



Peanut cultivars display susceptibility by triggering outbreaks of *Tetranychus ogmophallos* (Acari: Tetranychidae)

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Abstract

The peanut red spider mite, *Tetranychus ogmophallos* Ferreira and Flechtmann (Acari: Tetranychidae), is an important pest of peanut in Brazil and is considered a quarantine pest in other countries. This study investigates the development, reproduction, survival and life table parameters of *T. ogmophallos* on five peanut cultivars—three with high levels of oleic acid [high oleic] and recently released: Granoleico, IAC OL 3 and IAC 503; and two regular and previously used by farmers: Runner IAC 886, IAC Tatu ST 3—and two breeding lines (L. 8008 and L. 322) in the growth chamber. There were differences between the developmental times of all immature stages, the oviposition period, fecundity and adult longevity of *T. ogmophallos* reared on the peanut cultivars and breeding lines. The longest duration of the immature stage and lowest fecundity occurred on cultivars Granoleico and Runner IAC 886, and breeding line L. 322, which also displayed the lowest intrinsic rate of increase (r), finite rate of increase (λ) and net reproductive rate (R_0) and the shortest mean generation time (T). The highest fitness occurred on the IAC Tatu ST, IAC OL 3, IAC 503 and L. 8008. Our study shows that peanut cultivars belonging to the group with high oleic trait and recently released (IAC OL 3 and IAC 503) are susceptible to *T. ogmophallos*, except Granoleico, which is resistant. The regular and previously used cultivar Runner IAC 886 and breeding line L. 322 are resistant to the peanut red spider mite.

Keywords Peanut red spider mite · *Arachis hypogaea* · Demographic parameters · Age-stage two-sex life table

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Introduction

The peanut red spider mite, *Tetranychus ogmophallos* Ferreira and Flechtmann (Acari: Tetranychidae), is an important pest of peanut. This mite was first reported in the mid-west region of Brazil, and has now spread to both south and southeast regions, including the states Paraná, Santa Catarina, São Paulo and Minas Gerais, and Acre in the north (Ferreira and Flechtmann 1997; Lourenção et al. 2001; Flechtmann 2004; Chiaradia and Oliveira 2009; Santos 2016). Its rapid dissemination serves as an alert to other countries, because it is considered a quarantine pest mainly for countries bordering Brazil (Melville et al. 2018).

Treated as an emerging pest in peanut growing areas, *T. ogmophallos* has been reported to cause damage to all peanut plant developmental stages. Direct feeding injury causes a loss of leaf chlorophyll, reducing the photosynthetic rate, causing early leaf drop and reduces plant growth rate. These symptoms can result in a decrease in crop yield by reducing the number of pods, number of filled pods and individual seed weight, and, ultimately, in decline and death of the peanut plants (Melville et al. 2018).

In Brazil, the demand for peanut cultivars that would better meet the requirements of the confectionery, pharmaceutical and biofuel industry and that also fit into the rotation with sugar cane is challenging. Seed companies desire early cycle cultivars that serve the market, and high oleic cultivars (i.e., cultivars with high levels of oleic acid) stand out as good alternatives in the peanut 'chain'. In addition, the requirements of the new peanut market promoted changes and adoptions of new technologies that could guarantee peanut quality including agro-practice, harvesting and post-harvesting techniques (Santos et al. 2018). Since then, outbreaks of *T. ogmophallos* have been reported and its management has become a difficult task.

The needs of industry, farmers and cooperatives has accelerated breeding programs and import of peanut cultivars from other countries, such as Argentina. The breeding process of a given cultivar influences several metabolic and morphological mechanisms of pest resistance (Strauss et al. 2002). Cultivars that were resistant to herbivores may have become susceptible to diseases and pests as well (Alba et al. 2009).

Knowledge of cultivar susceptibility or resistance to a pest is an essential component of an Integrated Pest Management (IPM) program for any crop (Sedaratian et al. 2011). To date, however, there is no information on resistance of peanut cultivars to the peanut red spider mite. Life tables provide the most comprehensive analysis and description of the development, survival, and reproduction of arthropod populations (Rostami et al. 2018; Gong et al. 2018). The age-stage, two-sex life table theory (Chi and Liu 1985; Chi 1988) has been used to evaluate the population performance of several tetranychids mites and for the screening of resistant germplasm of various crops, including cultivars of tomato (Savi et al. 2019; Azadi-Qoort et al. 2019), common bean (Sepahvandian et al. 2019) and strawberry (Dana et al. 2018). Such detailed information is necessary and is the first step in developing an arthropod-resistant cultivar (Jyoti et al. 2001).

Determining life history traits will allow this study to make a connection between the cultivars present in the market today, those that were removed and served as progenitors and the resistance mechanism against *T. ogmophallos*. This information is crucial in order to recognize factors responsible for pest outbreaks, and to understand the adaptation processes. In this study, we present data on immature development, fecundity, survival and life table parameters of *T. ogmophallos* on peanut cultivars. We also bring detailed information of this mite on peanut breeding lines, which can serve as a source of resistance.

Materials and methods

Source and maintenance of the *Tetranychus ogmophallos* colony

Specimens of peanut red spider mite were collected from peanut fields Jaboticabal, São Paulo State, Brazil. Dr. Daniel Junior de Andrade (UNESP/FCAV) confirmed the mite species. They were reared on forage peanuts (*Arachis pintoi* Krapovickas and Gregory, cv. Amarillo) growing in 5-L pots in a greenhouse for at least 5 months (~10 generations, according to Bonato et al. 2000) before conducting experiments. Severely damaged plants were replaced with new plants every other week. The colony was maintained at 23 ± 5 °C, $65 \pm 10\%$ relative humidity (RH) and L12:D12 h photoperiod.

Peanut cultivars and breeding lines

Five peanut cultivars were considered in this study, namely Granoleico, Runner IAC 886, IAC Tatu ST, IAC OL 3 and IAC 503, and two breeding lines: L. 8008 and L. 322. Instituto Agronômico de Campinas (IAC) and Cooperativa Agroindustrial (COPLANA), São Paulo, Brazil, supplied the seeds. The cultivars and breeding lines were selected based on their economical relevance, the year in which the germplasm was registered and allowed for planting in Brazil, combined with reports of resistance to pests and diseases in the literature (Table 1). In addition, some breeding lines were tested to identify potentially useful sources of resistance to the mite (Table 1). Five seeds were sown in each 8-L plastic pots filled with a pasteurized substrate composed of soil, sand, and bovine manure (2:1:1) (pasteurized at 120 °C for 3 h) and kept in a greenhouse. About 15 days of germination thinning was done, leaving a single plant per pot. Plants were irrigated manually every other day or as needed and no fertilizers or pesticides were applied during the experiments.

