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Age-specific functional response of *Nephus arcuatus* (Col.: Coccinellidae), predator of *Nipaecoccus viridis* (Hem.: Pseudococcidae)

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Abstract

This study has evaluated the age-specific functional response of the females of *Nephus arcuatus* Kapur, as the major predator of *Nipaecoccus viridis* (Newstead). The varying density of *N. viridis* eggs (2, 4, 8, 15, 40, 65, 90, and 115) were offered to 3 to 33 days of the lifespan of the female adults under laboratory conditions (30 ± 1 °C, 65 ± 5% RH and a photoperiod of 14L: 10D h). The age of female adults affected functional responses, its parameters (handling time (T_h) and attack rates (a)), and predation rate by *N. arcuatus*. Females exhibited functional response type III during 16th, 24th and 28th days of their life. Conversely, the functional response during the other 30 days of female life changed from functional response type III to type II. The handling time decreased significantly from the 4th to 17th day as female age increases and then increased, whereas, the attack rates did not significantly change with higher age of the predator. The maximum attack rate values were found on the 12th, 14th, 15th, 17th, 18th, 20th and 25th days of female adults. The maximum mean predation rate was 156.6 eggs on the 17th and 18th days. Accordingly, the best time to use females of this predator in an inundative biocontrol agent is during the first 25 days of females' age, when the predator is more capable to attack the prey, especially when *N. viridis* is in the egg stage.

Keywords: Biological control, behavioral response, handling time, attack rate

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Introduction

The spherical mealybug, *Nipaecoccus viridis* (Newstead) (Hem.: Pseudococcidae) is a polyphagous pest, that feeds on many ornamental and horticultural plants throughout the tropical and subtropical regions and vast areas of Asia, Africa, North America, Oceania (CABI/EPPO, 2020) as well as the south and southwest of Iran (Asadeh and Mossadegh, 1983; Moghadam, 2013). An effective defensive behavior of mealybugs to protect themselves against insecticides is secreting waxy coating on their eggs and body which hides and protects them from insecticides (Gullan and Kosztarab, 1997). Thus, a safe and effective control of mealybugs is biological control with predators and parasitoids (Messelink et al., 2016; Chowdhury et al., 2015; Joodaki et al., 2018).

The coccidophagous coccinellid, *Nephus arcuatus* Kapur (Coleoptera: Coccinellidae) is an effective predator of mealybugs in afrotropical and Palearctic regions. This predator has been reported in Tago (Raimundo et al., 2008), Yemen, Syria (Kovar, 2007), Saudi Arabia (Ramindo and van Harten, 2000), United Arab Emirates (Raimundo et al., 2008) and Iran (Alizadeh et al., 2013; Mossadegh et al., 2015).

Over the warm southern regions of Iran, including Khuzestan province, various aspects including biological potential, life table parameters, optimal temperature of the activities, prey preferences, and the feeding behavior of *N. arcuatus*, as a newly recognized predator of *N. viridis*, have been studied (Zarghami et al., a, b and c 2014; Zarghami et al., 2016). Field observations show its important role in the suppression of mealybugs' population on field crops and citrus orchards (Alizadeh et al., 2013; Mossadegh et al., 2012; Mossadegh et al., 2015). However, more studies are needed to incorporate this predator into integrated pest management programs.

One of the most comprehensive diagnostic tests for understanding the predator-prey interaction is to investigate the functional response, which often correlates with the bio-control efficacy and the way a predator responds to the changing density of its prey (Holling, 1959; Farhadi et al., 2010; Bayoumy, 2011). Hence, we can evaluate the predator's performance and capability in the biological control programs (Murdoch and Oaten, 1975; Pervez and Omkar, 2005). Functional response is defined as the number of preys consumed per predator, as a function of prey density (Solomon, 1949; Holling, 1966). The functional response is generally classified into three shapes (types), named as linear (type I), non-linear with saturation (type II), and with sigmoid patterns (type III) (Holling, 1959). Two factors are important in determining the type of the functional response: the handling time, and the attack rate (Holling, 1965; Hassell, 1978). The coefficient of attack rate is the proportion of the predation rate to prey density, and the handling time could be used to estimate the satiation threshold (Pervez and Omkar, 2005). In many cases, the type of the functional response and its parameters are affected by different factors, such as the host plant (Cedola et al., 2001; Mahdian et al., 2007), temperature (Icsikber, 2005; Jalali et al., 2010), and the prey's age, size (Hassell et al., 1977; Rudolf, 2008; Milonas et al., 2011) and species (Hoddle, 2003; Sarmento et al., 2007), as well as the predator's characteristics, such as gender (Ding-Xu et al., 2007; Sahayara et al., 2015), age (Mukerji and LeRoux, 1969; Ding-Xu et al., 2007) and stage (Koch et al., 2003; Farhadi et al., 2010; Bayoumy, 2011; Zarghami et al., 2016). Studies on predation capacity of a predator and predatory-prey interaction during predator lifetime provides information how can promote its usage in biocontrol programs. Zarghami et al. (2014c) found a type III functional response of *N. arcuatus* feeding on *N. viridis* in 24h; however, this time is too short to evaluate its potential against this pest. Thus, the optimum age of *N.arcuatus* and the prey time on *N. viridis*, as well as the maximum attack rate and the lowest handling time can help develop efficient programs.

