus (all stages), T. pacificus (eggs + larvae) + M. crocea pollen, M. crocea, P. kawakamii, and avocado pol-

lens, 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 P. kawakamii, M. 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 & Scriven (1964b) observed that the oviposition rate of Amblyseius hibisci was significantly lower on spider mites than on pollen. Other authors have also shown the superiority of pollen as food (Swirski et al., 1967a, b; Elbadry & Elbenhawy, 1968b; Swirski & Dorzia, 1968; Knisley & Swift, 1971; Porres Arreaga, 1974; Elbenhawy, 1975b; McMurtry, 1977). However, spider mites are more favorable than pollen for some species (Chant, 1959; McMurtry & Scriven, 1964a; Zaher et al., 1969; McMurtry et al., 1970; McMurtry, 1977). Putman (1962) considered that the longer developmental time of T. 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.

A. citrifolius apparently was not hindered by the heavy webbing produced by T. pacificus on lima bean leaves. A. hibisci and Amblyseius limonicus were hindered by the webbing produced by T. cinnabarinus (McMurtry & Scriven, 1964b, 1965a). McMurtry et al. (1970) presented other examples of phytoseiids hindered by webbing, as well as of those favored by it.

Although H. 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%, 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 & Scriven, 1964a; McMurtry & Johnson, 1965; McMurtry, 1963, 1977; Teich, 1966; Swirski et al., 1967a, b, 1970; Elbadry et al., 1968a; Swirski & Dorzia, 1968; Knisley & Swift, 1971). Of 7 different sources of food offered to Amblyseius 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 & Johnson, 1965). Sometimes, the presence of a secondary source of food results in more effective control of the prey (Collyer, 1964; McMurtry & Scriven, 1966a, 1966b, 1968). On the other hand, Putman & 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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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.

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.

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
Protonymph	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.

Table 4

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

Stage	Replicate						Mean
	1	2	3	4	5	6	
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 1	2	3	4	5	6	Mean* ± SD
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.

Table 6

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

Temp.	Female				Male				Female & Male			
(°C)	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

Table 6 (Cont'd)

Temp.	Female				Male				Female & Male			
(°C)	Min	Max	Mean±SD	N	Min	Max	Mean±SD	N	Min	Max	Mean±SD	N
					(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.

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		r	t(°C)*	k**
	Developmental period (in days)	Velocity of development			(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	$y = 51.8510-6.0.54x + 0.2372x^2 - 0.00312x^3$	$y = 0.0938x=1.2050$	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).

Table 8

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

Temp.		Preoviposition (days)			Oviposition (days)			Postoviposition (days)			Longevity (days)		
(°C)	N	Min	Max	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean±SD
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

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

Table 10

PER CENT (±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.

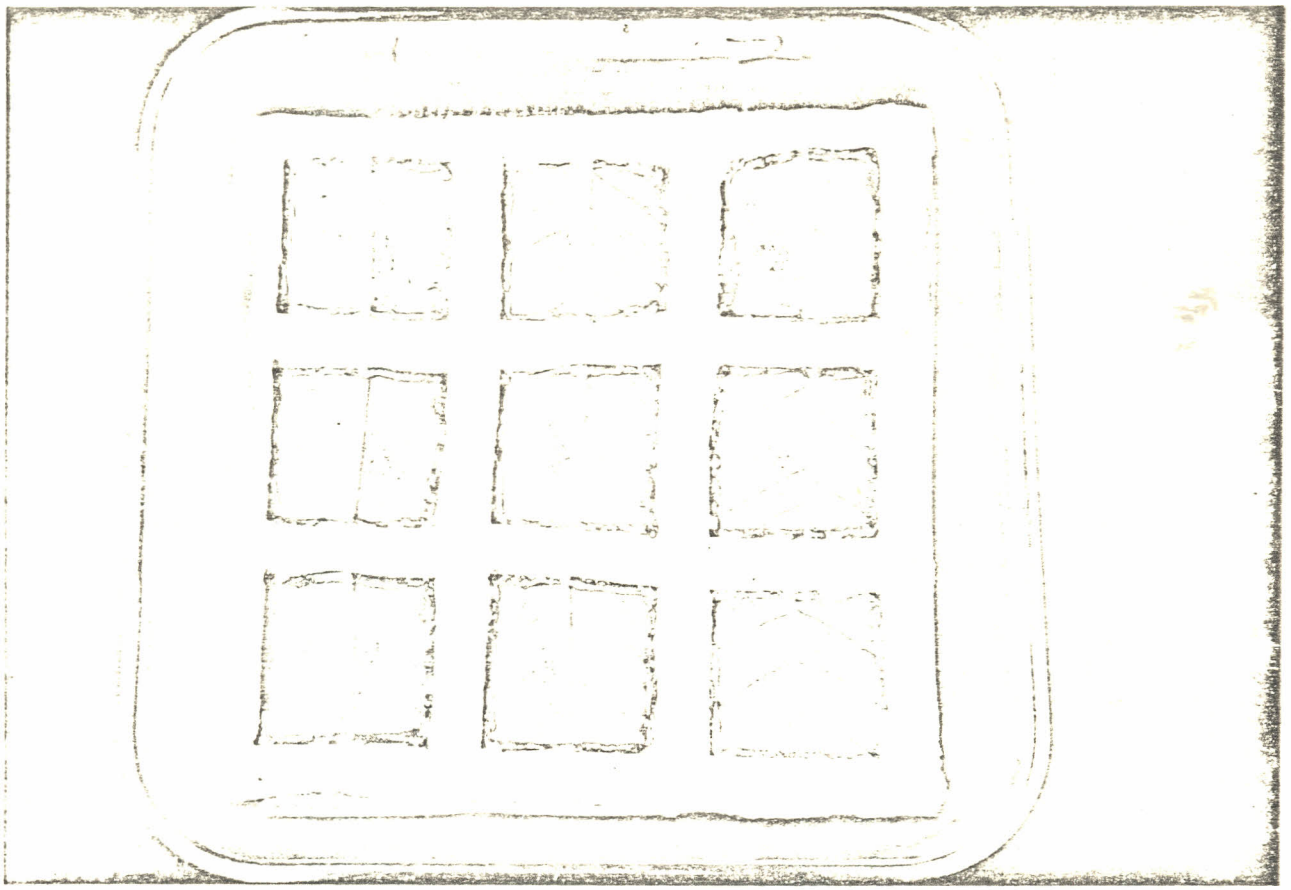

Figure 1. Arenas of lemon leaves utilized in the studies of the biology of A. citrifolius.