Experimental set-up

To perform the study, arenas were made with fully expanded young leaflets (fifth leaf below the apical meristem of plant at reproductive stage—R3) of plants of each cultivar and breeding line. Each leaflet was placed with the adaxial surface down in a Petri dish (9 cm diameter, 2 cm high) with the aid of an entomological pin stuck in the center of each arena (Petri dish) with hot glue. Each arena was filled daily with deionized water (~10 mL) to keep the leaflet floating, maintain leaflet turgor and serve as a barrier for the mites.

Immature development and survival

To determine the development times (egg–adult) of the immature stages and survival rate, two engorged adult females of *T. ogmophallos* were placed in each arena and allowed to lay eggs for 24 h. Females and extra eggs were removed, leaving a single egg per arena. For each treatment, a cohort of 120 eggs of *T. ogmophallos* was used (total $n = 840$). Observations were made twice daily (12-h interval) and the duration, survival of immature stages and their quiescent stages of each treatment were recorded. Body size, presence of exuvia and a silvery appearance (quiescent period) were used to identify the duration and molting to the next stage (Laing 1969). Experiments were carried out in a room at 25 ± 1 °C,

Table 1 Characteristics of peanut cultivars and breeding lines used in the experiment

	Cultivars					Breeding lines	
	Granoleico	Runner IAC 886	IAC Tatu ST	IAC OL3	IAC 503	L. 322	L. 8008
Year of registration in Brazil	2010	2002	2000	2013	2009	Not registered	Not registered
Origin	Tegua×I.J.S. 95-1	Florunner	IAC Tatu	Line 886×accession 2562	IAC Caiapó×accession 2562	Accession 69007×line 886	IAC Caiapó×accession 2562
Botanical type	Virginia	Virginia	Valencia	Virginia	Virginia	Virginia	Virginia
Cycle and growth habit	125–130 days, runner	125–130 days, runner	90–100 days, upright	125–130 days, runner	130–140 days, runner	140 days, runner	130–140 days, runner
Oleic trait	High oleic	Regular	Regular	High oleic	High oleic	Regular	High oleic
Resistance to foliar diseases	Low	Low	Low	Low	Moderate	High	Moderate
Resistance to thrips	–	Low (Pirootta et al. 2017)	Low (Lourenção et al. 2007)	Low (Michelotto et al., unpubl. data)	Low (Michelotto et al. 2017)	Low (Michelotto et al., unpubl. data)	–
*Estimated acreage	+++	++	+	++++	+++++	–	–

*Crop season 2018/2019

– no information available, +++++ widely grown; + less grown

70 ± 10% RH and L12:D12 h photoperiod. The leaflet of each arena was exchanged every 7 days, except when the mite was in the quiescent stage. A camel hairbrush was used to transfer the mites from old to new leaflet.

Reproduction and adult longevity parameters

When adults of *T. ogmophallos* emerged, virgin male and female mites were paired, and transferred into a new arena with a fresh leaflet of each treatment. The pre-oviposition, total pre-oviposition and oviposition periods, female daily fecundity (number of eggs) and female and male longevities were recorded. If males died while the experiments were running, additional males were obtained from the maintenance-rearing colony for mating purposes. Males obtained from the maintenance-rearing colony were excluded from the analysis. Observations were done also every 12 h. Eggs (F₂ generation) were counted and discarded daily, except eggs laid between days 3 and 10, which were preserved to calculate sex ratio.

Life table analysis

The computer program TWSEX-MSChart (Chi 2019) was used for the raw data analysis and calculation of population parameters. The developmental time, adult longevity, adult fecundity, and population parameters were estimated by using the bootstrap method (Efron and Tibshirani 1993; Huang and Chi 2012), with 100,000 resampling to estimate the variances and standard errors. We used the paired bootstrap method to compare differences (Efron and Tibshirani 1993; Akkopru et al. 2015). The raw life table data of all individuals (females, males and those dying during at immature stages) were analyzed according to the age-stage, two-sex life table procedure developed by Chi and Liu (1985) and Chi (1988). The age-stage specific survival rate (s_{xj} , where x =age in days, j =development stage), the age-specific survival rate (l_x), age-specific fecundity (m_x) and the population parameters (R_0 , net reproduction rate; r , intrinsic rate of increase; λ , finite rate of increase; T , mean generation time) were calculated accordingly. The adult pre-oviposition period (APOP) is considered the time from the emergence of the adult female to its initial oviposition, whereas the total pre-oviposition period (TPOP) is the total duration from the beginning of the egg stage to the female’s initial oviposition. The net reproduction rate (R_0) is defined as the mean number of offspring that an individual can produce during its life span. It was calculated as:

$$R_0 = \sum_{X=0}^{\infty} l_x m_x \tag{1}$$

The intrinsic rate of increase (r) was estimated using the Euler–Lotka formula with the age indexed from day 0 (Goodman 1982):

$$\sum_{X=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{2}$$

The finite rate (λ) was calculated as $\lambda = e^r$. The mean generation time (T) is defined as the period (days) that is required by a population to increase to R_0 -fold of its size at the

stable age-stage distribution, and was calculated as $T = (\ln R_0)/r$. The age-stage life expectancy (e_{xj}) is the period (days) that an individual of age x and stage j is expected to survive and it is calculated following the procedures described in Chi (1988) and Chi and Su (2006). According to Fisher (1993), the age-stage reproductive value (v_{xj}) is defined as the contribution of an individual of age x and stage j to the future population. The reproductive value (v_{xj}) was calculated according to Huang and Chi (2011) and Tuan et al. (2014).

