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LIFE TABLES OF TWO-SPOTTED SPIDER MITE *TETRANYCHUS URTICAE* KOCH (ACARI: TETRANYCHIDAE) AND ITS PREDATOR *PHYTOSEIULUS PERSIMILIS* ATHIAS-HENRIOT (ACARI: PHYTOSEIIDAE)

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Abstract

Life table of *Tetranychus urticae* and *Phytoseiulus persimilis* on bean leaflets were studied under laboratory conditions in three seasons. For *T. urticae* the development time from egg to adult varied from 7 to 24 days and the highest immature mortality was 78.70 % in winter. Eggs laid by females were 88.1 eggs in autumn and 70.6 eggs in summer season. The gross reproductive rate (GRR) was the highest (65.51) in autumn and 52.50 in summer. The net reproductive rate (R_0) was the highest (15.862) in autumn and 8.916 in summer. The intrinsic rates of increase (r_m) and finite capacity for increase (λ) reached maximal values (0.1873 and 1.206) in autumn, whereas minimal values (0.056 and 1.058) were in winter season. The mean generation time (T) was the shortest in summer and double (3.701) days in autumn. The development time of *P. persimilis* from egg to adult varied from 5 to 14 days. The highest immature mortality was 60 % in summer. Eggs laid by females were 39.4 eggs in autumn and 30.2 eggs in summer. The gross reproductive rate (GRR) was the highest (31.4) in autumn and 24.0 in summer. The net reproductive rate (R_0) was the highest (10.573) in autumn and 8.460 in winter. The intrinsic rates of increase (r_m) and finite capacity for increase (λ) reached maximal values (0.1823 and 1.200) in summer, whereas minimal values (0.1025 and 1.108) were in winter. The mean generation time (T) was the shortest in summer. The results suggested that *P. persimilis* could develop and reproduce within a wide range of temperatures.

Key words: *Tetranychus urticae, Phytoseiulus persimilis,* immature mortality, intrinsic rates of increase, reproductive rate, Survival

Introduction

It is widely believed that in most animal species, population growth rate is a decreasing function of density (Harrison and Cappuccino 1995). Thus, per capita growth rate is negatively associated with present and/or past population densities (negative density dependence). A persistent debate among ecologists has surrounded the question of whether and how herbivore populations are regulated. Early research focused on whether abiotic or biotic factors controlled populations (Cappuccino 1995). However, regulation was generally viewed as intuitively necessary, preventing populations from becoming infinitely large or extinct (Harrison and Cappuccino 1995). There is a growing body of evidence for density dependence in natural populations, especially from manipulative experiments (Sequeira and Dixon 1997, Hunter and Elkinton 1999, Karels and Boonstra 2000, Rotem and Agarwal 2003).

Difficulty in the detecting density dependence may be due to the great variance frequently associated with the effect of density on population growth, as herbivores can be limited by many factors that potentially act in a density dependent manner. These factors include resources, predators, parasitism, disease, competition, and plant resistance, all of which can cause herbivore populations to decrease in size (Cappuccino 1992, Hunter and Elkinton 1999, Krebs et al. 2001). Indeed, these multiple factors frequently interact to ultimately determine population dynamics (Hunter and Elkinton 1999, Krebs *et al*. 2001).

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Phytophagous insect populations exist at relatively low to extremely high density. Top-down factors (i.e. natural enemies) can act to depress herbivore population size, usually well below the host-plant's carrying capacity (Cappuccino 1992, Hunter and Elkinton 1999). Alternatively, bottom-up factors, such as plant defenses, can control herbivore population growth (Hunter and Price 1992).

A spider mite population can expand rapidly with up to 40% per day (Shih *et al*. 1976). But the population may suddenly falls due to overexploitation of the food and predation by the natural enemies. Two-spotted spider mite (TSSM) *Tetranychus urticae* Koch populations are generally longer in the exponential growth phase than in the phase in which the population approaches the carrying capacity. This makes them typically r_m-selected (Caswell and Hastings 1980, Sabelis 1985). A rapid population increase can be achieved by a high reproduction rate or a short developmental time. However, the relative contribution of those two parameters is not equal. How much a change in either parameter affects the r_m depends on the actual rate of population increase (Caswell and Hastings 1980). *Phytoseiulus* species all have a high potential for population increase, probably the highest in the Phytoseiidae (Zhang 1995). They have a short development time (Sabelis and Janssen 1994), with a usually nonfeeding larval stage that takes up only a small percentage of the developmental period, along with high fecundity, resulting in intrinsic rate of increase (r) values sometimes exceeding 0.4 (Takahashi and Chant 1992). However, the rate of increase of *Phytoseiulus persimilis* Athias-Henriot can vary according to the plant on which the prey, *T. urticae*, are feeding (Popov and Khudyakova 1989, Kazak 2008). With the models from Caswell and Hastings (1980), one can demonstrate that for r_m values higher than approximately 0.1/day a change in developmental time has a larger effect on the population growth rate than an equal proportional change in oviposition rate. For lower r_m values the opposite is true.

