Effect of Different Thermal Conditions on Biology and Number of Generations of Palpita forficifera (Lepidoptera: Crambidae)

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Effect of different thermal conditions on biology and number of generations of *Palpita forficifera* (Lepidoptera: Crambidae)

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Abstract

Palpita forficifera Munroe (Lepidoptera: Crambidae) is the principal pest in olive groves in Brazil and Uruguay, damaging buds and fruits. Therefore, this work was undertaken to understand the biology of *P. forficifera* at different temperatures, to determine thermal requirements, and to estimate the number of annual generations in different olive groves located in Brazil and Uruguay. The study was performed at 10, 15, 20, 25, 30, and 35 °C, 60 ± 10% RH, and a 14:10 h (L:D) photoperiod. The duration and survival stages of development, sex ratio, fecundity, and fertility were determined, and we elaborated the fertility life table at different temperatures. We also determined the thermal requirements, and the number of annual generations in olive producing areas were estimated. All immature stages of *P. forficifera* were affected negatively by the temperature at 10 and 35 °C, whereas 25 and 30 °C provided the shortest egg-to-adult periods. However, larval viability was affected at 30 °C (48.7%). Highest fecundity (325.5 eggs) was found for *P. forficifera* females kept at 25 °C. Additionally, the highest net reproduction rates (R_o) and intrinsic population growth rates (R_m) were verified at 25 and 30 °C. Lower thermal threshold (Tb) and thermal constant (K) for the egg-to-adult period were 10.7 °C and 549.45 degree-d, respectively. Based on the thermal requirements, *P. forficifera* can produce 4.0 to 6.3 generations per yr in the olive producing regions of Brazil and Uruguay. Results of the present study are important for understanding the occurrence of *P. forficifera* under field conditions and to aid strategic management designs.

Key Words: thermal requirements; lower thermal threshold; biology; caterpillar of the olive tree; life cycle

Resumo

Palpita forficifera Munroe (Lepidoptera: Crambidae) é a principal praga da oliveira no Brasil e Uruguai, causando danos nas brotações e nos frutos. Assim, o trabalho compreenderá a biologia de *P. forficifera* em diferentes temperaturas, determinar as exigências térmicas e estimar o número de gerações anuais para diferentes locais de cultivo de oliveira no Brasil e no Uruguai. O estudo foi realizado nas temperaturas de 10, 15, 20, 25, 30, e 35 °C, umidade relativa do ar de 60 ± 10% e fotoperíodo de 14:10 h (L:D). Foram avaliados parâmetros biológicos das fases imaturas e adulta e com esses dados foi elaborada a tabela de vida de fertilidade, estimado as exigências térmicas e o número de gerações anuais em áreas produtoras de oliveira. As temperaturas de 10 e 35 °C afetaram negativamente todas as fases imaturas de *P. forficifera* e as temperaturas de 25 e 30 °C proporcionaram as menores durações do período ovo-adulto. Porém, a viabilidade larval foi afetada na temperatura de 30 °C (48,7%). Fêmeas de *P. forficifera* mantidas a 25 °C resultaram na maior fecundidade (325,5 ovos). Em adição, as maiores taxas liquidas de reprodução (R_o) e a taxa intrínseca de aumento populacional (R_m) foram verificadas nas temperaturas de 25 e 30 °C. A temperatura base (Tb) e a constante térmica (K) para o período ovo-adulto foi de 10,7 °C e 549,45 graus-dia, respectivamente. Com base nas exigências térmicas *P. forficifera* pode ter de 4,0 a 6,3 gerações anuais em regiões produtoras de oliveira do Brasil e Uruguai. Os resultados do presente estudo são importantes para a compreensão da ocorrência de *P. forficifera* nas condições de campo e auxiliar no delineamento de estratégias para o seu manejo.

Palavras Chave: exigências térmicas; temperatura base; biologia; lagarta-da-oliveira; ciclo biológico

Olive farming is common in many regions of the world, particularly those of subtropical and temperate climate. While the traditional olive cultivation areas in Mediterranean countries have reached their limit due to little capacity to expand existing farms, South American countries (Chile, Argentina, Peru) have increased production and export, principally to the Brazilian market (Mesquita et al. 2006). Due to the large consumption in Brazil of both olive oil and olives, olive farming has been promoted in the country, hence the 10,000 ha allocated to this crop for the 2019/2020 harvest (Ibraoliva 2020). South and southeast micro regions of the country stand out due to their edaphoclimatic conditions (Alba et al. 2013). Similarly, olive farming in Uruguay has been quite productive, amounting to 6,300 tons for the 2019/2020 harvest (Asolur 2020), wherein cultivation, climate, and soil conditions are similar to those in southern Brazil (Paullier 2013).