Results

Immature development and survival

The immature development stages of *T. ogmophallos* on peanut cultivars and breeding lines are given in Table 2. All *T. ogmophallos* eggs hatched on the 5th day, showing no differences between egg incubation periods among treatments. The duration of development time of the larvae, protonymphs and deutonymphs were different among peanut cultivars and breeding lines tested. The longest duration of the larval developmental stage was observed on L. 322, Runner IAC 886 and Granoleico. The shortest duration was observed on IAC Tatu ST (Table 2). The mite had the longest protonymph development time on Granoleico, Runner IAC 886 and L. 322, whereas it was shortest on IAC 503 and L. 8008 (Table 2). The last developmental stage (deutonymphs) of *T. ogmophallos* was significantly longer on L. 322, Granoleico and Runner IAC 886 compared with the other hosts (Table 2). The duration of the protochrysalis stage of *T. ogmophallos* was affected by peanut cultivar and breeding lines—it was longer for mites reared on Granoleico and Runner IAC 886 than for mites reared on L. 8008. Conversely, no difference among the cultivars and breeding lines was observed for the deutochrysalis and teleiochrysalis stages (Table 2). Based on the duration of the immature stages, males of *T. ogmophallos* developed faster than females on peanut plants. The duration of development of male immature stages was longer on L. 322, compared with IAC Tatu ST and L. 8008. When female, this parameter was longer on Granoleico, L. 322 and Runner IAC 886. (Table 2). Survival of immature stages of *T. ogmophallos* was >65% on all tested hosts. Granoleico and L. 322 *T. ogmophallos* exhibited the lowest percentage of larval survival, whereas survival was highest on IAC 503 and IAC OL 3 (Table 2).

Reproduction and adult longevity parameters

Differences were observed in the sex ratio of *T. ogmophallos* (F_2 generation) on all peanut cultivars and breeding lines (Table 3). The lowest sex ratio occurred on L. 322, whereas the highest occurred on IAC 503 followed by L. 8008. The adult pre-oviposition period (APOP) of *T. ogmophallos* females was much longer on Granoleico and L. 322, whereas for IAC Tatu ST, IAC OL3 and IAC 503 it was significantly shorter (Table 3). Likewise, TPOP was longest on Granoleico, Runner IAC 886 and L. 322 compared with the other hosts (Table 3). The oviposition period was shorter for females reared on Granoleico, Runner IAC 886, IAC Tatu ST and L. 322 than on IAC OL 3, IAC 503 and L. 8008. Mean total fecundity of *T. ogmophallos* differed among peanut hosts: the lowest and highest values were observed on Granoleico and IAC 503, respectively (Table 3). Peanut cultivars and breeding lines affected *T. ogmophallos* female and male longevities. The lowest longevity for both sexes was recorded on Granoleico, Runner IAC 886 and L. 322 (Table 3).

Table 2 Mean (\pm SE) duration and survival of immature stages of *Tetranychus ogmophallos* on five peanut cultivars and two breeding lines

Parameters	Cultivars					Breeding lines	
	Granoleico	Runner IAC 886	IAC Tatu ST	IAC OL 3	IAC 503	L. 322	L. 8008
Egg incubation period (days)	5.41 \pm 0.10a	5.40 \pm 0.11a	5.39 \pm 0.10a	5.42 \pm 9.59a	5.38 \pm 0.10a	5.39 \pm 0.11a	5.40 \pm 9.20a
Larval duration (days)	2.23 \pm 0.21a	2.19 \pm 0.16a	1.12 \pm 0.13c	1.33 \pm 0.13b	1.33 \pm 0.10b	2.25 \pm 0.19a	1.43 \pm 0.10b
Prothrysalis duration (days)	1.13 \pm 2.55a	1.03 \pm 0.10a	0.90 \pm 3.31ab	0.87 \pm 4.50b	0.90 \pm 4.06ab	0.97 \pm 4.74ab	0.78 \pm 4.00c
Protonymph duration (days)	1.35 \pm 0.11a	1.33 \pm 9.24a	0.92 \pm 3.32b	0.95 \pm 5.34b	0.83 \pm 7.36c	1.30 \pm 4.43a	0.89 \pm 3.75bc
Deutochrysalis duration (days)	0.94 \pm 0.03a	1.00 \pm 4.89a	0.91 \pm 3.31a	1.05 \pm 4.89a	1.03 \pm 6.89a	1.07 \pm 0.10a	1.07 \pm 9.05a
Deutonymph duration (days)	1.36 \pm 0.06a	1.29 \pm 4.85a	1.23 \pm 7.75ab	1.00 \pm 3.48bc	1.06 \pm 7.86bc	1.40 \pm 0.12a	0.95 \pm 0.07c
Teleiochrysalis duration (days)	1.53 \pm 5.71a	1.52 \pm 3.38a	1.54 \pm 4.37a	1.5 5 \pm 5.30a	1.51 \pm 0.11a	1.55 \pm 4.4a	1.52 \pm 0.10a
Duration of the immature stage							
Female (days)	13.12 \pm 0.17a	13.04 \pm 0.18a	11.15 \pm 0.16c	12.23 \pm 0.12b	12.05 \pm 0.13b	13.05 \pm 0.31a	11.76 \pm 0.18bc
Male (days)	11.89 \pm 0.68ab	11.92 \pm 0.57ab	10.75 \pm 0.14c	11.33 \pm 0.30b	11.31 \pm 0.29b	12.33 \pm 0.77a	11.13 \pm 0.20bc
Survival of immature stage (%)	68.89 \pm 4.33c	70.47 \pm 3.24bc	73.42 \pm 0.70b	77.73 \pm 3.11a	79.44 \pm 1.66a	66.50 \pm 3.31c	75.00 \pm 0.25ab

Means within a row followed by the same letter are not significantly different by the bootstrap paired test ($P > 0.05$)

Table 3 Mean (\pm SE) sex ratio (females/females + males), duration of adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), oviposition period, fecundity and longevity of *Tetranychus ogmophallos* on five peanut cultivars and two breeding lines

