



Efficacy of *Amblyseius largoensis* (Muma) as a biocontrol agent of the red palm mite *Raoiella indica* (Acari: Tenuipalpidae)

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Abstract The red palm mite, *Raoiella indica* Hirst (Acari: Tenuipalpidae), is a severe pest of coconut (*Cocos nucifera* L.), banana (*Musa* sp.), and some ornamental palms. The predatory mite *Amblyseius largoensis* Muma (Acari: Phytoseiidae) has been reported in association with *R. indica* in several countries. Here, we assessed the interaction effect between prey density and population structure on predation and fecundity of this phytoseiid species. Specifically, we estimated the predation capacity of nymphs and females of *A. largoensis* based on their functional and numerical responses when fed on eggs, immature stages (deutonymphs or protonymphs), and females of *R. indica*. Nymphs and females of *A. largoensis* presented type II functional responses to *R. indica*, except for nymphs of the predator when consuming immature stages of the pest that exhibited a type III functional

response. Nymphs and females of the predator showed a higher attack rate and shorter handling time when feeding on eggs of *R. indica* than on immatures and females. The highest oviposition rates of *A. largoensis* were observed when eggs and immatures of the pest were offered as prey. The results indicate that nymphs and females of *A. largoensis* may be effective in suppressing *R. indica* populations, mainly at lower prey densities.

Keywords Biological control · Numerical response · Immature stages · Phytoseiid

Introduction

The red palm mite, *Raoiella indica* Hirst (Acari: Tenuipalpidae), is a severe pest with high reproductive capacity, rapid dissemination, and the ability to adapt to new hosts. It was first described from India (Hirst 1924) and remained restricted to the Old World until it was detected in the Caribbean by Flechtmann and Etienne (2004). Subsequently, this pest mite has been reported in Puerto Rico (Rodrigues et al. 2007), Venezuela (Vásquez et al. 2008), Mexico (Nappo 2009), Colombia (Carrillo et al. 2011), Brazil (Navia et al. 2011), and the United States of America (USA) (Peña et al. 2012). In Brazil, *R. indica* has spread to all coconut production regions in less than 10 years (Navia et al. 2011; Rodrigues and Antony 2011; Oliveira et al. 2016; Hata et al. 2017; Melo et al. 2018).

The coconut tree, *Cocos nucifera* L. (Arecaceae), is a main host for the red palm mite, and yield losses can

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reach up to 70% in Trinidad and Tobago (Peña 2013). Coconut cultivation has great socioeconomic importance for Brazil, the fourth greatest producer in the world (FAO 2014), with a cultivation area of approximately 250 thousand hectares (IBGE 2017). In addition to coconut plantations, *R. indica* can also attack other Arecaceae as well as species of Heliconiaceae, Musaceae, and Zingiberaceae (Vásquez and Moraes 2012; Carrillo et al. 2012a).

Strategies ranging from chemical control (Ramos et al. 2011; Rodrigues and Peña 2012; Assis et al. 2012) over plant resistance (Rodrigues and Irish 2012) to biological control (Rodríguez et al. 2010; Carrillo et al. 2012b, 2014; Domingos et al. 2012) have been investigated. Regarding biological control, several studies have been carried out aiming at identifying natural enemies (Carrillo et al. 2012c; Hoy 2012; Taylor et al. 2012; Domingos et al. 2012). Predatory mites of the family Phytoseiidae are common natural enemies of phytophagous mites (McMurtry et al. 2013), and some species have been found in association with *R. indica* (Taylor et al. 2012). *Amblyseius largoensis* Muma (Acari: Phytoseiidae) is a type III generalist predator, predominantly found in coconut palm leaflets around the world (McMurtry and De Moraes 1984; Demite et al. 2014), which, in addition to feeding on phytophagous mites and other arthropods, also feeds on pollen and sugary substances such as nectar (McMurtry and Croft 1997; Lawson-Balagbo et al. 2008; Melo et al. 2015). This species has been reported in association with *R. indica* in coconut plantations in several countries, including Brazil (Roda et al. 2008; Carrillo et al. 2011; Bowman and Hoy 2012; Rodríguez et al. 2010; Taylor et al. 2012; Gondim Jr et al. 2012). Several studies on *A. largoensis* against the red palm mite have been conducted, and the results indicate its potential as a biological agent of *R. indica*, prey preference, and plasticity in response to this pest (Carrillo et al. 2010, 2012b, 2014; Carrillo and Peña 2012; Domingos et al. 2012; Morais et al. 2016); however, there is limited information on the interaction between prey density, population structure, and fecundity of this predator.