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One of the most common phytosanitary issues of olive tree cultivation (*Olea europaea* L., Oleaceae) in Brazil and Uruguay has been the occurrence of the olive tree caterpillar, *Palpita forficifera* Munroe (Lepidoptera: Crambidae) (Ricalde et al. 2014), a species indigenous to South America that, in recent years, has become the principal pest of the crop (Scheunemann et al. 2017, 2019). The damage caused by the caterpillars is due to feeding on tender buds, compromising production in the following yr (Scheunemann et al. 2019). In higher infestations they also can damage fruits, reducing the quality of olives and olive oils (Scheunemann et al. 2017).

There are reports of 156 species of *Palpita* globally, although few of economic relevance (Bergant & Trdan 2006). Prominent among those is *Palpita unionalis* Hübner (Lepidoptera: Pyralidae), considered one of the principal pests to olive groves in the Mediterranean region; the species may cause as much as 90% reduction of leaf area and lead to fruit yield losses as high as 30% (Lopez-Villata 1999). In South America, 2 species are noteworthy, *P. forficifera* and *Palpita persimilis* Munroe (Lepidoptera: Crambidae). Although the distribution of *P. forficifera* is restricted to South America, there is growing concern that this species will be introduced in other continents, similar to *P. persimilis*, which was reported recently in Florida, USA (Hayden & Buss 2013).

Temperature performs a fundamental role in the development and establishment of insects in a given location (Bergant & Trdan 2006). Also, this climate variable can be used to determine the establishment potential of a new pest in a particular region, as well as to predict occurrence (Peterson & Vieglais 2001; Nava et al. 2007). Furthermore, based on the development of immature and adult stages of certain arthropods at different thermal conditions, it is possible to better define established monitoring and control strategies (Trudgill et al. 2005). Therefore, the goal of this study was to gain a better understanding of quantified growth, survival, and reproductive success of adults and immatures across a temperature gradient, to generate life tables of *P. forficifera* at different temperatures, and to determine thermal demands focused on estimating the number of generations the olive tree caterpillar could produce in 1 yr at different olive grove locations in Uruguay and Brazil.

Materials and Methods

REARING AND MAINTENANCE OF *PALPITA FORFICIFERA*

In order to establish rearing and maintenance in the laboratory, adults were collected from an olive orchard at Embrapa Clima Temperado, Pelotas, Rio Grande do Sul, Brazil (31.6797222°S, 52.4400000°W; 57 masl) with a light trap (Model 515, ISCA Tecnologias, Ijuí, Rio Grande do Sul, Brazil) equipped with ultraviolet light (300–390 µm). Adults were transported to the Embrapa Clima Temperado Entomology Lab and maintained in cages made from plastic tubes (12 cm diam × 22 cm high) (15 couples per cage). Insects were fed an aqueous solution of 10% honey and water. To collect eggs, a substrate made of tulle fabric (SSediada, São Bernardo do Campo, São Paulo, Brazil) was placed on top of the cage; above the fabric, a filter paper disc (15 cm diam) and a wet vegetable sponge cloth (Spontex, PaneSponja, Ilhéus, Bahia, Brazil) was employed to maintain egg viability (Scheunemann et al. 2019). The filter paper containing the eggs was removed daily and placed inside a Petri dish (10 cm diam × 1 cm high) so eclosion would occur. After eclosion, larvae were inoculated (about 500 larvae, 24 h old or younger per box) inside rectangular plastic boxes (Sanremo, Esteio, Rio Grande do Sul, Brazil) (39 cm long × 14 cm high × 30 cm wide) and fed cv. 'Koroneiki' olive tree buds and leaves. Food was added every 2 d until pupation. Upon emergence, adults were removed every 24 h, couples paired, and rearing proceeded as aforementioned. Rearing and maintenance of insects was carried out in a climate controlled room at 25 ± 2 °C, 60 ± 10% RH, and a 14:10 h (L:D) photoperiod. Likewise, in order to maintain the genetic variability of populations, insects from the field were introduced every 4 generations. The study was performed in 2017 and 2018.

