Predatory Behavior and Life History of Tenuisvalvae notata (Coleoptera: Coccinellidae) Under Variable Prey Availability Conditions

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PREDATORY BEHAVIOR AND LIFE HISTORY OF *TENUISVALVAE NOTATA* (COLEOPTERA: COCCINELLIDAE) UNDER VARIABLE PREY AVAILABILITY CONDITIONS

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ABSTRACT

Prey availability for predaceous insects can be uncertain in row crop ecosystems, requiring predators to employ flexible reproductive strategies to maintain their populations. In this study, we examined life history parameters and predatory behavior of the ladybeetle, *Tenuisvalvae notata* (Mulsant) (Coleoptera: Coccinellidae) under different conditions of prey availability. Females of *T. notata* exhibited a type III functional response when preying upon neonate striped mealybug [*Ferrisia virgata* Cockerell (Hemiptera: Pseudococcidae)] nymphs and a type II response when preying upon third instars and female adults. On average, *T. notata* females consumed 157.9 neonate nymphs, 3.6 third-instar nymphs and 2.2 adult females of *F. virgata* per day. When subjected to a one-day period of prey deprivation, *T. notata* females exhibited significant reductions in reproduction and survivorship. After 150 days of exposure 47, 13 and 20% of females were alive when fed daily or subjected to repeated one- or 2-day periods of prey deprivation, respectively. Prey consumption increased as a function of prey availability. Daily oviposition was observed for females fed daily, but a sharp reduction in egg production was observed under conditions of prey scarcity. These findings show that *T. notata* exhibits a positive response to prey availability preying upon the striped mealybug *F. virgata*.

Key Words: coccidophagy, *Ferrisia virgata*, functional response, numerical response

RESUMEN

La disponibilidad de presas en ecosistemas anuales puede ser incierta para insectos depredadores. Requiriendo estos insectos ajustar sus estrategias reproductivas para mantener con éxito sus poblaciones. Por lo tanto, este estudio determinó las características de la historia de vida y el comportamiento depredador de la mariquita *Tenuisvalvae notata* (Mulsant) (Coccinellidae) en condiciones variables de disponibilidad de presas. Las hembras de *T. notata* exhibieron respuesta funcional de tipo III cuando depredaron ninfas neonatas de la cochinilla *Ferrisia virgata* Cockerell (Pseudococcidae) e respuesta del tipo II cuando depredaron ninfas del tercer instar y hembras adultas. En general, hembras de *T. notata* consumieron hasta 157.9 ninfas neonatas, 3.6 ninfas del tercer instar y 2.2 hembras adultas de *F. virgata* por día. Cuando las hembras de *T. notata* fueron sometidas a escasez de presas por intervalos de un día, presentaron reducción significativa en la reproducción y supervivencia. Después de 150 días de exposición a varias condiciones de disponibilidad de presa, tasas de supervivencia de 47%, 13%, y 20% fueron observadas en hembras alimentadas diariamente o que estuvieron sometidas a intervalos de escasez de presas de 1 ó 2 días, respectivamente. El incremento en el consumo estuvo en función de la disponibilidad de presas. Cuando las hembras fueron alimentadas diariamente, fue observada producción diaria de huevos. Mientras que en condiciones de escasez de presas, hubo una fuerte reducción en la reproducción. Estos resultados muestran que *T. notata* exhibe una respuesta significativa a la disponibilidad de presa, e indican su potencial como depredadora de *F. virgata*.

Palabras Clave: coccidofagia, *Ferrisia virgata*, respuesta funcional, respuesta numérica

Predators undergo changes in their life history traits as a function of prey availability, allowing them to sustain their populations in crop ecosystems under conditions of prey scarcity. Prey availability in crop ecosystems can be unpredictable because of natural population dynamics, pest management practices, competition with other prey species, and even the activities of natural enemies. According to Stearns (1992), predator species experiencing food scarcity face a trade-off, i.e., they must reduce reproductive effort and shift energy to somatic functions to ensure their survival. Although predators may exhibit a temporary reduction of egg production in response to prey scarcity, it has been hypothesized that predators should be able to survive in the crop ecosystem with minimum prey consumption until prey availability increases enough to sustain their reproduction (Torres et al. 2004). Thus, it is critical to understand the functional and numerical responses of a natural enemy to changes in prey availability in any biological control program.

