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Temperature and prey assessment on the performance of the mealybug predator *Tenuisvalvae notata* (Coleoptera: Coccinellidae)

Larissa F Ferreira,[1] Christian S A Silva-Torres,[1] Robert C Venette[2] and Jorge B Torres[1]*

[1]*Department of Agronomy-Entomology, Rural Federal University of Pernambuco, Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, 52171-900 Recife, PE Brazil.*
[2]*Northern Research Station, USDA Forest Service, 1561 Lindig Street, St. Paul, MN 55108-6125, USA.*

Abstract *Tenuisvalvae notata* preys upon several mealybug species (Hemiptera: Pseudococcidae), a group of worldwide pests including *Planococcus citri* and *Ferrisia dasyrilii*. Although the consequences of variation in temperature for the development and reproduction of insects are generally appreciated, the consequences of potential interactions between temperature and prey for predatory insects are not. Thermal requirements and predation rates were determined for *T. notata* at different constant temperatures with both prey species. *T. notata* larvae developed to adults in experimental conditions > 18 to <38 °C. The upper thermal limit for egg hatch was 34 °C and for pupation was 33 °C. Adults reared at ≥ 32 °C did not lay eggs and survived less than 1 week. Prey species did not affect lower temperature thresholds or thermal constants for development from egg to adult. Furthermore, prey did not affect a number of reproductive traits, but the interaction between temperature and prey affected changes in developmental times and oviposition rate with age. Predation rate of *T. notata* increased as a function of temperature, and *T. notata* adults generally consumed more nymphs of *P. citri* than *F. dasyrilii*. These findings indicate that *T. notata* is well adapted to the tropical and sub-tropical temperatures and may prove useful for the biological control of some native and non-native mealybugs.

Key words development, predator–prey interaction, Pseudococcidae, thermal requirement.

INTRODUCTION

The lady beetle *Tenuisvalvae notata* (Mulsant 1850) is native to South America and prefers to prey upon some mealybug species (Dreyer *et al*. 1997a; Barbosa *et al*. 2014a,b). It was successfully introduced into Africa to control the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (1977) (Herren & Neuenschawabder 1991; Chakupurakal *et al*. 1994). In South America, its occurrence is recorded in Brazil, Bolivia, Colombia and Paraguay. In Brazil, it has been reported from the states of Amapá, Bahia, Mato Grosso do Sul, Rio de Janeiro, Rondônia, São Paulo and Pernambuco (Dreyer *et al*. 1997a; Barbosa *et al*. 2014a; Peronti *et al*. 2016). *T. notata* was associated with *Phenacoccus herreni* Cox and Williams, (1981) in Colombia and with *P. manihoti* in Brazil and Paraguay (Loehr *et al*. 1990; Sullivan *et al*. 1991). In the semi-arid region of Pernambuco state, *T. notata* was reported preying upon *Phenacoccus solenopsis* Tinsley (1898) and *Ferrisia dasyrilii* Cockerell (1896) on cotton. Also, it was found on prickly pear, *Opuntia ficus-indica* (L.), infested with the false cochineal scale *Dactylopius opuntiae* Cockerell (1896) (Barbosa *et al*. 2014a; Giorgi *et al*. 2018), but was unable to complete development when feeding exclusively on this scale (Barbosa *et al*. 2014b). Lastly, in São Paulo state, *T. notata* was found preying upon the pink hibiscus mealybug *Maconellicoccus hirsutus* (Green 1908) (Peronti *et al*. 2016). Therefore, this predator appears to exhibit some plasticity to different climates and prey, which is important for its distribution and activity as a natural enemy. In addition, *T. notata* can be produced under laboratory conditions and may be used in augmentative biological control programs of mealybugs.

Temperature and food quality are among the most important factors regulating insect development and reproduction (Davis *et al*. 1996; Hodek & Honěk 1996; Trudgill *et al*. 2005; Estay *et al*. 2009; Kang *et al*. 2009; Ju *et al*. 2011). Data about the effects of such factors are essential to improve rearing methods and to forecast field establishment and activity of natural enemies, which are core steps in biological control programs. Upper and lower temperature thresholds for insect development and the thermal constant (K) to complete development, measured in degree days, can be useful to forecast population growth and distribution of insects (Messenger, 1959), including coccinellids specifically (Samways *et al*. 1999; Koch *et al*. 2006; Nolan 2007; Poutsma *et al*. 2008). Furthermore, temperature can affect attack rate and prey handling times of predatory insects, changing encounter rates and predator–prey interactions (Vucic-Pestic *et al*. 2011; Dell *et al*. 2014). As a result, temperature plays a central role in lady beetle biology (summarised data in Nedvěd and Honěk 2012). Therefore, thermal requirements of *T. notata* preying upon mealybugs are important to better understand its potential for biological control programs.

Regarding food suitability, lady beetles complete development and reproduce when fed on essential prey (Hodek and Honěk 1996), but not all prey that are attacked or consumed

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*jorge.torres@ufrpe.br

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are of equal nutritive value, resulting in variation in development, growth and reproduction (Omkar & Srivastava 2003; Ferrer *et al.* 2008; Shera *et al.* 2010; Hodek & Evans 2012; Barbosa *et al.* 2014a,b; Lira *et al.* 2019). Therefore, the quality of targeted prey may affect the success of a biological control program with lady beetles (Michaud & Olsen 2004; Michaud 2005; Barbosa *et al.* 2014b; Lira *et al.* 2019).

Previous studies have addressed some aspects of developmental rates, prey consumption, functional response and reproduction of *T. notata* (Dreyer *et al.* 1997a,b; Barbosa *et al.* 2014a,b; Túler *et al.* 2017). However, little is known about the interaction of prey quality and thermal requirements on life history traits of *T. notata*. In fact, this is the first study to report thermal requirements and its possible interaction with prey species for *T. notata*. This information is important to support rearing and use of *T. notata* in biological control of mealybugs in different areas. Thus, this study aimed at determining the effects of different temperature on development, reproduction and predation rate of *T. notata* fed with two mealybug species, *F. dasyrilii* and *Planococcus citri* (Risso 1813), and estimating thermal requirements (threshold temperatures and thermal constant) for development.

MATERIALS AND METHODS

Insect cultures

Mealybug colonies of *F. dasyrilii* and *P. citri* were grown in the laboratory of Insect Behavior of the Universidade Federal Rural de Pernambuco (UFRPE), Recife, Pernambuco State, Brazil. *Ferrisia dasyrilii* was collected originally from cotton plants in the experimental area of the Crop Protection Unit at UFRPE (−8.017070°S and −34.944362°W), whereas *P. citri* was obtained from soursop plants (*Annona muricata* L.) at a field orchard in Chã Grande, Pernambuco State (8.25710°S and 35.49386°W). Both mealybug species were reared on 1-kg pumpkin fruits (*Cucurbita moschata* Duchesne var. 'Jacarezinho'), following Sanches and Carvalho (2010).