Parameters	Cultivars					Breeding lines	
	Granoleico	Runner IAC 886	IAC Tatu ST	IAC OL 3	IAC 503	L. 322	L. 8008
Sex ratio	0.89 \pm 0.02b	0.84 \pm 0.04b	0.88 \pm 0.03b	0.87 \pm 0.03b	0.95 \pm 0.01a	0.75 \pm 0.04c	0.93 \pm 0.01a
APOP (days)	0.53 \pm 2.48a	0.50 \pm 0.0b	0.45 \pm 4.54c	0.45 \pm 3.39c	0.45 \pm 3.38c	0.50 \pm 3.39a	0.48 \pm 3.39b
TPOP (days)	13.68 \pm 0.31a	13.56 \pm 0.15a	11.65 \pm 0.18c	12.68 \pm 0.12b	12.50 \pm 0.14b	13.54 \pm 0.19a	12.25 \pm 0.16b
Oviposition period (days)	15.02 \pm 0.62b	14.71 \pm 0.73b	15.33 \pm 0.73b	16.37 \pm 0.59a	17.7 \pm 0.78a	15.16 \pm 0.56b	16.41 \pm 0.81a
Mean total fecundity (no. eggs)	89.15 \pm 1.02c	98.15 \pm 2.67b	112.87 \pm 0.59a	115.54 \pm 1.74a	119.13 \pm 0.07a	101.61 \pm 1.73b	110.44 \pm 1.09a
Longevity							
Female (days)	32.84 \pm 0.88c	32.47 \pm 1.06c	34.31 \pm 0.88b	35.98 \pm 1.48a	36.42 \pm 0.66a	32.40 \pm 0.96c	36.01 \pm 0.78a
Male (days)	30.85 \pm 1.75b	29.70 \pm 3.60b	42.95 \pm 1.62a	43.11 \pm 1.8a	42.93 \pm 3.12a	31.12 \pm 2.63b	43.83 \pm 2.52a

Means within a row followed by the same letter are not significantly different by the bootstrap paired test ($P > 0.05$)

Age-stage-specific survival rate (s_{xj})

The overlap seen in the age-stage-specific survival rate curves (s_{xj}) (Fig. 1) found in successive stages clearly shows the differences between the stages of development and the survival that is found in individuals reared on all hosts (Fig. 1). The probability that a new hatched individual

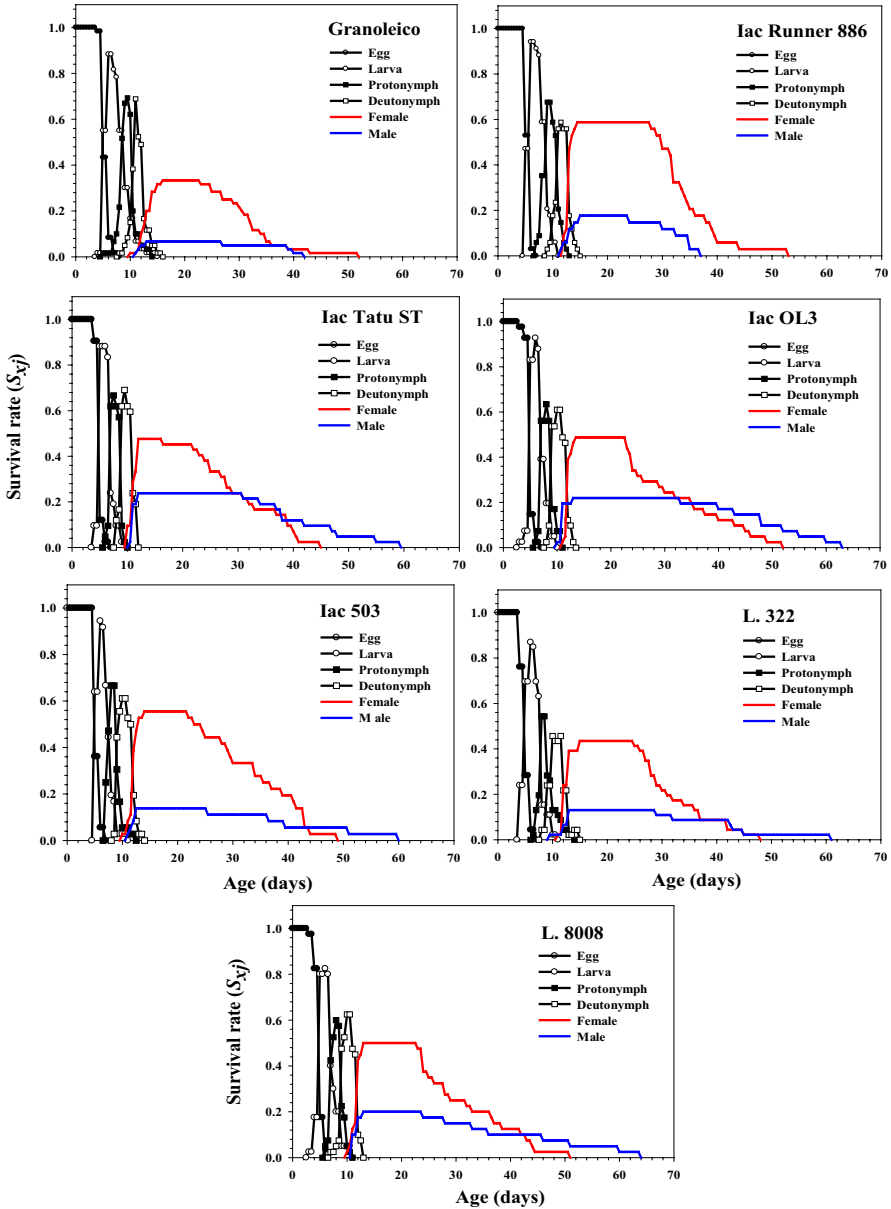


Fig. 1 Age-stage-specific survival rate of *Tetranychus ogmophallos* reared on five peanut cultivars and two breeding lines

of *T. ogmophallos* will survive to the adult ‘female’ stage was lower on Granoleico (0.33), followed by L. 322 (0.43), IAC Tatu ST (0.48), IAC OL 3 (0.49), L. 8008 (0.50), IAC 503 (0.56) and Runner IAC 886 (0.59) (Fig. 1). For ‘male’ individuals, this probability was lower on Granoleico (0.06) than on L. 322 (0.13), IAC 503 (0.14), Runner IAC 886 (0.18), L. 8008 (0.20), IAC OL 3 (0.21) and IAC Tatu ST (0.23) (Fig. 1).