The lady beetle, *Tenuisvalvae notata* (Mulsant) (= *Hyperaspis notata*) (Coleoptera: Coccinellidae), is a predator of mealybugs (Hemiptera: Pseudococcidae) (Dreyer et al. 1997a, 1997b). Native to South America, it was introduced into Africa in the 1980s to control the cassava mealybug, *Phenacoccus manihoti* Matille-Ferrero (Hemiptera: Pseudococcidae) (Herren & Neuenschwander 1991; Chakupurakal et al. 1994). Due to the importance of *T. notata* as a biological control agent, Dreyer et al. (1997a & b) studied its performance on different prey under various thermal conditions; however, parameters related to predation rate, survival and reproduction under conditions of prey abundance and scarcity were not investigated.

The striped mealybug, *Ferrisia virgata* Cockerell (Hemiptera: Pseudococcidae), is a polyphagous and cosmopolitan species that has been found on at least 80 families and 150 genera of cultivated plants and weeds (Anonymous 2004; Ben-Dov et al. 2013). *Ferrisia virgata* is considered one of the most important pests of cotton (*Gossypium* spp.; Malvales: Malvaceae) in Pakistan (Ghouri 1960), where it also damages other economically important plant species. In Brazil, this species has recently been observed damaging cotton (Silva-Torres et al. 2013).

Based on the predation and reproduction of a predator as a function of prey availability, Solomon (1949) introduced 2 important concepts that are still widely accepted: i) the functional response, which refers to prey consumption as a function of prey availability, and ii) the numerical response, which refers to the number of predators originating from prey consumption plus the number of predators attracted to the area of prey abundance. The application of these concepts became widely applied after the studies and revisions made by Holling (1961). The functional response is determined based on 2 parameters: handling time (T_h), which includes prey capture, subjugation and consumption, and the attack rate (a'), which represents the efficiency of searching for prey in a determined area (Hassell 1978; Casas et al. 1993; Aljetlawi et al. 2004). The numerical response is the number of predators that are added to the system by either reproduction or the attraction of immigrant predators according to prey availability. A simple predator-prey model might assume that the production of new predators is directly proportional to food consumption. The proportional constant of the predator response indicates the efficiency with which prey are converted into predator offspring (Torres et al. 2004). Therefore, prey consumption and reproduction of predators as a function of prey availability are important mechanistic data influencing the dynamics of predator-prey populations (Aljetlawi et al. 2004; Milonas et al. 2011).

Survivorship and reproduction of predators are often modelled by using the different prey densities and sizes to test the strength of the relationship between the prey and predator (Hodek & Honek 1996; Britto et al. 2009; Sabaghi et al. 2011). The effect of prey scarcity on predator performance is also meaningful (Oliveira et al. 2002). In crop ecosystems, especially in row crops such as cotton [*Gossypium hirsutum* L. (Malvales: Malvaceae)], soybean [*Glycine max* (L.) Merr. (Fabales: Fabaceae)], and cassava [*Manihot esculenta* Crantz (Malpighiales: Euphorbiaceae)], which are all hosts of *F. virgata*, predators likely face variable prey availability due to natural population dynamics and the effects of control methods. Thus, we hypothesize that *T. notata* under prey scarcity conditions is able to survive by reducing its egg production. Therefore, we investigated the reproduction, predation rate and survival rate of *T. notata* as a function of different levels of prey availability when *F. virgata* is the food source.

Materials and Methods

Environmental Conditions and Prey and Predator Species

The experiments were carried out in the Laboratory of Insect Behavior of the Universidade Federal Rural de Pernambuco (UFRPE) in Recife, Brazil at 25 ± 0.8 °C, 67 ± 8% RH and photoperiod of 12:12 h L:D. These physical conditions were maintained for insect rearing and all experiments, unless otherwise specified.

Adult *T. notata* were collected from cotton plants infested with the cotton mealybug *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae) in Furnas, Surubim County, Pernambuco

State, Brazil (S 07° 49' 59" W 35° 45' 17"). In the laboratory, *T. notata* were fed all life stages of *F. virgata* ad libitum. The coccinellid colony was maintained in transparent Plexiglas™ cages (30.0 × 20.0 × 40.0 cm) containing lateral openings of 10-cm diam and covered with a 2-mm nylon mesh to allow ventilation of the cages. Each rearing cage received one 'Jacarezinho' pumpkin [*Cucurbita* sp. (Cucurbitales: Cucurbitaceae)] weighing approximately 1 kg that was fully infested with *F. virgata* nymphs and adults. Each pumpkin was placed on folded paper towels on the bottom of the cage to catch excreted honeydew.