The colony of *T. notata* was established with adults collected from cotton plants infested with cotton mealybug *P. solenopsis* in Surubim County (−7.833056°S and −35.754722°W), Pernambuco State, Brazil. Lady beetle colonies were maintained in transparent Plexiglas™ cages (40 × 25 × 20 cm in length, width and height) lined on the bottom with paper towel, holding one pumpkin infested with *F. dasyrilii* nymphs and adults per cage as prey according to the procedures described by Barbosa *et al.* (2014a). Both lady beetle and mealybugs were maintained at 25 ± 2 °C, 60 ± 10% relative humidity and photoperiod of 12:12 h (L:D).

Biological and reproductive traits of *Tenuisvalvae notata*

Through this test, we determined the developmental times (egg-adult), sex ratio, fecundity, fertility and survival of females subjected to different constant temperatures and prey species. Initially, *T. notata* pupae were held separately in Petri dishes (5-cm diameter) and observed daily for adult eclosion. Newly emerged *T. notata* adults were separated by sex and fed *ad libitum* with either *F. dasyrilii* or *P. citri*. Pairs of 5-day-old adult females and males of the lady beetle were transferred to Petri dishes (5-cm diameter) containing a piece of paper towel (~0.5 cm^2) as oviposition substrate and provided with nymphs and adults of *F. dasyrilii* or *P. citri*. Fifteen pairs of adult beetles were used per prey species. The oviposited eggs of the lady beetle were identified under a stereomicroscope (Motic, SMZ-168, São Paulo, Brazil) and transferred twice a day ($<$12 h) to new Petri dishes (3.5-cm diameter). Dishes were placed in climatic chambers at constant temperatures of 16, 18, 20, 22, 25, 28, 32 and 38 °C; relative humidity of 70 ± 5%; and photoperiod of 12:12 h (L:D). A minimum of 30 eggs per mealybug species (n = 2) and temperature (n = 8) were monitored daily for survival and development.

Eggs were kept under temperature conditions for 30 days, and larval eclosion was recorded daily, and the presence of exuvia was used to determine the transition between instars. The duration and viability of each immature stage were recorded only for the temperatures between 20 and 32 °C because eggs were not viable at 16, 18 or 38 °C. Prey was offered daily *ad libitum* to the lady beetles as follows: 1st and 2nd instar larvae of *T. notata* were provided with neonate nymphs of *F. dasyrilii* or *P. citri*, according to the prey offered to the parental adult females. After reaching the 3rd instar, *T. notata* larvae were provided with 3rd-instar nymphs and adults of *F. dasyrilii* or *P. citri* as prey, according to the respective treatment. Developmental times (egg to adult), immature viability and sex ratio were recorded for each temperature and prey item.

To study adult reproductive output and survival of *T. notata*, 10 pairs of adult females and males were formed at adult eclosion date and reared in Petri dishes (5-cm diameter) under the same temperature conditions and prey species used during the larval stage. Females and males were kept paired for 10 days when males were discarded and female survival, fecundity and egg viability were recorded for 60 days consecutively. Adult *T. notata* can live up to 84 weeks at 20 °C and 60 weeks at 25 °C when fed with *P. manihoti* under laboratory conditions (Dreyer *et al.* 1997b), and single mated females are able to lay viable eggs for 60 days, but polyandry is most common in this species (Túler *et al.* 2017). Therefore, we monitored adult females for 60 days to determine fecundity, egg viability and female survival, a period that is sufficient to detect any significant impact of temperature and food quality on reproduction (Michaud & Jyoti 2008; Colares *et al.* 2015; Túler *et al.* 2017).

Additional tests were run with adults and eggs obtained from the insect colony reared at 25 °C and fed with *F. dasyrilii* or *P. citri*. The eggs and adults (n = 30) were kept in Petri dishes as previously described and were subjected to the temperatures of 33, 34, 35 and 36 °C, in climatic chambers at the respective constant temperature. Egg viability and larval development were monitored daily, whereas for the adults, survival and fecundity were recorded.

All data were analysed with the statistical package SAS version 9.0 (SAS Institute 2002). The relationship between temperature and developmental times was analysed by linear regression (Proc REG). The equations with all parameters significant, fitted to the biological data in analysis and with higher coefficient of determination, were selected. Further, the impact of temperatures and prey items on development and reproduction characteristic was submitted to homogeneity (Lavene; Proc ANOVA) and normality (Shapiro–Wilk; Proc Univariate) tests followed separately for each factor by one-way analysis of variance (ANOVA) and mean separations performed by either Tukey HSD test ($df > 1$) or Fisher's test from ANOVA ($df = 1$). Progeny sex ratio was calculated as the proportion of females in the progeny and subjected to chi-square (χ^2) test through Proc FREQ ($\alpha = 0.05$). Curves of survival for adult females reared during 60 days under different temperature and prey items were estimated by the Kaplan–Meier method and compared by the log-rank test using the Proc LIFETEST. Female fecundity and fertility were subjected to ANOVA, and the means compared by Tukey HSD test ($\alpha = 0.05$), using the Proc GLM.

Estimation of thermal requirements for development of *Tenuisvalvae notata*

The lower threshold temperature (LT) and thermal constant (K) of *T. notata* were obtained through the thermal sum model (Campbell *et al.* 1974), which describes the relationship between the inverse of the developmental times ($1/D$) and the environment temperature T (i.e., $1/D = y = \alpha + \beta * x$). In addition, based on the cumulative degree days model, the lower development threshold (i.e., when $1/D = 0$) was estimated by the relation of the intercept and the linear coefficient of the fitted linear equation (e.g., $LT = -\alpha/\beta$), whereas the thermal constant was calculated by the inverse of the linear coefficient ($K = 1/\beta$). The standard errors for the mean values of LT and K were estimated according to Campbell *et al.* (1974) and Zuim *et al.* (2017). The linear model does not allow estimations of the optimal temperatures for development nor the upper limiting temperatures. Thus, the nonlinear model Brière-1 (Brière *et al.* 1999) was fitted to the results of developmental rates of *T. notata* fed different prey as a function temperature studied (Rebaudo *et al.* 2018). (Other non-linear models did not fit as well; data not shown.) The optimal (T_{opt}) and upper (T_{max}) temperatures were obtained through the 'devRate' procedure of R (R Development Core Team 2013).

