DEVELOPMENTAL RATES, VITAL SCHEDULES, SEX RATIOS, AND LIFE TABLES FOR *TETRANYCHUS URTICAE, T. TURKESTANI* AND *T. PACIFICUS* (ACARINA : TETRANYCHIDAE) ON COTTON

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TETRANYCHIDS
DEVELOPMENTAL TIME
LONGEVITY
FECUNDITY
SURVIVORSHIP
LIFE TABLES

ABSTRACT : The life histories of *Tetranychus urticae* Koch, *T. pacificus* McGregor and *T. turkestani* (Ugarov and Nikolski) (Acarina : Tetranychidae) were studied at 5 constant temperatures ranging from 15.5° to 29.4°C on cotton cotyledons. Average developmental times of all 3 species were similar. These ranged from 25.8 to 29.0 days at 15.5°C and from 6.1 to 6.7 days at 29.4°C for females. Males required slightly less time. Total progeny at 23.8°C was 84.6, 103.3, and 78.9 eggs/female for *T. turkestani, T. urticae* and *T. pacificus*, respectively, and at 29.4°C was 73.5, 64.3 and 68.3 eggs/females for *T. turkestani, T. urticae* and *T. pacificus*, respectively. The percentage of female offspring was 74 % for *T. urticae*, 55 % for *T. turkestani* and 57 % for *T. pacificus*. Average female adult longevity at 23.8°C was 12.46, 14.71 and 12.71 days for *T. turkestani, T. urticae*, and *T. pacificus*, respectively, and at 29.4°C was 8.79, 9.71, and 8.91 days for *T. turkestani, T. urticae* and *T. pacificus*, respectively. Life tables were constructed from survivorship and fecundity data collected at 23.8 and 29.4°C. The intrinsic rate of increase for the 3 tetranychids ranged from 0.204 to 0.219 at 23.8°C and from 0.293 to 0.295 at 29.4°C. The results of this study are compared with other investigations of the same species.

TETRANYQUES
DURÉE DU DÉVELOPPEMENT
LONGÉVITÉ
FÉCONDITÉ
SURVIE
TABLES DE VIE

RÉSUMÉ : La biologie de trois espèces d'Acariens Tetranychidae : *Tetranychus urticae* Koch, *Tetranychus pacificus* McGregor et *Tetranychus turkestani* (Ugarov et Nikolski), élevées sur feuilles cotylédonaires de cotonnier, a été étudiée à cinq températures différentes échelonnées de 15,5°C à 29,4°C.

Les durées moyennes de développement des trois espèces sont comparables. Pour les femelles, elles varient selon l'espèce de 25,8 à 29,0 jours, pour une température de 15,5°C et de 6,1 à 6,7 jours, pour une température de 29,4°C. Les mâles se développent un peu plus rapidement. Pour *T. turkestani, T. urticae* et *T. pacificus* élevés à 23,8°C, la descendance totale est respectivement de 84,6, 103,3 et 78,9 œufs par femelle, tandis qu'à 29,4°C, les pontes correspondantes sont de 73,5, 64,3 et 68,3 œufs. Le pourcentage de femelles dans la descendance est de 74 % pour *T. urticae*, 55 % pour *T. turkestani* et 57 % pour *T. pacificus*. À 23,8°C, la longévité moyenne des femelles adultes est de 21,46 jours pour *T. turkestani*, de 14,71 jours pour *T. urticae* et de 12,71 jours pour *T. pacificus*, tandis qu'à 29,4°C les longévités correspondantes sont respectivement 8,79, 9,71 et 8,91 jours.

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Les tables de vie sont dressées à partir des données recueillies sur la survie et la fécondité à 23,8°C et à 29,4°C. Le taux intrinsèque d'accroissement des trois tétranyques varie de 0,204 à 0,219, pour une température de 23,8°C et de 0,293 à 0,295, pour une température de 29,4°C. Les résultats obtenus ont été comparés à ceux des travaux effectués sur les mêmes espèces.

INTRODUCTION

Spider mites have been reported infesting cotton in the United States since the late 1800's (TITUS, 1905) and are currently among the most destructive arthropod pests in California cotton fields (LEIGH and BURTON, 1976). At least 25 spider mite species in six genera have been reported as pests of cotton in the world (LEIGH, 1963). The majority are in the genus *Tetranychus*. In California's San Joaquin Valley the major tetranychid species are *Tetranychus turkestani* (Ugarov and Nikolski), the strawberry or atlantic mite ; *T. urticae* Koch, the twospotted mite ; and *T. pacificus* McGregor, the Pacific mite.

The strawberry mite is considered to be primarily an early-season pest of cotton in California and the twospotted and Pacific mites are thought to be pests chiefly in mid to late season (LEIGH, 1963). All are found throughout the cotton growing regions of the San Joaquin Valley. LEIGH and BURTON (1976) reported that *T. urticae* is found predominantly in the eastern and southern parts and *T. pacificus* mainly in the western regions. No regional pattern has been found for *T. turkestani*. It has been suggested (e.g., ANDRES, 1957 ; LEIGH, 1963) that these temporal and spatial patterns are related to temperature and humidity.

MCGREGOR and MCDONOUGH (1917) were the first researchers to examine the biology of a spider mite on cotton. They reported the life history of *T. urticae* reared in the field. Numerous researchers have investigated the field population dynamics and damage potential of several species of spider mites (e.g. CANERDAY and ARANT, 1964 ; SIMONS, 1964 ; FURR and PFRIMMER, 1968 ; GAABOUB *et al.*, 1976 ; CAREY, 1980). Others have examined *T. urticae* in life table studie (ANDRES, 1957 ; BENGSTON, 1969 ; LAING, 1969 ; SHIH *et al.*, 1976). CAGLE (1956) and ANDRES (1957) conducted studies on *T. turkestani*, although only ANDRES presented the information in life table form. LAMIMAN (1935) presented a brief sketch of the biology of *T. pacificus*. ANDRES (1957) conducted developmental fecundity and longevity studies on this species at different temperatures and humidities, as he did with *T. urticae* and *T. turkestani*.

This study is part of a 2-year investigation of the biology and ecology of the tetranychid mites found on cotton in California. The present paper reports the findings of the laboratory studies conducted in 1977 on the life history of the three major tetranychid pests of cotton in the San Joaquin Valley.

