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A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 55 • Number 5 • August 1987

Biology and Ecology of *Euseius scutalis* (Athias-Henriot) (Acarina: Phytoseiidae)

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ABSTRACT

The effects of some environmental factors on development and fecundity of *Euseius scutalis* (Athias-Henriot) were investigated. Although *E. scutalis* is a general feeder, pollen and *Tetranychus pacificus* McGregor eggs were found to be the most favorable foods. Development and fecundity were lowest on *Brevipalpus lewisi* McGregor.

Over a variety of different temperatures and humidities, *E. scutalis* showed a wider range of environmental tolerances than did *E. stipulatus.* Eggs of *E. scutalis* hatched at 19 percent relative humidity and immature stages developed at 35°C, indicating that this species is adapted to arid and hot areas. The rate of development varied in a quadratic manner with increase in temperature.

Euseius scutalis required mating for egg production, and multiple matings were necessary for full egg production. *Euseius scutalis* had the greatest intrinsic rate of natural increase (0.325) and the shortest generation time (9.32 days) at 30°C, indicating this as the optimum temperature for population increase.

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Biology and Ecology of *Euseius scutalis* (Athias-Henriot) (Acarina:Phytoseiidae)[1]

INTRODUCTION

HIGH REPRODUCTIVE RATES combined with rapid developmental times give spider mites the potential for population outbreaks that can cause severe economic damage (Jeppson, Keifer, and Baker 1975; Sabelis 1981). This potential danger from spider mites is greater in a modified agricultural system than in a natural habitat, due to the elimination of natural enemies and the acquisition of resistance to pesticides (van de Vrie, McMurtry, and Huffaker 1972). Many authors have reported the ability of spider mites to acquire resistance to acaricides (Helle 1965; Helle and van de Vrie 1974; Jeppson, Keifer, and Baker 1975).

Phytoseiid mites are the most important predators of spider mites. More than 100 species have been described, some of which have been studied extensively. Several species are now used in different integrated pest management programs (e.g., *Typhlodromus occidentalis* Nesbitt on apple in Washington and on grape in California, and *Phytoseiulus persimilis* Athias-Henriot on greenhouse crops in Europe).

The genus *Euseius* is equivalent to the *finlandicus* group of *Amblyseius* (Chant 1959). The cheliceral and ventrianal shield morphology, in combination with other features, clearly define *Euseius* as a genus (McMurtry 1983). Originally, *Euseius scutalis* was described from Algeria as *Typhlodromus scutalis* by Athias-Henriot (1958). Several species now are considered synonyms of *E. scutalis,* including *Amblyseius lebanesi* Dosse from Lebanon (Swirski and Amitai 1968), *T. (A.) rubini* Swirski and Amitai from Israel, *A. gossipi* ElBadry from Egypt, and *A. delhiensis* Narayanan and Kaur from India (Wysoki and Bolland 1983).

Euseius scutalis is widely distributed through North Africa (Morocco and Algeria) and the Middle East (Lebanon, Iran, Jordan, Egypt, and Israel), and is also known from southern Spain and India. Swirski and Amitai (1965, 1968, 1985) reported that *E. scutalis* (= *A. rubini*) was found in the coastal plain of Israel. ElBadry and ElBenhawy (1968b) reported that this species (= *A. gossipi*) was the most common predatory mite on cotton throughout Egypt. It also was found on other host plants of economic importance (ElBadry et al. 1968a). McMurtry and Bounfour (unpublished) have found the same mite in Morocco, where it occurs on various tree crops in the arid areas of the country. Table 1 gives a complete list of plant families from which *E. scutalis* has been collected. The species seems to be adapted to a wide range of botanical families, but mainly occurs on trees and shrubs. It has been associated with tetranychids (ElBadry and ElBenhawy 1968b; Narayanan and Kaur 1960), whiteflies (Meyerdirk and Coudriet 1986; Wysoki and Cohen 1983), and tenuipalpids (McMurtry and Bounfour, unpublished). Overall, the species seems to occur in warm climates.

The objectives of the present work were (1) to quantify and compare development and reproduction of *E. scutalis* when reared on food sources of pollen or various pests

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[1] Accepted for publication on February 6, 1987. This paper is from a thesis submitted in partial fulfillment of an M.S. degree, Department of Entomology, University of California, Riverside, in 1985.

TABLE 1. PLANT HOSTS OF *EUSEIUS SCUTALIS*

Family	**Genus, species, and collectors**
Anacardiaceae	*Schinus molle* (Swirski and Amitai 1968); *S. terebinthifolius, Pistacia atlantica* (Amitai and Swirski 1978); *P. palaestina* (Wysoki and Swirski 1971)
Asclepiadaceae	*Calotropis procera* (Swirski and Amitai 1965)
Asteraceae	*Inula* sp. (Swirski and Amitai 1968); *Artemisia* sp. (Swirski and Amitai 1985)
Bigoniaceae	*Jacaranda mimosifolia, Campsis radicans* (Amitai and Swirski 1978)
Caprifoliaceae	*Lonicera japonica* (Swirski and Amitai 1968)
Chenopodiaceae	Undetermined (Swirski and Amitai 1985)
Convolvulaceae	*Ipomoea* sp. (Swirski and Amitai; Daneshvar 1980)
Ebenaceae	*Diospyros virginiana* (Amitai and Swirski 1978)
Euphorbiaceae	*Ricinus communis* (Swirski and Amitai 1961; Dosse 1967)
Fabaceae	*Dalbergia sissoo, Dolichos lablab, Ceratonia siliqua, Cercis siliquastrum* (Swirski and Amitai 1965); *Acacia* sp., *Gleditsia sinensis* (Amitai and Swirski 1978)
Fagaceae	*Quercus ithaburensis* (Wysoki and Swirski 1971)
Juglandaceae	*Carya* sp. (Amitai and Swirski 1978)
Lauraceae	*Persea americana* (Swirski and Amitai 1965)
Malvaceae	*Hibiscus esculentus, Gossypium* sp. (Narayanan and Kaur 1960); *G. herbaceum* (Swirski and Amitai 1965); *G. barbadense* (ElBadry 1967); *Malva* sp. (McMurtry and Bounfour unpublished); *Abutilon* sp. (Swirski and Amitai 1985)
Moraceae	*Ficus sycomorus* (Swirski and Amitai 1968); *Morus nigra* (Swirski and Amitai 1968); *Morus* sp. (Daneshvar 1980); *Ficus* sp. (McMurtry and Bounfour unpublished)
Moringaceae	*Moringa aptera* (Swirski and Amitai 1985)
Myrtaceae	*Psidium guajava* (Swirski and Amitai 1965)
Oleaceae	*Phillyrea media* (Wysoki and Swirski 1971); *P. latifolia* (Amitai and Swirski 1978)
Platanaceae	*Platanus orientalis* (Amitai and Swirski 1978)
Punicaceae	*Punica granatum* (Swirski and Amitai 1968; Daneshvar 1980)
Rhamnaceae	*Zizyphus spina-christi* (Swirski and Amitai 1965)
Rosaceae	*Pyrus malus* (Swirski and Amitai 1965; McMurtry and Bounfour unpublished); *Prunus persica* (Swirski and Amitai 1965); *P. armeniaca* (Swirski and Amitai 1965); *Spiraea vanhouttei, Rosa* sp. (Amitai and Swirski 1978)
Rutaceae	*Citrus* sp. (Porath and Swirski 1965; Daneshvar 1980; McMurtry and Bounfour unpublished)
Solanaceae	*Solanum villosum* (Swirski and Amitai 1968); *Capsicum* sp. (Daneshvar 1980)
Salvadoraceae	*Salvadora persica* (Swirski and Amitai 1965)
Styracaceae	*Styrax officinalis* (Swirski and Amitai 1965)
Verbenaceae	*Lippia nodiflora* (Amitai and Swirski 1978)
Violaceae	*Viola* sp. (Swirski and Amitai 1968)
Vitaceae	*Vitis* sp. (Daneshvar 1980)