The *F. virgata* colony was initiated with insects collected from infested cotton plants growing in the experimental area of the Departamento de Agronomia of UFRPE. Infested leaves and plant terminals were collected and transferred to the laboratory, where they were placed on pumpkins held on plastic trays lined with paper towels. The colonies were maintained according to the methodology described by Sanches & Carvalho (2010) with some modifications. Before exposure to *F. virgata*, the pumpkins were washed with natural liquid soap and dried with paper towels. Adult infested pumpkins that were producing crawlers, i.e., first instars of *F. virgata*, were set on top of clean pumpkins in the same tray. The nymphs and adults used in the experiments were collected from the infested pumpkins as needed.

Functional Responses of *T. notata* Preying upon *F. virgata*

The predation rate of *T. notata* on *F. virgata* was assessed using different prey densities and developmental stages (2 nymphal stages and adult females). Neonate *F. virgata* were supplied at densities of 40, 80, 120, 140, 160, 200, and 240 per female predator, per day, in a 5.5-cm diam plastic Petri dish in 16, 14, 12, 10, 8, 6, and 6 replicates, respectively. Third-instar and adult female *F. virgata* were provided to adult *T. notata* at densities of 2, 4, 6, 8, and 10, and 1, 2, 4, 6, and 8, respectively, with 18, 16, 14, 12, and 10 replicates, respectively. These prey densities were selected based on preliminary observations to span a range of values both deficient and excessive relative to the mean daily predation rate. For example, at densities lower than 40, all neonate nymphs were completely consumed. Due to the time required to count the nymphs and correct for natural mortality, replicates were set up 24 h prior to the experiment and the number of nymphs per replicate double-checked immediately before they were offered to the beetles following morning. Due to the logistic demands of counting nymphs, the experiment was blocked in time, with 5 to 6 replicates per density performed each day.

The mealybugs were exposed to predation on infested cotton leaf discs (5.0-cm diam) offered in Petri dishes lined with filter paper disc moistened with distilled water. The appropriate life stage were then obtained from the stock colony and transferred to the cotton leaf discs with a paintbrush under a stereomicroscope at 10X magnification (SMZ-168, Motic™, São Paulo, SP, Brazil). The tops of the Petri dishes were covered with a perforated PVC film™ to allow gas exchange. The Petri dishes were left in the laboratory for 12 to 24 h to allow *F. virgata* to establish themselves on the leaf discs. During that time, 5- to 10-day-old *T. notata* females were randomly collected from the stock colony and maintained for 24 h without food to standardize hunger levels; water was made available on moistened cotton pads.

On the morning of the experiment, the number of live mealybugs established on each leaf disc was examined and their densities were adjusted as needed. Each ladybird beetle was weighed using a 0.001 g precision scale (FA-2104N, Bioprecisa™) and singly transferred to an arena containing prey. The Petri dishes were transferred to a growth chamber set to 25 ± 1 °C, 70% RH and a photoperiod of 12:12 h L:D for 24 h, and then the number of surviving prey in each replicate and the weight of each ladybird beetle were recorded.

The functional response was estimated in 2 steps based on the number of prey consumed (Na) as a function of the initial prey density (N0). In the first step, the general shape of the functional response curve, which is based on a logistic regression of the number of mealybugs consumed per density, was determined using the CATMOD procedure in SAS (SAS Institute 2002). The cubic model was initially tested because of its capacity to detect the most possible functional response types, and the sine of the linear coefficient of the equation obtained was used to determine the type of functional response, as described by Juliano (1993). The second step consisted of determining handling time (T_h) and attack rate (a') parameters which were estimated using nonlinear least square regression based on the proportion of prey eaten (Na/N0) as a function of initial prey densities (N0) (PROC NLIN, SAS Institute 2002). Comparisons of functional response parameters Th and a' determined for prey of different ages were performed using the 95% confidence interval mean overlapping procedure (Di Stefano 2005). In addition, the number of prey consumed by females and *T. notata* body weight gain as a function of prey availability were subjected to regression analysis using the REG procedure in SAS (SAS Institute 2002). The best fitted model was selected based on significance levels of the parameters ($P < 0.05$), a high adjusted coefficient of determination, and the *F*-value.

Survival and Reproduction of *Tenuisvalvae notata* Subjected to Prey Limitation

To investigate the survival and reproduction of *T. notata* as a function of prey availability, we evaluated 5 treatments based on different prey deprivation regimes: 0, 1, 2, 4, and 8 days. In regime "0", the predator was fed daily with 6 third-instar nymphs of *F. virgata*, and in the other regimes the predator was fed likewise except during the above-mentioned periods between feedings. A previous study showed that a density of 6 third-instar nymphs is adequate prey for a pair of *T. notata* during 24 h (Barbosa 2012). Thus, 5 treatments consisted of different feeding periods. Each treatment was replicated 15 times and each replicate consisted of an adult pair of 5-day-old *T. notata*.