EXPERIMENTAL METHODS

Mite colonies were established from infested cotton fields near Five Points, California in July 1977. Identification of the three species was virtually impossible based on live specimens. The only way to adequately distinguish the species was by using aedeagal characteristics as outlined by BAKER and PRITCHARD (1953). Since field colonies of the species on cotton are frequently mixed, even on the same leaves, approximately 75 field-collected females were isolated on leaf discs as a first step towards determining their identity. The sons produced by these solitary females were slide-mounted and their aedeagi examined to establish identity of each female and her progeny. Once the identity of a family unit was made, the daughters of the original field-collected female were used in initiating the experiments. All of the investigations were done using the F2-F4 generations from the field.

Developmental studies were done on each of the tetranychids at 5 constant temperatures — 15.5 ∓ 3°, 18.3 ∓ 2°, 21.1 ∓ 2°, 23.8 ∓ 2°, and 29.4 ∓ 2°C. The relative humidity ranged from 50-65 % and the diurnal cycle was 16 hours light and 8 hours dark. All mites were reared on the cotyledons of cotton seedlings placed in cotton-stoppered glass vials. Adult mites of both sexes were transferred from their respective colony to a cotton seedling with a small brush and the female allowed to oviposit. The mites and all but one egg from each seedling were later removed and the remaining egg was followed through to maturity. Approximately 24 individuals of each species were observed at each of the five temperatures. The experiments at the three lowest temperatures were checked once per day and the tests at 23.8° and 29.4°C were checked every 12 hours.

Fecundity and longevity data were collected at only the two highest temperatures, 23.8° and 29.4°C. For this, the individuals maturing as females in the rate of development tests were observed for oviposition and survival through their adulthood. Because up to 50 % of those maturing were males, female deutonymphs of the same species were added in order that the number of females observed through the ovipositional stage would remain around 24.

Cotton seedling cotyledons were used instead of detached leaf discs because we felt that it was important to provide the mites with a live food source of the same species and variety from which they were recovered from in the field (*Gossypium hirsutum*, cultivar SJ-4). Because of the size and shape of the cotyledons it was often impossible to determine whether an immature had crawled away or fallen off. In some cases the shriveled corpse could not be found or identified. This problem occurred at all temperatures and for all species in up to 20-25 % of the replicates. In such cases, the immature survivorship was felt to be unreliable. The lost replicate was replaced with a new egg. The developmental information of only those individuals surviving to adulthood is presented. Adult survivorship information is felt to be reliable because the dead female was usually found.

Life table calculations

A life table is a concise summary of certain vital statistics of a population (Deevy, 1947). Originally set forth as a tool for the study of human and animal populations, Birch (1948) and Andrewartha and Birch (1954) adopted and advocated life table techniques for use in insect population investigations.

The analysis of tetranychid mite populations through the use of life tables is important for several reasons. First, it helps to order the gathering of the major life history parameters — development, longevity, fecundity, and sex ratio. Second, it isolates age-specific relationships. Third, it helps answer questions, not only about individuals, but about cohorts and populations (Keyfitz, 1968). The consequences of certain population biology features as expressed in life table parameters are reviewed and critiqued in works by Cole (1954), Lewontin (1965), Gadgill and Bossert (1970) and Stearns (1977).

The intrinsic rate of increase, r, was calculated from data on survival and fecundity of individuals of known age. The data were combined in the form of a life table with the following columns :

l_x = proportion of females alive in age interval ×

m_x = the number of female offspring produced per surviving female in the age interval ×

$l_x m_x$ = the number of female offspring per original female produced in the age interval ×

Because the total daily progeny and the sex ratios were known rather than the actual number of progeny maturing as females, m_x was calculated using

$$m_x = P \cdot m_x'$$

where

P = proportion of females in the sex ratio

m_x' = total progeny produced per surviving female in the age interval ×

The parameter, r, was calculated using the following formula :

$$r = \log_e R_o / T$$

where R_o and T are specifically defined and derived as below.

The net reproductive rate, R_o, is the average number of newborn females produced by an average newborn female dyring its entire lifetime. It is the sum of the products of l_x and m_x. That is

$$R_o = \sum_{x=1}^{\infty} l_x m_x$$

The mean generation time, T, is the average age of parenthood. An accurate calculation of T is made by weighing each age by its total realized fecundity, $x l_x m_x$, and dividing by R_o. Thus

$$T = \sum_{x=1}^{\infty} x l_x m_x / \sum_{x=1}^{\infty} l_x m_x$$

The denominator is identical to R_o.

RESULTS

■ *Egg Stage*

The egg stage in all three species was about twice as long as any of the active stages plus their quiescent period (Table 1). The egg stage lasted the longest in *T. turkestani* all temperatures, except 21.1°C where the duration for *T. pacificus* was slightly greater. At the lowest temperature and the two highest temperatures, *T. urticae* and *T. pacificus* egg incubation times were similar while at 18.3 and 21.1°, *T. pacificus* eggs hatched in about 0.8 days less time than did *T. urticae* eggs. As in all the developmental studies, the greatest variation and the widest range occured at the lowest temperatures.

■ *Larval Stage.*

The average duration of the larval stages and their following quiescent stages for the three species at various temperatures are presented in Table 1. The quiescent stage for all species at all temperatures took about 30-40 % of the total time required to develop through both stages. In general, *T. turkestani* required more time to develop at all temperatures, except 29.4°C where the larval stage of *T. pacificus* took about 0.17 days longer.

■ *Protonymphal Stage*

The duration of this stage was usually shorter than the larval stage at corresponding temperatures (Table 1). Considerable variation in developmental times existed at all temperatures and in all species. On average, the quiescent stage lasted about 5-10 % longer than the active stage.

■ *Deutonymphal Stage*

The average duration of the deutonymph and its following quiescent stage are presenting in Table 1. As with the protonymphs and their quiescent stages, there was no consistent pattern among species. *T. turkestani* had the longest developmental times at 15.5°C for its deutonymphal and quiescent stages and also the greatest developmental time for its quiescent stage at 21.1°C. At all temperatures the quiescent stages of *T. turkestani* lasted longer than its preceding deutonymphal stage. The relative duration of these two stages varied considerably in the other two species.

■ *Total Maturation Time*

At the lowest temperature, 15.5°C, males of all three species required about 1-3 % more time to develop than the females. At the other temperatures the average male developmental time was about 6-11 % shorter than the female's (Table 2). There were only small differences in developmental times between species at similar temperatures.

TABLE 1. Duration in days of the egg (e), larva (l), protonymph (p), deutonymph (d) and quiescent (q_1, q_2, q_3) stages of *Tetranychus turkestani, T. urticae* and *T. pacificus* at 5 constant temperatures. Standard deviation in parentheses.