The aim of this study was, therefore, to investigate the biological life table and intrinsic rate of natural increase of TSSM and *P. persimilis* at three seasons, i.e. summer, autumn and winter. Knowledge of the life table and intrinsic rate of natural increase will enhance the possibilities for its more effective use as a biological control agent under the very diverse climatic conditions.

Materials and Methods

The duration of developmental stages of *T. urticae* was studied on excised leaf disc in the laboratory. Bean (*Lablab purpureus* L.) leaf discs were made which were circular in appearance with 2 cm diameter. The leaf discs were placed on cotton bed in petridish (5 cm × 1 cm) facing under surface upward. The cotton bed was kept wet by soaking with water twice daily so that the discs remained fresh. Two adult female *T. urticae* were transferred to each disc for laying eggs. The adult female mites were collected from the cultures by rearing *T. urticae* on potted bean plants maintained in the greenhouse for more than one year. During continuous rearing every times the eggs were collected from fresh adult female of lab culture and maintained in the same way. All life stages were recorded till the death of the adult. The experiment was conducted in three seasons viz., summer, autumn and winter. The average temperature was recorded as 26.03±1.37 ºC.

Developmental period of *P. persimilis* from egg to adult emergence was also examined in laboratory at average temperature of 25.18±1.23 ºC. Experiments were conducted on excised leaf discs without mite infestation. Two ovipositing female *P. persimilis* were kept on each excised bean leaf disc with sufficient composite stages of prey *T. urticae* as food. The male was also removed after laying the first egg by the female.

The life tables of both mite species i.e. *T. urticae* and *P. persimilis* at different seasons were constructed from the life history and fecundity data. The actual death occurred in the egg and immature stages were taken into account when the female survival rate at each temperature was determined. Life tables were constructed using the survival data of a specific age class (l_x) and the female offspring produced per female in each age class (m_x). The net reproductive rate (R_o), the mean generation time (T), the intrinsic rate of increase (r_m), the doubling time (D_t), and the finite rate of increase (λ) were calculated using the method recommended by Birch (1948):

$R_o = \sum(l_x \times m_x)$

$T = \sum(x \times l_x \times m_x) / \sum(l_x \times m_x)$

$r_m = \text{Ln}(R_o)/T$

$D_t = \text{Ln}(2)/r_m$

$\lambda = \exp(r_m)$

Here x is age l_x, the cumulative female survivorship, and m_x, the number of female descendants per female at x. Calculation of a corrected r_m value was performed by iteration. The method, aiming to find r_m for which $(1 - \sum\exp(-r_m \times x) \times l_x \times m_x)$ is minimal, was given by Maia *et al*. (2000), where e is the base of natural logarithms, x is the age of individuals in days, lx is the age-specific survival rate and mx is the age-specific fecundity rate. The population doubling time and the population trend index were also calculated. The different parameters were:

i) Gross reproductive rate (GRR) is the mean total number of eggs produced by a female over its lifetime, ($GRR = \Sigma m_x$) measured in female eggs/ female/generation.

ii) Net reproductive rate (R_0) is the number of times a population will multiply per generation, ($R_0 = \Sigma l_x m_x$) measured in females/female/generation.

iii) Finite rate of increase (λ) is the number of times the population will multiply itself per unit of time, (λ=e) measured in females/female/day. Hence the finite rate of increase (λ) is the natural antilogarithm of the intrinsic rate of increase (r_m = eggs/female/day).

iv) Mean generation time (T): The relation between numbers and time in a population growing exponentially is given by $N_T = N_0 e^t$, when T = the mean length of generation.

v) Doubling time (DT) is the time required for a given population to double its number, (DT - $\log_e 2/r_m$), measured in days.

vi) Capacity for increase (r_c) is an approximation for r_m. It is calculated as follows: $r_c = \log_e R_0/T_c$, where T_c is the cohort generation time, defined as the mean age of maternal parents in the cohort at birth of the female offspring, $Tc = \Sigma l_x m_x/R_0$.