From results obtained for LT and K with the Campbell linear model for temperatures between 20 and 32 °C, the probable number of generations of *T. notata* per year was estimated. The estimation considered 10 years' temperature averages (Ta) for four Pernambuco localities (Chã Grande, Belo Jardim, Surubim and Petrolina) where *T. notata* had been collected associated with mealybugs infesting fruit orchard and cultivated plants in these locations (Barbosa *et al.* 2014a; Pacheco-da-Silva *et al.* 2019). Thus, the annual (365 days) number of generations (NG) for *T. notata* was estimated using the following equation: $\text{NG} = 365\ (Ta - LT)/K$. The annual average temperatures for the respective Pernambuco localities were obtained from APAC ('Agência Pernambucana de Águas e Clima') and from Climatedata.org for the period of 2008 to 2018.

Predation of *Tenuisvalvae notata* upon two mealybug species under different temperatures

In order to measure the predation rate of *T. notata* under different temperatures showing successful development and reproduction (ca. 20, 22, 25, 28 and 32 °C) and prey species (*F. dasyrilii* and *P. citri*), 3rd- and 4th-instar larvae, and females of *T. notata* were monitored daily for prey consumption. Larvae of *T. notata* were reared individually in Petri dishes (3.5-cm diameter) up to the 2nd-instar feeding *ad libitum* upon neonate nymphs of *F. dasyrilii* or *P. citri* and were kept under the respective rearing temperature in the climatic chamber. When *T. notata* larvae reached the 3rd instar, they were provided daily with five nymphs of the respective mealybug species in the 3rd instar until moulting to pupal stage. This number of mealybug nymphs provided daily to 3rd-instar *T. notata* was determined based on previous consumption tests, which showed that they consumed an average of less than five nymphs per day. The number of mealybug nymphs consumed daily was tailed and replaced by new ones, always maintaining the initial number of prey available ($n = 5$). Further, prey consumption by adult female ladybird beetles was determined over 10 consecutive days. Each treatment (temperature × prey) had 25 replications.

All data (total number of prey consumed, daily predation rate) were submitted to homogeneity (Lavene; Proc ANOVA) and normality (Shapiro–Wilk; Proc Univariate) tests. Data were transformed when needed to satisfy assumptions of the ANOVA. Further, treatment means were separated by Tukey HSD test ($\alpha = 0.05$) when appropriate.

RESULTS

Biological and reproductive traits of *Tenuisvalvae notata*

Developmental times

Tenuisvalvae notata eggs did not hatch when kept at 16, 18 or 38 °C. Eggs were incubated at a constant 33, 34, 35 or 36 °C, and only those at 33 or 34 °C hatched (100% when females had been fed either *F. dasyrilii* or *P. citri*). Larval survival was reduced to about 40% at 34 °C. No larvae survived to adults at 35 °C. Furthermore, adults obtained at 25 °C and reared at the same upper temperatures (33, 34, 35 and 36 °C) failed to lay eggs and died within a week. However, juvenile *T. notata* developed to adults and reproduced when reared at 20, 22, 25, 28 or 32 °C feeding on either mealybug species. Further, all juvenile stages showed increased developmental rate ($1/D$) as function of temperature increase (Fig. 1). Mean egg developmental times varied from 10.1 ± 0.30 days at 20 °C to 4.2 ± 0.07 days at 32 °C when fed on *F. dasyrilii* ($y = -0.156 + 0.012x$, $r^2 = 0.969$, $F_{4,145} = 272.64$, $P < 0.0001$, Table 1). Similar results were obtained when *T. notata* fed on *P. citri*, with mean egg development varying from 11.3 ± 0.25 to 4.3 ± 0.12 days when incubated at 20 to 32 °C, respectively ($y = -0.157 + 0.013x$, $r^2 = 0.953$, $F_{1,158}$, $P < 0.0001$). Regarding the prey effect on *T. notata* egg

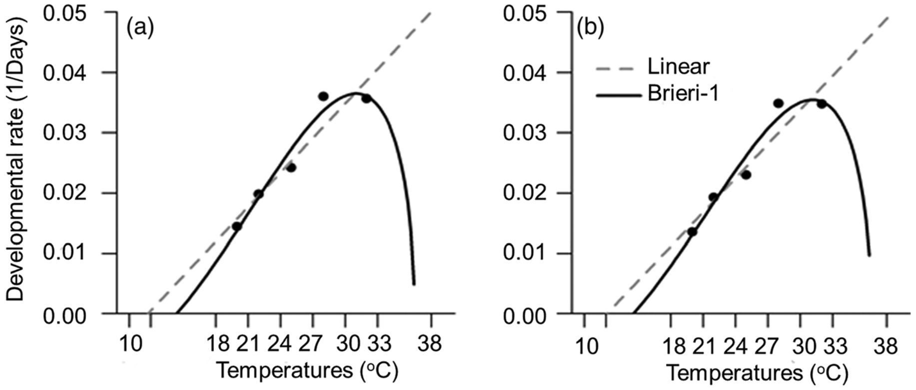

Fig. 1. Models of the developmental rate (1/*D*) from egg to adult of *Tenuisvalvae notata* preying upon the mealybugs *Ferrisia dasyrilii* (a) or *Planococcus citri* (b) as a function of temperatures between 18 and 32 °C. Closed symbols represent the observed data.

Table 1 Mean (±SEM) developmental times (days) of *Tenuisvalvae notata* reared under different temperatures (°C) and fed *Ferrisia dasyrilii* or *Planococcus citri*

	Temperature (°C)†					
Stage/preys	20	22	25	28	32	$F_{4,145}^{P\text{-value}}$
Egg						
F. dasyrilii	10.1 ± 0.30 Ba†	8.9 ± 0.73 Ab	6.6 ± 0.08 Ac	4.7 ± 0.09 Ad	4.2 ± 0.07 Ad	$272.64^{<0.0001}$
P. citri	11.3 ± 0.25 Aa	8.0 ± 0.25 Bb	6.7 ± 0.10 Ac	4.5 ± 0.14 Ad	4.3 ± 0.12 Ad	$230.73^{<0.0001}$
$F_{1,158}^{P\text{-value}}$	$8.55^{0.0049}$	$9.98^{0.0025}$	$0.95^{0.3345}$	$1.35^{0.2502}$	$1.36^{0.2483}$	
Larva (I–IV)						
F. dasyrilii	8.8 ± 0.12 Ba	5.8 ± 0.75 Bb	5.1 ± 0.11 Bc	3.3 ± 0.05 Bd	3.5 ± 0.07 Bd	$584.91^{<0.0001}$
P. citri	9.9 ± 0.20 Aa	6.3 ± 0.08 Ab	5.7 ± 0.14 Ac	3.7 ± 0.06 Ad	3.9 ± 0.08 Ad	$389.04^{<0.0001}$
$F_{1,158}^{P\text{-value}}$	$20.89^{<0.0001}$	$17.78^{<0.0001}$	$10.06^{0.0024}$	$16.51^{0.0001}$	$10.64^{0.0019}$	
Pupa						
F. dasyrilii	23.5 ± 0.26 Aa	18.0 ± 0.22 Ab	13.9 ± 0.15 Ac	9.5 ± 0.22 Ad	9.5 ± 0.24 Ad	$706.66^{<0.0001}$
P. citri	22.7 ± 0.30 Ba	18.3 ± 0.29 Ab	13.5 ± 0.19 Ac	9.0 ± 0.37 Ad	8.6 ± 0.16 Bd	$475.16^{<0.0001}$
$F_{1,158}^{P\text{-value}}$	$4.26^{0.0435}$	$0.52^{0.4743}$	$2.24^{0.1397}$	$1.67^{0.2015}$	$8.55^{0.0049}$	
Egg–adult						
F. dasyrilii	69.2 ± 0.58 Ba	50.4 0.28 Bb	41.2 ± 0.42 Bc	27.7 ± 0.27 Ad	28.0 ± 0.40 Ad	$1801.34^{<0.0001}$
P. citri	73.9 ± 0.77 Aa	51.8 0.53 Ab	43.4 ± 0.60 Ac	28.3 ± 0.40 Ad	28.7 ± 0.38 Ad	$1142.79^{<0.0001}$
$F_{1,158}^{P\text{-value}}$	$23.45^{<0.0001}$	$5.14^{0.0271}$	$8.41^{0.0053}$	$1.36^{0.2490}$	$1.73^{0.1935}$	