Species	Stage	Temperature (°C) 15.5°	18.3°	21.1°	23.8°	29.4°
T. turkestani	e	13.50 (1.50)	7.50 (0.93)	6.78 (0.73)	4.95 (0.71)	2.63 (0.49)
	l	3.29 (0.90)	2.00 (0.59)	2.21 (0.67)	1.21 (0.34)	0.93 (0.27)
	q_1	2.33 (0.73)	1.54 (0.72)	1.60 (0.72)	0.92 (0.29)	0.54 (0.14)
	p	2.19 (0.60)	1.54 (0.72)	1.17 (0.38)	0.79 (0.25)	0.54 (0.14)
	q_2	2.33 (0.48)	1.41 (0.58)	1.43 (0.59)	0.95 (0.15)	0.54 (0.14)
	d	2.48 (0.81)	1.54 (0.66)	1.43 (0.59)	0.93 (0.33)	0.50 (0.00)
	q_3	3.38 (1.02)	1.75 (0.53)	1.83 (0.72)	1.06 (0.29)	0.56 (0.17)
T. urticae	e	11.19 (1.51)	6.58 (0.78)	6.00 (0.83)	4.42 (0.24)	2.54 (0.29)
	l	2.59 (0.59)	1.88 (0.54)	1.96 (0.46)	1.10 (0.33)	0.75 (0.29)
	q_1	2.05 (0.49)	1.46 (0.51)	1.33 (0.56)	0.85 (0.23)	0.63 (0.30)
	p	2.27 (0.70)	1.42 (0.50)	1.29 (0.55)	0.81 (0.24)	0.63 (0.27)
	q_2	2.32 (1.34)	1.54 (0.66)	1.29 (0.46)	0.98 (0.28)	0.35 (0.28)
	d	2.45 (1.22)	1.83 (0.87)	1.38 (0.49)	1.04 (0.29)	0.52 (0.08)
	q_3	2.41 (0.67)	1.75 (0.61)	1.75 (0.74)	1.08 (0.43)	0.52 (0.28)
T. pacificus	e	11.91 (0.88)	7.33 (0.64)	6.88 (1.19)	4.41 (0.24)	2.58 (0.41)
	l	2.83 (0.76)	1.71 (0.55)	1.83 (0.38)	1.10 (0.33)	1.10 (0.42)
	q_1	2.38 (0.58)	1.38 (0.58)	1.50 (0.51)	0.85 (0.23)	0.50 (0.21)
	p	2.13 (0.99)	1.04 (0.20)	1.33 (0.48)	0.81 (0.25)	0.54 (0.14)
	q_2	2.42 (1.28)	1.67 (0.64)	1.50 (0.72)	0.98 (0.28)	0.52 (0.10)
	d	2.17 (1.00)	1.29 (0.46)	1.46 (0.72)	1.04 (0.29)	0.63 (0.27)
	q_3	3.13 (0.85)	1.79 (0.41)	1.58 (0.50)	1.08 (0.43)	0.58 (0.24)

TABLE 2. Average duration in days of female and male *Tetranychus turkestani, T. urticae* and *T. pacificus* at 5 constant temperatures. Standard deviation in parentheses.

Species	Sex	Temperature (°C) 15.5°	18.3°	21.1°	23.8°	29.4°
T. turkestani	♀	29.0 (3.14)	18.0 (1.96)	17.4 (1.26)	10.7 (0.86)	6.4 (0.62)
	♂	29.5 (3.38)	16.2 (1.89)	15.5 (1.13)	9.7 (0.65)	6.0 (0.47)
T. urticae	♀	25.8 (1.94)	16.5 (1.17)	15.0 (1.34)	10.5 (0.62)	6.1 (0.44)
	♂	26.6 (3.31)	15.0 (1.73)	14,4 (1.82)	9.8 (0.65)	5.6 (0.38)
T. pacificus	♀	26.4 (1.62)	16.5 (0.69)	16.9 (1.46)	10.5 (0.68)	6.7 (0.55)
	♂	28.0 (1.83)	15.9 (0.76)	15.6 (2.07)	9.9 (0.73)	6.2 (0.61)

Oviposition

The time from maturation to the first egg (preoviposition period) ranged from 1.17 days in *T. turkestani* and *T. pacificus* at 23.8° to 0.42 days in *T. pacificus* at 29.4°C (Table 3). At this higher temperature the preovipositional period of *T. pacificus* was only half that of *T. turkestani*, which averaged 0.79 days.

The daily ovipositional patterns for all three species at 23.8°C (Fig. 1) were quite similar. In general, the maximum egg production lasted from ca. day 5 to day 11 for all species, although *T. turkestani* laid eggs erratically towards the end of their lives.

The ovipositional patterns for these species at 29.4°C were similar to those at the lower temperature, with a few exceptions (Fig. 2). *T. turkestani* had the highest peak fecundities, laying ca. 11.8 eggs/female/day 3, 4, and 6. *T. pacificus* and *T. urticae* laid ca. 8-10 eggs/female/day over this same period. The peak production for all species lasted from day 2 to ca. day 8