Different life table parameters of TSSM and *P. persimilis* were calculated using the adult survival (l_x), number of female progeny per day (m_x) and female sex ratio with the help of QBASIC software (Jervis and Copland 1996).

Results

Life table of T. urticae: Generation mortality of *T. urticae* (egg to adult) varied from 71.6% in autumn to 83.8% in winter (Table 1). In winter egg stage suffered the highest mortality (56.9%). Handling of egg and larval stages in this study may have played a significant role in their high mortality rates. All stages except the egg stage demonstrated decreasing mortality with increasing temperature.

The sex ratio of *T. urticae* (1:2.9; male: female) was used for the life table calculation and the life table parameters of are given in Table 2 and 4. Highest gross reproductive rate (GRR) was observed in autumn season (65.51) followed by summer (52.50) and winter (42.38) season. Net reproductive rate (R_o) was similar rank like GRR in different seasons. Capacity of increase (r_c) was highest in autumn season (0.1735) and lowest in winter season (0.0544). The intrinsic rates of natural increase (r_m) was highest in autumn season (0.1873) followed by summer (0.1761) and winter season (0.0564).

Highest cohort generation time (T_c) was observed in winter season (28.972) followed by autumn (15.934) and summer season (13.057). The mean generation time (T) was greater in winter season (27.96) and among the 3 seasons of study it was 14.76 days in autumn and 12.42 days in summer season. Finite capacity for increase (λ) was highest (1.206) in autumn followed by summer (1.193) and winter season (1.058). Highest generation doubling time (DT) was observed in winter season (12.29) and lowest in autumn (3.70) season.

Life table of P. persimilis: The generation mortality (egg to adult) are presented in Table 1 which varied from 51.4% in winter to 68% in summer. In summer egg stage suffered the highest mortality (33.7%) whereas in autumn the larval stage suffered the highest mortality (61.6%). In winter larval stage suffered the highest mortality (39.9%). Handling of egg and larval stages in this study may have played a significant role in their high mortality rates. All stages except the egg stage demonstrated decreasing mortality with increasing temperature.

The sex ratio of *P. persimilis* was1:3.9 (male: female). The intrinsic rate of natural increased (r_m) was highest in summer season (0.1823) followed autumn (0.1806) and winter season (0.1025). In summer season *P. persimilis* completed its development within 5–6 days. Highest gross reproductive rate (GRR) was observed in the autumn season (31.4) and lowest in the winter season (21.3). Net reproductive rate (R_o) was highest (10.573) in autumn season than in winter (8.46) and summer (6.546). Capacity of increase (r_c) was highest in summer (0.1747) and lowest in winter (0.096) season (Tables 3 and 4).

Highest cohort generation time (T_c) was observed in winter season (22.252) followed by autumn (13.747 days) and summer (10.754 days) season. Generation time (T) was highest in the winter season (20.83 days) and lowest in summer season (10.31 days). Finite capacity for increase (λ) was highest (1.2) in summer followed by autumn (1.198) and winter season (1.108). Highest generation doubling time (DT) was observed in winter season (6.762) followed by autumn (3.838) and winter (3.802).

Table 1. Duration and survival of *Tetranychus urticae* and *Phytoseiulus persimilis* at different seasons.

Stage	*Tetranychus urticae*		*Phystseiulus persimilis*	
	Duration	Survival (%)	Duration	Survival (%)
Summer				
Egg	3-4	100.00	1-2	100.00
Larva	4-5	48.2 ± 2.60	2-3	66.3 ± 2.45
Protonymph	5-6	33.4 ± 2.40	3-4	50.6 ± 3.16
Deutonymph	6-7	23.6 ± 1.28	4-5	40.5 ± 3.16
Adult	7-8	20.0 ± 1.02	5-6	32.0 ± 3.74
Autumn				
Egg	3-5	100.00	2-3	100.00
Larva	5-7	53.7 ± 2.21	4-5	78.5 ± 2.00
Protonymph	7-8	39.1 ± 1.61	5-6	38.4 ± 5.10
Deutonymph	8-9	32.2 ± 1.92	6-7	48.0 ± 3.74
Adult	9-10	28.4 ± 1.79	8-9	40.2 ± 4.47
Winter				
Egg	7-9	100.00	4-5	100.00
Larva	9-12	43.1 ± 1.64	6-8	86.4 ± 2.45
Protonymph	13-15	29.6 ± 1.33	9-10	60.1 ± 3.16
Deutonymph	15-17	21.3 ± 0.99	10-11	54.3 ± 4.00
Adult	17-19	16.2 ± 1.15	12-14	48.6 ± 2.00

Table 2. Life table of *Tetranychus urticae* at different seasons.