†Values followed by the same capital letter (when present) in the columns are not significantly different between prey species (Fisher's test), whereas means followed by the same lowercase letter within the rows are not significantly different across temperatures ($P > 0.05$, Tukey HSD test).

developmental times, it varied significantly between prey species only at 20 ($F_{1,158} = 8.55$, $P < 0.0049$) and 22 °C ($F_{1,158} = 9.98$, $P = 0.0025$).

The period of larval development decreased significantly with increase in temperature, regardless of prey species (Table 1). It varied from 8.8 ± 0.12 to 3.5 ± 0.07 days at 20 to 32 °C ($y = -0.169 + 0.015x$, $r^2 = 0.958$, $F_{4,145} = 584.91$, $P < 0.0001$) when *T. notata* was fed *F. dasyrilii* and from 9.9 ± 0.20 to 3.9 ± 0.08 days at 20 to 32 °C ($y = -0.154 + 0.014x$, $r^2 = 0.955$, $F_{4,145} = 389.04$, $P < 0.0001$) when fed *P. citri*. In addition, there was significant effect of prey species on larval developmental times at all temperatures, with the overall larval development being faster when *T. notata* fed on *F. dasyrilii* than on *P. citri* (Table 1). Likewise, pupation time decreased with increases in temperature, regardless of prey species (Table 1). Developmental times for pupa varied from 23.5 ± 0.26 to 9.5 ± 0.24 days when *T. notata* was fed *F. dasyrilii* ($y = -0.072 + 0.006x$, $r^2 = 0.956$, $F_{4,145} = 706.66$, $P < 0.0001$), and from 22.7 ± 0.30 to 8.6 ± 0.16 days when fed *P. citri* ($y = -0.085 + 0.006x$, $r^2 = 0.956$, $F_{4,145} = 475.16$, $P < 0.0001$). In addition, there was an effect of prey species for pupal development at 20 °C ($F_{1,158} = 4.26$, $P = 0.043$) and 32 °C ($F_{1,158} = 8.55$, $P = 0.0049$).

The time required to complete development from egg to adult eclosion was variable depending on the temperature, regardless of prey species. The development from egg to adult eclosion varied from 69.2 ± 0.58 to 28.0 ± 0.40 days at 20 and 32 °C, respectively ($y = 0.002 - 0.023x$, $r^2 = 0.968$, $F_{4,145} = 1801.34$, $P < 0.0001$) when *T. notata* larvae fed with *F. dasyrilii*. Likewise, whole development varied from 73.9 ± 0.77 to 28.7 ± 0.38 days at 20 and 32 °C, respectively ($y = 0.002 - 0.023x$, $r^2 = 0.963$, $F_{4,145} = 1142.79$, $P < 0.0001$) when fed *P. citri*. In addition, there was a significant effect of prey species on developmental times from egg to adult at 20, 22 and 25 °C, with a longer period when *T. notata* was fed *P. citri* (Table 1).

Sex ratio

Sex ratio of *T. notata* was not affected by temperature when fed *P. citri* (χ^2 = 0.0238, *df* = 4, P = 0.09) nor *F. dasyrilii* (χ^2 = 0.0278, *df* = 4, P = 0.09). Similarly, sex ratio was not affected by prey species at all temperature tested (multiple chi-square outcomes resulted in $P > 0.05$).

Fecundity

The response of maintaining adult females at the same rearing temperature regimes resulted in decreased in the pre-oviposition period with an increase in temperature when females were fed with *P. citri* ($F_{4,45}$ = 3.67, P = 0.0114). Nonetheless, no significant difference was detected for pre-oviposition period when they were fed with *F. dasyrilii* ($F_{4,45}$ = 1.62, P = 0.1856). Female fecundity tailed during 60 days was affected by temperature, when *T. notata* was fed *F. dasyrilii* ($F_{4,45}$ = 67.59, $P < 0.0001$) or *P. citri* ($F_{4,45}$ = 39.97, $P < 0.0001$) (Table 2, Fig. 2). Each female fed *F. dasyrilii* laid an average of 5.2 ± 1.86 to 442.5 ± 37.88 eggs/female, whereas those females fed with *P. citri* laid an average of 13.7 ± 6.07 to 196.8 ± 22.66 eggs/female, with similar and lower fecundities at the lowest and highest tested temperatures (ca. 20 and 32 °C). Comparing prey species, higher fecundity was observed when females were fed *P. citri* at 28 °C ($F_{1,18}$ = 30.97, $P < 0.0001$; Table 2 and Fig. 2).

Fertility

Egg viability was also significantly affected across temperatures, varying from 16.2 ± 8.33 to 84.6 ± 5.83 when fed *F. dasyrilii* ($F_{4,45}$ = 17.74, $P < 0.0001$) and from 20.4 ± 7.75 to 91.1 ± 2.28 when fed *P. citri* ($F_{4,45}$ = 35.34, $P < 0.0001$), also with similar and lower egg viabilities at the lowest and highest tested temperatures (ca. 20 and 32 °C). However, again, there was no effect of prey on egg viability at all tested temperatures (Table 2).