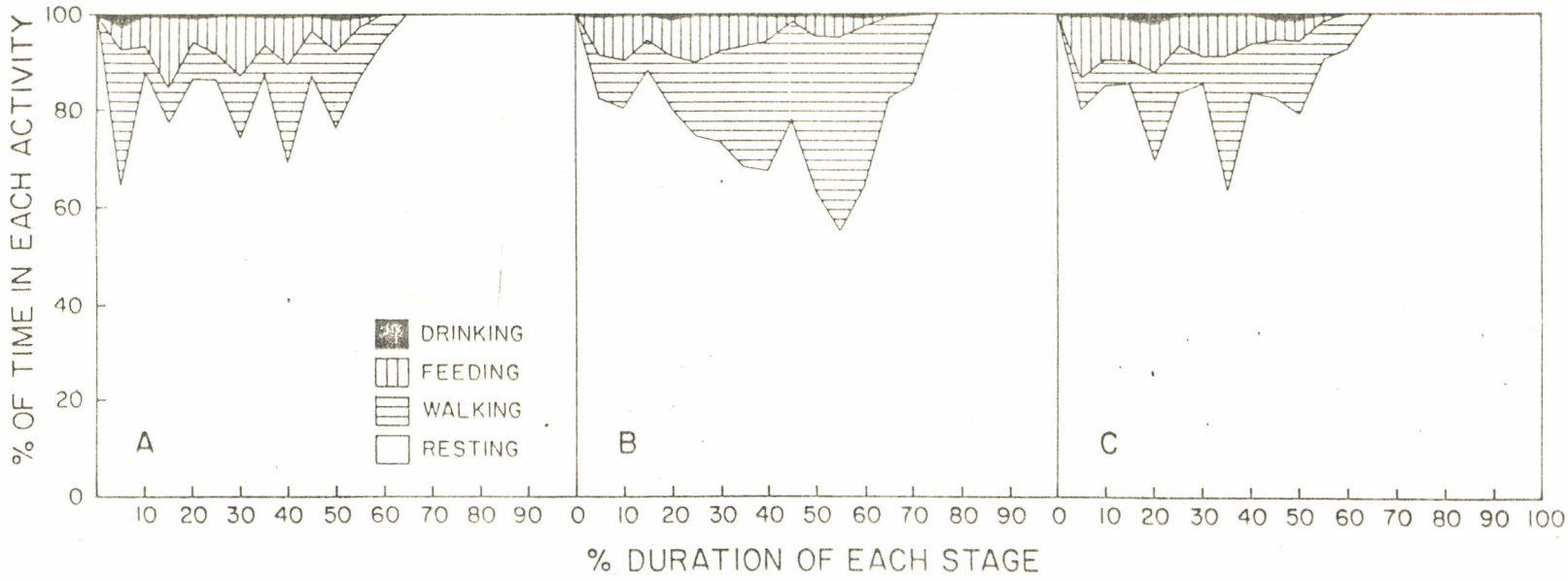

Figure 2. Variation in the percentage of time spent in each activity by larvae (A), protonymphs (B) and deutonymphs (C) of A. citrifolius. The total duration of each stage is 100%.

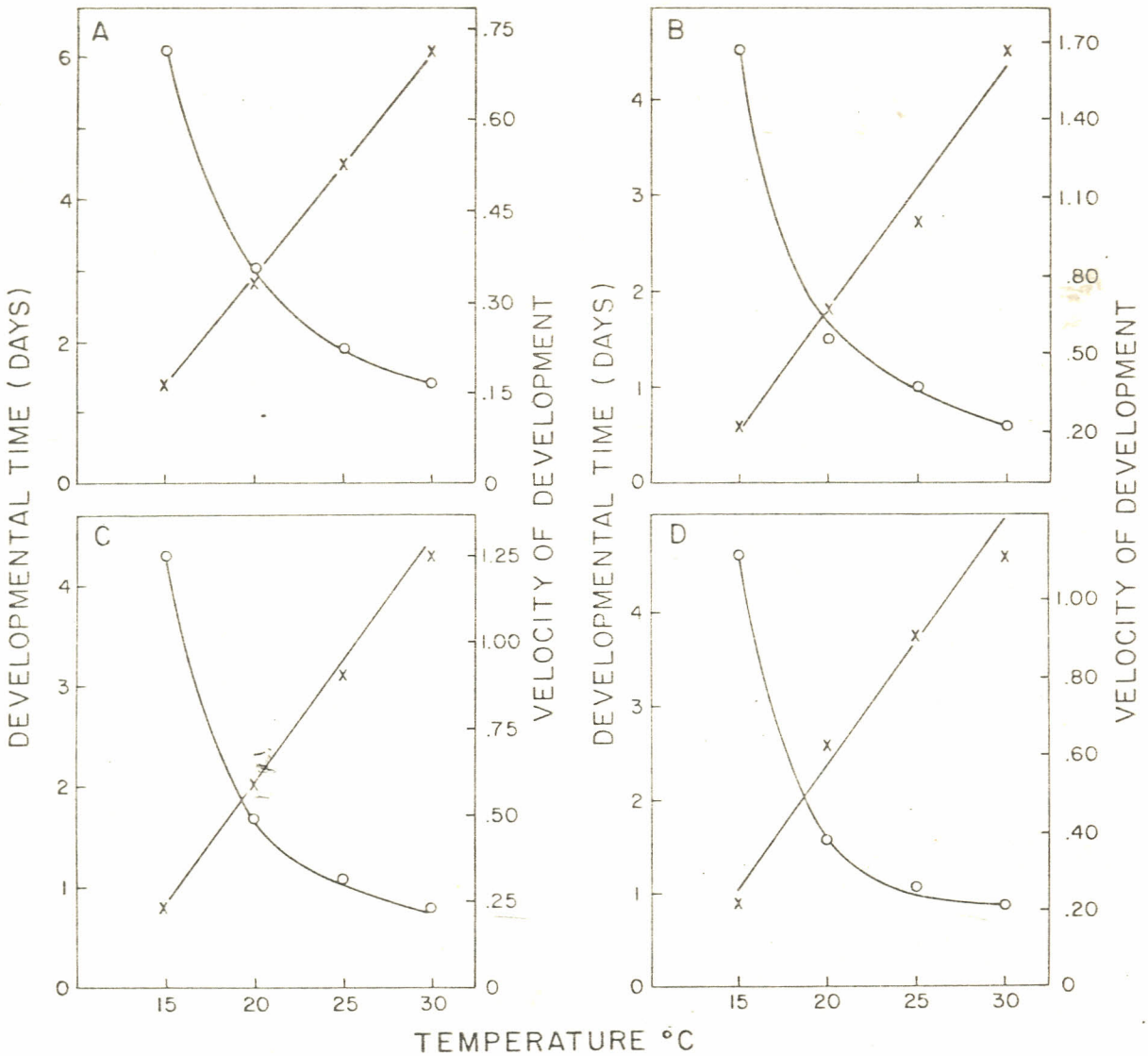

Figure 3. Relationship between temperature and developmental time (circles) and velocity of development (crosses) of each immature stage of A. citrifolius. A: egg; B: larva; C: protonymph; D: deutonymph. Velocity of development = 1/ developmental time (in days).