BIOLOGY OF IMMATURE AND ADULT STAGE OF *PALPITA FORFICIFERA* AT DIFFERENT THERMAL CONDITIONS

Bioassays were performed inside climate controlled chambers, using 6 constant temperatures (treatments) (10, 15, 20, 25, 30, and 35 °C), 60 ± 10% RH, and a 14:10 h (L:D) photoperiod. For the immature stages, 150 insects were used at each stage of development (egg, larva, and pupa), for each of the 6 treatments. For the egg stage, 150 eggs were grouped in 6 repetitions of 25 eggs each. Each group of 25 eggs correspond to a piece of the egg-laying substrate (filter paper, as aforementioned) containing 25 eggs that were placed inside glass tubes (9.0 cm high × 3.0 cm diam) and assigned to their respective temperatures. In order to stop caterpillars from escaping after eclosion, the top of the glass tubes were covered with plastic film. Daily observations were made to register date and number of eclosed larvae. For the larval stage, 150 larvae (< 12 h) were placed individually inside glass tubes (9.0 cm high × 3.0 cm diam) containing 25 mL of an agar-water (3.5%) solution and a bud with 3 leaves of cv. 'Koroneiki' olive tree. The purpose of the agar-water solution was to keep the olive tree leaves turgid. Leaves were replaced every 2 d until pupation occurred. For evaluations concerning the pupal stage, 12-h-old pupae were used (75 male pupae and 75 female pupae, separated by gender as described by Butt and Cantu [1962]). Then pupae were placed in plastic containers (Sanremo, Esteio, Rio Grande do Sul, Brazil) (400 mL), the tops of the containers were closed with their lids and they were housed at different temperatures until adults emerged. Duration (d) and viability (%) were determined for all stages of development (egg, pupa, and larva) as well as the egg-to-adult period and sex ratio (sr).

For the adult stage, couples from rearing and maintenance as old as 12 h were placed into transparent plastic cages (Senir Embalagens, Nova Odessa, São Paulo, Brazil) (17.0 cm high × 10.0 cm diam) (1 couple per cage), with both ends covered by tulle fabric. Then they were housed inside climate controlled chambers at 10, 15, 20, 25, 30, and 35 °C constant temperatures, 60 ± 10% RH, and a 14:10 h (L:D) photoperiod. Insects were fed distilled water and 10% honey aqueous solution, supplied via capillarity in 10 mL plastic containers (CRAL, Cotia, São Paulo, Brazil). To collect eggs, a filter paper (9 cm diam) was placed under the tulle fabric and above it a wet vegetable sponge cloth (Spontex, PaneSponja, Ilhéus, Bahia, Brazil), as described in the rearing and maintenance section. The number of eggs was counted daily, and when a second set of eggs were laid, the egg viability was evaluated. Also, daily mortality of adults was registered.

The experimental design was completely randomized with 6 treatments (10, 15, 20, 25, 30, and 35 °C), and 25 repetitions (couples) each. Biological parameters evaluated were: period (d) of pre-oviposition and oviposition, mean total fecundity, fertility, and longevity (d) of males and females.

After the death of females, the presence of spermatophore in the bursa copulatrix was verified in order to register the couple's percentage of matings. To do so, the abdomen was detached from the thorax using histology scissors and a scalpel. The abdomen was placed inside a glass tube (50 mL) containing 20 mL of potassium hydroxide solution (KOH 10%). This procedure was conducted so the excess tissue that ad-

hered to the copulatory bursa was removed. After 48 h, the abdomen was placed on a watch glass (Syracuse™) (Laborglas, São Paulo, São Paulo, Brazil) and dissected under a stereoscopic microscope (Leica, M80) (Leica, Barra Funda, São Paulo, Brazil) so spermatophores could be counted.

From the biological parameters obtained from immature and adult stages, such as duration and viability of development stages, sex ratio, fecundity, and longevity, the fertility life table was calculated estimating the following parameters: net reproduction rate (R_o), intrinsic population growth rate (R_m), mean generation time (T), and finite rate of increase (λ).