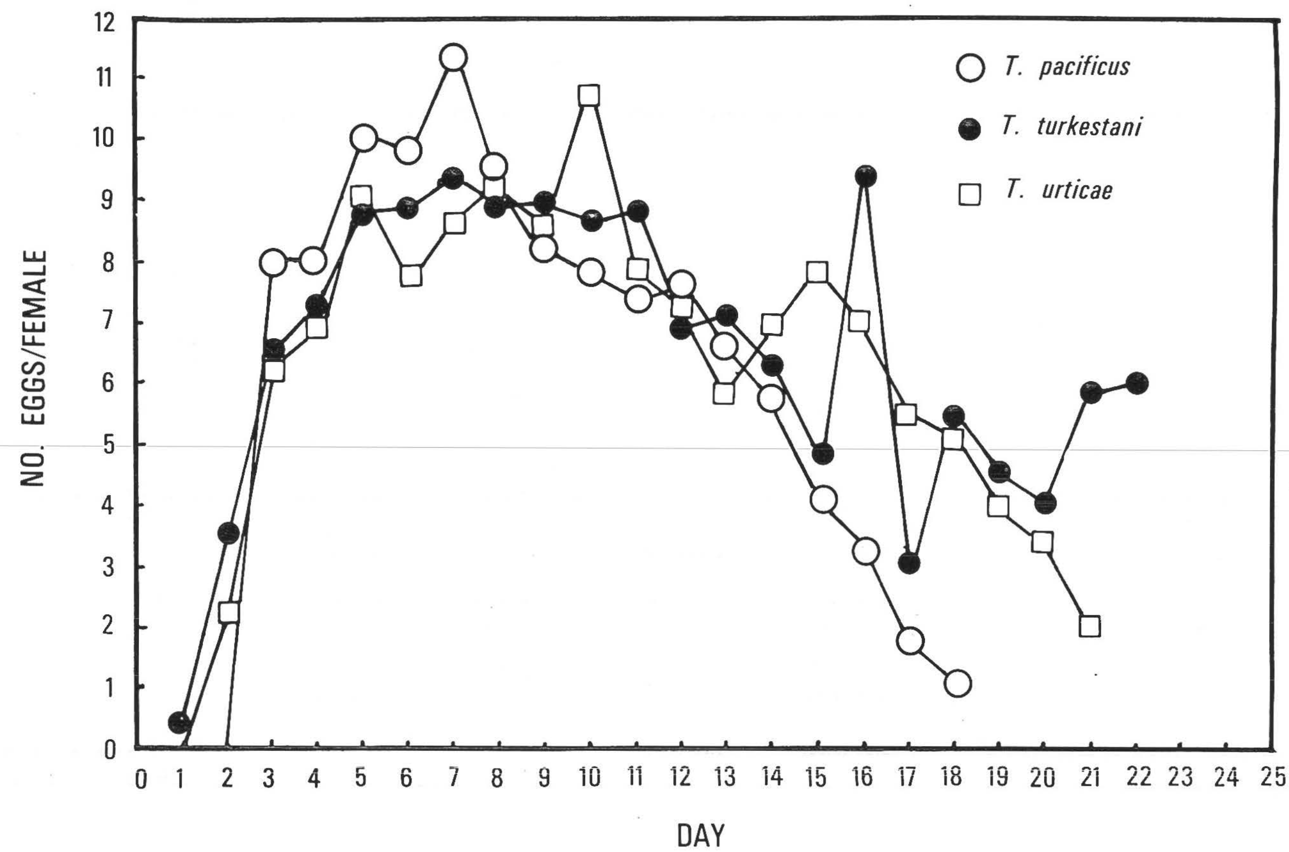

FIG. 1 : the average daily oviposition per living female of *Tetranychus turkestani, T. urticae*, and *T. pacificus* at 23.8°C.

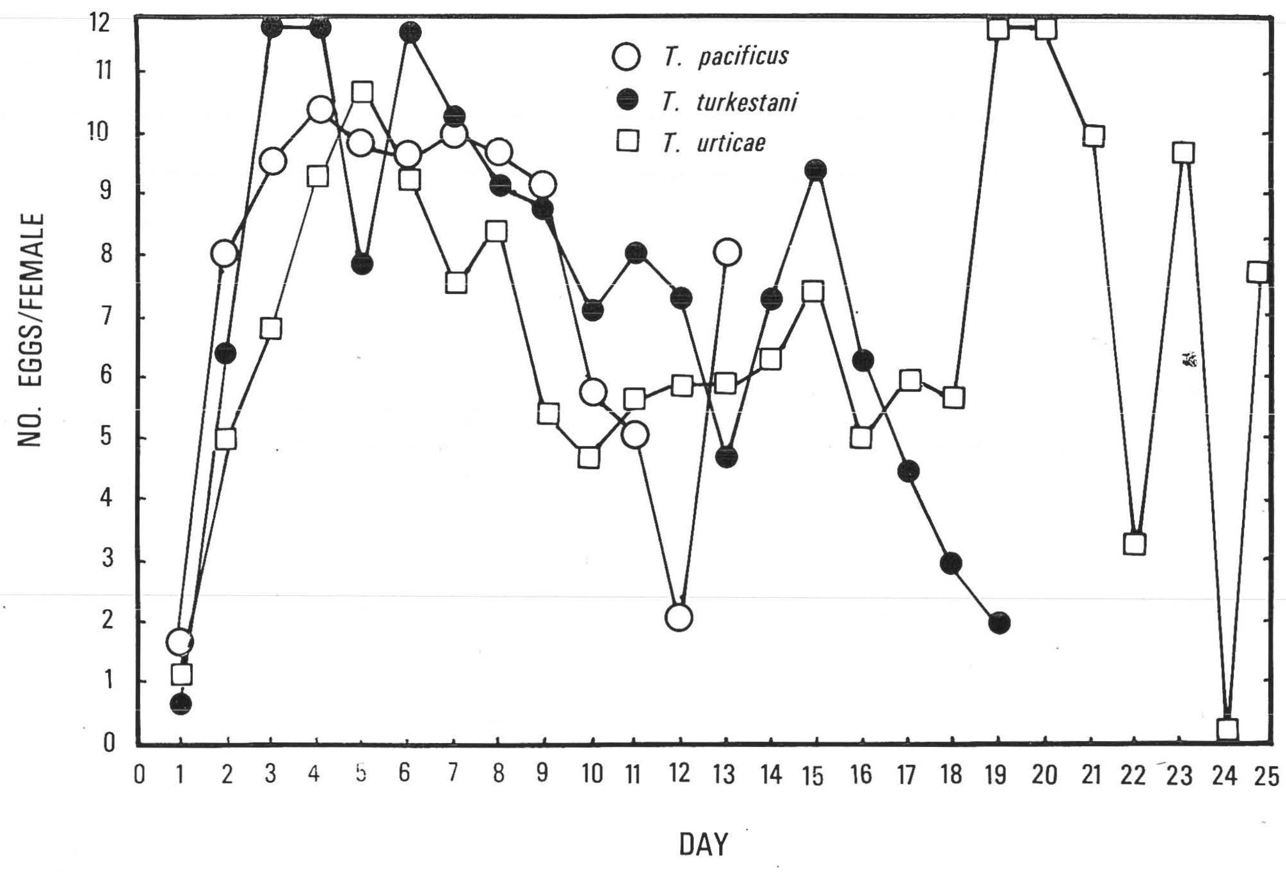

FIG. 2 : the average daily oviposition per living female of *Tetranychus turkestani, T. urticae*, and *T. pacificus* at 29.4°C.

TABLE 3. Average preovipositional periods for *Tetranychus turkestani*, *T. urticae*, and *T. pacificus* at 23.8° and 29.4°C. (Maximum and minimum in parentheses).

	Preovipositional period (days)	
	23.8°C	29.4°C
T. turkestani	1.17 (0-3)	0.79 (0-2)
T. urticae	1.08 (1-2)	0.71 (0-2)
T. pacificus	1.17 (1-4)	0.42 (0-1)

TABLE 4. Total progeny of *Tetranychus turkestani*, *T. urticae*, and *T. pacificus* at 23.8° and 29.4°C. (X̄ = average number/female ; SD = standard deviation ; RANGE = maximum and minimum values).