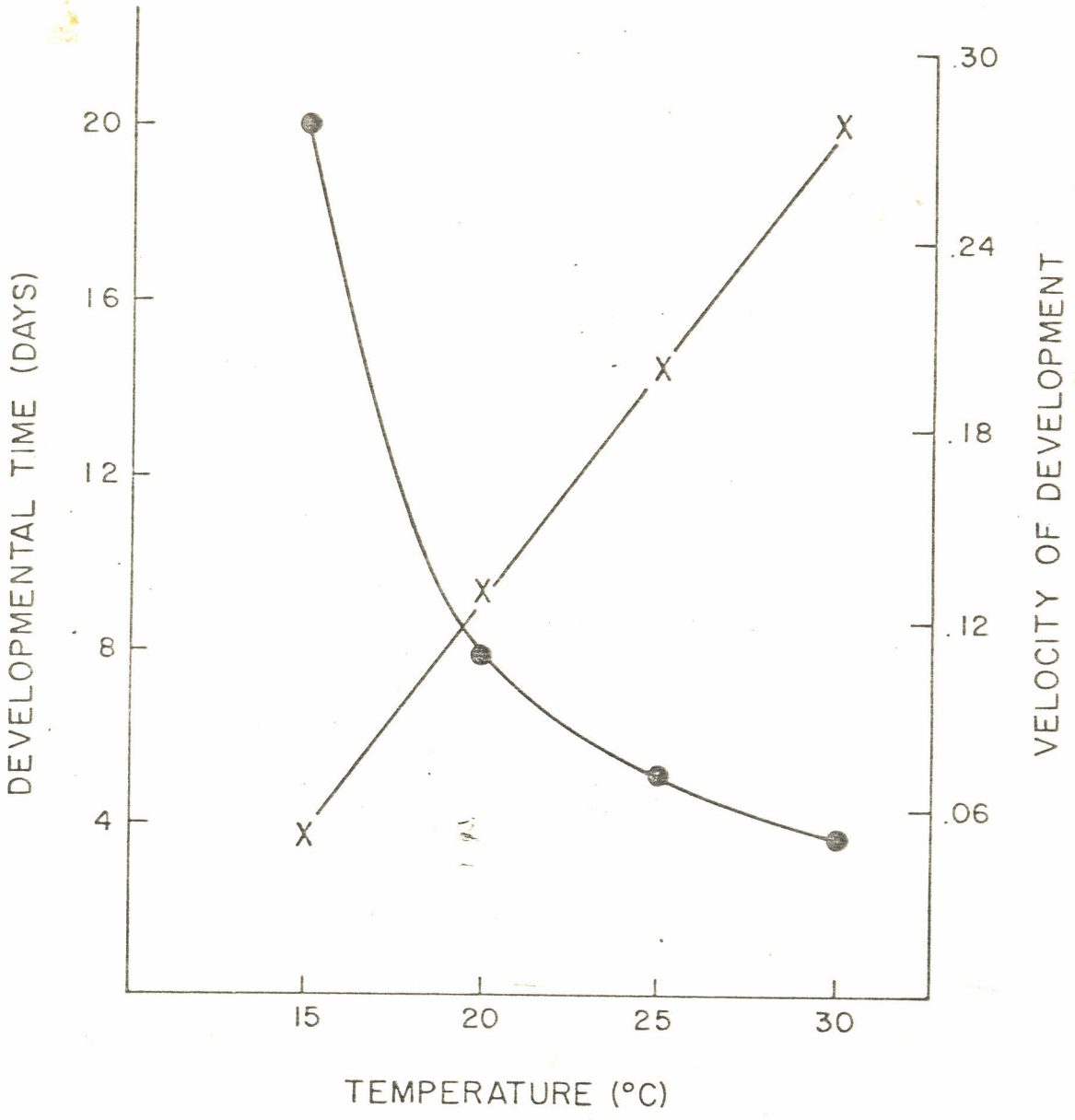

Figure 4. Relationship between temperature and developmental time (circles) and velocity of development (crosses) of the combined immatures stages of A. citrifolius. Velocity of development = 1/developmental time (in days).