Survival

Survival was not affected by temperature when *T. notata* females were fed *F. dasyrilii* (log-rank test; χ^2 = 7.46, *df* = 4, P = 0.1131) (Fig. 3). However, there was a significant effect of temperature on survival when females were fed on *P. citri*, since 100% of the females kept under 20 °C were alive up to 60 days, but females kept under temperatures from 22 to 32 °C had a reduction in survival varying from 55.5 to 82.2% (log-rank test; χ^2 = 12.52, *df* = 4, P = 0.0139) (Fig. 3).

Complementary tests showed that egg viability at 33 and 34 °C was 100% but were not viable at 35 and 36 °C. Larval viability decreased about 25% at 33 °C and 40% at 34 °C, but remaining larvae did not survive to pupation. Eggs or larvae were not viable at 35 and 36 °C. Average adult survival decreased from 23 to 7 days at 33 to 35 °C and did not reproduce when exposed to temperatures conditions from 33 to 36 °C.

Estimation of thermal requirements for development of *Tenuisvalvae notata*

As previously described, the developmental rate across all juvenile stages of *T. notata* exhibited a positive linear fashion that allowed the estimation of the *LT* and *K*. The lower threshold temperature (*LT*) and DD accumulation for development of *T. notata* from egg to adult did not show significant variation between prey items since there is overlap in the 95% confidence interval for both variables and prey species (Table 3). The *LT* estimated by the linear Campbell's model was 11.8 ± 0.40 and 12.1 ± 0.37 °C fed *F. dasyrilii* and *P. citri*, respectively. Meanwhile, the estimated values for thermal constant (*K*) for *T. notata* to reach adulthood was 520.8 ± 99.3 and 529.94.4 DD fed *F. dasyrilii* and *P. citri*, respectively (Table 3). In addition, the optimal (T_{opt}) and upper limiting ($T_{\max}$) temperatures estimated by the nonlinear Brière-1 model were 31.0 and 31.1 °C, and 36.4 ± 2.29 and 36.5 ± 2.54 °C, respectively, for *T. notata* fed *F. dasyrilii* and *P. citri* (Table 3 and Fig. 1). The nonlinear model Brière-1 predicted an optimal temperature that fits between the maximum developmental rate observed between

Table 2 Reproductive traits of *Tenuisvalvae notata* females exposed to different temperatures (°C) and fed *Ferrisia dasyrilii* or *Planococcus citri* for 60 days consecutively

	Temperature (°C)[†]					
Prey	20	22	25	28	32	$F_{4,45}^{P\text{-value}}$
Pre-oviposition period (days)						
F. dasyrilii	5.6 ± 2.41 a[†]	2.8 ± 0.41 a	2.2 ± 0.51 Aa	1.3 ± 0.21 a	3.5 ± 1.35 a	$1.62^{0.1832}$
P. citri	11.8 ± 3.43 a	4.7 ± 0.80 a	1.5 ± 0.22 Ab	1.7 ± 0.49 b	6.1 ± 3.36 ab	$3.67^{0.0102}$
$F_{1,18}^{P\text{-value}}$	$2.18^{0.1567}$	$0.41^{0.0501}$	$1.570^{\cdot\,2263}$	$0.55^{0.4680}$	$0.51^{0.4829}$	
Fecundity						
F. dasyrilii	8.1 ± 3.00 c	60.4 ± 13.40 bc	145.0 ± 28.87 b	442.5 ± 37.88 Aa	5.20 ± 1.86 c	$67.59^{<0.0001}$
P. citri	15.5 ± 4.58 c	44.3 ± 8.48 c	115.7 ± 11.36 b	196.8 ± 22.66 Ba	13.7 ± 6.07 c	$39.97^{<0.0001}$
$F_{1,18}^{P\text{-value}}$	$1.79^{0.1977}$	$1.03^{0.3145}$	$0.89^{0.3576}$	$30.97^{0.0001}$	$1.79^{0.1979}$	
Egg viability						
F. dasyrilii	16.2 ± 8.33 b	84.6 ± 5.83 a	75.2 ± 4.18 a	79.9 ± 1.25 a	34.2 ± 12.05 b	$17.74^{<0.0001}$
P. citri	23.4 ± 5.94 b	91.1 ± 2.28 a	75.4 ± 5.94 a	77.5 ± 4.38 a	20.4 ± 7.75 b	$35.34^{<0.0001}$
$F_{1,18}^{P\text{-value}}$	$0.49^{0.4911}$	$1.07^{0.3145}$	$0.00^{0.9821}$	$0.27^{0.6110}$	$0.92^{0.3496}$	

[†] Values followed by the same capital letter (when present) in the columns are not significantly different between prey species (Fisher's test), whereas means followed by the same lowercase letter within the rows are not significantly different across temperatures ($P > 0.05$, Tukey HSD test).

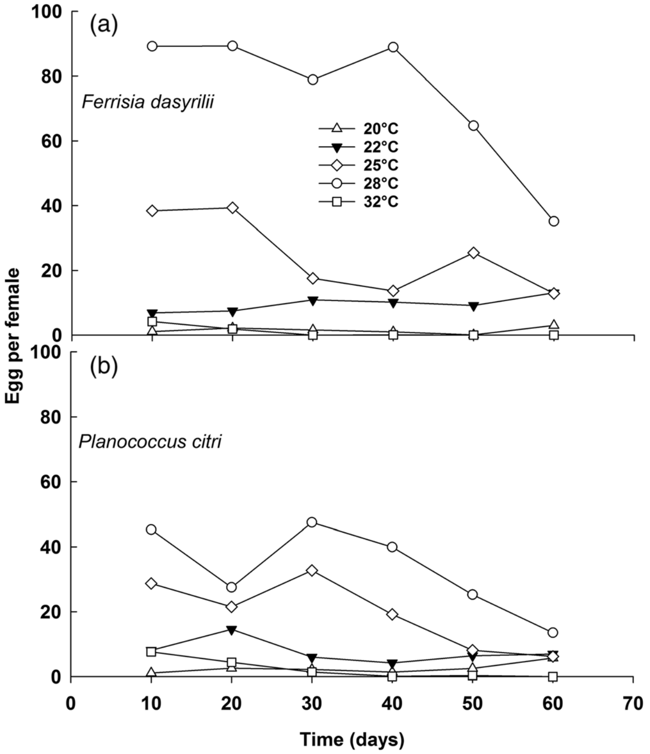

Fig. 2. Oviposition of *Tenuisvalvae notata* preying upon the mealybugs *Ferrisia dasyrilii* (a) or *Planococcus citri* (b) under different constant temperatures (°C).