		Progeny/female	
		23.8°C	29.4°C
T. turkestani	X̄	84.6	73.5
	SD	44.67	43.57
	RANGE	6-181	21-179
T. urticae	X̄	103.3	64.3
	SD	39.30	42.50
	RANGE	16-166	15-185
T. pacificus	X̄	78.9	68.3
	SD	40.13	36.90
	RANGE	13-163	5-150

TABLE 5. Ratio of female to male (female : male) *Tetranychus turkestani*, *T. urticae*, and *T. pacificus* at various temperatures. (Percentage females in parenthesis).

	Temperature (°C)					
	15.5°C	18.3°C	21.1°C	23.8°C	29.4°C	Total
T. turkestani	13 : 8 (62)	13 : 11 (54)	10 : 13 (43)	13 : 18 (62)	14 : 10 (58)	63 : 50 (55)
T. urticae	16 : 7 (69)	19 : 5 (79)	20 : 4 (83)	16 : 8 (67)	17 : 7 (71)	88 : 31 (74)
T. pacificus	17 : 7 (71)	11 : 13 (48)	12 : 12 (50)	15 : 9 (63)	13 : 11 (57)	68 : 52 (57)

or 9. However, *T. urticae* females tended to have erratic ovipositional patterns near the end of their lives. One female laid eggs at an high and erratic rate from day 18 to day 25. The average total fecondity at 23.8° and 29.4°C for all species is presented in Table 4.

TABLE 6. Longevity in days of *Tetranychus turkestani*, *T. urticae*, and *T. pacificus* females at 23.8° and 29.4°C. (X̄ = Mean ; SD = standard deviation ; Range = maximum and minimum values).

		Longevity (days)	
		23.8°C	29.4°C
T. turkestani	X̄	12.46	8.79
	SD	4.80	4.98
	RANGE	3-22	3-18
T. urticae	X̄	14.71	9.71
	SD	5.80	5.58
	RANGE	4-32	3-26
T. pacificus	X̄	12.71	8.91
	SD	3.64	3.87
	RANGE	6-19	1-13

TABLE 7. Life table of *Tetranychus turkestani* at 23.8°C. (m_x = P·m_x', where P represents the proportion of females (0.55), and m_x' represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m_x'	m_x	l_xm_x	$\times l_xm_x$
1	11.7	1.00	0.29	0.16	0.16	1.87
2	12.7	1.00	3.50	1.93	1.93	24.54
3	13.7	1.00	6.50	3.58	3.58	48.98
4	14.7	0.96	7.17	3.94	3.79	55.65
5	15.7	0.96	8.70	4.79	4.59	72.12
6	16.7	0.92	8.82	4.85	4.46	74.53
7	17.7	0.88	9.24	5.08	4.42	79.16
8	18.7	0.88	8.86	4.87	4.29	80.19
9	19.7	0.83	8.85	4.87	4.04	79.59
10	20.7	0.79	8.42	4.63	3.66	75.73
11	21.7	0.67	8.63	4.75	3.18	69.01
12	22.7	0.63	6.67	3.67	2.31	52.46
13	23.7	0.50	6.92	3.81	1.90	45.10
14	24.7	0.33	6.13	3.37	1.11	27.48
15	25.7	0.29	4.86	2.67	0.78	19.92
16	26.7	0.13	9.33	5.13	0.67	17.81
17	27.7	0.13	3.00	1.65	0.21	5.94
18	28.7	0.13	5.33	2.93	0.38	10.94
19	29.7	0.13	4.67	2.57	0.33	9.92
20	30.7	0.13	4.00	2.20	0.29	8.78
21	31.7	0.13	5.67	3.12	0.41	12.85
22	32.7	0.08	6.00	3.30	0.26	8.63
23	33.7	0.00	0.00	0.00	0.00	0.00
					46.79	881.11

R_o = 46.79 ; T = 18.83 ; r = 0.204

TABLE 8. Life table of *Tetranychus turkestani* at 29.4°C. (m_x = P·m'_x, where P represents the proportion of females (0.55), and m'_x represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m'_x	m_x	l_xm_x	× l_xm_x
1	7.4	1.00	0.67	0.37	0.37	2.73
2	8.4	1.00	6.42	3.53	3.53	29.66
3	9.4	1.00	13.50	7.43	7.43	69.80
4	10.4	0.96	13.17	7.24	6.95	72.32
5	11.4	0.79	7.84	4.31	3.41	38.83
6	12.4	0.67	11.94	6.57	4.40	54.56
7	13.4	0.50	10.17	5.59	2.80	37.48
8	14.4	0.50	8.83	4.86	2.43	34.97
9	15.4	0.46	8.55	4.70	2.16	33.31
10	16.4	0.38	6.67	3.67	1.39	22.86
11	17.4	0.33	7.75	4.26	1.41	24.48
12	18.4	0.29	7.14	3.93	1.14	20.95
13	19.4	0.17	4.50	2.48	0.42	8.16
14	20.4	0.17	7.00	3.83	0.65	13.35
15	21.4	0.17	9.25	5.09	0.86	18.51
16	22.4	0.17	6.00	3.30	0.56	12.57
17	23.4	0.17	4.25	2.34	0.40	9.30
18	24.4	0.08	3.00	1.65	0.13	3.22
19	25.5	0.04	2.00	1.10	0.04	1.12
20	26.4	0.00	0.00	0.00	0.00	0.00
					40.49	508.17

R_o = 40.49 ; T = 12.55 ; r = 0.295

TABLE 9. Life table of *Tetranychus urticae* at 23.8°C. (m'_x = P·m'_x, where P represents the proportion of females (0.74), and m'_x represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m'_x	m_x	l_xm_x	× l_xm_x
1	11.5	1.00	0.00	0.00	0.00	0.00
2	12.5	1.00	0.00	0.00	0.00	0.00
3	13.5	1.00	8.04	5.95	5.95	80.32
4	14.5	1.00	7.88	5.83	5.83	84.55
5	15.5	0.96	10.09	7.47	7.17	111.10
6	16.5	0.88	9.71	7.19	6.32	104.33
7	17.5	0.83	11.40	8.44	7.00	122.53
8	18.5	0.79	8.95	6.62	5.23	96.80
9	19.5	0.75	8.67	6.42	4.81	93.83
10	20.5	0.75	10.72	7.93	5.95	121.97
11	21.5	0.75	7.72	5.71	4.28	92.12
12	22.5	0.75	7.06	5.22	3.92	88.16
13	23.5	0.71	5.82	4.31	3.06	71.86
14	24.5	0.63	6.80	5.03	3.17	77.67
15	25.5	0.63	7.60	5.62	3.54	90.35
16	26.5	0.58	6.57	4.86	2.82	74.73
17	27.5	0.54	5.31	3.93	2.12	58.35
18	28.5	0.50	5.17	3.83	1.91	54.52
19	29.5	0.38	4.00	2.96	1.12	33.18
20	30.5	0.21	3.60	2.66	0.56	17.06
21	31.5	0.04	2.00	1.48	0.06	1.86
22	32.5	0.00	0.00	0.00	0.00	0.00
					74.84	1475.30