The object of this study is to evaluate the impact of age on the functional response, attack rate, and handling time of the female *N. arcuatus*. The results of this study could lead to a better understanding of the potential of *N. arcuatus* to suppress *N. viridis* population in citrus orchards in a biological control program.

Material and Methods

Stock culture

Nipaecoccus viridis mealybugs were collected from unsprayed orange trees, in an orchard in Dezful (48º30′ E, 32º20′ N), Khuzestan province, southwestern Iran, in the spring of 2013. They were then mass-reared on fresh potato sprouts, *Solanum tuberosum* L., in plastic rearing boxes (24×16× 10 cm) that were completely covered by a mesh net. *N. arcuatus* adults were collected from the same orchard and reared on sprouted potatoes infested with *N. viridis* for two generations before being used in the tests. The stock colonies of both *N. arcuatus* and *N. viridis* were kept in an incubator at 30±1ºC, 65±5% RH, and 14L: 10D photoperiod.

Functional response assessments

The age specific functional response of adult female of *N. arcuatus* to different densities of *N. viridis* eggs has been investigated during 3 to 33 days of the lifespan of the adult female. The adult females of *N. arcuatus* at the same age were kept in a stock colony of *N. viridis* and then used in the experiments. Before the experiment, individual females of *N. arcuatus* (3days old) were maintained without prey for 12h in a micro tube container (1.5 ml) in order to standardize their hunger level. Hence, each female was kept into a plastic container (9×7×3 cm) with different densities of the eggs of *N. viridis* as a kind of prey. Egg is the preferred developmental stage of *N. arcuatus*, as a prey (Zarghami et al., 2014c). Each container had a 20-mm diameter hole in the center of the lid, which was covered with a piece of fine muslin to make ventilation. The number of *N. viridis* eggs evaluated were 2, 4, 8, 15, 40, 65, 90 and 115. After 12h, each starved female was transferred to new prey density and the number of eggs consumed was recorded. The prey densities were substituted every day throughout 36 days of the female life. Each treatment (prey densities) was repeated 10 times. Each treatment was continued until the end of the experiment, although females in low densities (2, 4, and 6) showed a high mortality rate due to hunger. Experimental conditions were based on the optimal temperature for *N. arcuatus* activities and were 30 ± 1°C, 65 ± 5% RH, and a 14 L: 10 D photoperiod (Zarghami et al., 2014a).

Statistical analysis

The functional responses of *N. arcuatus* were evaluated in two processes (Juliano, 2001). Firstly, the shape of the functional response was indicated by evaluating the data equipped with the types I, II or III of functional response, using a polynomial logistic regression of the proportion of the prey eaten (N_a/N_0) as formula below:

$$\frac{N_a}{N_0} = \frac{\exp\left(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3\right)}{1 + \exp\left(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3\right)} \quad (1)$$

Where N_a is the number of preys eaten, N_0 is the initial prey density presented, and P_0, P_1, P_2, and P_3 are constant, linear, quadratic and cubic factors related to the slope of the curve. The mentioned parameters were predicted using the CATMOD procedure in SAS software (Juliano, 2001; SAS Institute Inc. 2003). The data sets for adult females of *N. arcuatus* were fitted individually with equation 1 and the types of functional response were tested by examining the signs of P_1 and P_2. If P_1 was positive and P_2 was negative, a type III functional response was indicated. However, if P_1 was negative the functional response was a type II (Juliano, 2001).

Secondly, a nonlinear least squares regression (PROC NLIN; SAS Institute Inc. 2003) has been used to predict the functional response parameters (T_h, and either a for type II functional response or b, c, and d for type III functional response) using Rogers` random predator equation 2, which is the most suitable type II functional response in states with prey reduction (Rogers, 1972); if this model failed to provide a good description of the data ($a$, $b$ or $T_h$ be negative), Holling`s disc equation 3 was employed instead (Madadi et al., 2011; Moayeri et al., 2013):

$$N_a = N_0\{1 - \exp[a(T_h N_0 - T)]\} \quad (2)$$

$$N_a = \frac{a T_h N_0}{1 + a T_h N_0} \quad (3)$$

Where T is the fine total time that predator and prey are exposed to each other (24h); a is the attack rate; and T_h is the handling time in hours (Trexler et al., 1988; Juliano, 2001).