Functional and numerical response studies are useful in assessing the potential of biological control agents (Holling 1959; Holling 1961; Costa et al. 2017). The functional response describes the predation rate as a function of prey density, and the numerical response describes changes in the predator's abundance due to changes in prey density (Solomon 1949; Holling 1959).

The functional response of a predator may vary depending on the stage of development of its prey and its own development stage (Santos 1975; Reis et al. 2000; Carrillo and Peña 2012; Costa et al. 2014). In this context, the objective of the present study is to assess the type of functional response of nymphs and females of *A. largoensis* fed on different developmental stages of *R. indica*, as well as its numerical response to this pest.

Materials and methods

Rearing of *A. largoensis*

The colony of *A. largoensis* was started with individuals collected from leaflets of a coconut plantation located in the city of Aracaju (10° 56' 46"S; 37° 03' 12"W), Sergipe State, Brazil, in March 2017. Individuals were identified using taxonomic keys, and voucher specimens were deposited in the mite collection of Maranhão State University, São Luís, Brazil. The mites were mass-reared in arenas made of pieces of PVC (23 cm long × 4 cm wide) placed on a polyurethane foam (24 × 5 × 3.0 cm), surrounded by a layer of hydrophilic cotton moistened with distilled water, and placed in a plastic tray saturated with distilled water. Cotton threads underneath a glass slide (18 × 18 mm) were placed on the arenas to serve as shelter and oviposition site (Oliveira et al. 2017). The predatory mites were fed castor bean pollen, *Ricinus communis* L. (Euphorbiaceae), all stages of *R. indica* and, 10% honey, and these sources were replenished every 2 days.

Population of *R. indica*

To obtain eggs, females of *R. indica* were collected from unsprayed coconut leaflets in the same plantation as described above, let to oviposit for 3 days on coconut leaflets placed on moistened polyurethane foam with distilled water, and inserted into open plastic tubes (52 cm long × 5.5 cm diameter). The tubes were kept in glass pots with distilled water up to the height of the foam to maintain the turgidity of the leaflet. Likewise, leaflets of coconut with protochrysalis, deutochrysalis, and teliochrysalis (quiescent stages) of *R. indica* were collected and maintained as mentioned above until the emergence of protonymphs, deutonymphs (immature stages) and adult females, respectively. The active stages were used in the bioassays up to 48 h after the

emergence. Larvae were not used due to their minute size (similar to eggs) and because they are very easy to wound and therefore difficult to handle. Unsexed protonymphs or deutonymphs were used due to the difficulty to separate immature males from females (Kane et al. 2012).

Functional and numerical responses

All experiments were conducted at standardized conditions (27 ± 3 °C temperature, $70 \pm 10\%$ relative humidity, and 12 h photoperiod). The arenas were made of PVC disks (6 cm diameter) placed on a polyurethane foam (6 cm diameter \times 0.33 cm depth) saturated with distilled water inside a plastic container (6.2 cm diameter \times 5 cm depth). A barrier of cotton wool soaked in water was placed around the edge of the PVC disk to prevent the predatory mites from escaping (Oliveira et al. 2017).

Functional response experiments were conducted separately for nymphs and females of *A. largoensis* and for each stage of *R. indica*. In each experiment, a nymph (deutonymph) (4–5 days old) or an adult female (8–10 days old) of *A. largoensis* was transferred to an arena with increasing densities (5, 10, 20, 30, 40, 60, 80, and 100) of eggs, immature stages (protonymph or deutonymphs), or females of *R. indica*. We carried out 10 replicates for each density of *R. indica* stages. The numbers of eggs, immatures, and females of *R. indica* consumed by nymphs of the predatory mite were recorded after 24 h, without prey replacement during the experiment. For females of the predator, in addition to evaluating the functional response within 24 h as for nymphs, their numerical response was recorded for 48 h with prey replenishment at the end of the first day. Oviposition data from the first day were excluded to minimize the effects of previous diets (Carrillo and Peña 2012).