Age-specific survival rate (l_x) and age-specific fecundity (m_x)

Considering the survival rate of the total population at different ages of *T. ogmophallos*, the l_x curve in general maintained a pattern from 10 to 25 days on all hosts tested (Fig. 2). A lower survival rate was recorded for *T. ogmophallos* when reared on cultivar Granoleico (0.4 at age 15) (Fig. 2). The age-specific fecundity (m_x) of *T. ogmophallos* obtained the lowest value on Granoleico (5.4 eggs) and Runner IAC 886 (5.7 eggs), followed by IAC OL 3 (6.2 eggs), L. 8008 (6.3 eggs), IAC 503 (6.3 eggs), L. 322 (6.4 eggs) and IAC Tatu ST (6.6 eggs) (Fig. 2).

Age-stage life expectancies (e_{xj}) and Age-stage-specific reproductive value (v_{xj})

The life expectancy (e_{xj}) of each age-stage group of *T. ogmophallos* (Fig. 3) indicates the time period that individuals of age x and stage j were expected to live after age x on different cultivars and breeding lines of peanut. The e_{01} (newly hatched mite) values on Granoleico, L. 322, L. 8008, IAC Tatu ST, IAC 503, Runner IAC 886 and IAC OL 3 were 19.32, 23.37, 27.31, 27.35, 27.82, 28.58 and 29.48 days, respectively (Fig. 3). The reproductive value (v_{xj}) describes the contribution of an individual mite of age x and stage j to the future population (Fig. 4). The v_{xj} of a newly hatched egg is exactly the finite rate of increase (λ). The major peak of v_{xj} of *T. ogmophallos* females occurred at 13 days when females reared on IAC OL 3 ($v_{13}=51.80$), IAC Tatu ST ($v_{13}=51.40$), IAC 503 ($v_{13}=49.93$) and L. 8008 ($v_{13}=48.72$); and 14 days when reared on Granoleico ($v_{14}=52.04$), L. 322 ($v_{14}=52.03$) and Runner IAC 886 ($v_{14}=46.83$) (Fig. 4).

Life table parameters

Peanut cultivars and lines affected the population parameters, intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0) and mean generation time (T) of *T. ogmophallos* (Table 4). The r value was lowest on Granoleico followed by Runner IAC 886 and L. 322, whereas mites reared on IAC Tatu ST, IAC OL 3 and L. 8008 obtained the highest value of r (Table 4). The finite rate of increase values for mites reared on Granoleico was higher than for mites reared on IAC Tatu ST, IAC OL 3, IAC 503 and L. 8008 (Table 4). The R_0 value was lower, while the mean generation time (T) was longer, in mites reared on Granoleico, Runner IAC 886 and L. 322, than in mites reared on IAC 503 (Table 4).

Discussion

Tetranychus ogmophallos performance differed among peanut cultivars and breeding lines, as was reported previously for the fitness of other tetranychid species among other crop cultivars (Gotoh et al. 2015; Gong et al. 2018; Rostami et al. 2018; Savi et al. 2019). By combining the estimated parameters, we obtained ample evidence that *T. ogmophallos*

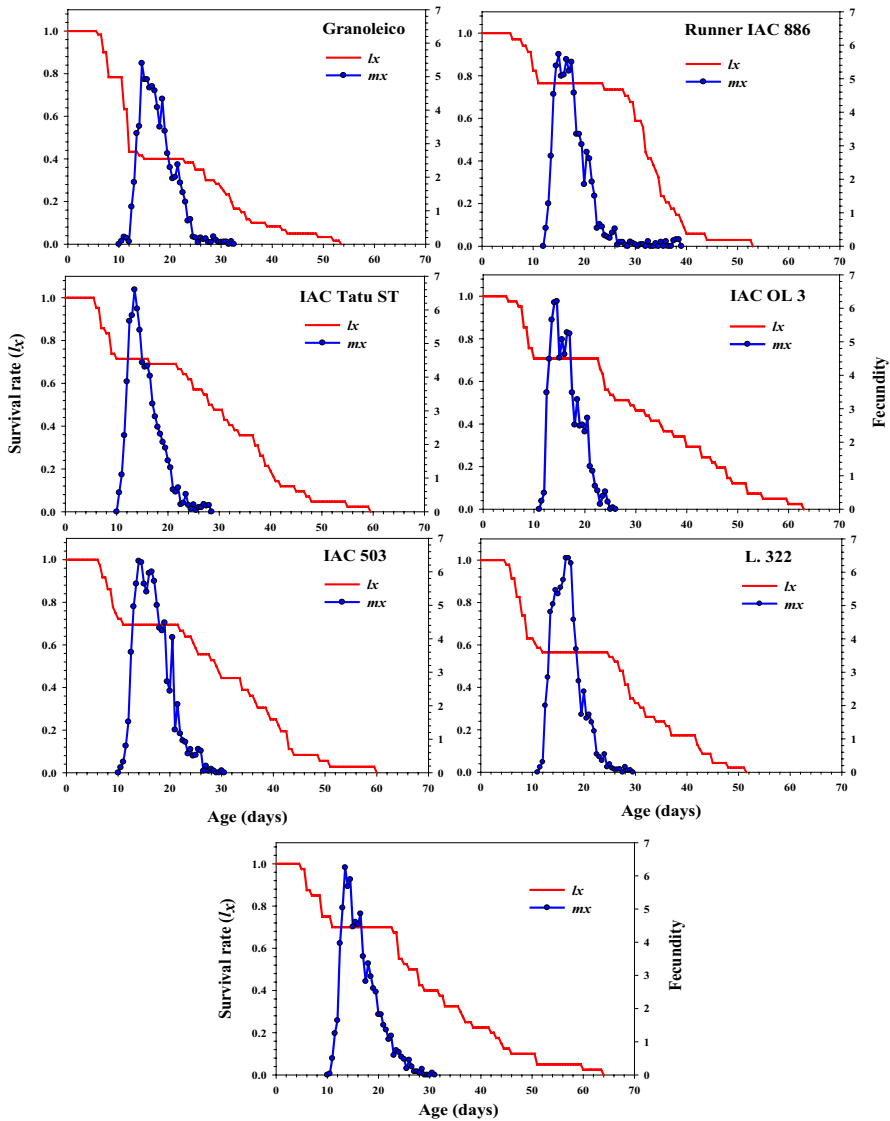


Fig. 2 Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Tetranychus ogmophallos* reared on five peanut cultivars and two breeding lines

population growth rate is extremely high on peanut plants and this may facilitate its exploitation of new peanut cultivars and therefore broaden its host range.