For modeling the type III functional response, attack rate (a) in equation 2 has been substituted in equation 3 as a function of prey density (Hassell, 1978; Pervez and Omkar, 2005). As the generalized simple form, attack rate (Equation 4) is a function of the initial number of preys:

$$a = (d + bN_0)/(1 + cN_0) \quad (4)$$

Where *b*, *c* and *d* are constants that must be estimated. The simplest form arises when *a* is a function of initial density, as in equation 5:

$$N_a = N_0\{1 - \exp[(d + bN_0)(T_h N_a - T)(1 - cN_0)]\} \quad (5)$$

If the results of the nonlinear least square regression indicated that parameters *c* and *d* did not show a significant difference from 0 (not shown), they were to be removed from the model, and a reduced model could be used as follows (Juliano, 2001):

$$a = bN_0 \quad (6)$$

Differences in the estimates of the attack rates (type II) and the handling times (type II and type III) in relation to predator age were fitted to nonlinear regressions using Sigmaplot 12. Also, discrepancies in the estimates of the constant *b* (type III) have been analyzed with an indicator variable as follows (Juliano, 2001):

$$N_a = \frac{\exp[b + D_b(j)]N_0^2 T}{1 + \exp[b + D_b(j)]N_0^2\left[T_h + D_{T_h}(j)\right]} \quad (7)$$

Where *j* is an indicator variable, respectively equal to 0 and 1 for the first and second data sets. For a type III response (equation 7), the parameters D_b estimates the different values of parameter *b* between the data sets and indicates the discrepancies (D_b) of *b* in different stages (Juliano, 2001). If the parameter D_b is significantly different from zero, then *b* for the two data sets is different. The maximum predation rate (T/T_h), which represents the maximum number of prey that can be consumed by one predator during 24h (Hassell, 2000), has been calculated using the estimated T_h.

Results

The relationship between the consumption of the mean number of prey with specific densities, and the age of the female *N. arcuatus* during 33 days of predator life in the three dimensional plot indicated that with higher age, the number of prey consumed tended to increase from the 4th day and reached to a threshold value in the 17th day, and then declined with age (Figure 1). For example, the mean number of preys consumed with a density of 115 individuals was estimated 62.9±6.01, 61.9±6.80, 80.5±9.05, 58.2±7.64, 54±5.33, and 40.2±4.48 prey in 4th, 10th, 17th, 20th, 26th, and 36th day of the female lifetime, respectively.

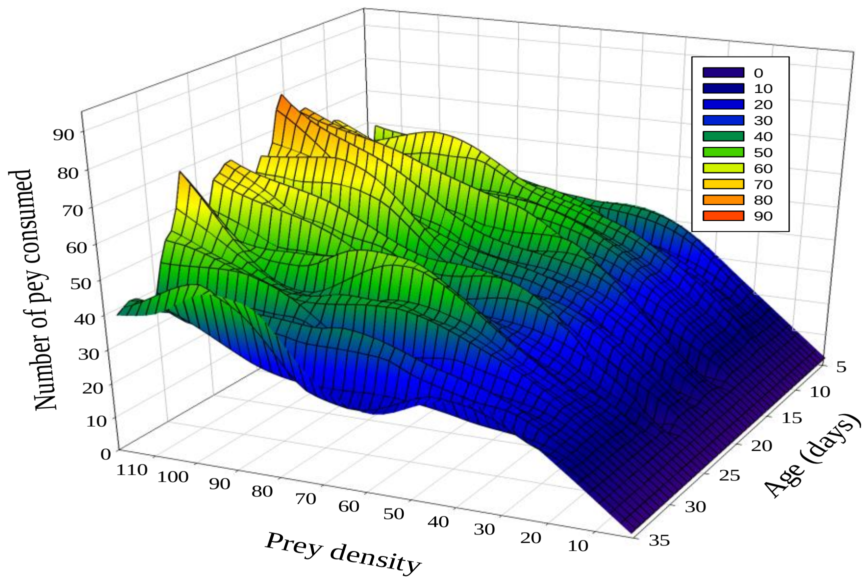

Figure 1. The three dimensional plot showing the effect of the age of *N. arcuatus* and *N. viridis* density on mean number of prey consumed.

Table 1. Results of logistic regression analysis of the proportion of *N. viridis* eggs consumed by adult female of *N. arcuatus* as a function of initial prey density at different age of life.