considered important in California, (2) to characterize the mating response and estimate the sex ratio of *E. scutalis,* (3) to compare the development at different temperatures and the egg hatching at different humidities of both *E. scutalis* and *E. stipulatus,* and relate the information obtained to the habitat distribution of the two species, and (4) to construct life tables and quantify life table parameters for *E. scutalis* at different constant temperatures.

MATERIALS AND METHODS

Culture Maintenance and General Procedures

Predator cultures for this study were started in 1983 using 30 females taken from each of three University of California, Riverside insectary cultures: *E. stipulatus* originating from Kenitra (humid coastal); *E. scutalis* originating from Marrakech (inland arid); and *E. scutalis* from Agadir (coastal arid). These species were collected in Morocco in 1982 and introduced to California for biological control of mite pests on citrus in California (McMurtry and Bounfour, unpublished). The mites were reared according to the method described by McMurtry and Scriven (1975). The rearing substrate was a leaf of *Ficus auriculata* Loureiro for *E. scutalis* and a citrus leaf for *E. stipulatus.* The leaves were placed on water-saturated foam pads 12 mm thick, in 20 × 20 cm stainless steel baking pans. Each leaf was surrounded by a strip of water-saturated cellucotton 1 cm wide, as a barrier to prevent escape of the mites and to keep the leaf moist. Plastic coverslips, slightly bent to form the shape of a tent, were placed in the middle of each arena with a few strands of cotton underneath to provide mites resting and oviposition sites. The food, provided twice weekly, consisted of *Malephora crocea* Jacq. pollen and *Tetranychus pacificus* McGregor eggs and larvae, using extraction methods described by Scriven and McMurtry (1971). The culture units were kept in aerated boxes and maintained in a laboratory room at approximately 24° C at ambient relative humidity and photoperiod.

Unless otherwise stated, experiments were conducted in small modified refrigerators (Platner, Scriven, and Braniger 1973) in which temperature and photoperiod could be controlled.

Except for the temperature test, all tests were conducted at 25° C ± 0.5°, 40 to 70 percent relative humidity, and 12:12-hour photoperiod. The predatory mites were transferred with a camel-hair brush (size 00000). The other experimental mites were transferred by means of a specially designed aspirator. The data were analyzed using analysis of variance, Student t-test, and Sidak Multiple Comparison Test (Ray 1982; Steel and Torrie 1980).

Developmental and Fecundity Effects of Different Foods

The foods tested included (1) pollen of iceplant, *Malephora crocea* Jacq.; (2) eggs of the Pacific spider mite, *Tetranychus pacificus;* (3) all life stages of *T. pacificus;* (4) all life stages of citrus red mite, *Panonychus citri* McGregor; (5) nymphs of citrus thrips, *Scirtothrips citri* Moulton, obtained from UC Riverside greenhouse colonies; (6) all life stages of avocado brown mite, *Oligonychus punicae* Hirst, reared in the laboratory; and (7) all life stages of the citrus flat mite, *Brevipalpus lewisi* McGregor, collected locally from citrus trees. Pollen was tested on both citrus and lima bean leaves; all stages of *O. punicae* were tested on avocado leaves; all stages of *T. pacificus* were tested on lima bean leaves; and the other prey were tested on citrus leaves. Except for the arenas of avocado leaves, which were placed top side up, all arenas were placed top side down on water-saturated foam pads. The types and positions of leaf arenas were chosen to simulate the natural substrate preferred by the prey.

The Marrakech strain was used in these tests. For the developmental studies, 10 females from the stock culture were introduced to each leaf arena and removed 24 hours later. The progeny from those females were observed daily and their developmental stages recorded. For the oviposition tests, each newly emerged female was isolated individually with a male on an arena. Eggs laid by these females were counted and removed daily for 2 weeks.

Mating and Sex Ratio

To study the effect of a single mating on oviposition, 20 females were chosen at random from the Marrakech stock culture and put in citrus leaf arenas for 24 hours. The resulting progeny were fed with pollen and reared to the adult stage. After one mating, 10 females of the new generation were isolated in individual arenas. The eggs oviposited were counted and removed daily.

To determine progeny sex ratio, 27 pairs of *E. scutalis* females and males of the same age were reared at 25° C. The eggs laid were collected every 3 days, labeled as to date and parentage, and reared under the same conditions as the parents. At the adult stage, they were sexed by visual observation. Individuals of questionable sex were mounted in Hoyer's media and sexed with the aid of a phase contrast microscope. The experiment ended after 12 days of ovipositon.

Temperature and Humidity Effects on Immature *E. scutalis* and *E. stipulatus*

For the temperature study, the arenas consisted of squares of citrus leaves (2.5 × 2.5 cm) that were placed top side down on foam pads. Twenty-five females per temperature were chosen arbitrarily from each of the three cultures (two *E. scutalis* and one *E. stipulatus*), and placed into individual arenas for oviposition. The females were removed 12 hours later, and all eggs but one were removed from each arena.

Temperatures used were 15°, 20°, 25°, 30°, 35°, and 40° C at 28 to 76 percent relative humidity. The mites were observed every 6 to 8 hours during development, except those at 15° C, which were checked once a day after the first week. Except for the hexapod larval stage, which is easy to recognize, the stages were determined at the time of observation by the presence or absence of exuviae. Estimates of the duration of each stage were based on the equations of Perring and coworkers (1984).