DETERMINATION OF THERMAL REQUIREMENTS AND NUMBER OF ANNUAL GENERATIONS OF *PALPITA FORFICIFERA*

From the duration of egg, larval, and pupal stage, and the egg-to-adult period, we estimated the termal requirements, calculating the lower thermal threshold (Tb) and the thermal constant (K) using the hyperbole method (Haddad & Parra 1984). Based on the lower thermal threshold, the thermal constant, and the accumulated degree-d, we estimated the anual number of generations of *P. forficifera* in olive producing regions from Brazil and Uruguay. For this study we considered that the thermal requirements of *P. forficifera* is the same for all other populations evaluated. We used the methodology proposed by other authors (Haddad & Parra 1984). Therefore, we used mean historical monthly temperatures (1981–2010) for each region in Brazil (INMET 2020) and in Uruguay (INIA 2020). The anual number of generations was estimated for 7 municipalities in Brazil: Santana do Livramento (Rio Grande do Sul), Encruzilhada do Sul (Rio Grande do Sul), Campo Novos (Santa Catarina), São Carlos (São Paulo), Maria da Fé (Minas Gerais), and Venda Nova do Imigrante (Espírito Santo), and the munipality of Treinta y Tres in Uruguay. The climatological data (mean monthly temperature) of each location studied were collected from weather stations at the site or located at a maximum of 30 km from the study site.

STATISTICAL ANALYSES

Duration of egg, larval, and pupal stages, and egg-to-adult, preoviposition, oviposition (x) (d) were tested for normality by the Shapiro and Wilk (1965) test, and homoscedasticity according to Hartley (1950) and Bartlett (1937). Subsequently, the means were subjected to analysis of variance (ANOVA) through the F test ($P \leq 0.05$) using the SAS® GLM procedure (SAS Institute 2011). When statistically significant, the means were compared by Tukey's test ($P \leq 0.05$). Sex ratio was analyzed by chi-square (χ^2) test ($P \leq 0.05$) (PROC FREQ) (SAS Institute 2011). Fertility life table parameters such as net reproduction rate ($R_{o)}$, intrinsic population growth rate (R_m), mean generation time (T), and finite rate of increase (λ) were estimated by the Jackknife technique, using Lifetable SAS (Maia et al. 2000) programming, and means were compared by the t bilateral test ($P \leq 0.05$) in the SAS™ software (SAS Institute 2011). Longevity of *P. forficifera* adults was estimated by survival curves using the Kaplan-Meier Estimator, and subsequently compared with each other using the log-rank test with the R statistical system (R Development Core Team 2011). From the mean duration of the development stages of *P. forficifera* (egg, larval, and pupal), and egg-to-adult at different temperatures, the lower thermal threshold for development and thermal constant was determined using the hyperbole method (SAS Institute 2011).

Results

BIOLOGY OF IMMATURE AND ADULT STAGES OF *PALPITA FORFICIFERA* AT DIFFERENT THERMAL CONDITIONS

Temperature affected the duration of all development stages, and viability of egg and larval stages of *P. forficifera* (Table 1). Out of all temperatures evaluated, 35 °C did not allow the development of any *P. forficifera* stage, whereas at 10 °C only the embryonic period (35 d) was observed to be successful, but with the lowest embryonic viability of 20% (Table 1). Meanwhile, 25 and 30 °C provided

Table 1. Mean values (± SE) of duration (d) and viability (%) of the egg, larval, and pupal stages, and egg-to-adult period of *Palpita forficifera* at different temperatures.

	Duration (d)			
Temperature (°C)	Egg	Larva	Pupa	Egg-to-adult
10	35.0 ± 0.8 a	*	*	*
15	8.0 ± 0.0 b	41.8 ± 1.1 a	23.5 ± 1.3 a	73.4 ± 9.8 a
20	5.0 ± 0.0 c	24.3 ± 0.5 b	12.1 ± 0.5 b	41.4 ± 5.6 b
25	3.5 ± 0.1 c	15.9 ± 0.5 c	9.2 ± 0.5 c	28.6 ± 3.6 c
30	3.0 ± 0.0 c	14.8 ± 0.4 c	7.2 ± 0.3 c	25.0 ± 3.5 c
F	32.8	22.8	19.5	27.7
d.f.	4	3	3	4
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001
		Viability (%)		
10	20.0 ± 6.5 b	*	*	6.7 ± 4.7
15	86.0 ± 3.4 a	76.7 ± 4.6 a	78.7 ± 4.3 ^{ns}	80.4 ± 2.8 ^{ns}
20	80.0 ± 6.3 a	80.0 ± 5.7 a	88.7 ± 3.2	82.9 ± 2.9
25	88.6 ± 5.2 a	74.7 ± 4.1 a	89.3 ± 4.0	84.2 ± 4.8
30	84.7 ± 5.2 a	48.7 ± 5.0 b	74.2 ± 12.9	74.2 ± 12.9
F	23.5	17.6	21.3	19.1
d.f.	4	3	3	3
P	> 0.0001	> 0.0001	0.5632	0.3211

Means followed by the same letters in columns do not statistically differ from one another by Tukey's test ($P > 0.05$).
*There was no development; ^{ns} = not significant.