Age	Param.	Estim.	SE	X^2	P	Age	Param.	Estim.	SE	X^2	P	Age	Param.	Estim.	SE	X^2	P
4	Linear	-0.2811	0.0694	16.41	<.0001	**15**	Linear	-0.1440	0.0404	12.69	0.0004	**26**	Linear	-0.1123	0.0345	10.57	0.0011
	Quadratic	0.00252	0.000896	7.89	0.0050		Quadratic	0.00154	0.000569	7.29	0.0069		Quadratic	0.000701	0.000488	2.06	0.1514
5	Linear	-0.7372	0.1289	32.73	<.0001	**16**	Linear	0.0562	0.0178	10.01	0.0016	**27**	Linear	-0.1128	0.0315	12.82	0.0003
	Quadratic	0.00799	0.00154	26.87	<.0001		Quadratic	-0.00152	0.000300	25.67	<.0001		Quadratic	0.000964	0.000454	4.50	0.0338
6	Linear	-0.6118	0.0889	47.36	<.0001	**17**	Linear	-0.2308	0.0651	12.59	0.0004	**28**	Linear	0.0584	0.0274	4.55	0.0329
	Quadratic	0.00695	0.00111	38.90	<.0001		Quadratic	0.00221	0.000855	6.69	0.0097		Quadratic	-0.00224	0.000424	27.73	<.0001
7	Linear	-0.3296	0.0555	35.31	<.0001	**18**	Linear	-0.2787	0.0618	20.37	<.0001	**29**	Linear	-0.1610	0.0460	12.25	0.0005
	Quadratic	0.00371	0.000744	24.78	<.0001		Quadratic	0.00273	0.000814	11.24	0.0008		Quadratic	0.00123	0.000631	3.81	0.0510
8	Linear	-0.1468	0.0457	10.32	0.0013	**19**	Linear	-0.5773	0.0859	45.14	<.0001	**30**	Linear	-0.1646	0.0504	10.65	0.0011
	Quadratic	0.00109	0.000619	3.12	0.0773		Quadratic	0.00673	0.00109	38.24	<.0001		Quadratic	0.00131	0.000684	3.67	0.0554
9	Linear	-0.1791	0.0423	17.93	<.0001	**20**	Linear	-0.0645	0.0203	10.09	0.0015	**31**	Linear	-0.4881	0.0703	48.15	<.0001
	Quadratic	0.00192	0.000582	10.89	0.0010		Quadratic	0.000654	0.000324	4.06	0.0439		Quadratic	0.00617	0.000939	43.20	<.0001
10	Linear	-0.2018	0.0449	20.18	<.0001	**21**	Linear	-0.3783	0.0659	32.95	<.0001	**32**	Linear	-0.2408	0.0410	34.53	<.0001
	Quadratic	0.00236	0.000617	14.63	0.0001		Quadratic	0.00419	0.000864	23.53	<.0001		Quadratic	0.00272	0.000570	22.67	<.0001
11	Linear	-0.2121	0.0755	7.90	0.0050	**22**	Linear	-0.2548	0.0719	12.54	0.0004	**33**	Linear	-0.1773	0.0362	23.91	<.0001
	Quadratic	0.00155	0.000964	2.58	0.1080		Quadratic	0.00192	0.000923	4.35	0.0371		Quadratic	0.00187	0.000513	13.35	0.0003
12	Linear	-0.2291	0.0843	7.38	0.0066	**23**	Linear	-0.3386	0.0763	19.70	<.0001	**34**	Linear	-0.2882	0.0427	45.51	<.0001
	Quadratic	0.00173	0.00106	2.64	0.1043		Quadratic	0.00372	0.000993	14.03	0.0002		Quadratic	0.00331	0.000593	31.15	<.0001
13	Linear	-0.4626	0.1061	19.01	<.0001	**24**	Linear	0.0899	0.0160	31.46	<.0001	35	Linear	-0.8897	0.0790	126.69	<.0001
	Quadratic	0.00474	0.00131	13.17	0.0003		Quadratic	-0.00208	0.000279	55.58	<.0001		Quadratic	0.0117	0.00105	123.60	<.0001
14	Linear	-0.3290	0.0693	22.55	<.0001	**25**	Linear	-0.3551	0.0628	32.00	<.0001	**36**	Linear	-0.2404	0.0365	43.47	<.0001
	Quadratic	0.00338	0.000901	14.05	0.0002		Quadratic	0.00421	0.000836	25.39	<.0001		Quadratic	0.00271	0.000515	27.67	<.0001

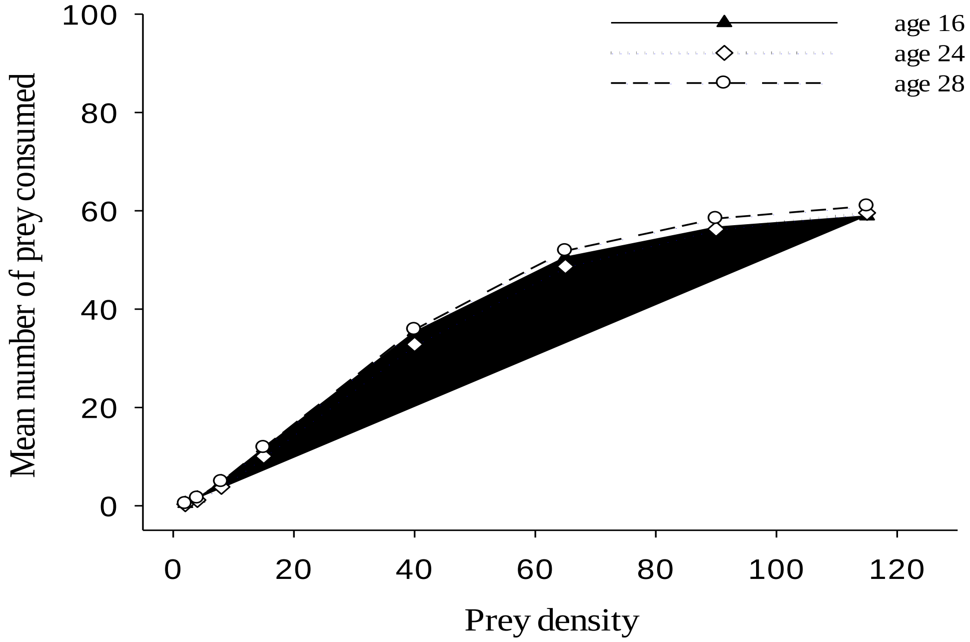

Figure 2. Type III age specific functional responses at the age of 16, 24 and 28 day old of *N. arcuatus* female to densities of *N. viridis* eggs. Symbols are observed data and lines were predicted by model.