Mealybugs were provided to the predators on cotton leaf discs as described above, but only third-instar mealybug nymphs were used as prey. For each replicate of each feeding period, the surviving prey were counted and recorded after 24 h of prey exposure. Egg production and prey consumption were evaluated under a stereomicroscope at 10X magnification. Female mortality was recorded daily. If the male of a pair died earlier than the female, it was replaced with a male of the same age to avoid any effect of mate deprivation on the reproduction and survival of the female.

The survival curves for females subjected to different prey deprivation intervals were determined using the Kaplan-Meier method (Klein & Moeschberger 2003), and prey deprivation intervals were compared using the Log-Rank test (PROC LIFETEST, SAS Institute 2002). Additionally, female fecundity was tracked for 150 d and subjected to analysis using the regression Wizard-Equation procedure in SigmaPlot® 10.0 for Windows. Vari-

ous nonlinear regression models were tested, and the best-fitted model was determined to be single exponential decay based on significance of parameters ($P < 0.05$), a high adjusted coefficient of determination and the largest F-value.

Food conversion based on prey consumption was calculated as the ratio of the total number of eggs produced to the total number of third-instar nymphs consumed per female predator across the feeding intervals. However, this estimate did not take into account the eggs that were produced during the first 3 days after the predator females had been subjected to the feeding intervals to minimize any influence of previous prey consumption. Thus, the number of eggs and egg masses and the food conversion for 147 days of observation were subjected to a Kolmogorov-D normality test and Bartlett's test for homogeneity of variance. The numbers of eggs produced per female were log (x+1) transformed to normalize the data and subjected to analysis of variance (ANOVA). Means were separated with Tukey's HSD test (α = 0.05; SAS Institute 2002).

RESULTS

Functional Response of *Tenuisvalvae notata* Preying upon *Ferrisia virgata*

Female *T. notata* preying upon neonate *F. virgata* (< 24 h old crawlers) exhibited a type III functional response with an average consumption of 157.89 nymphs per day (Table 1). In contrast, when *T. notata* females were offered older prey, i.e., third-instar nymphs and adult females of *F. virgata*, they exhibited a type II functional response, demonstrating that a longer time was required to handle and attack older prey, especially the adult females (Table 2).

TABLE 1. ESTIMATED PARAMETERS OF THE PROPORTIONS OF *FERRISIA VIRGATA* NYMPHS AND ADULTS CONSUMED BY ADULT *TENUISVALVAE NOTATA* FEMALES AT DIFFERENT PREY DENSITIES AND ACCORDING TO PREY AGE.

Prey	Parameter	Value (± SE)	Df	χ^2 value	P
Newly hatched nymphs	Intercept	-0.7263 ± 0.1305	1	30.99	< 0.0001
	Linear	0.0123 ± 0.0018	1	45.72	< 0.0001
	Quadratic	-0.00004 ± 0.0000059	1	44.11	< 0.0001
	Cubic	ns*	—	—	—
Third-instar nymphs	Intercept	2.5397 ± 0.3593	1	49.97	< 0.0001
	Linear	-0.3361 ± 0.0477	1	49.66	< 0.0001
	Quadratic	ns	—	—	—
	Cubic	ns	—	—	—
Adult females	Intercept	1.3155 ± 0.3390	1	15.06	< 0.0001
	Linear	-0.3278 ± 0.0607	1	29.19	< 0.0001
	Quadratic	ns	—	—	—
	Cubic	ns	—	—	—

*ns, stand for parameters lacking statistical significance requiring reduction to lower level equation models.

TABLE 2. VALUES (MEAN ± 95% CONFIDENCE INTERVALS) OF ATTACK RATE [A (H^{-1})] AND HANDLING TIME [T_H (H)] FOR *TENUISVALVAE NOTATA* FEMALES ATTACKING NEWLY HATCHED NYMPHS, THIRD-INSTAR NYMPHS OR ADULT FEMALES OF *FERRISIA VIRGATA* AND THE ESTIMATED NUMBER OF PREY KILLED PER DAY (T/T_H).

Prey	Attack rate	Handling time	T/T_h
Newly hatched nymphs	0.00048 ± 0.00012 b*	0.152 ± 0.033 c*	157.89
Third-instar nymphs	0.106 ± 0.075 a	6.63 ± 0.96 b	3.62
Adult females	0.130 ± 0.069 a	11.04 ± 2.66 a	2.17

*Means within a column followed by the same letter are not significantly different (pairwise comparisons through 95% confidence intervals).