For the humidity study, eggs 12 to 14 hours old were taken from leaf arenas in the laboratory and placed in small watchglasses. The humidity chambers consisted of small dessicators containing different concentrations of sulfuric acid solutions (specific gravity = 1.84) to obtain relative humidities of 19, 22, 25, 38, 43, 51, 60, 80, and 100 percent (Buxton and Mellanby 1934). Humidities were measured using psychrometric methods. Dessicators were placed in a temperature cabinet at 25° C and 12:12 photoperiod. Observations were made daily until the eggs hatched or dessicated.

Effects of Temperature on Reproductive Potential

About 50 females were chosen arbitrarily from the Marrakech stock culture and confined in citrus leaf arenas for oviposition at each of the study temperatures. They were removed 12 hours later and the eggs laid were reared to the adult stage at the same temperatures. Each newly emerged female was isolated individually with a male for oviposition. Eggs laid were counted and removed daily. Rearing and experimental units consisted of young excised citrus leaves placed top side down in a steel pan as described by McMurtry and Scriven (1964a). Three or four small pieces of plastic coverslip (1 × 0.5 cm) were bent and placed, with a few strands of cotton, in different corners of each arena to provide resting and oviposition sites for the predators, and to form an obstacle to mite escape. Pollen of *Malephora crocea* Jacq., provided daily and amply as food, was lightly dispersed over all the surface of each arena. The leaf was replaced as necessary, and an additional male was added whenever the previous male died or escaped.

Life tables were constructed daily by recording the number of individuals alive for one cohort. The intrinsic rate of natural increase was calculated by resolving the formula

$$\Sigma\, l_x m_x \exp(-r_m \cdot x) = 1,$$

where x is the individuals' age in days, l_x is the proportion of individuals alive at age x, and m_x is the number of female offspring per female per day (Birch 1948; Southwood 1978). For a comparison with data reported in the literature, we derived the rate of fecundity by dividing the total number of eggs per female by the oviposition period (measured in days).

RESULTS AND DISCUSSION

Developmental and Fecundity Effects of Different Foods

There were no significant differences between the durations of development for nymphs fed on *Tetranychus pacificus* eggs, on all stages of *Oligonychus punicae,* and on pollen tested both on citrus and bean leaves (table 2). The longest development durations occurred on *Panonychus citri, Scirtothrips citri,* and all stages of *T. pacificus.* Predator larvae were observed to pierce and feed on pollen grains and eggs of *T. pacificus* and *O. punicae,* but did not feed on other stages of those mites. Larvae of the

TABLE 2. MEAN DURATION (IN DAYS) OF IMMATURE STAGES OF *EUSEIUS SCUTALIS* ON VARIOUS FOODS

	Egg		**Larva**		**Nymph**[*]		
Food	**Mean, ± standard deviation**	**N**[†]	**Mean, ± standard deviation**	**N**	**Mean, ± standard deviation**	**N**	**Mortality**
							%
Pollen[‡]	2.7 ± 0.5a[§]	58	0.9 ± 0.2b	52	1.8 ± 0.4a	29	15
Pollen[¶]	2.1 ± 0.3b	36	0.9 ± 0.3b	36	1.9 ± 0.2a	33	8
T. pacificus (eggs)	2.6 ± 0.5a	65	1.4 ± 0.6a	48	1.9 ± 0.5a	35	17
T. pacificus (all stages)	2.2 ± 0.4b	38	0.8 ± 0.2b	34	4.3 ± 0.5c	12	32
O. punicae	2.9 ± 0.3a	31	0.9 ± 0.1b	31	2.1 ± 0.4a	29	17
P. citri	2.7 ± 0.5a	44	1.1 ± 0.4b	42	3.2 ± 0.7b	33	25
S. citri	2.1 ± 0.7b	36	1.2 ± 0.4a	27	3.2 ± 0.4b	25	17
B. lewisi	2.2 ± 0.4ab	17	0.9 ± 0.1b	13	—[#]	—	100

[*] Protonymph plus deutonymph.

[†] Sample size.

[‡] Pollen tested on citrus leaf arenas.

[§] Means followed by the same letters are not significantly different ($p = 0.05$, Sidak test).

[¶] Pollen tested on bean leaf arenas.

[#] No survivors.

predator also showed a red coloration in the gut when offered *Brevipalpus lewisi,* indicating that they fed on this prey. We did not determine which stage of the prey was consumed. Nymphs and adults of the predator fed on all stages of *P. citri.* High proportions of females and eggs were always left in the arenas, however, indicating that the feeding was concentrated on larvae, nymphs, and adult males. The predator rarely was observed feeding on eggs and adult females of *P. citri;* this might be attributed to the stalk attached to the eggs and to the size of *P. citri* females. However, Keetch (1972) observed that even when the stalk was removed, *Euseius addoensis* (Van der Merwe and Ryke) did not feed on eggs of *P. citri. Euseius scutalis* had difficulty capturing and handling the adult females of this spider mite.

Euseius scutalis did not complete development on *B. lewisi.* On the sixth day of development, only two nymphs remained in the arena; one nymph showed a coloration only at the end of the opisthosoma, and the other showed no coloration. This indicated that feeding had ceased. The next day, both individuals died.

The predator seemed to develop faster on *O. punicae* than on other spider mites. All stages were easily attacked and consumed. Development time of *E. scutalis* when fed on *O. punicae* was similar to that reported by ElBadry et al. (1968b) when this predator was offered *Oligonychus mangiferus* (Rahman and Sapra).

Compared to other spider mite prey, the highest immature mortality of *E. scutalis* was observed when all stages of *T. pacificus* were offered as food, probably because of the webbing produced by this spider mite. The webbing interfered with the movement of the predator, isolating it from the prey located under the webbing. Swirski, Amitai, and Dorzia (1967) reported that *E. scutalis* (= *Amblyseius rubini*) larvae and nymphs moved readily in the webbing of *Tetranychus cinnabarinus* Boisduval. Moreover, mortality when fed on this prey was much lower than when fed on other prey species, but higher than when fed on pollen. ElBadry and coworkers (1968a) reported similar results for *E. scutalis* (= *A. gossipi*). The same authors (1968a), however, indicated that this predator consistently consumed more individuals of *O. mangiferus* than of *T. cinnabarinus.* McMurtry and Scriven (1946a) reported that the webbing of *T. cinnabarinus* and *T. pacificus* created a favorable environment for resting and oviposition of *Typhlodromus rickeri* (Chant). All the stages of the predator remained near the prey. The webbing of *Tetranychus cinnabarinus* entangled and isolated *E. hibisci* (Chant) and *Amblyseius limonicus* (Garman and McGregor) from the prey, thus causing high mortality (McMurtry and Scriven 1964a, 1965).

Nymphs and adults of *E. scutalis* readily attacked and consumed nymphs of *Scirtothrips citri.* Unsuccessful attempts to prey on winged individuals were also observed. Developmental time when fed on this prey was shorter than that reported by Tanigoshi, Nishio-Wong, and Fargerlund (1983) for *E. hibisci.* Immature mortality of *E. scutalis* on thrips was 17 percent. Swirski, Amitai, and Dorzia (1967) reported that this species had 84.2 percent immature mortality when offered *Retithrips syriacus* Mayet.