Pivotal Age	Summer				Autumn				Winter			
X	l_x	m_x	l_xm_x	xl_xm_x	l_x	m_x	l_xm_x	xl_xm_x	l_x	m_x	l_xm_x	xl_xm_x
0-8	0.20	-	-	-	-	-	-	-	-	-	-	-
9	0.20	2.45	0.491	4.417	-	-	-	-	-	-	-	-
10	0.20	7.58	1.517	15.169	0.28	-	-	-	-	-	-	-
11	0.20	6.99	1.398	15.377	0.28	6.92	1.936	21.299	-	-	-	-
12	0.20	4.83	0.967	11.600	0.28	5.80	1.624	19.488	-	-	-	-
13	0.20	3.87	0.773	10.053	0.28	6.77	1.895	24.631	-	-	-	-
14	0.20	6.17	1.234	17.281	0.28	5.28	1.478	20.696	-	-	-	-
15	0.18	4.02	0.723	10.842	0.28	5.06	1.416	21.237	-	-	-	-
16	0.16	3.49	0.559	8.947	0.28	4.16	1.166	18.655	-	-	-	-
17	0.15	2.83	0.424	7.205	0.28	3.72	1.041	17.697	-	-	-	-
18	0.12	3.42	0.410	7.388	0.28	3.87	1.083	19.488	-	-	-	-
19	0.09	3.27	0.294	5.595	0.26	3.64	0.947	17.999	0.16	-	-	-
20	0.05	1.78	0.089	1.785	0.25	3.42	0.855	17.103	0.16	1.04	0.167	3.331
21	0.02	1.78	0.036	0.750	0.24	3.72	0.892	18.738	0.16	1.86	0.297	6.246
22	0.00	0.00	0.000	0.000	0.16	3.20	0.512	11.255	0.16	1.78	0.286	6.282
23					0.14	3.20	0.448	10.296	0.16	1.78	0.286	6.567
24					0.12	2.38	0.286	6.853	0.16	2.60	0.416	9.994
25					0.08	1.93	0.155	3.867	0.16	1.93	0.309	7.733
26					0.06	1.19	0.071	1.856	0.16	1.64	0.262	6.805
27					0.05	0.74	0.037	1.004	0.16	1.64	0.262	7.067
28					0.04	0.52	0.021	0.583	0.16	2.53	0.405	11.326
29					0.02	0.00	0.000	0.000	0.16	1.86	0.297	8.626
30					0.00	0.00	0.000	0.000	0.14	1.19	0.167	4.997
31									0.14	0.30	0.042	1.291
32									0.13	2.08	0.271	8.661
33									0.12	1.41	0.170	5.595
34									0.12	1.78	0.214	7.281
35									0.10	1.78	0.178	6.246
36									0.09	1.04	0.094	3.373
37									0.09	1.78	0.161	5.943
38									0.08	1.71	0.137	5.199
39									0.07	0.97	0.068	2.639
40									0.06	0.74	0.045	1.785
41									0.05	1.78	0.089	3.658
42									0.04	1.34	0.054	2.249
43									0.04	1.41	0.057	2.430
44									0.03	2.08	0.062	2.748
45									0.02	0.89	0.018	0.803
46									0.02	1.04	0.021	0.958
47									0.02	0.37	0.007	0.349
48									0.01	0.00	0.000	0.000
49									0.00	0.00	0.000	0.000
		52.50	8.916	116.409		65.51	15.862	252.745		42.38	4.839	140.184

Table 3. Life table of *Phytoseiulus persimilis* at different seasons.