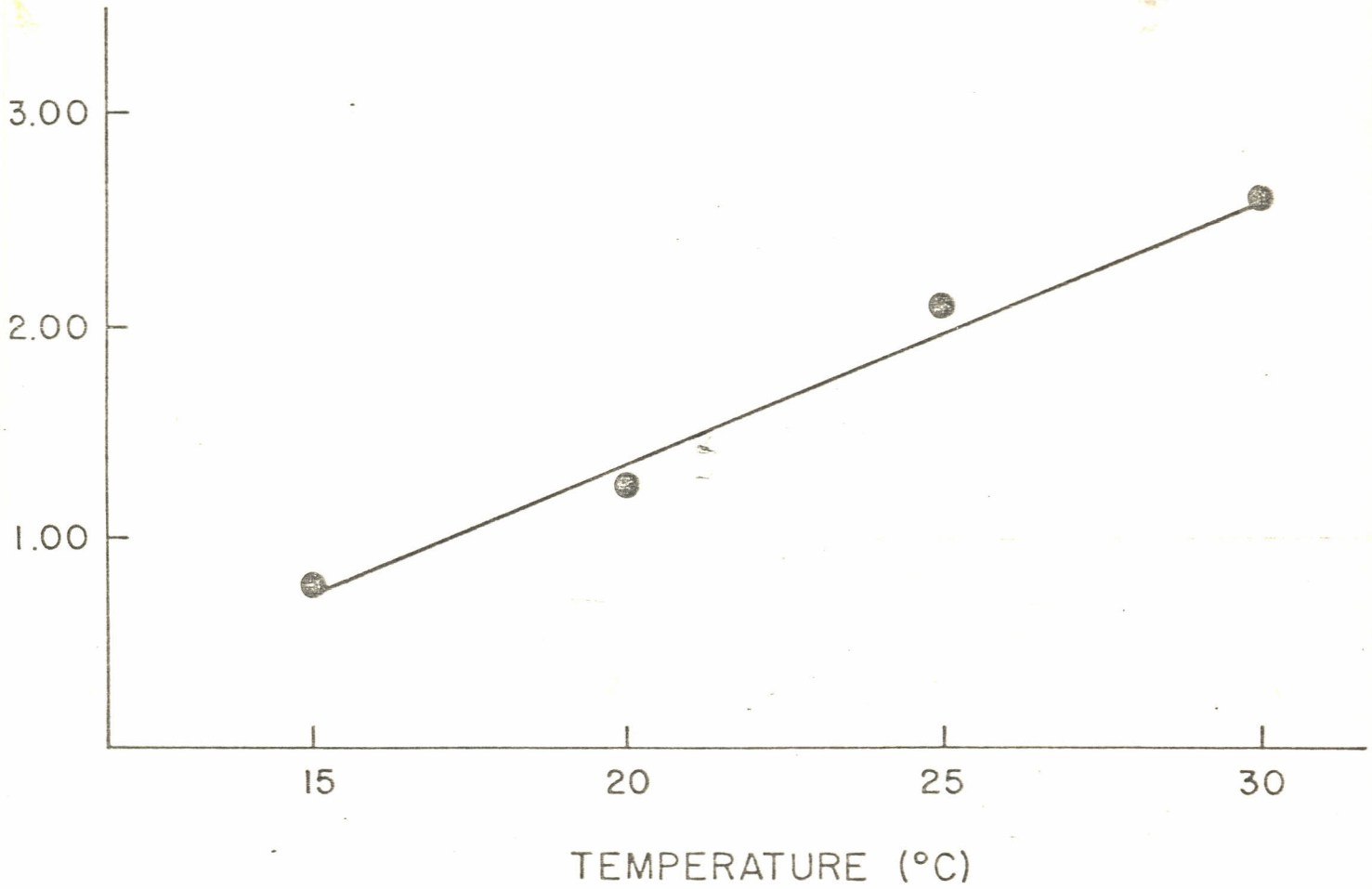

Figure 5. Relationship between the average daily rate of oviposition of A. citrifolius and temperature. y = .122x - 1.087 r = .9912

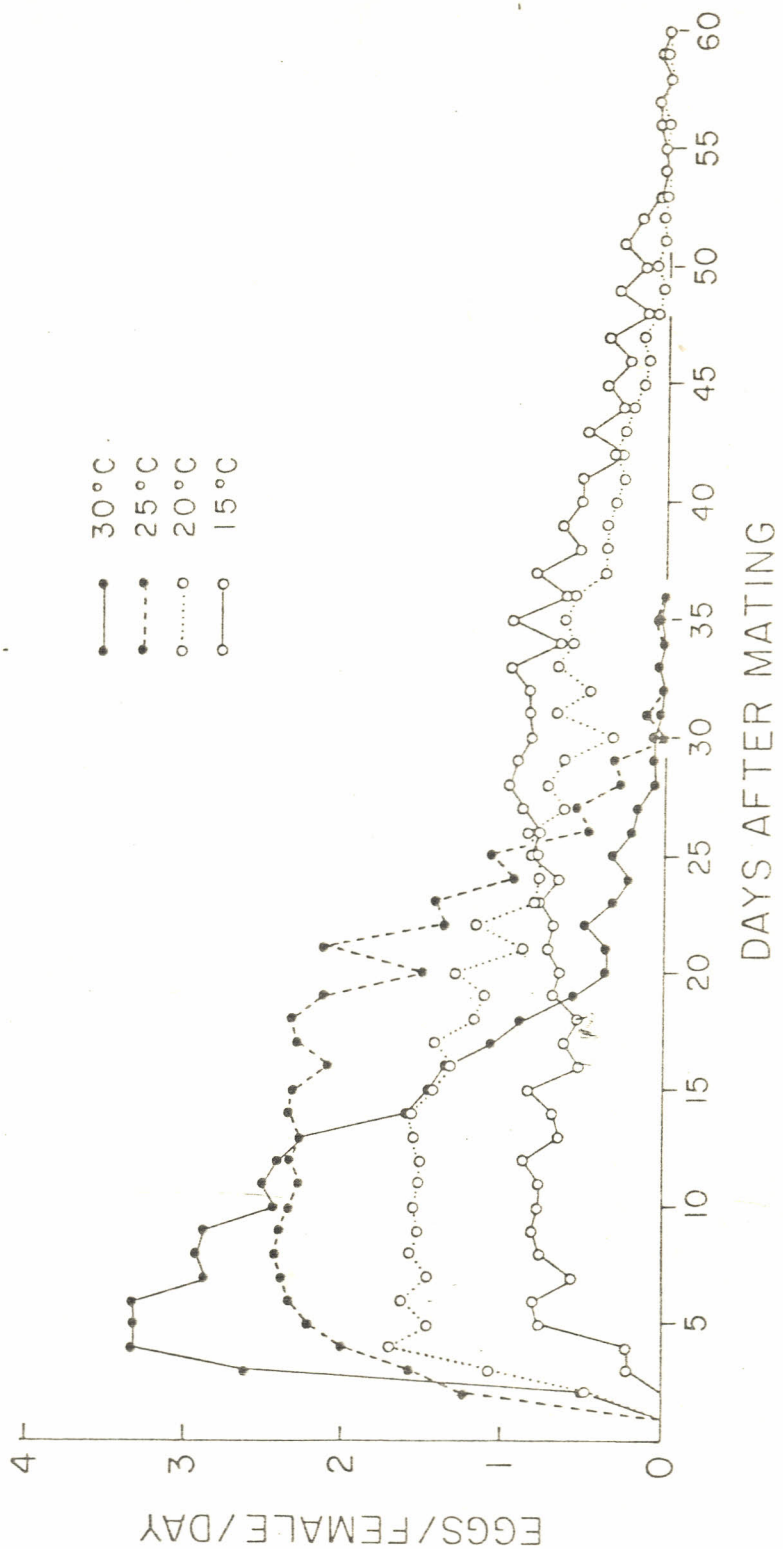

Figure 6. Daily oviposition rate of A. citrifolius. Day zero = day of mating. Rate calculated on the basis of number of females at the beginning of the experiment.