Both handling time and the attack rate were reduced when *T. notata* preyed on neonate compared to third-instars or adult females (Table 2). The ratio between the exposure and handling time presents the potential number of prey consumed per day (T/T_h; Table 2). Therefore, *T. notata* females consumed up to 157.9 crawlers nymphs, 3.6 third-instar nymphs and 2.2 adult females of *F. virgata* per day.

Although there was an increase in the number of prey killed as a function of the density, weight gain was similar across all prey densities offered (females: 0.56 ± 0.02 mg; $F_{df = 4, 65}$ = 1.25, P = 0.3003, Fig. 1a; third-instar nymphs: 0.62 ± 0.09 mg; $F_{df = 4, 65}$ = 0.53, P = 0.7168; Fig. 1b). On the other hand, the weight gain was increased as function of prey availability stabilizing only at higher densities of crawlers ($F_{df = 6, 69}$ = 3.94, P = 0.0019) (Fig. 1c). Females needed to consume over 80 neonate nymphs to achieve a level of weight gain comparable to that attained when subjected to low densities of older *F. virgata* nymphs and adults (Fig. 1c).

Survival and Oviposition of *Tenuisvalvae notata* Subjected to Prey Scarcity

Over 40% of female *T. notata* fed daily survived more than 150 days; whereas females subjected to progressively longer periods of prey deprivation exhibited significantly shorter survivorships, especially those fed only every 4 or 8 days (Fig. 2). Thus, many females in the 8 day prey deprivation treatment did not survive to the second feeding (Fig. 2).

There was an abrupt reduction in female fecundity in response to increased periods of prey deprivation (Fig. 3). A one-day period of starvation was sufficient to cause a significant reduction in egg production (Table 3, Fig. 3). Females fed daily laid 6 times more eggs and 4 times more egg masses than those fed every other day. Thus, female beetles fed ad libitum converted more of the food they consumed into eggs than those fed on alternate days (Table 3).

At the end of 150 days of observation, the consumption of third-instars *F. virgata* was at least 2-fold greater for females fed daily than for those fed at 1-day or longer intervals, which characterized conditions of food scarcity. Females subjected to one-day periods of prey deprivation
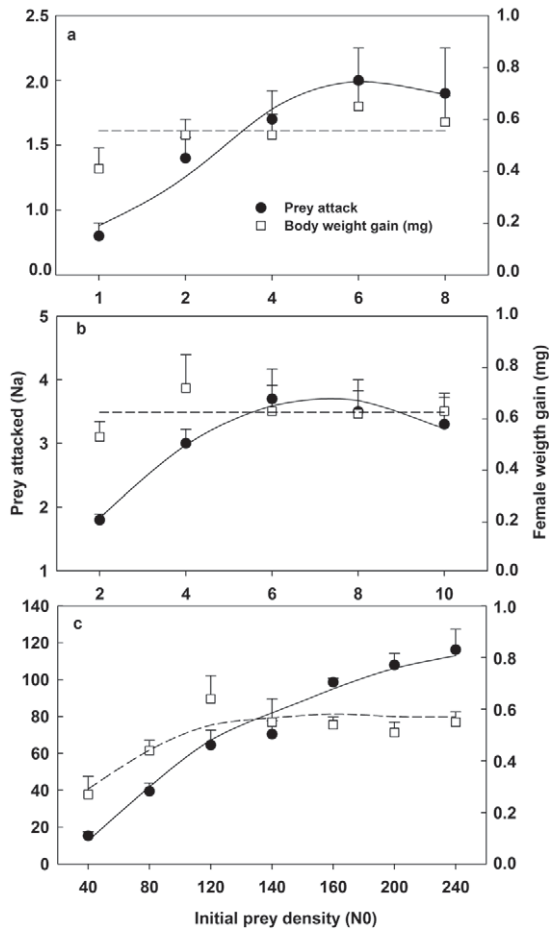