R_o = 74.84 ; T = 19.71 ; r = 0.219

TABLE 10. Life table of *Tetranychus urticae* at 29.4°C. (m_x = P·m'_x, where P represents the proportion of females (0.74), and m'_x represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m'_x	m_x	l_xm_x	× l_xm_x
1	7.1	1.00	0.88	0.65	0.65	4.62
2	8.1	1.00	5.04	3.73	3.73	30.21
3	9.1	1.00	6.75	5.00	5.00	45.45
4	10.1	0.96	9.26	6.85	6.58	66.44
5	11.1	0.88	10.90	8.07	7.10	78.79
6	12.1	0.75	9.11	6.74	5.06	61.18
7	13.1	0.71	7.29	5.39	3.83	50.18
8	14.1	0.63	8.27	6.12	3.86	54.36
9	15.1	0.46	5.27	3.90	1.79	27.09
10	16.1	0.33	4.75	3.52	1.16	18.68
11	17.1	0.25	5.33	3.94	0.99	16.86
12	18.1	0.25	5.50	4.07	1.02	18.42
13	19.1	0.25	5.67	4.20	1.05	20.03
14	20.1	0.25	6.00	4.44	1.11	22.31
15	21.1	0.25	7.50	5.55	1.39	29.28
16	22.1	0.17	5.00	3.70	0.63	13.90
17	23.1	0.17	5.75	4.26	0.72	16.71
18	24.1	0.08	5.50	4.07	0.33	7.85
19	25.1	0.04	12.00	8.88	0.36	8.92
20	26.1	0.04	12.00	8.88	0.36	9.27
21	27.1	0.04	10.00	7.40	0.30	8.02
22	28.1	0.04	3.00	2.22	0.09	2.50
23	29.1	0.04	10.00	7.40	0.30	8.61
24	30.1	0.04	0.00	0.00	0.00	0.00
25	31.1	0.04	8.00	5.92	0.24	7.36
26	32.1	0.00	0.00	0.00	0.00	0.00
					47.60	627.03

R_o = 47.60 ; T = 13.17 ; r = 0.293

TABLE 11. Life table of *Tetranychus pacificus* at 23.8°C. (m_x = P·m'_x, where P represents the proportion of females (0.57), and m'_x represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m'_x	m_x	l_xm_x	× l_xm_x
1	11.5	1.00	0.00	0.00	0.00	0.00
2	12.5	1.00	2.17	1.24	1.24	15.46
3	13.5	1.00	6.04	3.44	3.44	46.48
4	14.5	1.00	6.83	3.89	3.89	56.45
5	15.5	1.00	8.88	5.06	5.06	78.45
6	16.5	1.00	7.50	4.28	4.28	70.54
7	17.5	0.92	8.59	4.90	4.50	78.83
8	18.5	0.83	8.95	5.10	4.23	78.33
9	19.5	0.83	7.95	4.53	3.76	73.34
10	20.5	0.79	7.42	4.23	3.34	68.50
11	21.5	0.79	7.16	4.08	3.22	69.32
12	22.5	0.67	7.13	4.06	2.72	61.27
13	23.5	0.58	6.36	3.63	2.10	49.41
14	24.5	0.50	5.50	3.14	1.57	38.40
15	25.5	0.33	3.88	2.21	0.73	18.61
16	26.5	0.25	2.83	1.61	0.40	10.69
17	27.5	0.13	1.67	0.95	0.12	3.40
18	28.5	0.04	1.00	0.57	0.02	0.65
19	29.5	0.00	0.00	0.00	0.00	0.00
					44.65	818.13