Oviposition rates for *E. scutalis* fed on various foods are shown in table 3. The female predators fed on each of the foods offered, and also oviposited in each case. The highest oviposition rate (more than 2 eggs per female per day) was obtained from females fed on pollen and *T. pacificus* eggs. The lowest oviposition rate (0.06 egg per female per day) was obained on *Brevipalpus lewisi.* Swirski, Amitai, and Dorzia (1967) reported an oviposition rate of 0.04 egg per female per day when fed on *Brevipalpus phoenisis* (Geijskes). Unlike immature stages, adult females moved more readily within the webbing of *T. pacificus* when all stages were offered. The oviposition rate on this prey was 1.2 eggs per female per day, lower than that obtained when only eggs were

TABLE 3. MEAN OVIPOSITION RATE OVER 14 DAYS AND SURVIVAL OF *EUSEIUS SCUTALIS* ON VARIOUS FOODS

Food	Eggs per female per day			
	Mean*	**Standard deviation**	**N**†	**Survival**
				%
Pollen on citrus leaves	2.3a	± 0.6	16	75
Pollen on bean leaves	2.1ab	± 0.5	20	75
T. pacificus (eggs)	2.2a	± 0.7	15	60
T. pacificus (all stages)	1.2cd	± 0.7	16	44
O. punicae	1.5bc	± 0.4	20	50
P. citri	1.0cd	± 0.4	37	5
S. citri	1.4cd	± 0.5	12	86
B. lewisi	0.06e	± 0.5	12	8

*Means followed by the same letter are not significantly different (p = 0.05, Sidak test).

†Sample size.

offered. This indicated that perhaps female predators fed at less than their capacity, probably due to the presence of webbing. In addition to feeding on nymphs of *S. citri,* female predators occasionally were observed to feed on winged thrips that were stuck to the cellucotton. There were no significant differences between the rates of oviposition for females fed with pollen on bean leaves and those for females fed with pollen on citrus leaves, and with *T. pacificus* eggs ($p = 0.05$).

The data in tables 2 and 3 indicate that *E. scutalis* can utilize a variety of food, and that pollen is favorable for development and fecundity of the predator. All species of *Euseius* that have been studied feed and reproduce readily on pollen (McMurtry 1977, 1980, 1983; Muma and Denmark 1970). Moreover, some species were found to reproduce better on pollen than on tetranychid mites (McMurtry and Scriven 1964b; Swirski, Amitai, and Dorzia 1967). Although *E. aleyrodis* (ElBadry) developed faster on pollen of *Gossipium* sp., the reproduction was higher on whitefly *Bemesia tabaci* Genn. nymphs (ElBadry 1968). *Euseius scutalis* individuals had similar development durations when fed on date and corn pollen, but longer durations when fed on tetranychid mites (ElBadry and ElBenhawy 1968b). The ability of *E. scutalis* to survive on a wide variety of foods might partly explain its wide distribution on different plants. This is important in the case of prey scarcity. Alternative food sources allow the predator to survive in the absence of prey and to reproduce before the pest attains a high population level (McMurtry, Huffaker, and van de Vrie 1970; McMurtry and Johnson 1966).

Mating and Sex Ratio

Usually, males molted earlier than females. Some males were observed to guard female deutonymphs, with mating occurring immediately after deutonymph females molted. The mated females laid an average of 31 eggs (range 22 to 41) in 13.1 days (range 8 to 20). The mean rate of oviposition was 2.5 eggs per female per day.

Most phytoseiid mites require mating for egg production (McMurtry, Huffaker, and van de Vrie 1970). All the eggs are fertilized, but during embryo development some eggs lose the paternal set of chromosomes. Diploid eggs result in females, and haploid eggs develop into males (Helle et al. 1978; Hoy 1979; Nelson-Rees, Hoy, and Roush 1980). This condition is called parahaploidy (Hoy 1979) or paternal genome loss (PGL) (Bull 1983), or pseudo-arrhenotoky (Schulten 1985).

When the females stopped laying eggs, males were added to the arenas. Once males were added, oviposition would resume the following day. In one case, a female resumed oviposition, after 9 days of interruption, with the same rate as at the beginning of oviposition.

These results showed that, although mating and insemination occurred in the beginning of adult life, at least 2 matings were necessary for full egg production. Similar results were recorded for *Typhlodromus caudiglans* Schuster (Putman 1962), *T. rickeri* Chant (McMurtry and Scriven 1964a), and *Amblyseius andersoni* Chant (Amano and Chant 1978a). *Euseius scutalis* females that mated only once oviposited fewer eggs and had a shorter oviposition period than females that mated repeatedly (ElBadry and ElBenhawy 1968a). Most females were observed to mate twice, but in a few cases they mated three or four times (ElBadry and ElBenhawy 1968a).

A higher percentage of males was produced during the first days of oviposition than in subsequent days. This is consistent with observations reported for other phytoseiid mites (Amano and Chant 1978b; Putman 1962; Sanderson 1983; Schulten et al. 1978). The mean numbers of female and male progeny per female parent were 12.26 and 9.3, respectively (table 4). Thus, the ratio favors females slightly (1.25 ♀:1 ♂). Although female insemination is insured at the beginning of adult life, a high proportion of males of this species would be advantageous, increasing the chances of male and female encounters, for two reasons.

First of all, *E. scutalis* is a general feeder. Unlike the eggs of specialized predators oviposited within prey colonies, the eggs of *E. scutalis* can be expected to be dispersed at random according to food availability. Other species of *Euseius* show similar behavior (McMurtry and Johnson 1966; Sanderson 1983). Random dispersion of food increases the chances of outbreeding. Production of a high proportion of males is a strategy common in outbreeding populations (R. F. Luck, personal communication).

Second, females of *E. scutalis* require multiple mating for full egg production. This condition also increases the chances of outbreeding. In contrast, specialized predators (e.g., *Phytoseiulus persimilis*) that have strongly female-biased sex ratios usually require one mating for full egg production (Amano and Chant 1978b; Schulten et al. 1978; Smith and Newsom 1970). Since female oviposition sites are a function of prey distribution, the probability of sibmatings is high. The strategy for these species is to produce just enough males to ensure insemination of females as predicted by Hamilton (1967). Sabelis (1985) divides phytoseiid mites into two types: (1) general feeders adapted to low prey density, which produce Fisherian sex ratios, and (2) specialized predators, which produce Fisherian sex ratios at low prey density.