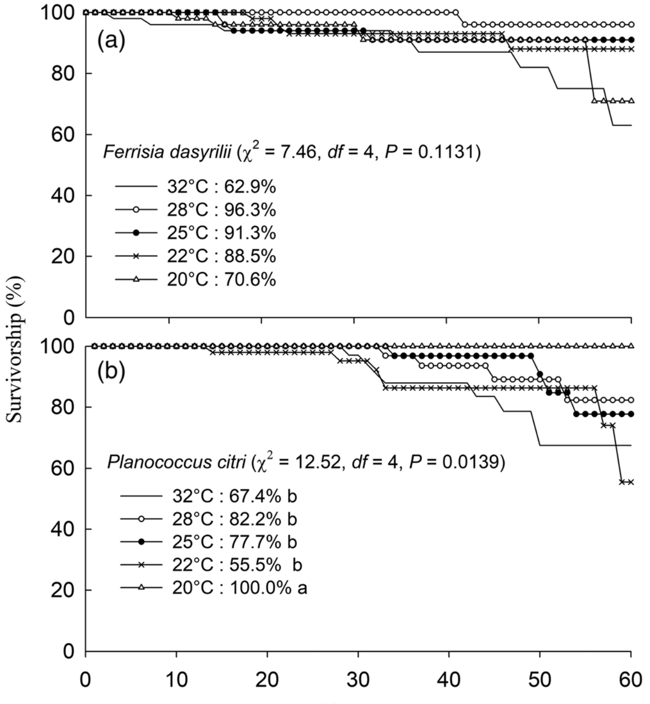

Fig. 3. Survival of *Tenuisvalvae notata* females preying upon the mealybugs *Ferrisia dasyrilii* (a) or *Planococcus citri* (b) under different temperatures during 60 days within adult stage. Curves were calculated by the Kaplan–Meier method and compared by log-rank test ($\alpha = 0.05$).

Table 3 Parameters adjusted from the linear Campbell and nonlinear Brière-1 models, which better described the development of *Tenuisvalvae notata* preying upon *Ferrisia dasyrilii* or *Planococcus citri* as a function of constant temperatures

Model/prey	Parameters	Estimate (±SE)	Models	Parameters	Estimate (±SE)
Ferrisia dasyrilii					
Linear (Campbell)[†]	α	−0.02276 ± 0.00945	Nonlinear Brière-1[‡]	a (10^{-5})	3.04 ± 1.03
	β	0.00192 ± 0.00036		T_0	14.5 ± 2.32
	LT	11.8 ± 0.40 (11.4–12.2)[§]		$T_{\max}$	36.4 ± 2.29
	K	520.8 ± 99.3 (421.5–620.1)[§]		T_{opt}	31.0
Planococcus citri					
Linear (Campbell)[†]	α	−0.02282 ± 0.00869	Nonlinear Brière-1[‡]	a (10^{-5})	3.65 ± 1.07
	β	0.00189 ± 0.00033722		T_0	14.5 ± 2.42
	LT	12.1 ± 0.37 (11.7–12.4)[§]		$T_{\max}$	36.5 ± 2.54
	K	529.1 ± 94.4 (434.6–623.5)[§]		T_{opt}	31.1

[†] α and β stand for intercept and slope of linear regression ($y = \alpha + \beta x$), *LT* stands for lower threshold temperature for development, and *K* is a thermal constant.

[‡] T_0, $T_{\max}$ and T_{opt} are respectively the lower temperature threshold, the upper temperature threshold and the optimal temperature for development, whereas a is the coefficient determined by the nonlinear model Brière-1 = $aT\,(T - T_0)(T_{\max} - T)^{1/2}$ in which data were best adjusted.

[§] Values between parentheses are 95% confidence interval.

28 and 32 °C (Fig. 1), with a decline after this temperature, and stopping at about 36 °C (Fig. 1).

Based on the results of the *LT* and *K* calculated by the linear model, the annual average number of generations that *T. notata* accomplishes varied from 6.8 to 7.1 in Chã Grande, from 6.9 to 7.2 in Belo Jardim, from 8.4 to 8.7 in Surubim and from 8.8 to 9.1 in Petrolina, feeding on *F. dasyrilii* and *P. citri*, respectively.

Predation of *Tenuisvalvae notata* upon two mealybug species under different temperatures

There was a significant increase in predation rate by larvae and adults of *T. notata* as a function of temperature increase from 20 to 32 °C (Table 4). The average daily consumption varied from 1.7 ± 0.08 to 2.9 ± 0. 14 ($F_{1,120} = 12.87$, $P < 0.0001$), from 1.4 ± 0.06 to 2.7 ± 0.09 ($F_{1,120} = 33.89$, $P < 0.0001$) and from 1.3 ± 0.11 to 2.7 ± 0.11 ($F_{1,120} = 40.61$, $P < 0.0001$) nymphs of *F. dasyrilii*, for 3rd- and 4th-instar larvae and adults of *T. notata*, respectively (Table 4). Similarly, the daily average of prey consumption when *T. notata* fed *P. citri* varied from 1.9 ± 0.08 to 3.6 ± 0.18 ($F_{1,120} = 23.16$, $P < 0.0001$), from 1.9 ± 0.06 to 3.1 ± 0.07 ($F_{1,120} = 25.73$, $P < 0.0001$) and from 1.9 ± 0.12 to 3.4 ± 0.22 ($F_{1,120} = 34.63$, $P < 0.0001$) nymphs of *P. citri* for 3rd- and 4th-instar larvae and adults of *T. notata* (Table 4).

Overall predation outcome comparing the two mealybug species shows higher predation upon *P. citri* across all tested temperatures ($P < 0.0001$) for both larvae and adults of *T. notata* (Table 4). For 3rd-instar larvae, there was a significant higher predation upon *P. citri* at 20 °C ($F_{1,48} = 5.42$, $P = 0.0242$), 28 °C ($F_{1,48} = 17.36$, $P < 0.0001$) and 32 °C ($F_{1,48} = 8.78$, $P = 0.0047$), whereas for 4th-instar larvae, there was a greater consumption only at 20 °C ($F_{1,48} = 31.31$, $P < 0.0001$) and 32 °C ($F_{1,48} = 12.59$, $P = 0.0009$). For *T. notata* adults, the higher predation upon *P. citri* occurred across all tested temperatures (Table 4).

DISCUSSION

The lady beetle *T. notata* fulfilled development and reproduction under constant temperatures from 20 to 32 °C. Moreover, the failure of *T. notata* to develop and reproduce when reared at temperatures greater than 32 °C was unexpected considering the predator occurs naturally in the semiarid areas of Pernambuco State, Brazil (Barbosta *et al*. 2014b; Giorgi *et al*. 2018). Temperature in the Semiarid areas may exceed 40 °C, but such temperatures likely occur for short periods of the day and in some periods of the year only. In contrast, the daily average temperature from 2008 to 2019 was 24.8 °C (e.g., Petrolina location, APAC 2019). Therefore, we can hypothesise that the impact from heat stress on part of the day is compensated by mild temperatures during the night differently from constant (25 °C) day–night temperature maintained in the laboratory.