Pivotal Age	Summer				Autumn				Winter			
X	l_x	m_x	l_xm_x	xl_xm_x	l_x	m_x	l_xm_x	xl_xm_x	l_x	m_x	l_xm_x	xl_xm_x
0-6	0.32	-	-	-	-	-	-	-	-	-	-	-
7	0.32	1.1	0.357	2.496	-	-	-	-	-	-	-	-
8	0.32	2.7	0.866	6.928	-	-	-	-	-	-	-	-
9	0.32	3.3	1.070	9.627	0.40	-	-	-	-	-	-	-
10	0.32	3.3	1.070	10.697	0.40	3.50	1.401	14.008	-	-	-	-
11	0.32	1.4	0.458	5.043	0.40	3.66	1.464	16.109	-	-	-	-
12	0.29	4.1	1.200	14.403	0.40	4.14	1.656	19.866	-	-	-	-
13	0.26	2.5	0.662	8.609	0.40	2.87	1.146	14.900	-	-	-	-
14	0.22	2.5	0.560	7.845	0.40	2.71	1.082	15.154	0.48	-	-	-
15	0.18	0.8	0.143	2.149	0.40	2.55	1.019	15.282	0.48	0.96	0.458	6.876
16	0.10	1.1	0.111	1.783	0.39	1.91	0.745	11.920	0.48	1.91	0.916	14.670
17	0.05	1.0	0.048	0.812	0.36	1.59	0.573	9.742	0.48	1.59	0.764	12.989
18	0.02	0.0	0.000	0.000	0.32	1.91	0.611	11.003	0.48	1.27	0.611	11.002
19	0.00	0.0	0.000	0.000	0.20	2.07	0.414	7.864	0.48	1.43	0.687	13.065
20					0.15	1.75	0.263	5.253	0.48	1.43	0.687	13.753
21					0.10	1.27	0.127	2.674	0.48	0.64	0.305	6.418
22					0.05	1.43	0.072	1.576	0.48	1.59	0.764	16.809
23					0.04	0.0	0.000	0.000	0.48	0.64	0.305	7.029
24					0.00	0.0	0.000	0.000	0.48	0.80	0.382	9.168
25									0.47	0.64	0.299	7.481
26									0.46	0.32	0.146	3.807
27									0.42	0.96	0.401	10.830
28									0.42	0.32	0.133	3.744
29									0.37	0.96	0.353	10.248
30									0.36	1.11	0.401	12.034
31									0.29	0.48	0.138	4.293
32									0.24	0.64	0.152	4.890
33									0.24	0.48	0.114	3.782
34									0.24	0.64	0.152	5.195
35									0.13	0.64	0.082	2.897
36									0.12	0.96	0.114	4.126
37									0.09	0.48	0.042	1.590
38									0.08	0.48	0.038	1.451
39									0.04	0.00	0.000	0.000
40									0.00	0.00	0.000	0.000
		24.0	6.546	70.391		31.4	10.573	145.351		21.3	8.46	188.158

Table 4. Life table parameters of *Tetranychus urticae* during different seasons

Life table parameters	*Tetranychus urticae*			*Phytoseiulus persimilis*		
	Summer	Autumn	Winter	Summer	Autumn	Winter
Gross Reproductive Rate (GRR=$\sum m_x$) eggs/female/generation	52.50	65.51	42.38	24.0	31.4	21.3
Net Reproductive Rate ($R_0=\sum l_x m_x$) females/ female/generation	8.916	15.862	4.839	6.546	10.573	8.460
Capacity of increase ($r_c=[\log_e R_0]/T_c$) Female offspring/ female/day	0.1676	0.1735	0.0544	0.1747	0.1715	0.0960
Intrinsic rate of increase (r_m) eggs/female/day	0.1761	0.1873	0.0564	0.1823	0.1806	0.1025
Cohort Generation Time ($T_c=\sum x l_x m_x/\sum l_x m_x$) days	13.057	15.934	28.972	10.754	13.747	22.252
Generation Time ($T=[\log_e R_0]/r_m$) days	12.42	14.76	27.96	10.31	13.06	20.83
Finite Capacity for increase ($\lambda=\text{antilog}_e\ r_m$) Female offspring/ female/day	1.193	1.206	1.058	1.200	1.198	1.108
Doubling Time ($DT=[\log_e 2]/r_m$) days	3.936	3.701	12.290	3.802	3.838	6.762

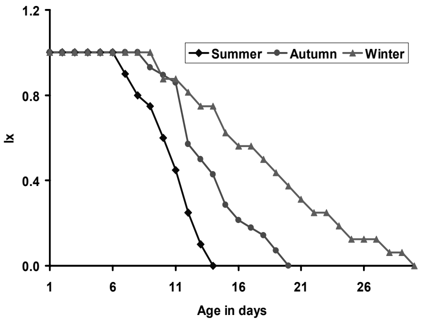

Fig. 1. Age-specific survival (*lx*) curves for *Tetranychus urticae* at three different seasons.