TABLE 4. PROGENY SEX RATIO OF 27 FEMALES OF *EUSEIUS SCUTALIS* AT 25° C

Sex	Days of age				Total	Mean	Standard deviation
	1-3	4-6	7-9	10-12			
Female individuals	92	87	74	82	335	12.26*	3.64
Male individuals	92	53	50	73	268	9.3	4.04
Female-to-male ratio	1.0	1.6	1.5	1.1	1.25		

*Means are not significantly different ($p = 0.05$, t-test).

Temperature and Humidity Effects on Immature *Euseius scutalis* and *E. stipulatus*

Development at different constant temperatures

Tables 5, 6, and 7 give the average duration of each immature stage of male and female *E. stipulatus, E. scutalis* from Agadir, and *E. scutalis* from Marrakech, respectively. Eggs of *E. stipulatus* did not hatch at 35° C. Those of both populations of *E. scutalis* did not hatch at 40° C. The duration of development decreased as temperature increased, except at 35° C, where the developmental time for both populations of *E. scutalis* increased. The longest developmental durations occurred at 15° C. The egg took the longest time and, usually, the larva took the shortest time to develop. Many authors have reported that the egg is the longest stage (Badii and McMurtry 1984; Ball 1980; de Moraes and McMurtry 1981; Sabelis 1981). In general, for each temperature, there were no significant differences ($p>0.05$) between sexes, but the data showed that males developed slightly faster than did females. This trait would have a selective advantage for males, since they search for a molting female deutonymph for mating (Amano and Chant 1978a; Badii and McMurtry 1984). Although *E. scutalis* completed development at 35° C, high mortality of the developing individuals was observed at this temperature. Usually, death occurred during molting. Charlet and McMurtry (1977) observed that molting *Metaseiulus validus* (Chant) took a longer time to emerge from the old cuticle at high temperatures, and that individuals frequently were unable to free themselves from the exuviae and died.

The behavior of *E. scutalis* at 35° C was characterized by a high level of activity. They attempted to escape from arenas, probably seeking a more suitable environment.

TABLE 5. DURATION IN HOURS OF EACH DEVELOPMENT STAGE OF *EUSEIUS STIPULATUS* AT DIFFERENT TEMPERATURES

	Females			**Males**		
Temperature (° C)	**Mean**	**Standard deviation**	**N***	**Mean**	**Standard deviation**	**N**
Egg stage						
15	169.2	19.1	12	152.2	20.1	5
20	70.9	7.2	13	70.4	5.6	10
25	59.2	4.4	9	58.3	5.6	5
30	28.8	2.8	10	28.7	2.8	7
Larva stage						
15	84.0	19.1	12	86.4	13.1	5
20	24.7	5.0	13	24.3	5.1	10
25	18.1	1.5	9	17.2	1.9	5
30	19.2	3.7	10	18.5	5.2	7
Protonymph stage						
15	104.0	11.8	12	115.2	20.1	5
20	30.9	7.0	13	31.7	8.7	10
25	28.4	4.3	9	26.5	3.0	5
30	18.9	2.7	10	18.3	5.7	7
Deutonymph stage						
15	83.6	15.9	12	72.0	16.9	5
20	37.9	4.2	13	32.9	6.3	10
25	23.7	5.2	9	20.0	2.5	5
30	17.5	3.2	10	16.2	3.7	7
Combined immature stages						
15	439.2	20.4	12	425.8	10.7	5
20	162.8	4.3	13	159.2	9.8	10
25	128.6	7.9	9	118.5	2.7	5
30	84.4	2.6	10	81.7	4.3	7

*Sample size.

Some individuals remained next to the cellucotton, where the temperature may have been lower and where drinking water was available. In contrast, the mites at 15° C showed reduced activity and moved less than those at the other temperatures. They remained under the coverslips most of the time.

Usually, individuals of the population of *E. scutalis* from Agadir developed slightly faster than those from Marrakech ($p<0.05$). Because of the sample size used in this study, however, it is difficult to determine whether the difference in development reflects a difference in the two populations. Marrakech and Agadir are separated by the High Atlas Mountains.

Euseius stipulatus developed faster than either population of *E. scutalis* at 15° C. Its development times were intermediate between those of the two *E. scutalis* populations at 20°, 25°, and 30° C, however, and it did not develop at all at 35° C. These data

TABLE 6. DURATION IN HOURS OF EACH DEVELOPMENT STAGE OF *EUSEIUS SCUTALIS* FROM AGADIR AT DIFFERENT TEMPERATURES

	Females			Males		
Temperature (° C)	**Mean**	**Standard deviation**	**N***	**Mean**	**Standard deviation**	**N**
Egg stage						
15	210.0	27.7	7	190.8	46.2	5
20	70.8	6.3	10	78.6	10.9	8
25	56.9	0.9	8	54.9	2.1	8
30	24.2	2.3	12	23.1	1.9	7
35	36.0	4.4	8	39.6	6.7	4
Larva stage						
15	123.4	32.3	7	148.8	54.7	5
20	21.0	2.7	10	21.5	2.9	8
25	19.1	3.9	12	18.5	1.9	8
30	10.0	2.3	12	12.3	2.4	7
35	14.8	2.7	8	12.7	2.4	4
Protonymph stage						
15	150.9	18.1	7	129.6	13.2	5
20	25.5	4.9	10	20.4	3.2	8
25	21.7	2.8	8	25.0	5.1	8
30	19.5	2.3	12	18.6	3.2	7
35	33.5	9.4	8	30.3	0.1	4
Deutonymph stage						
15	87.4	15.0	7	91.2	20.1	5
20	35.2	4.7	10	28.3	6.7	8
25	25.9	4.3	8	22.0	5.0	8
30	25.2	4.0	12	18.6	2.1	7
35	16.2	0.5	8	16.4	0.1	4
Combined immature stages						
15	571.7	10.8	7	560.0	13.1	5
20	152.5	5.9	10	148.8	7.6	8
25	122.9	3.7	8	120.4	3.4	8
30	77.2	4.2	12	72.2	2.7	7
35	97.2	2.7	8	99.0	5.6	4

*Sample size.

indicate that *E. scutalis* is intolerant of high temperatures. Sanderson (1983) reported high mortality among immature stages of *E. stipulatus* at 32.2° C. The upper developmental limit for *E. stipulatus* is probably between 32.2° and 35° C. Differences in development between *E. scutalis* and *E. stipulatus* are more obvious at high (35° C) and low (15° C) temperatures rather than at intermediate temperatures (20°, 25°, and 30° C). These differences define the temperature range tolerances of the two species, and are consistent with their distribution. While *E. stipulatus* is the most common phytoseiid mite in the cooler northern coastal areas of Morocco, *E. scutalis* occurs in the dry inland areas and the warm coastal regions of the country. Its distribution extends to the presaharian oasis areas.