The lower threshold temperature estimated to *T. notata* (*LT* = 14.5 °C) falls within the range of threshold temperature of other coccinellids. For example, Morales-Ramos and Rojas (2017) found an *LT* = 13 °C for *Coleomegilla maculata* (DeGeer 1775), while Saeedi *et al*. (2015) determined an *LT* = 11.5 °C for *Cryptolaemus montrouzieri* Mulsant, 1853. In addition, Pachú *et al*. (2018) also used the nonlinear model of Brière and estimated the *LT* = 16 °C for *Cycloneda sanguinea* (L., 1763), whereas Stathas *et al*. (2011) estimated an *LT* = 11 °C for *Harmonia axyridis* (Pallas 1773). In this context, one might be cautious with model estimations, as they might be helpful to predict possible insect survival and development in a determined habitat, but other factors also might affect the outcome in the habitat, for instance, the origin of the insect population and how long it has been reared under those environmental conditions. For instance, *C. montrouzieri* is indigenous to Australia and has been successfully introduced in various continents. Models indicates that *C. montrouzieri* has potential to establish in areas of the world with tropical climate (Ferreira 2019), whereas the estimated *LT* for this species was 11.5 °C (Saeedi *et al*. 2015), a temperature usually not common in tropical areas. However, if the population has been reared under colder or

Table 4 Mean number (±SEM) of *Ferrisia dasyrilii* or *Planococcus citri* nymphs consumed daily by larvae and adults of *Tenuisvalvae notata* under different constant temperatures (°C)

Predator age/prey	20	22	25	28	32	$F_{1,120}^{P\text{-value}}$
3rd-instar larvae						
F. dasyrilii	1.7 ± 0.08 Bc	2.3 ± 0.11 b	2.2 ± 0.10 b	2.5 ± 0.16 Bab	2.9 ± 0. 14 Ba	12.87 $^{<0.0001}$
P. citri	1.9 ± 0.08 Ac	2.6 ± 0.14 b	2.4 ± 0.14 bc	3.4 ± 0.16 Aa	3.6 ± 0.18 Aa	23.16 $^{<0.0001}$
$F_{1,48}^{P\text{-value}}$	5.42 $^{0.0242}$	3.13 $^{0.0832}$	1.29 $^{0.2618}$	17.36 $^{<0.0001}$	8.78 $^{0.0047}$	
4th-instar larvae						
F. dasyrilii	1.4 ± 0.06 Bb	2.4 ± 0.09 a	2.3 ± 0.09 a	2.5 ± 0.08 a	2.7 ± 0.09 Ba	33.89 $^{<0.0001}$
P. citri	1.9 ± 0.06 Ad	2.2 ± 0.09 cd	2.3 ± 0.11 cb	2.6 ± 0.08 b	3.1 ± 0.07 Aa	25.73 $^{<0.0001}$
$F_{1,48}^{P\text{-value}}$	31.31 $^{<0.0001}$	2.04 $^{0.1593}$	0.05 $^{0.8188}$	0.13 $^{0.7170}$	12.59 $^{0.0009}$	
Adult						
F. dasyrilii	1.3 ± 0.11 Bc	1.2 ± 0.04 Bc	1.5 ± 0.09 Bcb	1.8 ± 0.09 Bb	2.7 ± 0.11 Ba	40.61 $^{<0.0001}$
P. citri	1.9 ± 0.12 Acb	1.6 ± 0.06 Ac	2.2 ± 0.11 Ab	3.4 ± 0.22 Aa	3.3 ± 0.13 Aa	34.63 $^{<0.0001}$
$F_{1,48}^{P\text{-value}}$	13.03 $^{0.0007}$	26.29 $^{<0.0001}$	18.87 $^{<0.0001}$	45.44 $^{<0.0001}$	9.56 $^{0.0033}$	
3rd instar–adult						
F. dasyrilii	1.4 ± 0.05 Bd	2.0 ± 0.05 Bc	2.0 ± 0.06 Bcb	2.2 ± 0.06 Bb	2.7 ± 0.08 Ba	58.72 $^{<0.0001}$
P. citri	1.9 ± 0.06 Ac	2.0 ± 0.04 Acb	2.3 ± 0.07 Ab	3.1 ± 0.12 Aa	3.3 ± 0.07 Aa	60.08 $^{<0.0001}$
$F_{(gl = 1.48)}^{P\text{-value}}$	37.52 $^{<0.0001}$	4.31 $^{0.0432}$	9.48 $^{0.0034}$	47.82 $^{<0.0001}$	23.38 $^{<0.0001}$	

Values followed by the same capital letter (when present) in the columns are not significantly different between prey species (Fisher's test), whereas means followed by the same lowercase letter within the rows are not significantly different across temperatures ($P > 0.05$, Tukey HSD test).

warmer conditions, it could adapt to the climate, and the model's estimates are therefore accurate. Some studies have shown that insect populations are able to adapt to environmental conditions over time (Zeilstra & Fisher 2005; Weldon *et al.* 2011; Maes *et al.* 2012, 2015).

In this regard, the maximum estimated temperatures for development of *T. notata* by the model on either prey (36.4 and 36.5 °C) were superior to the temperature where there was development, reproduction and survival of this species in the laboratory (32 °C). In addition, when we ran complementary tests evaluating egg viability, larval development, adult survival and reproduction at 33 to 36 °C, we found that those temperatures were negative to *T. notata* development and reproduction. The population of *T. notata* used in this study has been reared in the laboratory for many generations at 25 °C. Therefore, we assume it has been acclimated to such conditions. Probably, the best development and reproduction of *T. notata* falls within the temperature range of 20 to 32 °C, as seen in Fig. 1. However, depending on the origin of the population due to possible adaptation to more extreme temperatures throughout generations, development and reproduction happen at such extreme temperatures or over a broader estimated by the models. In fact, a previous study conducted by Dreyer *et al.* (1997b), showed that development of *Hyperaspis* (= *Tenuisvalvae*) *notata* was possible on temperatures varying from 18 to 34 °C, which are slightly broader than our population's temperature range. It is possible that divergence on results is due to differences in populations used in both studies due to environmental (temperature) adaptation, ours being originated from the warmer region of Brazil (Semiarid of Pernambuco State) and the other having originated from the colder south region of Brazil. Further studies are under way to investigate the possible effects of temperature acclimation on *T. notata* development, survival and reproduction.