the shortest periods for egg (3.5 and 3.0 d, respectively), larval (15.9 and 14.8 d, respectively), pupal (9.2 and 7.2 d, respectively) stages, and egg-to-adult (25.0 and 25.0 d, respectively) (Table 1). In contrast, at 15 °C we observed the longest development period at larval (41.8 d) and pupal (23.5 d) stages, as well as egg-to-adult (73.4 d). The 30 °C temperature negatively influenced larval viability (48.7%) compared to the other temperatures under consideration (Table 1). Nevertheless, no statistical difference was observed regarding pupal viability and egg-to-adult period (Table 1). Sex ratio varied between 0.44 and 0.55 and did not significantly differ among treatments (Table 2).

The duration of pre-oviposition periods was inversely proportional to the temperature, ranging from 6.0 d at 30 °C to 22.7 d at 15 °C, significantly differing from 20 °C (12.4 d) and 25 °C (10.2 d) (Table 2). Furthermore, at 15 °C (15.1 d), 20 °C (15.5 d), and 30 °C (19.9 d) the longest oviposition periods were observed, when compared to 25 °C (10.2 d) (Table 2). However, despite presenting the shortest oviposition period, females exposed to 25 °C were the ones with the largest values for fecundity (total number of eggs) (325.5) (Table 2). Females kept at 35 °C did not lay eggs, because they lived only for a few days. Regarding copulation, adults kept at 10, 15, and 35 °C did not mate, statistically differing from insects kept at 20, 25, and 30 °C (Table 2), whose copulatory bursa contained spermatophores, although at 20 °C the percentage of matings was lower than that found at 25 and 30 °C (Table 2). *Palpita forficifera* fertility at 20, 25, and 30 °C was above to 80%, and at 15 °C, a temperature at which eggs were obtained, fertility was not observable because no spermatophores were found inside the copulatory bursa (Table 2).

Regarding longevity, females (χ^2 = 66.3; gl = 4; P < 0.0001) (Fig. 1A) and males (χ^2 = 33.1; gl = 4; P < 0.0001) (Fig. 1B) significantly differed at all of the tested temperatures, and only at 10 °C did females live longer (around 11.5 d) than males. However, at the other evaluated temperatures, males tend to live longer (15 °C = 7.32 d; 20 °C = 9.40 d; 25 °C = 7.40 d; 30 °C = 5.88 d) (Fig. 1B) compared to females (Fig. 1A).

With the fertility life table it was possible to verify that the mean time of a generation (T) varied from 107.4 d (15 °C) to 36.6 d (30 °C), statistically differing from the other temperatures (Table 3). At 43.9 d (25 °C) and 36.6 d (30 °C) of development, the net reproduction rates (R_o) were 121.5 and 98.6, respectively (Table 3). These values were, respectively, 83 and 78% above that found for insects kept at 15 °C (R_o = 21.4) (Table 3). Furthermore, insects kept at 15 and 20 °C were affected negatively regarding intrinsic population growth rate (R_m) and finite rate of increase (λ) compared to 25 and 30 °C treatments (Table 3).

DETERMINATION OF THERMAL REQUIREMENTS AND NUMBER OF ANNUAL GENERATIONS OF *PALPITA FORFICIFERA*

The lower thermal threshold and thermal constant of the egg stage was 7.4 °C and 64.6 degree d (y = −0.11454 + 0.01547x; R^2 = 0.98; P = 0.0006); the larval stage was 10.0 °C and 322.6 degree d (y = −0.00310 + 0.00310x; R^2 = 0.95; P = 0.0209); the pupal stage was 10.7 °C and 158.7 degree d (y = −0.06727 + 0.00630x; R^2 = 0.99; P = 0.0050); and egg-to-adult period was 10.7 and 549.5 degree d (y = −0.01943 + 0.00182x; R^2 = 0.98; P = 0.0087), respectively. Based on the lower thermal threshold, accumulated degree-d necessary to complete the adult stage of *P. forficifera* and the monthly average temperatures for each municipality, the number of annual generations was 4.6 (Santana do Livramento, Rio Grande do Sul), 4.5 (Encruzilhada do Sul, Rio Grande do Sul), 4.0 (Campos Novos, Santa Catarina), 6.6 (São Carlos, São Paulo), 4.2 (Maria da Fé, Minas Gerais), 6.3 (Venda Nova do Imigrante, Espírito Santo), and 4.2 (Treinta y Tres, Uruguay) (Table 4).