Compared with data in the literature, the three populations developed from egg to adult within the usual time range for phytoseiid mites. Putman (1962) reported that

TABLE 7. DURATION IN HOURS OF EACH DEVELOPMENT STAGE OF *EUSEIUS SCUTALIS* FROM MARRAKECH AT DIFFERENT TEMPERATURES

	Females			Males		
Temperature (° C)	**Mean**	**Standard deviation**	**N***	**Mean**	**Standard deviation**	**N**
Egg stage						
15	215.1	46.8	5	207.9	32.2	5
20	65.5	8.9	11	62.2	3.6	8
25	59.1	6.6	11	59.3	6.4	7
30	29.3	2.5	9	28.8	2.3	11
35	35.5	0.01	5	35.5	0.01	4
Larva stage						
15	129.6	21.5	5	135.6	16.6	5
20	32.2	5.5	11	28.1	4.6	8
25	25.7	7.3	11	21.1	8.9	7
30	16.4	2.4	9	13.6	3.4	11
35	17.3	1.2	5	17.1	1.5	4
Protonymph stage						
15	276.0	89.9	5	264.0	58.8	5
20	37.7	8.2	11	40.5	11.3	8
25	31.6	5.9	11	30.2	9.1	7
30	19.8	3.5	9	20.9	3.4	11
35	31.1	5.7	5	26.6	3.9	4
Deutonymph stage						
15	177.6	27.4	5	182.4	21.5	5
20	33.6	4.4	11	30.5	7.6	8
25	23.1	5.1	11	20.6	4.4	7
30	21.7	2.6	9	21.4	3.4	11
35	22.6	5.2	5	19.9	3.9	4
Combined immature stages						
15	798.3	64.4	5	771.9	21.5	5
20	170.6	8.3	11	160.8	10.9	8
25	139.4	4.8	11	130.3	7.8	7
30	87.2	4.9	9	83.3	5.9	11
35	105.9	4.9	5	99.7	1.5	4

*Sample size.

Typhlodromus caudiglans Schuster developed in 6.7 days at 24.8° C, in 10.4 days at 20.1° C, and in 33.4 days at 14.7° C. *Amblyseius bibens* Blommers developed in 21.2 days at 15° C and in 4 days at 30° C (Sabelis 1981). *Amblyseius chilenensis* (Dosse) females completed development in 5.1 days at 25° C and 3.9 days at 32° C (Ma and Laing 1973). Other species of *Euseius* have similar durations of immature stages except at 15° C, where *E. scutalis* seems to require a longer time to complete development. *Euseius citrifolius* (Denmark and Muma) developed in 19.7 days at 15° C, 7.7 days at 20° C, and 5.0 days at 25° C (de Moraes and McMurtry 1981). At 24° C, *E. addoensis addoensis* (Van der Merwe and Ryke) and *E. addoensis rubicolus* (Van der Merwe and Ryke) developed in 8 and 7 days, respectively, when fed on pollen (McMurtry 1980). Concerning *E. stipulatus,* Porres-Arreaga (1974) reported results similar to those presented here except at 15° C, at which he observed shorter developmental time (10.83 days). McMurtry (1977) found that this species developed in 8 days at 23° C when fed on *Tetranychus pacificus.* When fed on pollen, *E. hibisci* had a developmental time of 12.08 days at 21° C, 7.39 days at 24° C, 4.82 days at 29° C, and 4.59 days at 35° C (Tanigoshi, Fargerlund, and Nishio-Wong 1981).

Figure 1 shows the relationship between the rate of development (1 ÷ duration of development) of immature stages of *E. scutalis* from Marrakech, and temperature. The developmental rate increased between 15° and 25° C and leveled off at 30° C. Development decreased slightly at 35° C, indicating that the optimum temperature was probably about 30° C. However, deutonymphs seemed to have a higher optimum development temperature, as there was no decrease in the rate at 35° C. Tanigoshi and coworkers (1975) reported similar results for both the protonymph and deutonymph of *Typhlodromus occidentalis* Nesbitt. The curve relating rate of development of *E. scutalis* to temperature does not have the sigmoid shape common to the curves of most insects (Davidson 1944; Howe 1966), nor the straight-line appearance common to the curves of most phytoseiids (Badii and McMurtry 1984; Blommers 1976; Hamamura, Shinkaji, and Ashihara 1976; de Moraes and McMurtry 1981; Sabelis 1981). Hence, a second-degree polynomial regression was fitted to the data.

The data in table 8 show the coefficient estimates with R^2 and upper and lower predicted thresholds. All the regressions explain a significant ($p = 0.0001$) portion of variation. This shows that the predicted low threshold for development is 10.6° C while the upper threshold is higher than 35° C.

TABLE 8. REGRESSION COEFFICIENTS AND PREDICTED TEMPERATURE THRESHOLDS FOR THE DEVELOPMENT OF *EUSEIUS SCUTALIS*

	Regression				Predicted threshold temperatures (° C)	
Stage	B_0	B_1	B_2	R^2	min.	max.
Egg	−1.04	0.1	−0.001	0.82	11.8	—*
Larva	−3.57	0.32	−0.005	0.73	14.4	49.6
Protonymph	−2.82	0.27	−0.005	0.57	14.2	39.9
Deutonymph	−2.98	0.28	−0.005	0.79	14.3	41.7
Total	−0.45	0.05	−0.0007	0.88	10.6	—

*No maximum is predicted.

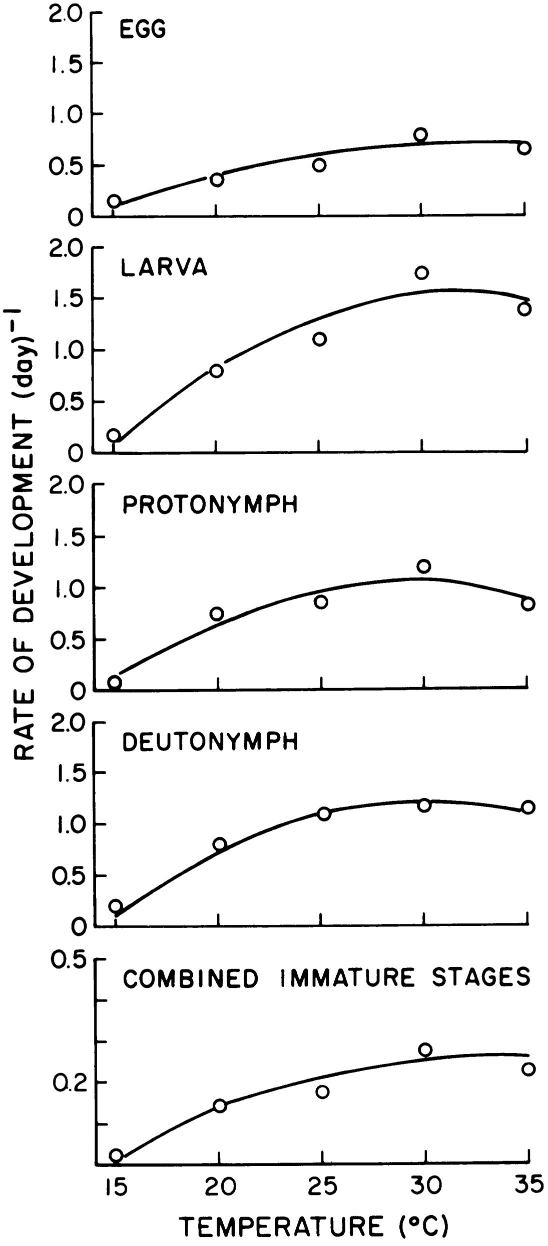

Fig. 1. Relationship between temperature and rate of development of *Euseius scutalis*.