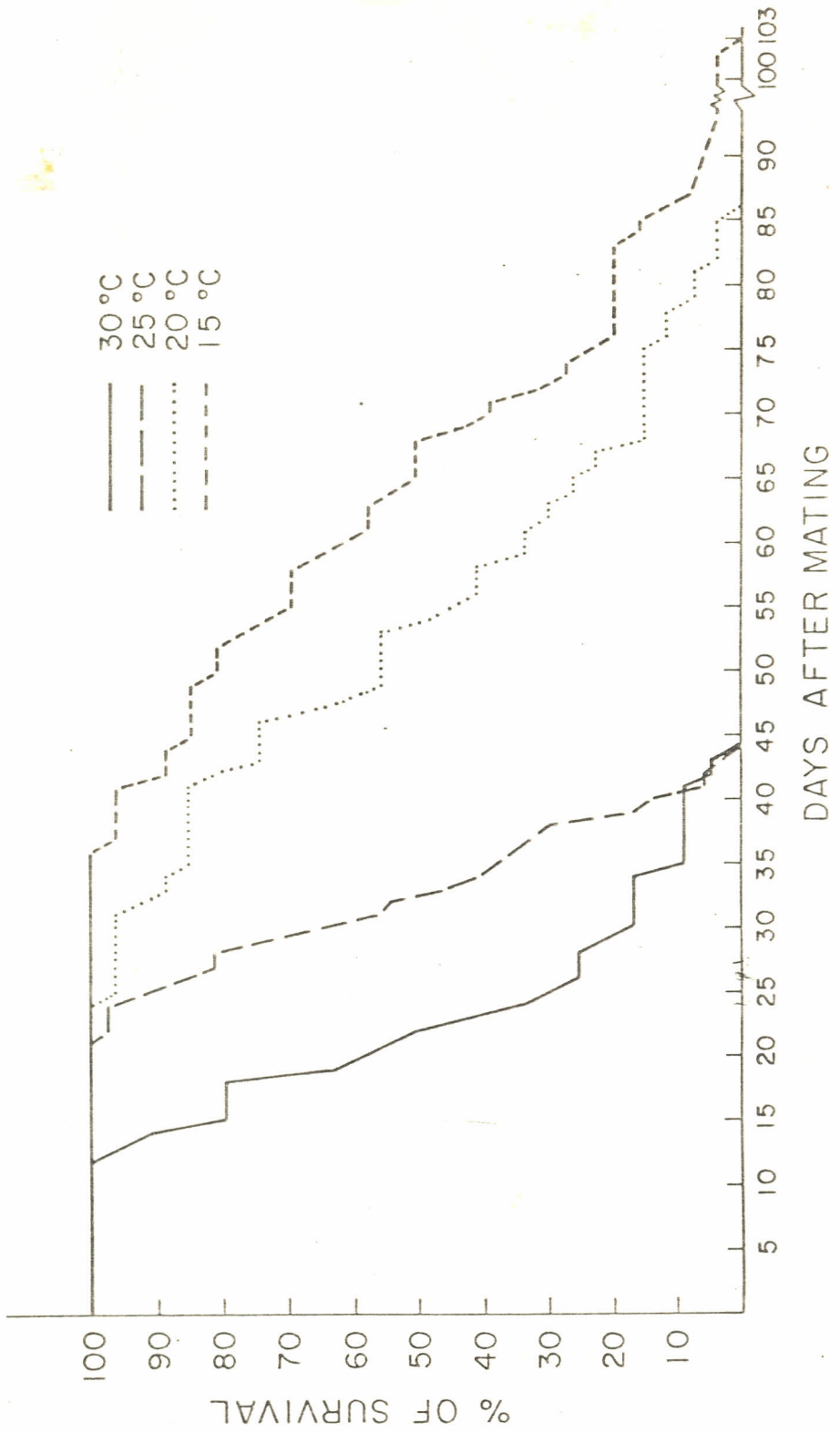

Figure 7. Survivorship of A. citrifolius at 4 temperatures. Day zero = day of mating.

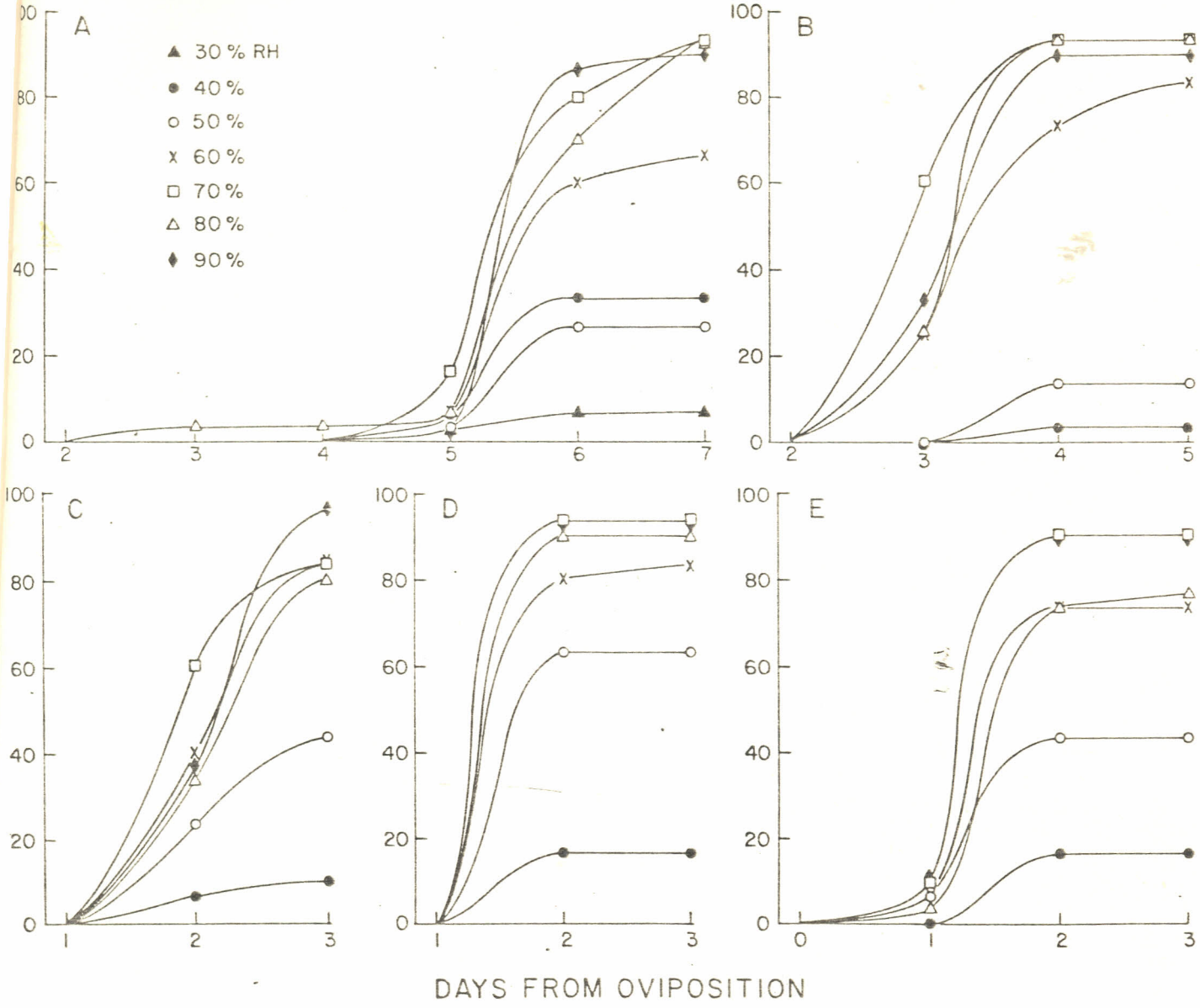

Figure 8. Daily percentage of eclosion of A. citrifolius at each temperature and relative humidity. A: 16°C; B: 20°C: C: 24°C; D: 28°C; E: 32°C.