The logistic regression analysis of the proportion of *N. viridis* eggs consumed (N_a) by female adult of *N. arcuatus* against the number of prey (N_a/N_0) indicates that the type of functional responses was affected by *N. arcuatus* female age. Females exhibited a functional response type III during 16th, 24th, and 28th days of their lifetime.

The linear coefficient was positive (P_1>0) and the quadratic coefficient was negative (P_2<0) (Table 1), meaning that the density of females is directly proportional to the prey consumed (Figure 2). Conversely, the negative sign of the linear coefficient for the other 30 days of female life time reveals that the functional response changed from type III to type II during these days. Thus, the proportion of prey consumed declines monotonically with larger proposed initial number of prey (Figure 3).

The functional response parameters of female adult of *N. arcuatus* at the ages of 5th, 7th, 9th, 12th, 20th, 32th, 33th, 34th, and 35th could be described by Holling's disc equation (Equation 3), whereas the remaining parts of females life were described by Rogers` random predator equation 2 (Table 2).

Table 2 indicates the estimates of attack rates (a) and handling times for type II and type III functional responses model of *N. arcuatus* female. In the days that *N. arcuatus* female showed a functional response of type III, the relationships between the attack rate and the initial number of prey was linear (a=bN_0), and the ranges of the rates of successful attacks (a) were from 0.0104 to 0.598 h^{-1}, from 0.00732 to 0.4209 h^{-1}, and from 0.01066 to 0.61295 h^{-1} for 16th, 24th, and 28th days of adult females lifetime.

Regression analysis of attack rates of *N. arcuatus* female at different female ages (Figure 4b) and the asymptotic 95% confidence interval for D_b (Table 3) show no clear trend and no significant difference in attack rates (F=0.857; df=3,26; P=0.476) and for constant b. However, the handling time (T_h) decreases significantly from 4th to17th as females age increased and is then raised (F=8.873; df=3, 29; P=0.002) (Fig. 4b, Table 2). The lowest handling times were observed during 17th, 18th, and 20th day of female life, with 0.1490 h, 0.1579 h, and 0.1511 h, respectively; and the highest were observed when females were older (0.4789 h, 0.4089 h, and 0.5360 h in 32th, 34th, and 36th day of female life, respectively).The Maximum attack rate (T/T_h) values were found during the 12th, 14th, 15th, 17th, 18th, 20th, and 25th days of female life (Table 2). The value of the coefficient of determination (r^2=1- residual sum of squares/corrected total sum of squares) indicated that Rogers` random predator equations (Equations 2 and 4) and Holling`s disc equation (Equation 3) adequately described the functional responses of female age of *N. arcuatus* (see values for R^2, Table 2).

Discussion

Over the recent years, using *N. arcuatus* in controlling mealybugs has been given more attention. For the first time, Mossadegh et al. (2012) and Alizadeh et al. (2013) reported it as the most effective predator of *Phenacoccus solenopsis* Tinsley, and *Maconellicoccus hirsutus* Green respectively, because of its large populations and improved periods of activity, particularly during Jun, July and August. Zarghami et al. (2014a) reported it as the most efficient predator of *N. viridis* in citrus orchards and noted that *N. arcuatus* could develop at a broad range of temperatures (20-35 ^{0}C), with the best temperature of 30 ^{0}C. Moreover, Forouzan et al. (2016) reported that 35^{0}C is the optimal temperature for growth and reproduction of *N. arcuatus* when feeding on *P. solenopsis*. It indicated that it could thrive and develop in warm environmental conditions. Further research showed that *N. arcuatus* also has high predation rate on *Planococcus citri* Risso, and found that when this predator was introduced with two prey species (*N. viridis* and *P. citri*), other factors such as prey stage, prey size and previous unique feeding experience had no impact on its prey selection behavior (Zarghami et al., 2014b). In other research, Zarghami et al. (2014c) investigated some behavioral response of *N. arcuatus* to *N. viridis* as prey, and reported that adult female of *N. arcuatus* showed a type III functional response and their numerical response was exponentially related to prey density in 24h. Joodaki and Zandi (2017) investigated the mutual interference of *N. arcuatus* feeding on *P. solenopsis* during 12h. They reported that as the density of *N. arcuatus* in the patch increased the searching efficiency (area of discovery) of predator due to negative effect of mutual interference is lowered (dependent density). Thus, each adult female of *N. arcuatus* spends less time searching prey and more time interacting with other conspecifics and handling prey which caused a reduction in predation rate. However, the whole duration of research is too short (12h, 24h) to arrive at a sensible conclusion on its predation response.