Effect of relative humidities on egg hatching

Eggs of *E. stipulatus* required higher humidities than those of *E. scutalis* in order to hatch (table 9). The eggs that did not hatch shrivelled. At 19 percent relative humidity, no eggs of *E. stipulatus* hatched, while 16 and 13 percent of the *E. scutalis* eggs hatched for the populations from Agadir and Marrakech, respectively. All eggs of both species hatched at 60 percent relative humidity or higher. *Euseius scutalis* seems to have a greater ability to hatch at low relative humidities than *E. stipulatus.*

Other species of phytoseiids studied also showed increasing percentages of eggs hatching as relative humidity increased (Badii and McMurtry 1984; McMurtry 1980; McMurtry, Mahr, and Johnson 1976; de Moraes and McMurtry 1981). The percentage hatching at lower humidity ranges depended on the area of origin for the species. Both populations of *E. scutalis* showed similar responses to relative humidities.

Eggs required a longer time to hatch at low humidities. De Moraes and McMurtry (1981) and Badii and McMurtry (1984) did not find any relation between the time required to hatch or shrivel and the relative humidity. However, Knisley and Swift (1971) found that *A. umbraticus* took longer to develop at lower humidities.

Phytoseiid eggs are reported to require a high relative humidity in order to hatch (Badii and McMurtry 1984; Knisley and Swift 1971; McMurtry and Scriven 1965). As a protection from dessication, females generally place their eggs in high-humidity microhabitats (e.g., on the underside of leaves) (McMurtry and Scriven 1965; Swift and Blaustein 1980). Moreover, development, predation, and behavior of phytoseiid mites also are affected by humidity. Mori and Chant (1966a, b) showed that the activity and number of prey consumed by *P. persimilis* were higher at low than at high humidities.

The differences in developmental time at different temperatures, although only obvious at the extremes, and the differences in response to the relative humidity may explain in part why *E. scutalis,* known only from the arid environments of Morocco,

TABLE 9. EFFECT OF DIFFERENT RELATIVE HUMIDITIES ON EGG HATCHING OF *EUSEIUS STIPULATUS* AND *E. SCUTALIS*

	E. stipulatus			***E. scutalis* Agadir**			***E. scutalis* Marrakech**		
Relative humidity	**Eggs hatched**	**Incubation time**	**N***	**Eggs hatched**	**Incubation time**	**N**	**Eggs hatched**	**Incubation time**	**N**
%	%	*days*		%	*days*		%	*days*	
19	0	4	17	16	3	19	13	3	16
22	0	3	14	24	3	21	14	3	21
25	5	3	22	45	3	20	41	3	22
38	6	3	16	48	3	25	30	3	15
43	9	3	22	50	3	16	44	3	23
51	75	3	15	83	2	12	78	2	22
60	100	2	15	100	2	20	100	2	18
80	100	2	15	100	2	20	100	2	18
100	100	2	18	100	2	16	100	2	28

*Sample size.

has been recovered in the Riverside area, also an arid environment. In contrast, *E. stipulatus* was released in many areas of southern California but has become established only in the mild, more humid coastal areas.

Effects of Temperatures on Reproductive Potential

Preoviposition, oviposition, and postoviposition periods decreased as temperature increased, except at 25° C, where the oviposition period was longer than at 15° or 20° C (table 10). The maximum fecundity occurred at 25° C, while the highest daily rate of oviposition was at 30° C (table 11). These data fall within the usual range of reproductive parameters for phytoseiid mites (McMurtry, Huffaker, and van de Vrie 1970; de Moraes and McMurtry 1981; Sabelis 1985; Swirski, Amitai, and Dorzia 1967; Tanigoshi 1981). The oviposition period of *Amblyseius fallacis* (Garman) increased from 8.6 days at 32° C to 35.0 days at 21° C (Smith and Newsom 1970). At temperatures ranging from 15° to 30° C, the preoviposition, oviposition, and post-

TABLE 10. EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON DURATION (IN DAYS) OF PREOVIPOSITION, OVIPOSITION, AND POSTOVIPOSITION OF *EUSEIUS SCUTALIS*

Tempera-	Preoviposition				Oviposition				Postoviposition			
ture (° C)	Range	Mean	S.D.*	N†	Range	Mean	S.D.	N	Range	Mean	S.D.	N
		days				*days*				*days*		
15	1.0-5	3.0	1.5	22	6-51	23.4	14.9	17	2.0-29	10.5	15.3	17
20	1.0-4	2.2	1.1	25	12-33	23.4	6.9	17	0.5-12	5.0	2.7	17
25	0.5-5	2.2	1.4	31	25-40	32.2	3.5	20	1.0-5	3.5	1.7	20
30	0.5-1	0.6	0.2	26	13-31	19.4	4.3	16	0.5-6	2.4	1.9	16
35	0.5-2	0.9	0.3	20	8-23	13.3	5.3	12	0.5-6	2.5	2.5	12

*Standard deviation.

†Sample size.