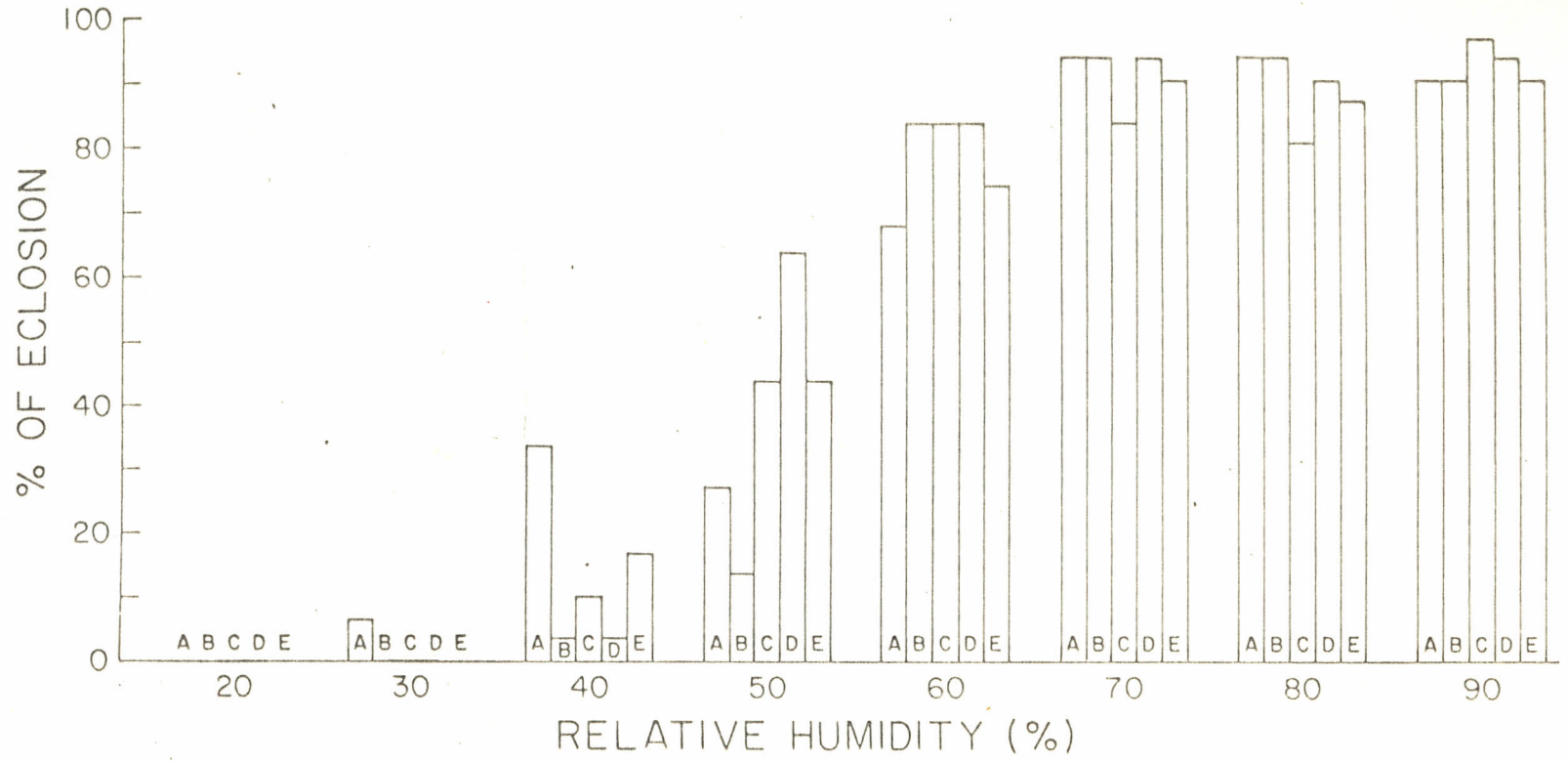

Figure 9. Maximum percentage of eclosion of A. citrifolius at each temperature and relative humidity.

A: 16°C; B: 20°C; C: 24°C; D: 28°C; E: 32°C.