Fig. 1. Mean (± SE) number of prey attacked and body weight gain (solid and dashed lines) for *Tenuisvalvae notata* as a function of prey densities of adult females mealybug (a) [prey attacked, $y = 0.425 + 0.493x - 0.038x^2$, R^2 = 0.86, F = 27.09, P = 0.035; weight gain, y = mean = 0.556 mg], third-instar nymphs (b) [prey attacked, $y = 0.160 + 0.968x - 0.066x^2$, R^2 = 0.88, F = 44.82, P = 0.0212; weight gain, y = mean = 0.626 mg], and newly hatched nymphs (c) [prey attacked, $y = 20.122 + 0.871x - 0.0012x^2$, R^2 = 0,87, F = 81.52, P = 0.006; weight gain, $y = 0.088 + 0.0057x - 0.000016x^2$, R^2 = 0.77, F = 7.02, P =0.048] of *Ferrisia virgata*. Note: Different scales on the y-axis due to different predation rate according to prey age.
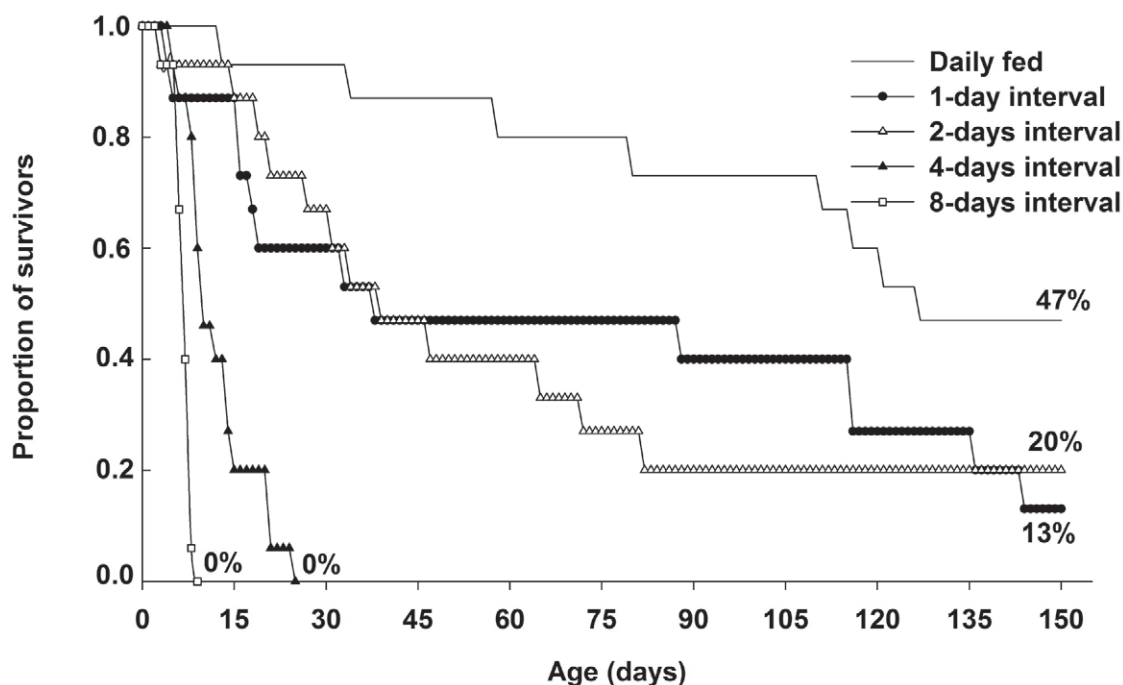
Fig. 2. Age-specific survivorship of *Tenuisvalvae notata* females over the 150 days following adult emergence preying upon *Ferrisia virgata* third-instar nymphs at different feeding intervals (Log-rank test: χ^2 = 84.40, *P*< 0.0001, df = 4).

consumed similar number of nymphs as did females fed at 2-day intervals, and these females exhibited greater consumption than did those fed at 4- or 8-day intervals (Table 3) ($F_{df = 4, 70}$ = 36.04, *P* < 0.0001). Because food conversion is assessed directly based on fecundity and prey consumption, the conversion of prey into eggs was superior for females fed daily ($F_{df = 4, 70}$ = 73.51, *P* < 0.0001). However, in this case, the food conversion calculation was also influenced by female survival. Because *T. notata* females exposed to prey scarcity lived for a certain period without laying eggs, the conversion also varied according to the prey deprivation period. For instance, females that were fed at 8-day intervals died earlier than others; inflating the conversion value for this group compared to that of females fed at intervals of 2 or 4 days, which lived longer and consumed more prey, but laid fewer eggs (Table 3, Fig. 3).

DISCUSSION

Fig. 3. Egg production of *Tenuisvalvae notata* females fed 6 third-instar nymphs of *Ferrisia virgata* at different intervals: daily (interval 0) or at 1-, 2-, 4-, or 8-day intervals over 150 days of evaluation.

Functional Response of *Tenuisvalvae notata* Preying upon *Ferrisia virgata*

Female *T. notata* preying on neonate nymphs exhibited a type III functional response, indicating that the predator can have a significant impact on this particular life stage. A type III functional response is characterized by a sigmoid curve, representing an initially rapid increase in the proportion of prey consumed as a function of prey availability that then decelerates. According to Beddington et al. (1976) and Hassell (1978), natural enemies exhibiting a type III functional response are able to regulate their prey population within a certain range of prey densities.