Discussion

In this study, it was verified that 25 and 30 °C were considered ideal temperatures for *P. forficifera*, as observed from biological parameters and the results obtained from the fertility life table. However, at 15 °C the species is able to develop at a slower growth rate. Biological results found for *P. forficifera* concur with findings about *P. unionalis*, the principal pest in most olive-growing countries of the Mediterranean basin (Dahi et al. 2009; Khaghaninia & Pourabad 2009; Yilmaz & Genç 2012). Nevertheless, at constant temperatures of 10 and 35 °C, a negative effect was verified over *P. forficifera* at egg, larval, and pupal stages, and the egg-to-adult period. Furthermore, in field conditions, the biological development of the species may be affected by changes not observed in the laboratory. This may occur due to thermal variations during the d in the field, exposing insects to a range of temperatures and not constantly the same conditions (Haddad & Parra 1984), especially in subtropical regions like those found in southern Brazil and Uruguay.

In the field, *P. forficifera* caterpillars feed on olive tree leaves, particularly those located in apical regions of the plant and shooting buds (Scheunemann et al. 2020). During the feeding process, there is a formation of webs over the leaves, which causes them to close (Scheunemann et al. 2017). This ecological relationship between insect and plant may provide an adequate microclimate, allowing the pest to survive through critical periods for the development of the species, especially during cold seasons (May through Jul) (temperatures lower

Table 2. Mean values (± SE) of biological parameters at different temperatures.

		Duration (d)				
Temperature (°C)	Sex ratio	Pre-oviposition	Oviposition	Fecundity	Fertility (%)	Copulation (%)
10	*	*	*	*	*	0.0 c
15	0.55 ^{ns}	22.7 ± 3.0 a	15.1 ± 2.3 ab	52.7 ± 14.8 c	0.00 b	0.0 c
20	0.53	12.4 ± 1.1 b	15.5 ± 1.7 a	183.8 ± 32.8 b	80.0 ± 6.3 a	24.0 b
25	0.44	10.2 ± 1.3 b	10.2 ± 0.9 b	325.5 ± 48.1 a	88.6 ± 5.2 a	68.0 a
30	0.55	6.0 ± 0.3 c	19.9 ± 1.7 a	242.3 ± 36.5 b	84.7 ± 5.2 a	68.0 a
H	3.95	40.0	16.0	28.54	23.5	53.6
d.f.	3	3	3	3	3	4
P	< 0.2672	< 0.0001	< 0.0011	< 0.0001	< 0.0001	< 0.0001

Means followed by the same letters in columns do not statistically differ from one another by Tukey's test (P > 0.05).
*Insects did not lay eggs.