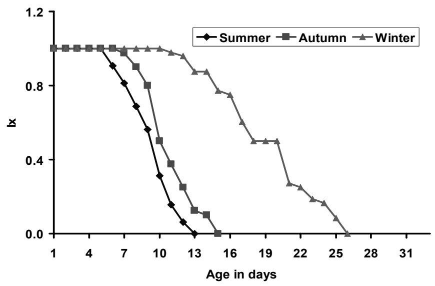

Fig. 2. Age-specific survival (*lx*) curves for *Phytoseiulus persimilis* at three different seasons.

Discussion

Sabelis (1991) gives an extensive review for life history data of tetranychid mites. For *T. urticae* he found a range in r_m values at 25°C from 0.219 to 0.336. Values of r_m obtained by Badii (1981) and Takahashi and Chant (1994) for the South African strain of *P. longipes* were higher than in the present study, with 0.366 at 25°C and 0.465 at 26°C, respectively. Badii (1981) and Takahashi and Chant (1994) based their estimation of the sex ratio on the generation considered in their studies for immature development, while in the present study calculations were made from the offspring of the generation considered for immature development. This difference leads to an underestimation of the r_m in the present paper compared to the others cited above. Krips *et al*. (1998) observed large differences in r_m values of *T. urticae* on ornamental crop gerbera ranging from 0.088 on cultivar Bianca to 0.242 on cultivar Sirtaki. This variation in *r*m was mainly caused by differences in developmental time of the spider mites.

Sakunwarin *et al.* (2003) studied the life table of *T. truncatus* Ehara and observed the net reproductive rate (R_o) was the highest (37.39) at 24°C, followed by 37.00 at 31°C. The innate capacity for increase (r_m) and finite rate of increase (λ) reached maximal values (0.321 and 1.378) at 31°C, whereas minimal values (0.134

and 1.143) were at 20°C. The mean generation time was the shortest at 35°C and the shortest time for a population to double was 2.16 days at 31°C. The r_m value in the present study was slightly lower than 0.34 of *T. mcdanieli* and *T. piercei* at 32°C (Tanigoshi *et al*. 1975, Congdon and Logan 1983, Aponte and McMurtry 1997, Fu *et al*. 2002). Normally, higher r_m is related to shorter developmental and generation times (Tanigoshi *et al*. 1975, Sabelis 1981) which is in confirmatory with the present case. Mean generation time (T) declined as the temperature increased. This result was quite similar to *T. mcdanieli* which required 14.31 and 10.50 days at 32 and 35°C (Tanigoshi *et al.* 1975). Bonato *et al.* (1990) reported a slightly longer generation time (20.7 and 17.2 days) for *E. carpini* at 26 and 30°C where Fu *et al*. (2002) reported a shorter generation time of 8.5 and 7.2 days for *T. piercei* at 32 and 36°C. Tommaso *et al.* (2007) studied the relationship between the number of immature individuals of *T. urticae* used to calculate life table parameters (sex ratio, development time, immature survival and the intrinsic rate of increase) and the accuracy of such determinations has been estimated.

Silva *et al.* (2005) studied the average duration of a generation (T) of *P. macropolis* (Banks) varied from 24.3 to 18.5 days at the temperatures from 20 to 26°C. The highest net reproduction (R_0 = 35.3) and the intrinsic rate of increase (r_m = 0.19) were obtained at 23ºC. The highest fecundity rate was registered at 26ºC. Similar values of r_m as obtained in the present study are reported in the literature for other phytoseiid species (Sabelis 1985), for instance for *Amblyseius longispinosus* (Evans) and *Amblyseius deleoni* Muma and Denmark (Sabelis 1985) and for *N. californicus* (Ma and Laing 1973). On the other hand, they are very low compared to other Type I species as defined by McMurtry and Croft (1997). At 26°C, for *P. persimilis*, *P. macropilis* (Banks) and *P. fragariae* Denmark and Schicha, Takahashi and Chant (1994) reported r_m values of 0.4282, 0.3862 and 0.3263, respectively. Despite these differences, the values obtained are relatively high and could be considered as sufficient to control *T. evansi* populations effciently (Gerson *et al*. 2003), even if more information about the specific predator/prey relation between *P. longipes* and *T. evansi* are needed to prove *P. longipes* effectiveness at a field scale (Janssen and Sabelis 1992). The intrinsic rate of increase (r_m) of *P. longipes* ranged from 0.091 to 0.416 female/female/day, at 15 and 30°C as observed by Ferrero *et al*. (2007).

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