Statistical analyses

The functional response curve type was determined by logistic regression of the proportion of prey consumed as a function of prey density, using the CATMOD procedure in the SAS statistical software (SAS Institute 2008), to determine the significance of the regression coefficients and the sign of the linear coefficient. Initially, the cubic model was tested because of its ability to capture all possible variations in functional response. The data were adjusted to the polynomial function to determine the functional response (Juliano 2001):

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}$$

Where (N_e) is the number of attacked mites and (N_0) is the offered density, P_0 , P_1 , P_2 , and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, related to the slope of the curve. The signs P_1 and P_2 are used to determine the type of functional response. When the linear term is not significantly different from zero, it indicates a type I functional response. When the linear coefficient is significantly negative ($P_1 < 0$), the predator displays a type II functional response, which indicates that the proportion of prey consumed declines monotonically with the initial prey density. When the linear coefficient is significantly positive ($P_1 > 0$) and the quadratic coefficient is negative ($P_2 < 0$), the predator presents a type III functional response, which indicates a positively density-dependent proportion of prey consumed (Juliano 2001).

As the experiments were conducted without prey replacement during the functional response experiment, we used the random predator equation (Juliano 2001; Rogers 1972) as a description of the functional responses of types II and III.

$$N_e = N_0 \{1 - \exp[\alpha(T_h N_e - T)]\}$$

$$N_e = N_0 \left\{ 1 - \exp \left[\left(d + b N_0 \right) \left(T_h N_e - T \right) / (1 + c N_0) \right] \right\}$$

where N_e = number of prey attacked, T = exposure time (24 h), N_0 = initial prey density, α = attack rate, a constant rate of successful search, and T_h = handling time. The consumption peak was estimated based on the reciprocal of $-Th \left(\frac{1}{Th} \right)$ and compared based on confidence intervals. Subsequently, T_h (handling time) and α (attack rate) parameters of the functional response were estimated using the nonlinear least square regression PROC NLIN procedure in SAS (SAS 2008), as described in Juliano (2001).

The oviposition rate of *A. largoensis* as a function of *R. indica* density was analyzed via regression analysis between the number of eggs and the density of prey offered, using the PROC REG of the SAS program (SAS 2008). Consumption among the densities and at the highest prey density (100) for nymphs and females of *A. largoensis* was compared using ANOVA, followed by Tukey's test at 5% of probability.

Results

Nymphs of *A. largoensis* presented a type II functional response to eggs and *R. indica* females, as indicated by the negative and significant linear coefficient ($P < 0.0001$). This contrasts with a sigmoid increase in consumption when *R. indica* immatures were offered as prey to *A. largoensis* nymphs, characterizing a type III functional response as also indicated by the positive and significant linear coefficient ($P < 0.0193$). Females of *A. largoensis* presented a type II functional response to all stages of *R. indica* (Table 1).

The number of *R. indica* preys consumed by nymphs of *A. largoensis* varied. When the prey consisted of eggs and immatures, the increase was up until the densities 20 and 60, respectively, after which it stabilized with an average consumption of 21.3 ± 2.77 (eggs) and $17.93 + 5.46$ (immatures), contrasting with a low consumption when adults females were offered as prey 5.01 ± 0.87 , except for the densities 40 and 100, which increased average consumption to 9.0 ± 1.55 (Fig. 1a). For *A. largoensis* females, average consumption varied with prey stage and density. The consumption stabilized after the density of 30 for eggs (27.52 ± 1.67) and adult females (11.07 ± 0.92) preys. However, at a density of 80 of these stages, an increase in consumption for eggs (36.7 ± 9.67) and adult females (15.6 ± 3.02) was found. For immatures, consumption stabilized until the density of 60 (23.2 ± 1.04) (Fig. 1b). For the highest prey

density (100), nymphs of the predator consumed more eggs and immatures of *R. indica* than females of the prey ($F_{2,25} = 14,59$; $P < 0.0001$) (Fig. 2a). Also, females of *A. largoensis* consumed more eggs than immatures and females ($F_{2,27} = 33,71$; $P < 0.0001$) (Fig. 2b).