Bonato et al. (2000) assessed the performance of the peanut red spider mite on three legumes, and found high rates of increase of *T. ogmophallos* when reared on bean (*Phaseolus vulgaris* L.) and soybean (*Glycine max* (L.) Merrill). Surprisingly, Bonato et al. (2000) reported poor performance of *T. ogmophallos* on peanut as a host compared to bean and soybeans. We assume that this mite has now found better environmental conditions for its development in peanuts growing area, based on the management

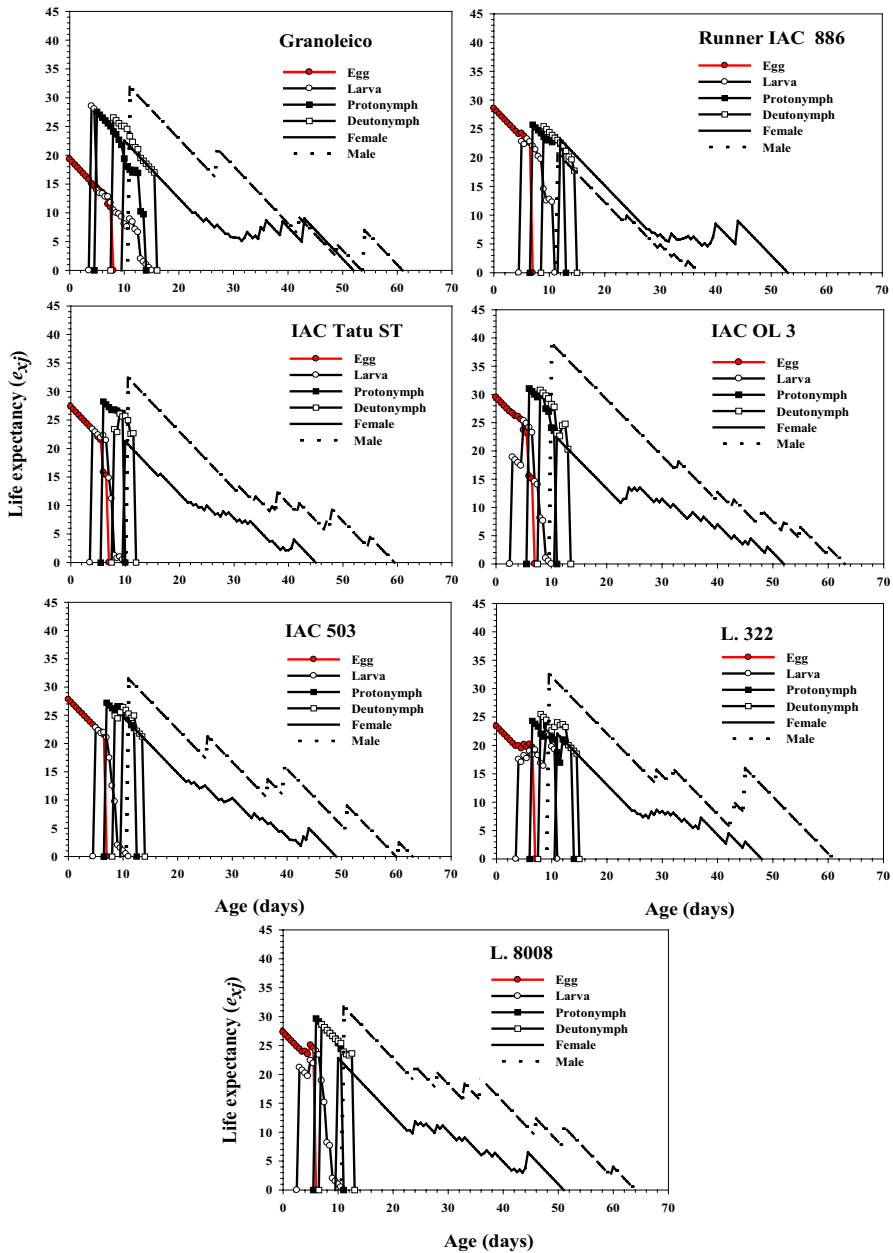


Fig. 3 Age-stage-specific life expectancy of *Tetranychus ogmophallos* reared on five peanut cultivars and two breeding lines

practices currently used by the farmers, extensive and overlapping planting dates, green bridge effects (Andrade et al. 2016), key pest increase—e.g., *Enneothrips flavens* Moulton (Thysanoptera: Thripidae) and *Stegasta bosquella* (Chambers) (Lepidoptera:

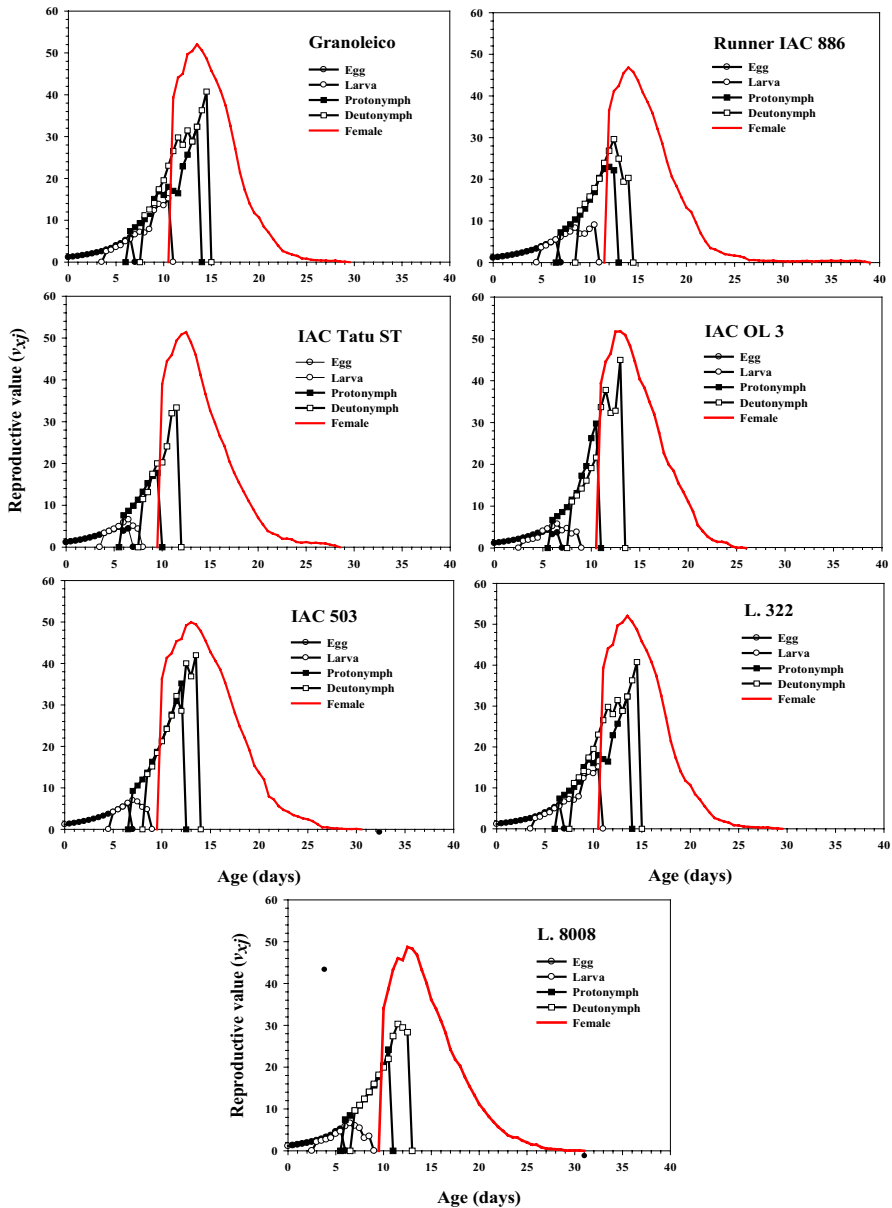


Fig. 4 Age-stage-specific reproductive value of *Tetranychus ogmophallos* reared on five peanut cultivars and two breeding lines

Gelechiidae)—, high frequency of pesticide applications that reduce beneficials (Pirota et al. 2017), and new high oleic peanut cultivars, in addition to Granoleico.

In this study Granoleico, Runner IAC 886 and the breeding line L. 322 promoted longer mobile (active) immature stages (larva, protonymph, and deutonymph) and longer duration of quiescent stages for *T. ogmophallos*. Feeding on these cultivars and breeding lines, mites

Table 4 Mean (\pm SE) life table parameters of *Tetranychus ogmophallos* on five peanut cultivars and two breeding lines

	Cultivars					Breeding lines	
	Granoleico	Runner IAC 886	IAC Tatu ST	IAC OL 3	IAC 503	L. 322	L. 8008
r (day^{-1})	$0.20 \pm 1.26c$	$0.21 \pm 1.05c$	$0.26 \pm 1.27a$	$0.26 \pm 1.11a$	$0.25 \pm 1.17b$	$0.21 \pm 1.41c$	$0.26 \pm 0.01a$
λ (day^{-1})	$1.22 \pm 1.54c$	$1.26 \pm 1.32b$	$1.30 \pm 1.64a$	$1.28 \pm 1.50a$	$1.29 \pm 1.44a$	$1.25 \pm 0.09b$	$1.29 \pm 1.63a$
R_0 (no. offspring/ individual)	$45.68 \pm 1.55c$	$46.14 \pm 3.69c$	$53.71 \pm 3.01b$	$53.41 \pm 0.13b$	$70.06 \pm 1.62a$	$45.46 \pm 2.34c$	$55.2 \pm 1.30b$
T (day)	$17.09 \pm 0.43a$	$17.06 \pm 0.25a$	$16.20 \pm 0.28b$	$16.02 \pm 0.20b$	$14.00 \pm 0.24c$	$17.83 \pm 0.26a$	$15.69 \pm 0.28b$

Means within a row followed by the same letter are not significantly different by the bootstrap paired test ($P > 0.05$)

had an increase of approximately 1–2 days in the total duration of the immature stage for both sexes. In addition, the strongest effect was verified in the larval stage, mites had a day of delay in development when compared to the susceptible cultivars (IAC Tatu ST, IAC OL3 and IAC 503) and breeding line (L. 8008). Bonato et al. (2000) reported total immature stages (egg-adult) of *T. ogmophallos* (without sex distinction) on soybean (11.9 days), bean (11.7 days) and peanut (14.2 days). These results are similar to ours obtained for males on soybean and bean, but the days to maturity are longer on peanut for both sexes. Extended developmental periods in the immature stages may be detrimental to mites and other pests because they prolong their exposure to natural enemies (Price et al. 1980).

The variation in the development period for *T. ogmophallos* among peanut cultivars and breeding lines, can be linked with an individual's gender, host acceptance and/or consumption, plant nutritional quality, morphological or allelochemical features (Wilson 1994; Awmack and Leather 2002; Steinite and Ievinsh 2002; van den Boom et al. 2003; Razmjou et al. 2009). Cultivars may differ in chemical profiles, thereby affecting arthropod physiology (Ode 2006). A previous study on *T. urticae* attributed variation in immature development to be related to plant antifeedant and deterrent factors such as the presence of secondary metabolites, leaf surface structure (trichomes) and leaf waxiness (Dabrowski 1973; Potter and Anderson 1982; Skorupska 2004; Najafabadi et al. 2014; Bensoussan et al. 2016). Differences in these characteristics among peanut cultivars may be involved too, but require further study.

The lower immature survival of *T. ogmophallos* on L. 322, Granoleico and Runner IAC 886 could explain why a mite species may have benefited from the change of cultivars and found better conditions for its development on the cultivars currently used (IAC 503 and IAC OL 3). According to Marinosci et al. (2015), responses of herbivore populations to environmental changes, such as a host plant shift, can range from local extinction to adaptation. In this study, it is very likely that mites feeding on less susceptible cultivars (Granoleico, Runner IAC 886, L. 322) encounter a higher fitness cost than on the others (IAC Tatu ST, IAC 503, IAC OL 3 and L. 8008). It is reasonable to say that the cultivar Runner IAC 886 played an important role in regulating the mite population in the recent past, mainly in maintaining the mite population below the economic threshold and avoiding outbreaks.