R_o = 44.65 ; T = 18.32 ; r = 0.207

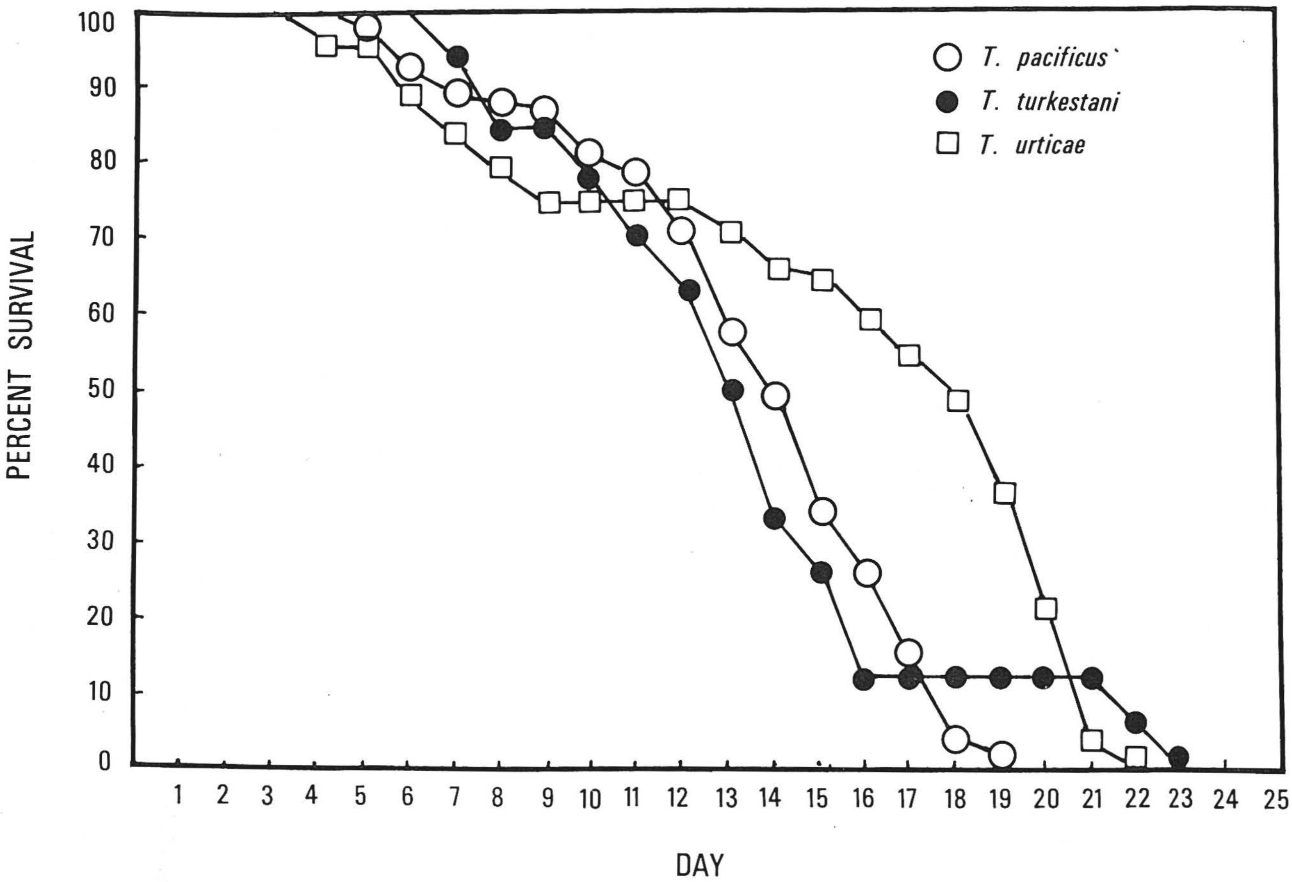

FIG 3 : longevity of *Tetranychus turkestani, T. urticae* and *T. pacificus* females at 23.8°C.

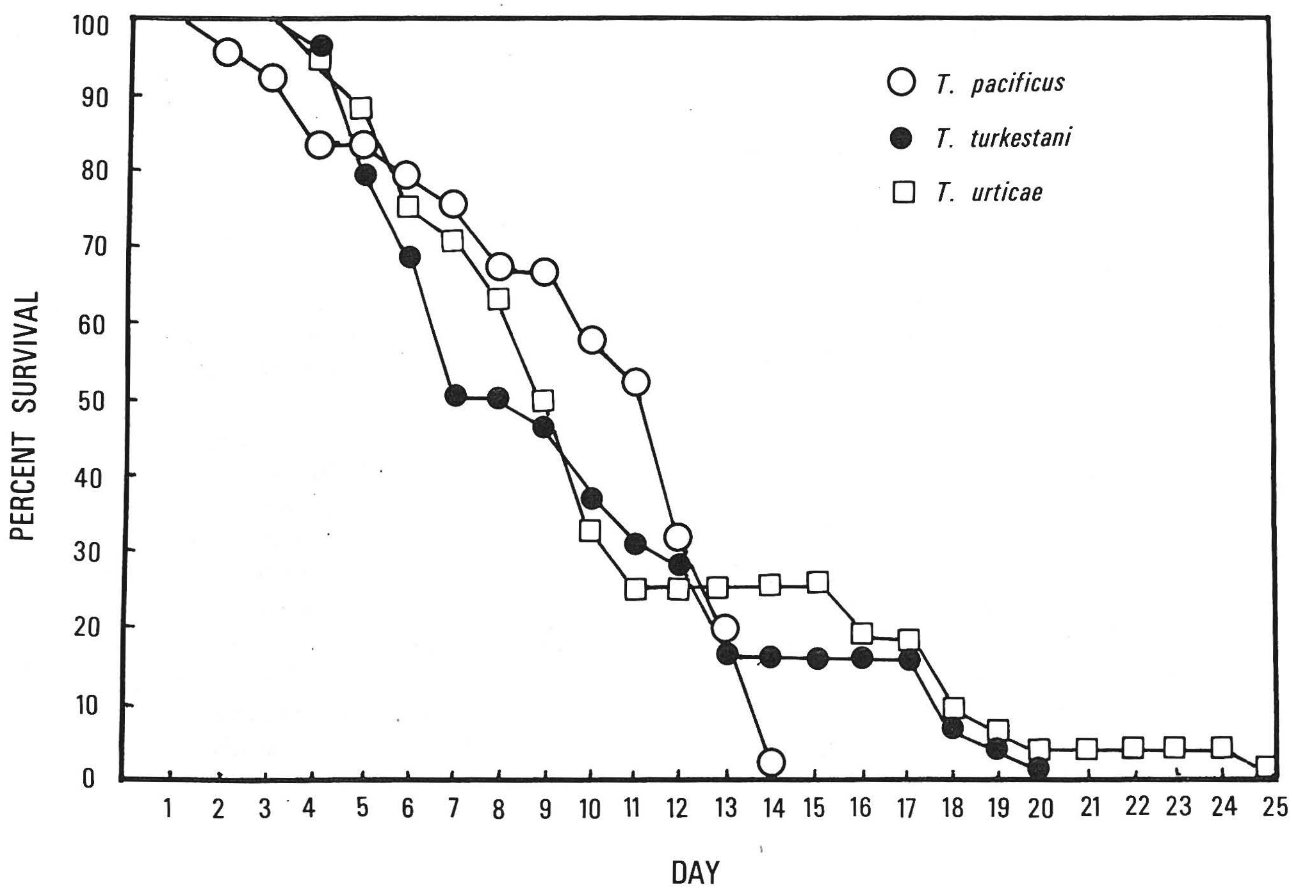

FIG. 4 : longevity of *Tetranychus turkestani, T. urticae* and *T. pacificus* females at 29.4°C.

TABLE 12. Life table of *Tetranychus pacificus* at 29.4°C. (m_x = P·m'_x, where P represents the proportion of females (0.57), and m'_x represents the total number of eggs laid per female).

Adult age (days)	Pivotal age (×)	l_x	m'_x	m_x	$l_x m_x$	$\times l_x m_x$
1	7.7	1.00	1.57	0.89	0.89	6.89
2	8.7	0.96	8.00	4.56	4.38	38.09
3	9.7	0.91	9.67	5.51	5.02	48.65
4	10.7	0.83	10.26	5.85	4.85	51.94
5	11.7	0.83	9.79	5.58	4.63	54.19
6	12.7	0.78	9.06	5.16	4.03	51.16
7	13.7	0.74	10.18	5.80	4.29	58.83
8	14.7	0.65	9.33	5.32	3.46	50.81
9	15.7	0.65	8.73	4.98	3.23	50.78
10	16.7	0.57	5.38	3.07	1.75	29.19
11	17.7	0.52	5.08	2.90	1.51	26.65
12	18.7	0.30	1.71	0.97	0.29	5.47
13	19.7	0.17	7.75	4.42	0.75	14.79
14	20.7	0.00	0.00	0.00	0.00	0.00
					39.08	487.44

R_0 = 39.08 ; T = 12.47 ; r = 0.294

Sex Ratio

The normal mode reproduction in all three species is arrhenotoky (OLIVER, 1971). The number of eggs for each species maturing as females and as males is presented in Table 5. The sex ratio of *T. turkestani* and *T. pacificus* was slightly greater than 1 : 1 (female to male) and for *T. urticae* it was almost exactly 3 : 1 (female to male).