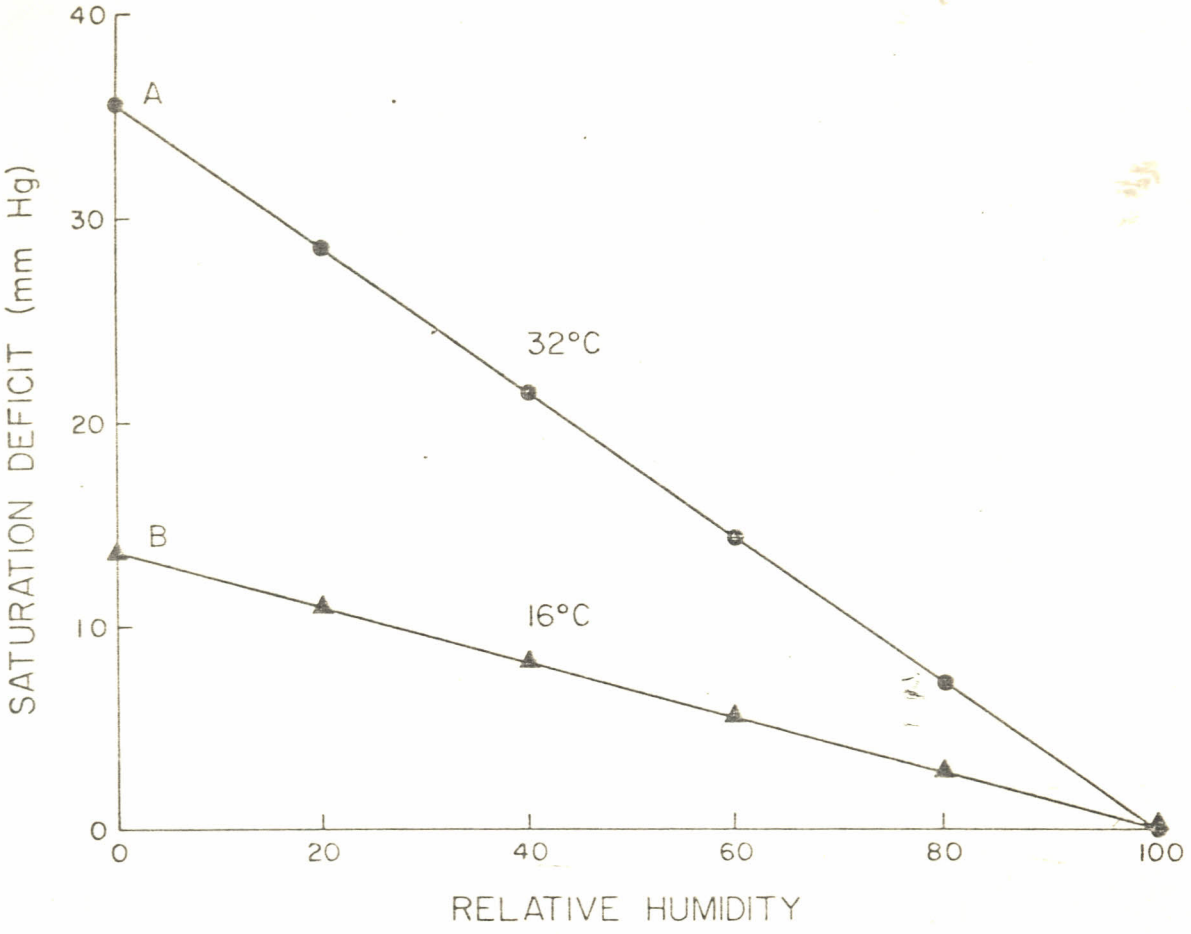

Figure 10. Relationship between relative humidity and saturation deficit at 2 temperatures. A: saturated vapor pressure at 32°C. B: saturated vapor pressure at 16°C.

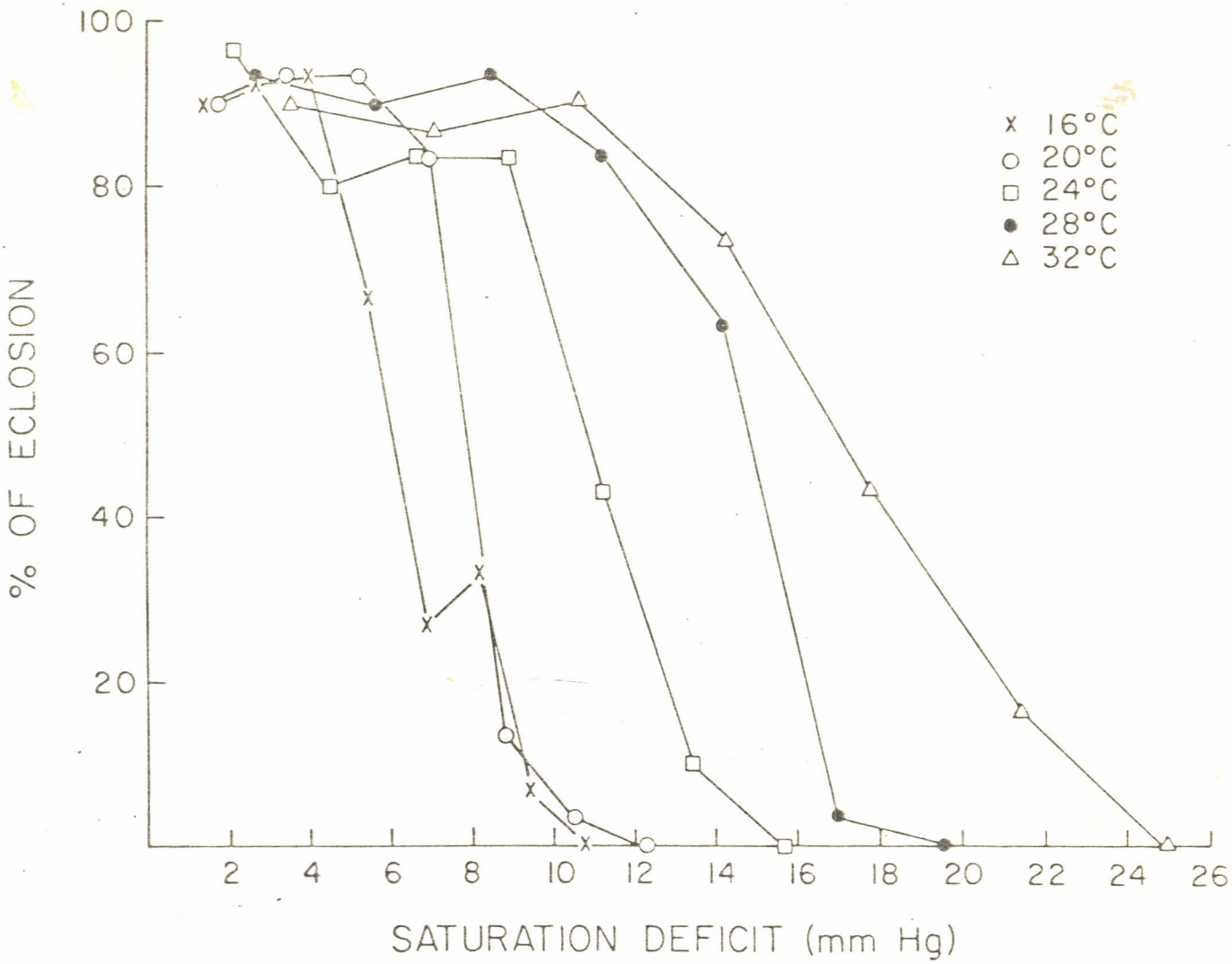

Figure 11. Percentage of eclosion of the larvae of A. citrifolius at 16, 20, 24, 28, and 30°C at different saturation deficits.