The proportion of eggs and adults of *R. indica* consumed by nymphs of *A. largoensis* decreased with increasing prey density. However, when nymphs of the predator fed on immatures of the pest, the proportion of prey consumed increased with density, peaking at 30 (Fig. 3a). On the other hand, the consumed proportion of all the stages of prey by females of the predatory mite decreased with increasing prey density (Fig. 3b).

There were no significant differences in the attack rate (α) of nymphs and females of the predator to eggs, immatures, and females of *R. indica* (except for a lower α of nymphs preying on immatures stages of the pest). Lower handling times (Th) and higher consumption peaks ($1/Th$) were found for nymphs of the predator preying on eggs and immatures when compared with females of *R. indica*. Females of *A. largoensis* presented the shortest handling time and the highest consumption peak when fed with eggs compared to immatures and adult females of the pest (Table 2).

Oviposition of *A. largoensis* females increased linearly with prey density for all developmental stages of *R. indica*. When *R. indica* eggs were offered as prey ($Y = 0.793 + 0.014x$; $P = 0.011$;

Table 1 Estimated parameters of the logistic regression of the proportion of eggs, immatures and females of *Raoiella indica* consumed by nymphs and adult females of *Amblyseius largoensis*

Prey stage	Parameter	<i>A. largoensis</i> nymphs				Type FR	<i>A. largoensis</i> females				
		Estimate	SD	χ^2	<i>p</i>		Estimate	SD	χ^2	<i>P</i>	Type FR
Eggs	Intercept (P_0)	6.1318	0.6619	85.82	<.0001	II	8.8956	0.8824	101.63	<.0001	II
	Linear (P_1)	-0.2320	0.0367	39.92	<.0001		-0.3783	0.0464	66.49	<.0001	
	Quadratic (P_2)	0.00245	0.000619	15.71	<.0001		0.00533	0.000748	50.69	<.0001	
	Cubic (P_3)	-8.53E-6	3.215E-6	7.04	0.0080		-0.00003	3.759E-6	45.07	<.0001	
immatures	Intercept (P_0)	-0.9326	0.1899	24.13	<.0001	III	1.6547	0.1565	111.75	<.0001	II
	Linear (P_1)	0.0302	0.0129	5.48	0.0193		-0.0417	0.00439	90.38	<.0001	
	Quadratic (P_2)	-0.00077	0.000252	9.23	0.0024		0.00089	0.000400	5.02	0.0251	
	Cubic (P_3)	4.218E-6	1.452E-6	8.43	0.0037		1.327E-6	3.798E-7	12.20	0.0005	
Females	Intercept (P_0)	1.2996	0.2748	22.37	<.0001	II	2.6155	0.3138	69.47	<.0001	II
	Linear (P_1)	-0.1207	0.0200	36.37	<.0001		-0.1619	0.0209	60.20	<.0001	
	Quadratic (P_2)	0.00145	0.000407	12.63	0.0004		0.00225	0.000401	31.45	<.0001	
	Cubic (P_3)	-5.88E-6	2.407E-6	5.96	0.0146		-0.00001	2.295E-6	22.50	<.0001	

Negative and positive linear terms in boldface indicating types II and III functional response respectively