TABLE 11. EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON TOTAL OVIPOSITION AND ON OVIPOSITION RATE OF *EUSEIUS SCUTALIS*

		Total oviposition			Eggs/female/day		
Tempera- ture (° C)	N*	Range	Mean	Standard deviation	Range	Mean	Standard deviation
15	17	5-27	15.3	6.9	0.5-1	0.69	0.19
20	17	15-38	28.5	6.6	1.0-1.5	1.26	0.38
25	20	43-91	64.8	13.2	1.8-2.5	1.98	0.19
30	16	41-87	55.9	11.3	2.4-3.7	2.90	0.38
35	12	20-59	34.6	5.9	1.6-3.7	2.46	0.70

*Sample size.

oviposition of *E. citrifolius* ranged from 5.3 to 1.7 days, 40.1 to 16 days, and 20.7 to 5.3 days, respectively (de Moraes and McMurtry 1981). These periods are comparatively longer than those of *E. scutalis.* The oviposition period of *E. hibisci* decreased from 25.19 days at 18° C to 8.9 days at 35° C (Tanigoshi, Fargerlund, and Nishio-Wong 1981). *Euseius scutalis* has an oviposition rate comparable to those of *E. hibisci* and *E. citrifolius* when fed on pollen (de Moraes and McMurtry 1981; Tanigoshi, Fargerlund, and Nishio-Wong 1981). In contrast, *E. scutalis* has a lower oviposition rate than *T. occidentalis, P. persimilis, A. bibens,* or *A. chilenensis* (Blommers 1976; Hamamura, Shinkaji, and Ashihara 1976; Ma and Laing 1973; Sabelis 1981; Tanigoshi et al. 1975), but relatively higher than that of *E. concordis* (McMurtry, Badii, and Johnson 1984). Usually, the rate of oviposition of phytoseiid mites increases with an increase in temperature (Badii and McMurtry 1984; Blommers 1976; de Moraes and McMurtry 1981; Tanigoshi et al. 1975; Tanigoshi, Fargerlund, and Nishio-Wong 1981).

Life table parameters are given in table 12. The intrinsic rate of natural increase (r_m) of *E. scutalis* increased from 0.019 at 15° C to 0.325 at 30° C, and declined to 0.15 at 35° C. Some workers have reported that the intrinsic rate of natural increase of phytoseiids has a linear relation to temperature (Blommers 1976; Ma and Laing 1973; Tanigoshi, Fargerlund, and Nishio-Wong 1981). Tanigoshi (1981) found that the linear relationship holds between 17° and 32° C. The net reproductive rate (R_o) increased from 2.56 at 15° C to 20.67 at 30° C and declined to 5.04 at 35° C. At 15° C, egg laying frequently stopped for periods of 1 to 10 days, and then resumed. This resulted in low oviposition over a long life span. Mean generation time (τ) decreased with an increase in temperature, but re-increased at 35° C.

The survivorship curves in figure 2 show that the longevity increased at lower temperatures. The greater mortality at high temperatures was accompanied by an earlier and higher peak in the fecundity. Similar observations were reported by Smith and Newsom (1970), Ma and Laing (1973), Sabelis (1981), and Badii and McMurtry (1984). In addition, a high daily reproductive rate seemed to be related to a shorter oviposition period. The peaks of fecundity were maintained for a relatively longer time at the intermediate temperatures of 20°, 25°, and 30 °C, and especially at 25 °C, than at low or high temperatures. The lowest r_m values at 15° and 35 °C can be attributed to high mortality at 35 °C and to a low rate of development and oviposition at 15 °C.

TABLE 12. EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON LIFE TABLE PARAMETERS OF *EUSEIUS SCUTALIS*

	Life table parameters*				
Temperatures (° C)	r_m	R_o	r_c	τ	T_c
15	0.019	2.56	0.019	47.6	48.7
20	0.151	10.58	0.126	15.56	18.73
25	0.188	19.46	0.143	15.76	20.72
30	0.325	20.67	0.245	9.32	12.33
35	0.150	5.04	0.136	10.78	11.97

*r_m = intrinsic rate of natural increase; R_o = net reproductive rate; r_c = capacity for increase; τ = mean generation time; and T_c = cohort generation time.

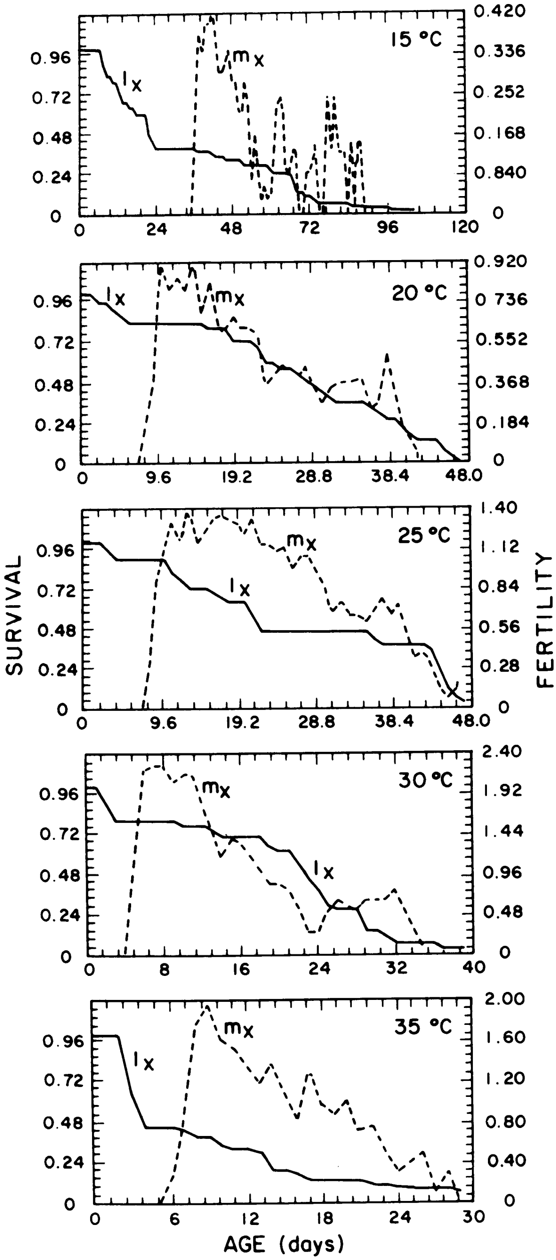

Fig. 2. Daily proportion of female progeny per female (m_x) and survival (l_x) of *Euseius scutalis*.

The daily egg production was relatively more stable for young females at the intermediate temperatures than at upper or lower temperatures. Although the maximum fecundity occurred at 25° C, life table parameters suggested that 30° C was the most favorable temperature for population increase of *E. scutalis.* This resulted from a high reproductive rate at early female age. The mean generation time, net reproductive rate, and intrinsic rate of increase illustrate this point. The unfavorable influence of low temperature on population increases and on the oviposition of *E. scutalis* is probably due to a direct influence on the reproductive system of the female, slowing the maturation of the oocytes. Data reported by Wysoki and Swirski (1971) showed that, although *E. scutalis* reproduces throughout the winter, more than 80 percent of the females collected in winter contained no eggs.

CONCLUSIONS

The literature and our field observations show that *Euseius scutalis* is adapted to a wide variety of trees and perennial crops that support various kinds of potential prey. Its sex ratio and its feeding habits are adapted to this type of habitat.

The data reported here on development and oviposition at different temperatures indicate that this species is also adapted to warm and arid areas, with the ability to survive in temperatures that prevail during the relatively short and mild winters in those areas.

No *Euseius* species is known to occur in the low desert regions of California and Arizona on citrus, but if established, *E. scutalis* might become a factor in the biological control of mites and thrips in those areas.

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