The difference in predation rate across prey age depicted in functional response models can
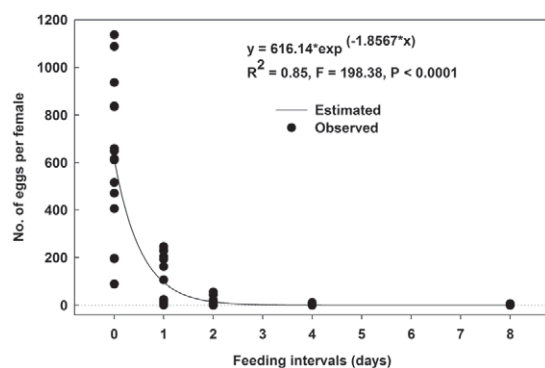
TABLE 3. MEAN VALUES OF LIFE HISTORY TRAITS FOR *TENUSIVALVAE NOTATA* FEMALES FED WITH THIRD-INSTAR NYMPHS OF *FERRISIA VIRGATA* AT DIFFERENT INTERVALS OVER 150 DAYS OF OBSERVATION. EACH FEEDING CONSISTED OF SIX THIRD-INSTAR *F. VIRGATA* NYMPHS.

Feeding intervals[a]	No. of eggs per female over 150 days	No. of egg masses per female over 150 days	Nymphs consumed per female/male pair over 150 days	Food conversion[b]
Daily	606.7 ± 81.52 a	101.8 ± 11.27 a	488.4 ± 54.07 a	1.23 ± 0.06 a
1 day	92.7 ± 25.87 b	25.5 ± 6.53 b	194.0 ± 42.72 b	0.31 ± 0.07 b
2 days	12.4 ± 4.19 b	7.0 ± 2.21 bc	114.3 ± 25.79 bc	0.09 ± 0.02 c
4 days	0.5 ± 0.19 b	0.4 ± 0.16 c	14.2 ± 1.52 c	0.03 ± 0.01 c
8 days	0.9 ± 0.38 b	0.4 ± 0.16 c	5.5 ± 0.19 c	0.18 ± 0.07 bc
Statistics	$F_{4,70}= 46.88, P< 0.0001$	$F_{4,70}= 52.97, P < 0.0001$	$F_{4,70}= 36.04, P < 0.0001$	$F_{4,70}= 73.51, P < 0.0001$

[a]Means within columns (± SE) followed by the same letters are not significantly different by Tukey's HSD test ($P > 0.05$).
[b]Number of eggs produced by one *T. notata* female for each third-instar nymph of *F. virgata* consumed.

be attributed to the fact that in older stages of *F. virgata* the body is covered with wax, which could make them more difficult to capture and thus less attractive to predators, although *T. notata* does capture and consume these older stages. Third-instar nymphs and adult female *F. virgata* made up 90% and 80% of prey at the lowest density, but only 33% and 24% of prey at the highest prey density. According to Atlihan et al. (2010), a predator exhibiting a type II functional response is more effective in regulating its prey population at lower densities than at high densities. This type of functional response has been detected in several ladybird beetles (Coleoptera: Coccinellidae), including *Harmonia axyridis* Pallas (Lee & Kang 2004), *Propylea dissecta* Mulsant, *Cheilomenes sexmaculata* Fabr. and *Coccinella transversalis* Fabr. (Omkar & Pervez 2004; Pervez & Omkar 2005), *Stethorus tridens* Gordon (Britto et al. 2009), *Adalia fasciatopunctata revelierei* Mulsant (Atlihan et al. 2010), *Hippodamia variegata* Goeze (Saleh et al. 2010), *Nephus includens* Kirsch (Milonas et al. 2011), and *Scymnus syriacus* Marseul (Sabaghi et al. 2011). In contrast, the consumption of neonate nymphs demonstrated a type III functional response, with 44% of the prey consumed at the lowest initial prey density, increasing to 61% of prey consumed at a density of 160 nymphs, and decreasing at the highest prey densities offered, 200 and 240 nymphs (Fig. 1c). Based on the assumptions of functional response models (Solomon 1957; Beddington et al. 1976; Hassell 1978), *T. notata* females should be best able to control *F. virgata* when 40 to 160 neonate nymphs are encountered per female, per day, with higher relative densities exceeding the ability of *T. notata* to control the population.

The size of both prey and predator affect the functional response because these factors affect the consumption rate and the attack rate, respectively, and are reflected in the resulting functional response (Aljetlawi et al. 2004). Similar results were reported by Milonas et al. (2011). These authors found a reduction in the attack rate and an increase in the handling time for the ladybird beetle *Nephus includens* Kirsch preying upon adult *Planococcus citri* Risso and *Planococcus ficus* Signoret mealybugs compared to second instar nymphs of these species.