Regarding developmental times of *T. notata* from egg to adult, results showed a reduction in duration across all developmental stages due to increase in temperature up to 32 °C. Similarly, Dreyer *et al.* (1997b) found that *T. notata* developmental times reduced from 90 to 21 days when reared at 18 and 32 °C, respectively. Thus, we could predict that in warmer climate (around 30–32 °C), *T. notata* would have more generations a year, hence, a faster population growth than on places with lower temperatures (18–20 °C). In fact, when we used the software CLIMEX (Climate Change Experiment, Hearne Software, version 4.0, Australia) to preview population geographic distribution, we found that *T. notata* has more potential to establish at tropical areas of the globe (Ferreira 2019). For the environmental conditions in the Semiarid of Pernambuco, from where *T. notata* population was originated, the average temperature is around 26 °C to 27.5 °C (APAC 2019), and this predator seems to be well adapted to local conditions with 6.8–9.1 generations per year. Similar temperature conditions are found in the Africa region where *T. notata* was introduced to control the cassava mealybug, *P. manihoti* (Herren & Neuenschawabder 1991; Chakupurakal *et al.* 1994).

The effects of food type on thermal requirements of lady beetles are not well documented in literature, but some studies suggest that prey suitability may affect the developmental times of the predator. Our results did not show much effect of mealybug species on development or thermal requirements of *T. notata*. However, some better performance preying upon *P. citri* than *F. dasyrilii* was detected. This preference could be related to the production of honeydew, which is more intense in *P. citri* in comparison to *F. dasyrilii*. There are reports of coccinellids feeding on the honeydew released by prey (Hagen 1962; Carter & Dixon 1984), which could indicate the presence of prey as well as be a food supplement for the predator. Another possible explanation for *T. notata* to prefer preying upon *P. citri* could be related to prey wax density, as nymphs and adults of *F. dasyrilii* produce a dense amount of wax covering their body, which might impair prey attack and handling as happen in chrisopids (Tapajós *et al.* 2016). Therefore, both factors honeydew production and wax density may affect predator preference and need to be considered when investigating predation on mealybug species.

Tenuisvalvae notata sex ratio was not affected by either prey species or temperature. In addition, other studies with coccidophagous lady beetles have shown that prey or temperature typically does not affect the sex ratio (Omkar & Kumar 2010; Yazdani & Zarabi 2011; Satar & Uygun 2012; Sayed & El Arnaouty 2016). When we consider the reproduction of *T. notata*, the higher oviposition rate was obtained at 28 °C, which seems to fit very well within the temperature range from where this population was originated, the semiarid regions of Pernambuco State. Similarly, Singh *et al.* (2018) showed that the lady beetle *Menochilus sexmaculatus* (Fab., 1781) also has higher fecundity at this temperature range. It is important to mention that in insects, there is a trade-off between reproduction and survival; for those individuals favouring reproduction, they usually have a reduction on survival (and vice versa), due to the high energetic cost of reproduction (Mirhosseini *et al.* 2014). However, when we look at the results of reproduction and survival of *T. notata* females at 25 and 28 °C, there were higher survival and reproduction at those temperatures, suggesting that these temperatures are the best conditions for this predatory species. Also, *T. notata* has a very long lifespan, and females after one mating are able to lay viable eggs for about 60 days (Túler *et al.* 2017). In case of multiple matings and ideal temperature conditions, *T. notata* females can live and reproduce for more than 150 days (Dreyer *et al.* 1997a; Túler *et al.* 2017), which benefits the biological control of mealybugs. Thus, *T. notata* females should also invest in long survival if they are to guarantee higher reproduction rates, even with just one mating that might happen just after emergence or after 100 days (Túler *et al.* 2017).

For higher temperatures, above the optimal or maximum thresholds, studies have shown that the response of organisms to thermal stress is dependent on the temperature itself and the duration of exposition to it (Nguyen *et al.* 2013; Walsh *et al.* 2019). Therefore, the reduction in *T. notata* reproductive output in higher temperatures could be due to males being more susceptible to thermal stress than females. Moreover, higher temperatures could affect spermatogenesis and/or increase spermatozoid mortality (Ponsonby & Copland 1998). Also, heat waves can reduce the number and viability of spermatozoids compromising their capacity to reach the spermatheca of females and posterior egg fertilisation (Sales *et al.* 2018). For instance, the beetle *Tribolium castaneum* (Herbst, 1797) suffered a negative impact of heat on its reproduction when adults were subjected to 5 to 7 °C above the optimum for 5 days. Females did not suffer a direct impact of heat, but male reproduction potential was significantly reduced, and females mated with heat-treated males had lower fitness, with only 40% egg viability (Sales *et al.* 2018). In fact, physiological studies are underway to test whether temperature affects spermatogenesis or oogenesis in *T. notata* and will shed more light and better our understanding of the effects of temperature on *T. notata* fitness.

Besides the effects of temperature on insect development, reproduction and survival, predation behaviour can also be dependent on temperature in ectothermic organisms such as insects, due to the locomotion activity, which can vary with the temperature (Dell *et al.* 2011). When both prey and predator are ectothermic organisms, they tend to have a lower locomotion activity at lower temperatures; hence, predator–prey interactions regarding predator attack and prey escape rate are less successful at lower temperatures (Dell *et al.* 2011). In addition, feeding rate is also dependent on temperature similarly to metabolic rates (Brown *et al.* 2004). In *T. notata* there was an increase of prey consumption with temperature, regardless of prey species available, in agreement with the hypothesis of higher metabolic rate and faster development of beetles in warmer temperatures, leading to a higher daily consumption rate. In another study with the ladybird beetle *Rhyzobius lophanthae* (Blaisdell 1892), the larvae also increased the number of prey (*Aspidiotus nerii* Bouché) consumed from 24.3 to 33.5 at 25 and 30 °C, respectively (Alloush 2019). Moreover, similar results were found for other coccinellid species, such as *Coccinella undecimpunctata* L.,1758 (Cabral *et al.* 2009), *C. montrouzieri* (Kaur & Virk 2012), *Harmonia dimidiata* (Fab., 1781) (Yu *et al.* 2013) and *Hyperaspis polita* Weise (Farhadi *et al.* 2017). Interestingly, for *T. notata*, there was a higher predation rate by 4th-instar larvae than adults, and this could be due to needs of food and energy uptake prior to pupation (Nedvěd & Honěk 2012).

Finally, we can conclude that larvae and adults of *T. notata* can be important predators of *F. dasyrilii* and *P. citri* since both predator and prey have been found in association in the field. This lady beetle can have a significant contribution on biological control of mealybugs in tropical areas where temperature ranges from 20 to 32 °C. In contrast, for non-adapted *T. notata* populations, there will be a negative impact on its potential establishment. Additionally, indigenous *T. notata* populations might survive and reproduce on lower and higher temperature than 20 and 32 °C, respectively, as found on *T. notata* populations from South of Brazil and on Colombian plains, but they need to acclimate to those temperatures for many generations in order to thrive. Therefore, further studies are under way to address this possibility and how it might affect biological control of mealybug.

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CONFLICT OF INTEREST

The authors declare 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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