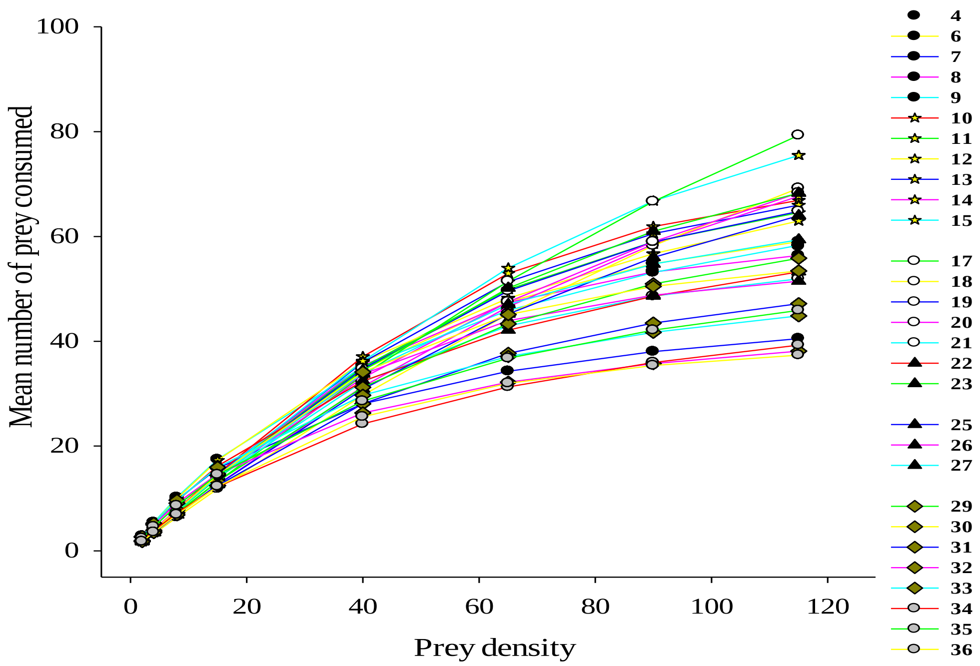

Figure 3. Type II age specific functional responses at different age of *N. arcuatus* female to densities of *N. viridis* eggs. Symbols are observed data and lines were predicted by model.

Table 2. Parameters estimated by the random predator equation(2) or disc equation(3) as well as R^2 and maximum predation rate (T/T_h) for the female adults of *N. arcuatus* fed on *N. viridis* eggs at different stage of life.

Age	Model	Type	Param.	Estim.	SE	CI 95% Lower	CI 95% Upper	T/T_h	R^2	Age	Model	Type	Param.	Estim.	SE	CI 95% Lower	CI 95% Upper	T/T_h	R^2
4	Rogers	II	a	0.1309	0.0483	0.0347	0.2270	74.89	0.89	**21**	Rogers	II	a	0.1411	0.0694	0.00296	0.2791	61.13	0.84
			T_h	0.3205	0.0503	0.2204	0.4207						T_h	0.3802	0.0631	0.2545	0.5059		
5	Holling	II	a	0.0647	0.00958	0.0456	0.0838	75.83	0.93	**22**	Rogers	II	a	0.0562	0.0120	0.0323	0.0801	81.08	0.84
			T_h	0.3165	0.0323	0.2521	0.3808						T_h	0.2960	0.0509	0.1947	0.3973		
6	Rogers	II	a	0.1585	0.0465	0.0661	0.2510	72.77	0.95	**23**	Rogers	II	a	0.1280	0.0446	0.0393	0.2167	74.98	0.92
			T_h	0.3298	0.0338	0.2624	0.3971						T_h	0.2484	0.0481	0.1526	0.3442		
7	Holling	II	a	0.0622	0.0137	0.0349	0.0896	53.03	0.84	**24**	Rogers	III	b	0.00366	0.00142	0.000835	0.00648	62.26	0.86
			T_h	0.4526	0.0552	0.3427	0.5624						T_h	0.3735	0.0297	0.3145	0.4326		
8	Rogers	II	a	0.1937	0.0913	0.0118	0.3755	65.95	0.90	**25**	Rogers	II	a	0.0875	0.0229	0.0418	0.1332	104.44	0.93
			T_h	0.3639	0.0459	0.2725	0.4553						T_h	0.2298	0.0500	0.1301	0.3295		
9	Holling	II	a	0.0600	0.0110	0.0381	0.0820	90.02	0.88	**26**	Rogers	II	a	0.1773	0.0772	0.0236	0.3311	104.44	0.93
			T_h	0.2666	0.0406	0.1858	0.3474						T_h	0.4013	0.0454	0.3109	0.4918		
10	Rogers	II	a	0.1997	0.0736	0.0532	0.3461	81.90	0.94	**27**	Rogers	II	a	0.1429	0.0558	0.0317	0.2541	75.31	0.90