Female Longevity

Adult female survivorship at 23.8° and 29.4°C is presented in Figures 3 and 4, respectively. Average longevity is presented in Table 6. Survivorship and longevity were higher in all species at the lower temperature. On average *T. urticae* lived slightly longer than did *T. pacificus* and *T. turkestani* at similar temperatures.

Life Tables

Life tables for all 3 species at both 23.8° and 29.4°C are presented in Tables 7-12. *T. urticae* had the highest net reproductive rates and the longest mean generation times at both temperatures and the highest intrinsic rate of increase at 23.8°C. At 29.4°C the intrinsic rate of increase for the 3 tetranychids was almost identical.

DISCUSSION

The findings of these studies are in general agreement with similar studies by other workers on these tetranychids in many respects but differ markedly in others. The times required to develop from egg to adult were quite consistent among studies and tended to confirm our findings. INGLINSKI and RAINWATER (1954) reported that *T. urticae* required an average of 6.5 days to develop from egg to adult at about 30°C, SHIH *et al.* (1976) found that this species matured in about 7.5 days at 27°C, LAING (1969) reported males and females required an average of around 16.5 days to mature at a mean temperature of 23°C, and ANDRES (1957) reported maturation times of 10.5 and 7.0 days at 24° and 35°C, respectively. In our study the maturation times of *T. urticae* at 23.8° and 29.4°C of 10.5 and 6.2 days, respectively, coincide with previous findings quite closely. The fact that none of the workers used cotton seedlings as the experimental host source may suggest that developmental times are only slightly affected by host plant and that temperature is the overriding environmental influence in this life history parameter.

Only two studies were found which reported developmental rates for *T. turkestani*, one by CAGLE (1956) and the other by ANDRES (1957). CAGLE reported that *T. turkestani* required about 13 days to mature at 21.9°C and around 7 days to mature at 25°C. ANDRES found that *T. turkestani* required 10.8 days to mature at 24°C and 6.0 days to mature at 34°C. The time required for maturation of *T. turkestani* at 24°C in our study was 10.7 days, almost identical to ANDRES' findings but differed from CAGLE's report by about 4 days. In the same study ANDRES showed that *T. pacificus* matured in 10.5 days at 24.°C and 5.3 days at 34°C. In our study, *T. pacificus* also matured in an average of 10.5 days at 24°C.

The average fecundity of the various species reported by other workers varies extensively and is occasionally quite different from our findings. MCGREGOR and MCDONOUGH (1917) reported that the average number of eggs laid by adult females under field weather conditions was around 84. ANDRES (1957) found that the two-spotted mite laid an average of about 100 eggs at 13°C, 180 eggs at 24°C and 60 eggs at 34°C. We found that *T. urticae* females laid around 103 eggs at 23.8°C and 64 eggs at 29.4°C, the former considerably lower than ANDRES reported at the comparable temperature but within the general range of the others. ANDRES reported that *T. pacificus* laid an average of 130 eggs/female at 23°C and 160 eggs/female at 34°C. We never found this species to lay more than an average of 70-80 eggs/female. ANDRES also reported that *T. turkestani* females laid an average of 160 eggs/female at 24°C and 80 eggs/female at 34°C. His finding at 24°C was almost double what we found at 23.8°C.

Of the *T. urticae* eggs which developed to maturity, 74 % were females in this study, almost identical to what LAING (1969) found. In constrast, CAGLE (1949) found that around 55 % of all eggs that matured were females in this species. CAGLE (1956) reported that the percent of *T. turkestani* eggs maturing as females was around 66-69 %, somewhat higher than our study in which only 55 % of all *T. turkestani* eggs matured as females. No sex ratios were found in the literature for *T. pacificus*.

The intrinsic rate of increase calculated by other workers for these species is difficult to compare with our findings because this parameter is a composite statistic, taking into account many aspects of the life history including developmental rate, fecundity, longevity, and sex ratio. Since there is sometimes considerable variation in reports of individual parameters within a species, it is not surprising to find disparities among studies which determined the intrinsic rate of increase, r. For *T. urticae*, WATSON (1964) determined r to be between 0.202 and 0.256 depending on the age of the host leaf. SHIH *et al.* (1976) determined the r to be 0.336 at 27°C whereas LAING reported an r of 0.143 for the same species at an average temperature of 23°C. BENGSTON (1969) determined the value of r for this species to be 0.282, which was the maximum under high temperature (34.5°C) and low humidity (25 %). The r-values in this study for *T. urticae* were 0.219 at 23.8°C and 0.293 at 29.4°C, considerably higher than LAING's findings at a comparable lower temperature but much lower than the findings of SHIH *et al.* (1976).

The intrinsic rates of increase for *T. turkestani* and *T. pacificus* were not found in the literature. ANDRES (1957) calculated the net reproductive rates, R_o, of these species as well as for *T. urticae*, under various conditions. At 24°C he found that the R_o of *T. urticae* was 150 eggs/female. In our study the R_o for this species at this temperature was about 75 eggs/female or around 1/2 that of ANDRES' findings. At this same temperature ANDRES determined the R_o of *T. turkestani* to be 124 eggs/female. We found the R_o was about 47 eggs/female or less than 1/2 that of ANDRES'. At 24°C ANDRES calculated the R_o of *T. pacificus* to be 146 eggs/female. We determined the R_o of the Pacific mite at this temperature to be about 45 eggs/female or less than 1/3 that of ANDRES. In all cases, ANDRES' study showed 2-3 times greater net reproductive rates in these species than in our study. There may be 2 possible reasons for this. First, ANDRES used alfalfa rather than cotton as his experimental host. Second, he chose only those females which laid eggs consistently for data collection.

We feel that the life history features of the three species are too similar to explain their reported differences in distribution and abundance both regionally and globally. There may be important ecological differences (e.g., dispersion, overwintering) which account for this, in part, and which are beyond the scope of a laboratory life history study.

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