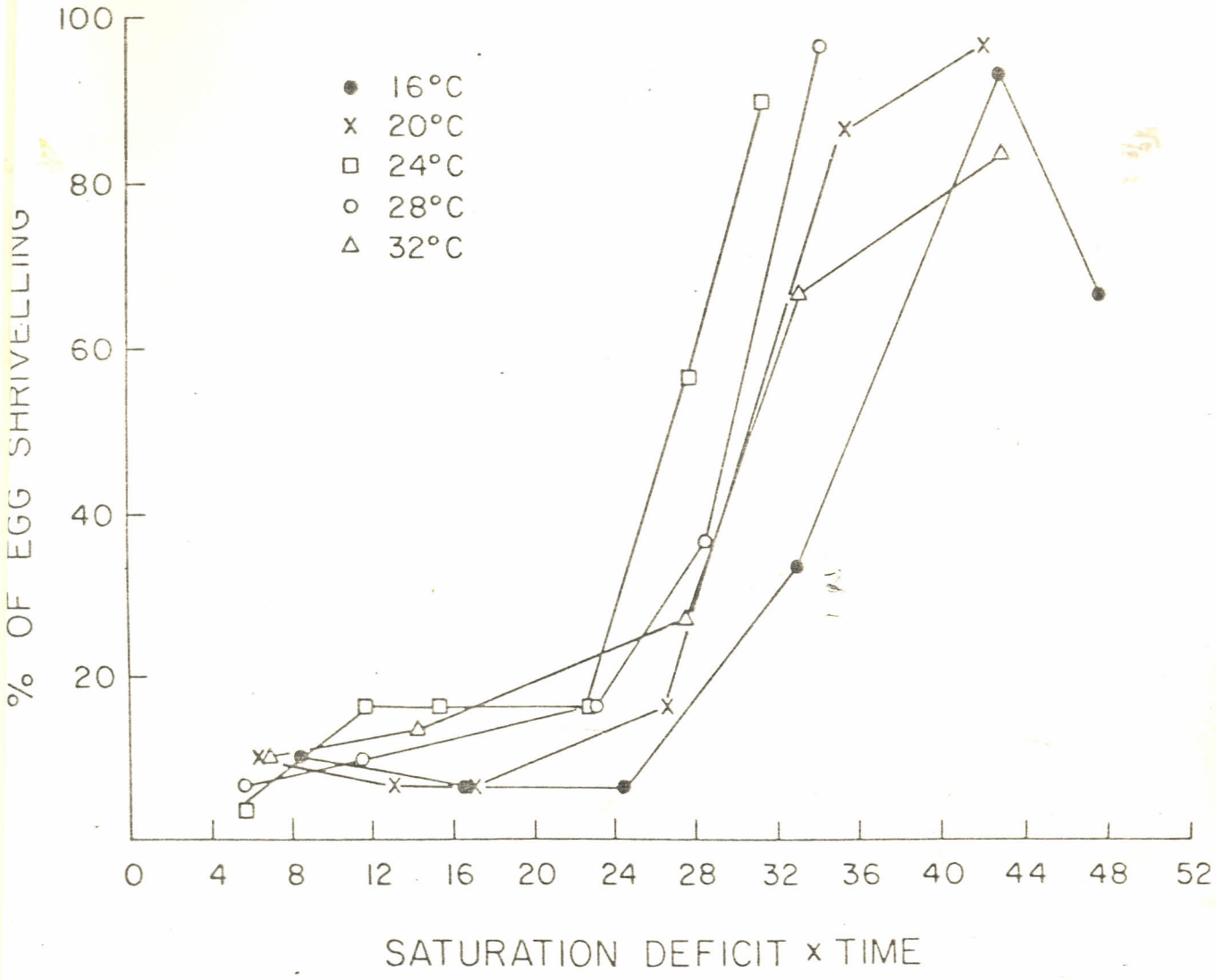

Figure 12. Egg shrivelling of A. citrifolius at different values of saturation deficit X time (in days) at various temperatures.

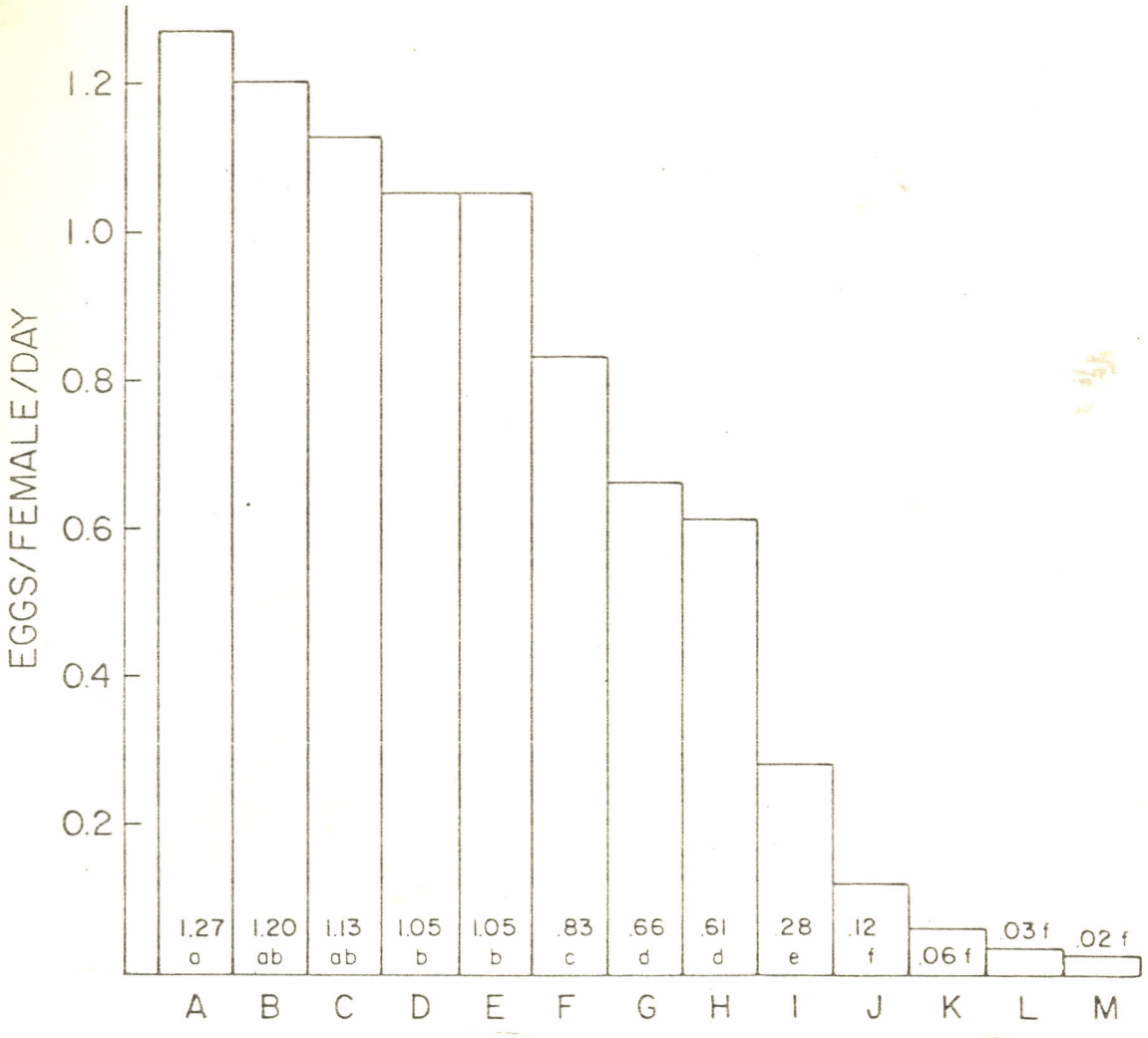

Figure 13. Oviposition rate (eggs/female/day) of A. citrifolius fed different kinds of food. Numbers followed by the same letter are not significantly different at 5% level. A: P. kawakamii pollen; B: M. crocea pollen; C: avocado pollen; D: T. pacificus (eggs + larvae) + M. crocea pollen; E; T. pacificus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