Another interesting correlation is that the cultivars IAC 503, IAC OL 3 and the breeding line L. 8008 carry the high oleic trait and all were susceptible to *T. ogmophallos*. Additionally, when we look at the origin of these cultivars, it is verified that these cultivars have in common the progenitors IAC Caiapó and accession 2562 (Table 1). The first report of *T. ogmophallos* outbreaks in peanuts was observed in areas growing large acreages of cultivar IAC Caiapó for two consecutive years (Lourenção et al. 2001). We assume that the progenitors IAC Caiapó and/or accession 2562 as well as their descendants may exhibit susceptibility to *T. ogmophallos*. In contrast, the cultivar Granoleico (Argentina cultivar) presents the high oleic trait and was the most used by the farmers recently, but its origin is completely different from the others. Together with the breeding line L. 322, these sources have the potential to be used for breeding new cultivars resistant to *T. ogmophallos*.

Besides the poor performance of *T. ogmophallos* in the immature stages on Granoleico, Runner IAC 886 and L. 322, these cultivars and breeding line exhibited longer APOP and TPOP, a short oviposition period, lower fecundity and shorter adult longevity. Fecundity of *T. ogmophallos* on Granoleico was nearly 26% lower than on IAC 503. These values differ from those previously estimated for *T. ogmophallos* on bean (63 eggs/female) and peanut (60 eggs/female), but are similar to those for females that developed on soybean (104.3 eggs/female) (Bonato et al. 2000). Fecundity (reproductive performance) is a highly suitable parameter for demonstrating the susceptibility of

a host plant (Awmack and Leather 2002). Tetranychid females perform poorly when exposed to less suitable or resistant host plants (Johnson et al. 1982; Khanamani et al. 2013; Zanardi et al. 2015; Savi et al. 2019). The reduced performance in females individuals developed on Granoleico may be directly related to differences in nutrient contents among host plants. According to Islam et al. (2017), adult females need a nitrogen source to develop mature ovaries and produce eggs, and a carbohydrate source for energy. Low quantity and quality of these compounds result in decreased herbivorous fecundity (Wekesa et al. 2011; Maleknia et al. 2016). In addition, females that reached reproductive maturity by feeding on low-quality substrate (leaf) and acquired low energy during its development may allow females to precisely control the sex ratio of their offspring (Roeder et al. 1996). In *T. urticae*, males result from smaller eggs than females (Macke et al. 2011), and may thus be less costly to produce in a poor environment (Marinosci et al. 2015). These reports are in agreement with the results described here, noted by the values of sex ratio on L. 322 as 0.75, while on IAC 503 was 0.95, and followed by L. 8008 with 0.93. We could thus hypothesize that the female of *T. ogmophallos* when reared on L. 322 increased the percentage of male individuals in the population, in response to the poor quality of the substrate and as a strategy to enhance its fecundity.

The results obtained in this study showed that feeding on Granoleico, Runner IAC 886 and L. 322 decreased the *T. ogmophallos* male and female longevities. This shorter longevity may be linked with lower suitability of host plants due to the presence of some phytochemicals in them acting as antibiotic compounds or the absence of essential nutrients (Wilson 1994; Sedaratian et al. 2009). Bonato et al. (2000) reported *T. ogmophallos* female longevity ranging from 16.5 to 25.3 days in peanut, soybean and bean. An additional interesting finding from the present study is that males had shorter longevity compared to females when fed on less susceptible cultivars and breeding line, and longer on susceptible cultivars (IAC Tatu ST, IAC OL 3, IAC 503 and L. 8008). This emphasizes the male's role in maintaining and stimulating the female's reproductive traits and in increasing the longevity (Saito 2010). We observed that males of *T. ogmophallos* share the costs of offspring care with the female during the oviposition process. We hypothesize that this male's behavior allows females to redirect part of parental care costs (gained energy) to spend on feeding and the oviposition process. However, the detailed physiological and/or behavioral mechanisms and major factors related to these differences among cultivars need further study.

Using the age-stage, two-sex life table allowed us to demonstrate the differences in all aspects of demographic parameters of *T. ogmophallos* between the peanut cultivars and breeding lines. Accordingly, the intrinsic rate of increase (r), finite rate of increase (λ) and net reproductive rate (R_0) of *T. ogmophallos* reared on Granoleico, Runner IAC 886 and L. 322 presented lower values. A similar trend was observed for *T. ogmophallos* fed on peanut, bean and soybean (Bonato et al. 2000). The variation of demographic parameters suggests that the local cultivars IAC 503 and IAC OL 3 were substantially more susceptible to *T. ogmophallos*. These factors, combined with the increased use of these cultivars and the expansion of cultivation areas, may explain the recurrent population outbreaks of this mite species.

Secondary pest outbreaks are not always solely caused by cultivar shift, but may result from changes in the cropping system. The rapid dissemination of *T. ogmophallos* in peanut growing areas is a product of a complex agroecosystem including environmental cues, intra- and inter-specific competition, reduction in populations of natural enemies due to pesticide applications, and drought-stressed plants (Gerson and

Cohen 1989; Wermelinger et al. 1991; Hill et al. 2017; Ruckert et al. 2018). Investigations on the effect of biotic and abiotic factors on *T. ogmophallos* population dynamics should be conducted to determine the main factors responsible for changes in population parameters.

Based on the results obtained in this study, it is possible to infer that the cultivars Granoleico, Runner IAC 886 and breeding line L. 322 are less favorable or more resistant hosts for development and reproduction of *T. ogmophallos*. Furthermore, the resistant germplasm identified in this study should be useful in future breeding trials to impart resistance to the peanut red spider mite. Best of all, our data provide farmers with good perspectives and alternatives to cultivars currently available on the market and relevant information in the design and control strategies as part of an IPM program.

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Author contributions DJA and CCM conceived the ideas and designed methodology; CCM collected the data and analysed the data; CMM, SFZ, PJS, MDM and DJA led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This article does not contain any studies with human participants performed by any of the authors.

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