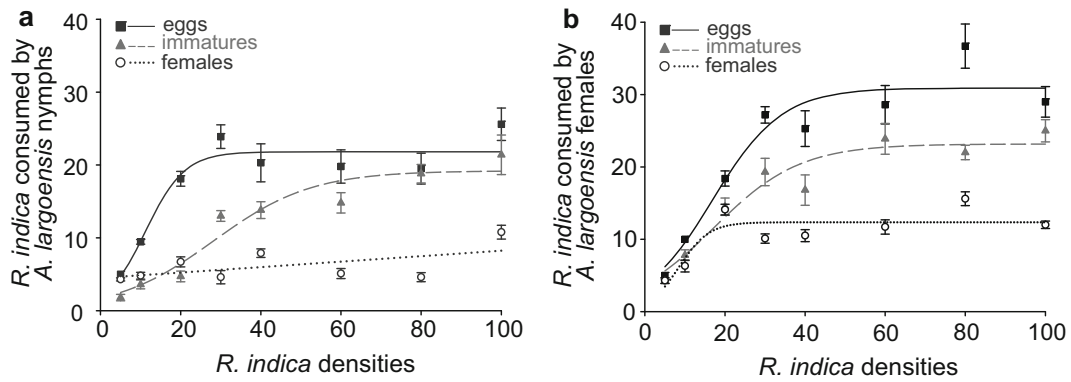


Fig. 1 Mean (\pm SE) numbers of eggs, immatures and females of *Raoiella indica* consumed by nymphs (a) and females (b) of *Amblyseius largoensis* as a function of prey density

$R^2 = 0.682$), the maximum oviposition rate of *A. largoensis* was 2.10 ± 0.31 eggs/female/day at a density of 80. With immatures as prey ($Y = 0.459 + 0.001x$; $P = 0.008$; $R^2 = 0.713$), oviposition peaked at a density of 30 (2.00 ± 0.33 eggs/female/day). When fed with *R. indica* females ($Y = 0.869 + 0.103x$; $P = 0.023$; $R^2 = 0.602$), the maximum oviposition rate was 1.70 ± 0.22 eggs/female/day at a density of 100 (Fig. 4).

Discussion

Our results show that nymphs of *A. largoensis* presented either type II or III functional responses, depending on the *R. indica* developmental stage.

However, females of this predator showed a type II functional response irrespective of prey stage. In type II functional responses, the number of prey consumed increases with prey supply until the satiation of the predator; however, the proportion of consumed prey decreases with prey density, tending to stabilize. This contrasts with a sigmoid increase in prey consumption for type III functional responses (Holling 1959). Natural enemies with the ability to regulate pests in the range where the proportion of deaths increases with density are regarded as efficient (Pervez and Omkar 2005). However, predators with a decreasing consumption at high densities can also be efficient at low prey densities.

Amblyseius largoensis also exhibited type II functional responses to the mites *Polyphagotarsonemus*

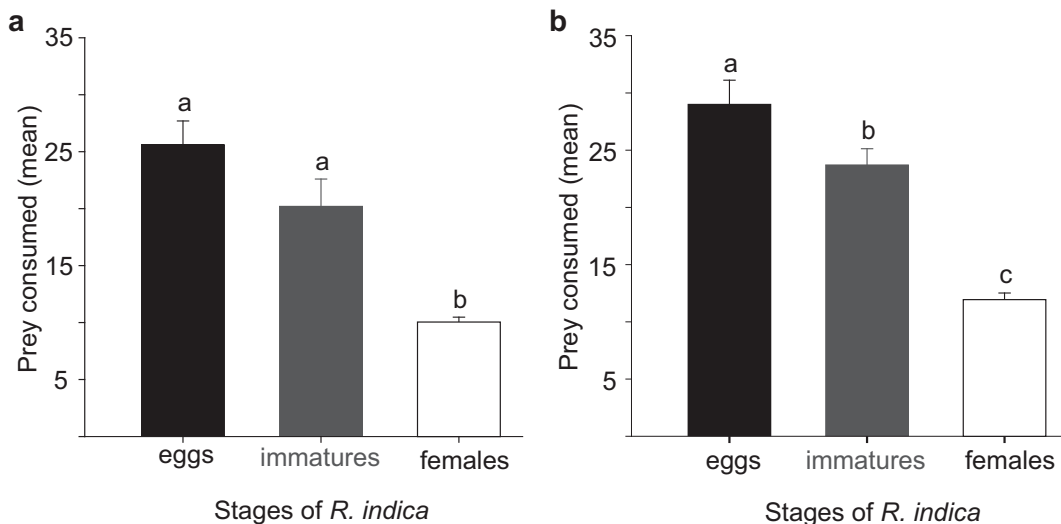


Fig. 2 Mean (\pm SE) numbers of eggs, immatures and females of *Raoiella indica* consumed by nymphs (a) and females (b) of *Amblyseius largoensis* at 100 prey density. Different letters indicate significant differences by the Tukey test ($P < 0.05$)