			T_h	0.2934	0.0348	0.2241	0.3627						T_h	0.3187	0.0484	0.2222	0.4152		
11	Rogers	II	a	0.1507	0.0699	0.0115	0.2898	83.50	0.87	**28**	Rogers	III	b	0.00533	0.00264	0.000062	0.0106	64.28	0.86
			T_h	0.2871	0.0561	0.1754	0.3987						T_h	0.3734	0.0275	0.3186	0.4281		
12	Holling	II	a	0.0575	0.00945	0.0386	0.0763	104.39	0.90	**29**	Rogers	II	a	0.1085	0.0468	0.0153	0.2018	74.98	0.86
			T_h	0.2299	0.0365	0.1571	0.3026						T_h	0.3201	0.0653	0.1898	0.4504		
13	Rogers	II	a	0.1686	0.0555	0.0581	0.2790	83.65	0.94	**30**	Rogers	II	a	0.1758	0.0812	0.0140	0.3377	62.73	0.91
			T_h	0.2869	0.0361	0.2151	0.3588						T_h	0.3826	0.0464	0.2902	0.4751		
14	Rogers	II	a	0.0871	0.0282	0.0309	0.1433	117.71	0.89	**31**	Rogers	II	a	0.0922	0.0365	0.0194	0.1650	62.10	0.85
			T_h	0.2039	0.0637	0.0772	0.3306						T_h	0.3871	0.0694	0.2487	0.5255		
15	Rogers	II	a	0.1481	0.0566	0.0354	0.2609	107.87	0.92	**32**	Holling	II	a	0.0578	0.0116	0.0346	0.0809	50.11	0.87
			T_h	0.2225	0.0482	0.1265	0.3185						T_h	0.4789	0.0529	0.3734	0.5843		
16	Rogers	III	b	0.00520	0.00214	0.000947	0.00946	62.03	0.89	**33**	Holling	II	a	0.0597	0.0116	0.0366	0.0828	61.67	0.88
			T_h	0.3869	0.0256	0.3359	0.4379						T_h	0.3892	0.0468	0.2959	0.4826		
17	Rogers	II	a	0.0960	0.0334	0.0296	0.1625	161.07	0.90	**34**	Holling	II	a	0.0430	0.00997	0.0231	0.0629	58.69	0.82
			T_h	0.1490	0.0665	0.0166	0.2814						T_h	0.4089	0.0714	0.2664	0.5513		
18	Rogers	II	a	0.0705	0.0208	0.0290	0.1119	152.10	0.89	**35**	Holling	II	a	0.0515	0.0130	0.0256	0.0773	67.84	0.79
			T_h	0.1579	0.0704	0.0178	0.2980						T_h	0.3538	0.0654	0.2234	0.4842		
19	Rogers	II	a	0.143	0.0427	0.0583	0.2285	85.33	9.94	**36**	Rogers	II	a	0.0992	0.0474	0.00466	0.1936	44.78	0.79
			T_h	0.2812	0.0376	0.2062	0.3561						T_h	0.5360	0.0828	0.3710	0.7011		
20	Holling	II	a	0.0435	0.00687	0.0298	0.0571	158.84	0.90										
			T_h	0.1511	0.0420	0.0676	0.2347												