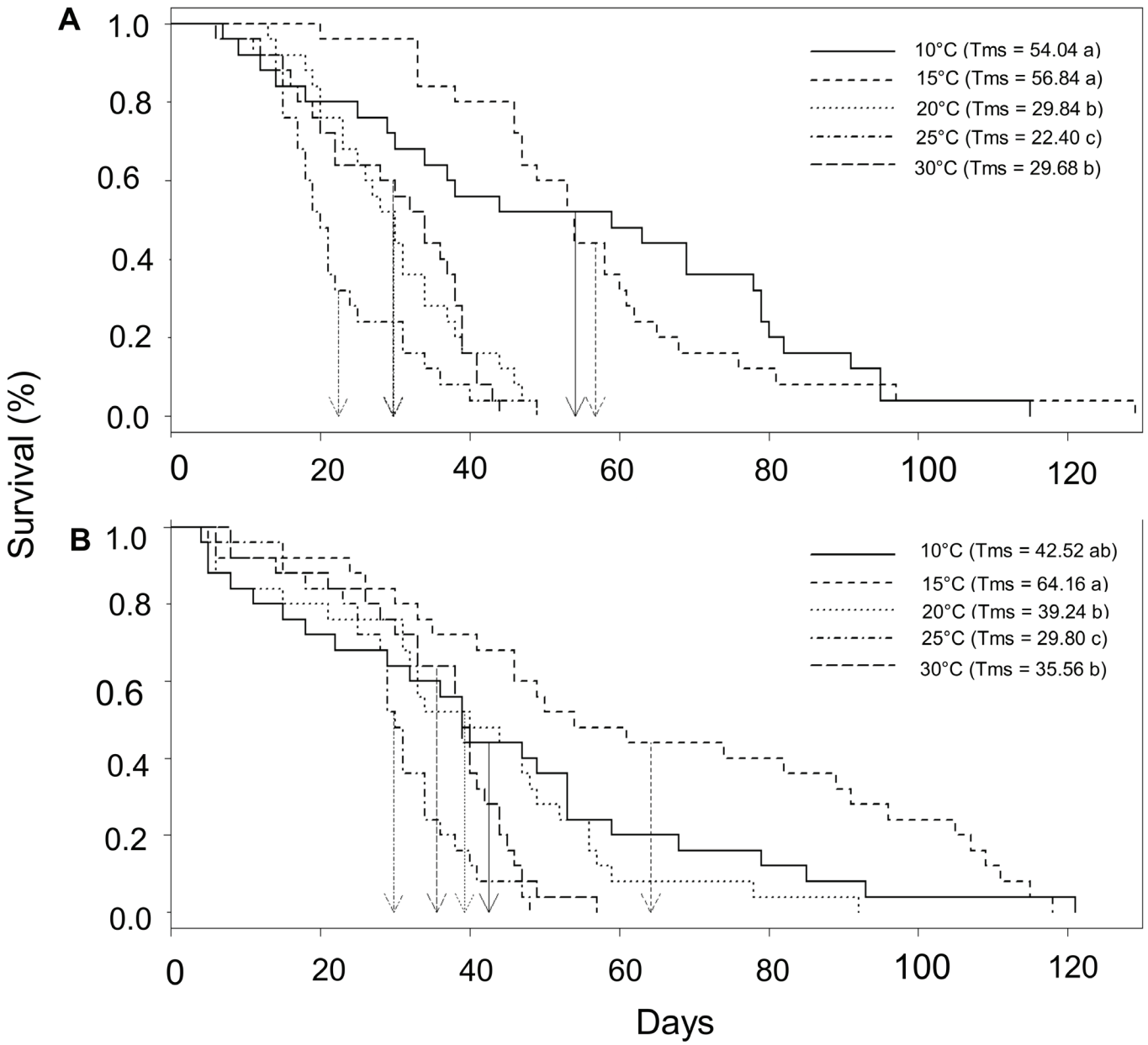

Fig. 1. Survival curves for female (A) and male (B) survival of *Palpita forficifera* at different temperatures (10, 15, 20, 25, and 30 °C), 60 ± 10% relative air humidity, and 14:10 h (L:D) photoperiod. Curves followed by the same letters for each gender did not differ from one another by the log-rank test (Tms = mean time of survival).

than or close to 10 °C). The diapause phenomenon has not yet been verified for *P. forficifera*, as has been observed in *Grapholita molesta* Busck (Lepidoptera: Tortricidae) (Silva et al. 2014), an important pest of apple and peach orchards in Brazil. However, it is relevant to note that at 15 °C copulation was not observed in lab conditions, indicating that low temperatures are not suitable for mating to occur, and the low temperatures must have interfered in sexual maturity or production of pheromones (Milano et al. 2008).

Table 3. Fertility life table of *Palpita forficifera* at different temperatures.

Temperature (°C)	T (d)	Ro (♀ per ♀)	R_m (♀ per ♀ *d)	λ
15	107.4 ± 2.76 a	21.4 ± 6.23 c	0.029 ± 0.002 c	1.029 ± 0.002 b
20	60.1 ± 1.22 b	80.9 ± 14.44 b	0.073 ± 0.003 b	1.076 ± 0.003 b
25	43.9 ± 0.59 bc	121.5 ± 17.69 a	0.109 ± 0.003 a	1.116 ± 0.003 a
30	36.6 ± 0.55 c	98.6 ± 14.84 ab	0.126 ± 0.003 a	1.134 ± 0.004 a

T = mean generation time; R_o = net reproduction rates, R_m = intrinsic population growth rate, and λ = finite rate of increase. Values represent mean ± SE obtained with the Jackknife method by the SAS program. For each evaluated parameter, means followed by the same letters in columns do not statistically differ from one another by Tukey's test ($P > 0.05$).

Table 4. Average temperatures (T) (°C) for olive producing regions of Brazil and Uruguay, accumulated degree-d (GD) and estimated number of generations (Num) based on the thermal constant (K) of *Palpita forficifera*.