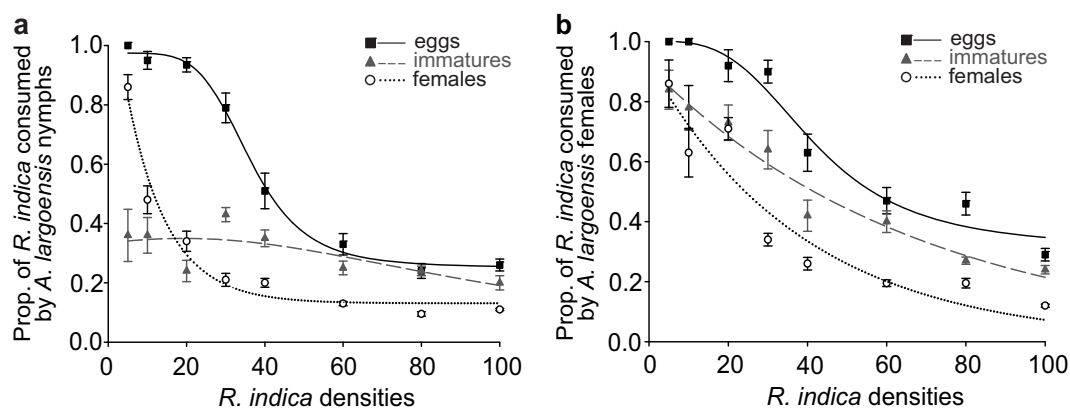


Fig. 3 Proportion of eggs, immatures and females of *Raoiella indica* consumed (mean \pm SE) by nymphs (a) and females (b) of *Amblyseius largoensis* as a function of prey density

latus (Banks) (Acari: Tarsonemidae) (Morell et al. 2010), *Oligonychus punicae* (Hirst) (Acari: Tetranychidae) (Sandness and McMurtry 1970) and to eggs of *R. indica* (Carrillo and Peña 2012). In line with our results, nymphs of *Euseius concordis* (Chant) (Acari: Phytoseiidae) also presented different functional responses when preying on eggs, immatures, and females of the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae). Nymphs of the predator exhibited a type III response when preying on eggs and females and a type II functional response when feeding on immatures of *M. tanajoa* (Costa et al. 2014). The functional response of a predator may vary depending on several factors, including its own stage of development and that of its prey (Santos 1975; Reis et al. 2000; Carrillo and Peña 2012). This could be explained by the fact that predators in early stages consume less and prefer small preys due to difficulties in handling larger preys, while the opposite pattern

occurs for adult predators. Other factors, such as the origin of the population of *A. largoensis* may also influence its potential as a biological control agent of *R. indica* (Gómez-Moya et al. 2018).

Nymphs and females of *A. largoensis* consumed more eggs than the other developmental stages of *R. indica*, most likely because of the preference of this predatory mite for eggs (Carrillo et al. 2012b; Carrillo and Peña 2012). Similar results have been observed for first and second instars of the lacewing *Ceraeochrysa caligata* (Banks) (Neuroptera: Chrysopidae), which consumed more eggs and immatures than females of *R. indica* (Viteri Jumbo et al. 2019). The consumption behavior found here may stem from the fact that early stages, such as eggs and immatures, have a lower biomass than adults of *R. indica*, leading predators to consume more eggs to obtain adequate nutrient amounts and satiety. As eggs of *R. indica* last approximately 9 days, longer than other developmental stages

Table 2 Estimates mean \pm SE and confidence intervals (CI) for the parameters attack rate (a'), handling time (T_h) and consumption peak ($1/T_h$) of nymphs and adult females of *Amblyseius largoensis* preying on eggs, immatures and females of *Raoiella indica* for 24 h