Neonate *F. virgata* nymphs are small and wax-free, unlike older nymphs and adult females. Thus, newly hatched nymphs were easily handled and attacked by *T. notata*, consistent with the results observed for *Pentilia egena* Mulsant, which exhibited greater predation on earlier instars of *Chrysomphalus ficus* Ashmead (Bortoli et al. 2001). Greater predation on neonate nymphs than on other stages can be expected in the field because the predators can access large numbers of crawling nymphs as they leave female ovisacs. Therefore, concentration of prey in both space and time would likely stimulate predatory behavior and result in a type III functional response, as found in this study.

Handling time is another important parameter in the prey-predator interaction that allows assessment of predator efficacy by encompassing the behavioral steps of capturing, subduing and consuming a prey item, usually denoted as the number of prey killed (Veeravel & Baskaran 1997). Therefore, predators were able to ingest more food per unit time when preying upon older *F. virgata* nymphs or adult females because they are so much larger than first-instar nymphs, even though they consumed fewer of them. The pattern of weight gain for *T. notata* preying upon neonate nymphs at low densities is indicative of suboptimal nutrition (Torres et al. 2004), resulting in a stimulating of predation. This explains the type III functional response observed when *T. notata* prey upon first-instar nymphs of *F. virgata*, but not on older stages.

Survival and Oviposition of *Tenuisvalvae notata* Subjected to Prey Scarcity

Female *T. notata* deprived of food for 1- or 2-day intervals showed a significant reduction in reproductive output, and only 13% and 20% survivorship, respectively, after 150 days. These trends in reproduction and survival suggest that female *T. notata* trade-off energy expenditure between reproduction and survival under conditions of prey scarcity in favor of survival. As demonstrated by Michaud & Qureshi (2006) and Seagraves (2009), ladybird beetles must ingest food above some maintenance level to reproduce. Notably, female *T. notata* lived longer without reproducing under intermediate periods of prey deprivation (i.e., 2 and 4 days). Michaud & Qureshi (2006) and Seagraves (2009) concurred that the decision to reproduce is directly affected by the quantity and quality of available food. Therefore, our results suggest that *T. notata* drives large amounts of energy to reproduce, since females lay egg every day during their reproductive period. This outcome reinforces the strong potential of *T. notata* as a biocontrol agent of *F. virgata*, which typically becomes available in large numbers for a short period in a limited space (Silva-Torres et al. 2013). This mealybug species can produce up to 450 neonates within about 16 days of adulthood, but less than 10% reach the adult stage (Oliveira et al. 2014) and they exhibit a low capacity for dispersal (Silva-Torres et al. 2013), facilitating the predator response.

The way in which organisms allot energy to growth, storage, and reproduction under conditions of food scarcity can be crucial to their fitness (Stearns 1992). Our results demonstrate that a single day without prey constituted food scarcity with respect to reproduction by *T. notata* females, which survived at similar rates when fed at 1- or 2- day intervals but abruptly curtailed reproduction (Fig. 3). These results support the hypothesis that *T. notata* uses available energy to sustain metabolism when prey becomes scarce only allocating to reproduction energy obtained in excess of this threshold (Beddington et al. 1976; Hassell 1978).

Based on our results, we can conclude that *T. notata* has the potential to regulate a *F. virgata* population when these mealybugs are in an early developmental stages, but when prey are readily available, *T. notata* also consumes older nymphs and adults beyond the level necessary for survival and reproduction (Fig. 1a and 1b). We also described the response of *T. notata* to an extended period of prey scarcity, which is characterized by a significant reduction in reproduction but not in survival. This life history trade-off would favor the persistence of *T. notata* in areas of low prey infestation, such as during periods of initial mealybug colonization or following the application of control measures. Furthermore, the generation time of *F. virgata* is approximately 41 days when reared on cotton plants at 25 °C (Oliveira et al. 2014). In contrast, *T. notata* that were fed *F. virgata* third-instar nymphs under the same conditions can complete one generation in approximately 30 days (Barbosa 2012). These data indicate that the predator can increase numerically faster than its prey. It is also notable that 40% of *T. notata* fed *F. virgata* daily remained alive after 150 days of observation. In fact, *T. notata* can live for up to 60 weeks in the adult stage when reared on mealybugs at 25 °C (Dreyer et al. 1997b). Therefore, coupling the daily predation rate observed in this study with the behavior of daily oviposition plus the long lasting adult stage, *T. notata* is a potential agent for effective mealybug biological control.

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