	Brazil										Uruguay	
	Santana do Livramento		Encruzilhada do Sul		Campos Novos		São Carlos		Maria da Fé		Venda Nova do Imigrante		Trinta y Tres	
Mo	T	GD	T	GD	T	GD	T	GD	T	GD	T	GD	T	GD
Jan	23.8	409.2	22.5	368.9	20.8	316.2	22.7	375.1	19.9	288.3	22.6	372.0	23.6	386.3
Feb	22.9	344.4	21.9	316.4	20.5	277.2	22.9	344.4	19.9	260.4	22.9	344.4	22.3	327.6
Mar	21.5	337.9	21.1	325.5	19.5	275.9	22.5	368.9	19.2	266.6	22.9	359.6	19.4	274.0
Apr	18.0	222.0	18.1	225.0	17.1	195.0	21.1	315.0	17.3	201.0	20.8	306.0	16.4	172.8
May	14.5	120.9	14.8	130.2	13.6	93.0	18.2	235.6	14.4	117.8	18.7	251.1	13.3	83.1
Jun	12.1	45.0	12.4	54.0	12.6	60.0	17.1	195.0	12.7	63.0	17.6	210.0	11.1	15.6
Jul	12.5	58.9	11.7	34.1	12.1	46.5	17.2	204.6	13.1	77.5	17.1	201.5	10.8	4.6
Aug	12.5	58.9	13.3	83.7	13.7	96.1	18.8	254.2	14.1	108.5	17.3	207.7	12.8	67.6
Sep	14.0	102.0	14.3	111.0	14.5	117.0	20.2	288.0	16.4	174.0	18.6	240.0	14.6	120.0
Oct	17.5	213.9	17.1	201.5	16.9	195.3	21.8	347.2	18.1	232.5	20.2	297.6	17.6	215.5
Nov	20.0	282.0	19.3	261.0	18.8	246.0	22.2	248.0	18.8	246.0	21.0	312.0	19.5	268.2
Dec	22.2	359.6	21.5	337.9	20.4	303.8	22.4	365.8	19.4	272.8	21.9	350.3	22.3	361.8
Total		2,195.1		2,449.2		1,918.2		3,641.8		2,035.6		3,101.9		2,297.0
K		549.45		549.45		549.45		549.45		549.45		549.45		549.45
Num		4.6		4.5		4.0		6.6		4.2		6.3		4.2

The net reproduction rate, in other words the ability of a given population increase in each generation, is an important indicator of the population dynamic that sums up the physiological ability of an insect (Richards 1961; Kumral et al. 2007). In a previous study, *P. forficifera* reared on the olive cv. 'Koroneiki' at 25 °C produced a net reproductive rate of 106.58, which is close to that found in this study of 121.5 (Scheunemann et al. 2019).

The lack of development during larval and pupal stages and, consequently, the egg-to-adult period, as well as the non-occurrence of copulation between *P. forficifera* adults exposed to 10 °C demonstrates that, at this temperature, the species is near its lower thermal threshold, as estimated (7.4 °C). Based on the values of the lower thermal threshold and the thermal constant, it was verified that the number of annual generations of *P. forficifera* may vary according to location. That said, a lower number of generations of olive tree caterpillars is expected to be found in places where temperatures are lower, as happens in the southern part of Brazil (Campos Novos, Rio Grande do Sul) and in Uruguay (Treinta y Tres), and in higher altitudes, as observed for some olive farming regions in the southeastern part of the country (São Carlos, São Paulo). Such variation in the number of annual generations of *P. forficifera* confirms what was observed for *P. unionalis*. For the latter, the number of annual generations may vary from 4 to 5 in Italy (Martelli 1915), 6 in Israel (Avidov & Harpaz 1969), 5 in Spain (Fodale et al. 1988), 2 in France (Balachowsky 1972), 2 to 3 in Turkey (Kovanci et al. 2006), and 3 in Greece (Mazomenos et al. 2002).

Still, considering a global climate change scenario with rising temperatures, the number of generations tends to increase, intensifying economic damages caused by the pest, as was demonstrated for *G. molesta* and other species of pest-insects that threaten temperate climate fruit trees in southern Brazil (Nava et al. 2017). Thereafter, data obtained in this study, ideally associated with data regarding the development of the species according to other environmental variables, such as humidity and photoperiod, allow ecological zoning and the estimation of bioecological behavior of the species in different locations and global warming scenarios.

Knowledge about thermal requirements of the species can help optimize rearing of *P. forficifera* and the multiplication process in the lab (Scheunemann et al. 2019), aid monitoring of the pest in orchards in order to verify initial occurrence of the species, and predict population outbreaks in the field. This information can help the development of new control strategies, such as biological control, as well as planning and implementing management programs, integrating control techniques, and assuring rational use of chemical pesticides.

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