<i>A. largoensis</i>	Prey stage	$a' \pm SE$	95% CI		$T_h \pm SE$	95% CI		$1/T_h$	95% CI	
			Lower	Upper		Lower	Upper		Lower	Upper
Nymphs	Eggs	0.0089 \pm 0.0013a	0.0062	0.0115	1.0585 \pm 0.0496 a	0.9597	1.1573	0.94 a	0.86	1.05
	immatures	0.0014 \pm 0.0002 b	0.0008	0.0019	1.2190 \pm 0.0678 a	1.0841	1.3540	0.82 a	0.74	0.92
	Females	0.0068 \pm 0.0017a	0.0033	0.0102	2.9337 \pm 0.1240 b	2.6869	3.1805	0.34 b	0.31	0.37
Females	Eggs	0.0095 \pm 0.0028a	0.0028	0.0152	0.7400 \pm 0.0314 a	0.6774	0.8026	1.35 a	1.25	1.49
	immatures	0.0076 \pm 0.0021a	0.0033	0.0119	1.0499 \pm 0.0423 b	0.9657	1.1341	0.96 b	0.88	1.04
	Females	0.0090 \pm 0.0022a	0.0046	0.0134	1.9055 \pm 0.0750 c	1.7563	2.0547	0.52 c	0.50	0.58

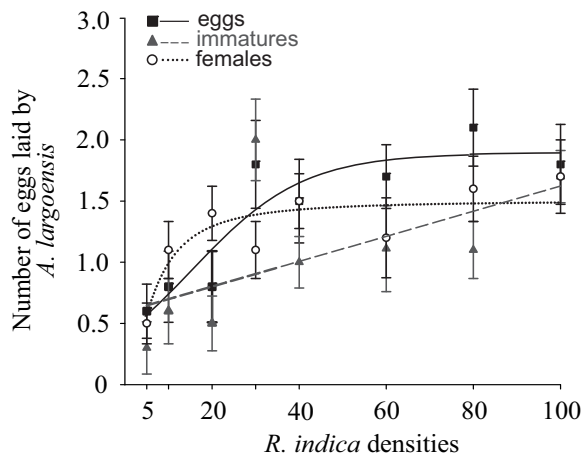


Fig. 4 Daily number of eggs laid (mean ± SE) by a female of *Amblyseius largoensis* feeding on increasing densities of eggs, immatures and adult females of *Raoiella indica*

(Nageshachandra and Channabasavanna 1984), they are available to predators for a long period. From an applied point of view, a high consumption of eggs is desirable for preventing pest population build-up.

The attack rate and the handling time are parameters used to determine the magnitude of the functional response (Pervez and Omkar 2005). Handling time includes the period required for the predator to identify, capture, attack, and consume prey and is therefore indirectly proportional to prey consumption (Holling 1959). The longest handling times and lowest consumption peaks were observed when nymphs and females of *A. largoensis* consumed females of *R. indica*. The reduced consumption of *R. indica* females by *A. largoensis* may be related to the greater size and mobility of the adult females compared with other stages of the prey (Costa et al. 2017). Since eggs are immobile and immatures present a reduced antipredator behavior, they may have been easier to handle compared to *R. indica* females (Ganjisaffar and Perring 2015). Carrillo et al. (2012b) observed that females of *A. largoensis* penetrate the chorion and imbibe all of the egg content in only one attack. In contrast, females probed several times in order to penetrate the larval cuticle of *R. indica*, which led to a longer handling time. In addition, other defense mechanisms, such as the possible existence of allomones on females of *R. indica*, may further protect against predators.

According to Sabelis and Janssen (1994), phytoseiid predation matches oviposition, as they allocate a major fraction of food ingested to egg production. The

oviposition peak of *A. largoensis* females was higher when the predator consumed eggs and immatures of *R. indica* in comparison with females. This pattern paired with the consumption behavior of *A. largoensis* emphasizing the suitability of this predator in controlling mainly eggs and immatures of *R. indica*. Overall, our results suggest that nymphs and females of *A. largoensis* could be effective biological control agents of the red palm mite, mainly at initial infestation.

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Compliance with ethical standards

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

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