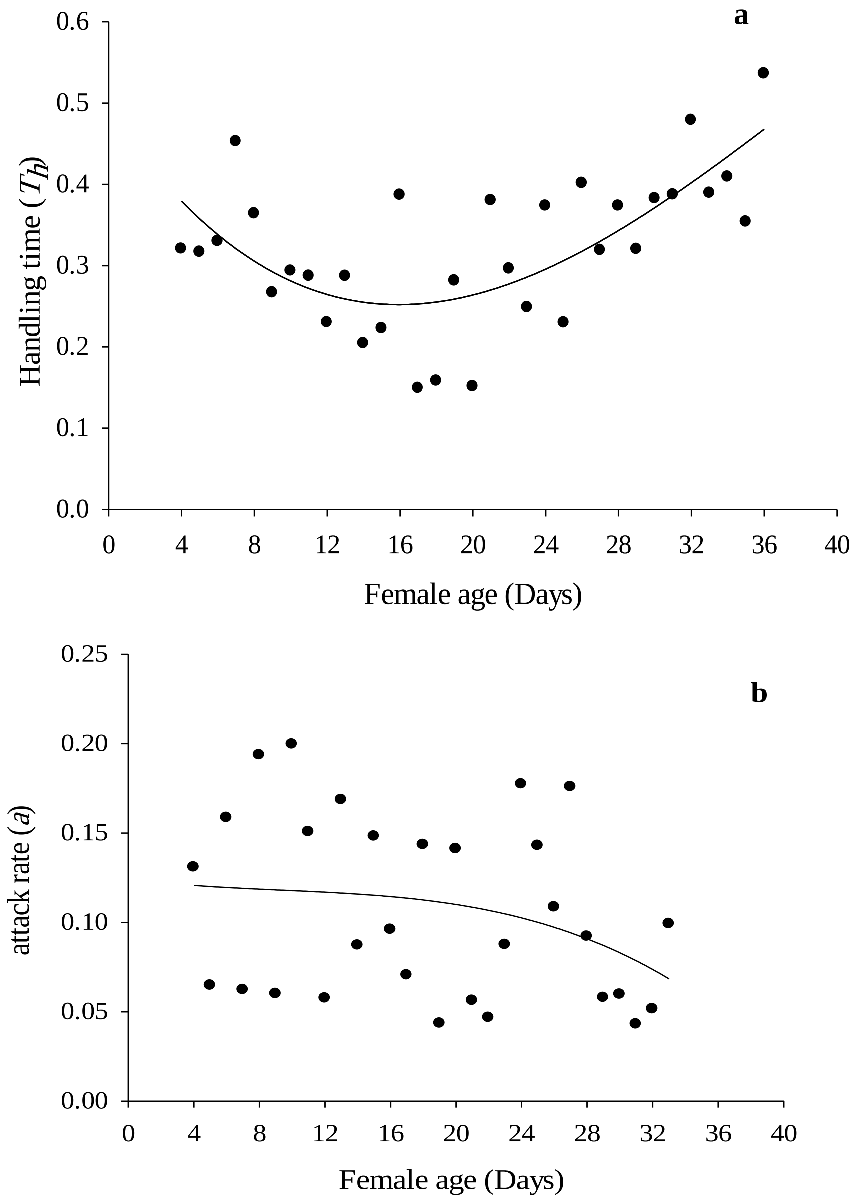

Figure 4. Regression trends showing handling times (a) and attack rates (b) for the different female ages estimated from fitting the type II responses model. Symbols are observed data and lines were predicted by model.

This is the first study to assess the age specific functional response of *N. arcuatus* feeding on *N. viridis*. We found that the age of the female predator can modify predator-prey interactions via effects on the predator's foraging behavior, i.e., the functional response and its parameters (attack rate and handling time). Similarly, Ding-Xu et al. (2007) found that the type of the functional response of *Scolothrips takahashii* Priesner to *Tetranychus viennensis* Zacher differs according to the gender and age of the adult predatory thrips. Females of various ages exhibited Type-II functional responses, but type-I functional responses has been determined for males, with the age of 12 days or more. Nikbin et al. (2014) reported a type III functional response for the one-day-old females of hymenopterous parasitoid *Trichogramma brassicae* Bezdenko on *Ephestia kuehniella* Zell eggs and a type II for two- to nine-day-old ones. However, Asadi et al. (2012) found that functional response of *Psyllaephagus zdeneki* Noyes & Fallahzadeh parasiting *Euphyllura pakistanica* Loginova was not correlated with parasitoid age (showing type II).

The most common functional response for coccinellids is type II which has been found in many studies, such as larvae and adults of *N. ryuguus* feeding on *O. acuta* (Li et al., 2005), larvae of *Propylea dissecta* Mulsant feeding on *Aphis gossypii* Glover (Omkar and Pervez 2004), all four larval instars and adults of *Hippodamia variegate* Goeze feeding on *Aphis fabae* Scolpoli (Farhadi et al., 2010), 2nd and 4th instar larvae of *N. includes* feeding on *Planococcus ficus* (Signoret) and *P. citri* (Milonas et al., 2011), 4th instar larvae and adults of *Hyperaspis polita* Weise feeding on adult female of *P. solenopsis* (Nakhaei et al., 2017), and 4th instar larvae and adults female of *H.polita* feeding on 1st instar, 2nd instar, 3rd instar, and adult female of *P. solenopsis* (Seyfollahi et al., 2018). In contrast, unlike type II functional response, the type III appears to be rare among coccinellids, such as adults of *Cycloneda sanguine* L. feeding on *Aphis gossypii* Glover at 25^0C (Icsikber, 2005), adults of *Eriopis connexa* Germar feeding on *Macrosiphum euphorbiae* Thomas (Sarmento et al., 2007), 4th instar larvae and adults female of *N. includes* feeding on *A.gossypii* (Bayoumy, 2011), adult male of *H.polita* feeding on egg of *N. viridis* (Farhadi et al., 2017), and adult female of *H.polita* feeding on 1st instar nymph of *P. solenopsis*, which has also been reported for *N. arcuatus* feeding on *N. viridis* by Zarghami et al. (2014c) and Zarghami et al. (2016).

A predator with a type II functional response can eliminate the prey-predatory population stability because it causes inverse density-dependent mortality in the prey population. In contrast, a predator with the type III functional response could more effectively regulate the density of the prey population and suppressing prey populations than a predator with the type II response (Holling, 1959; Murdoch, 1969; Murdoch and Oaten, 1975). Researchers attributed such ′sigmoidal′ behavior (type III) to the existence of learning behavior in the predatory population (Holling, 1965; Murdoch and Oaten, 1975) or switching behavior (the presence of alternative prey) (Murdoch, 1969). A predator with the type III functional response is supposed to learn more sophisticated techniques for hunting, prey handling or focusing to search in particular places within the environment (Real, 1977), whereas a predator with type II response feeds on prey without any initial delay in learning (Sarmento et al., 2007). Thus, with respect to different types of functional response of *N. arcuatus* during its 33 days lifetime (specially types III responses), and the result of Zarghami *et al.* (2014 and 2016), which also confirms the ability of this predator to show a type III response, we can conclude that *N. arcuatus* has the ability to suppress and regulate prey population during outbreaks of *N. viridis* in citrus orchards.

Our results indicate that estimated attack rates and constant *b* did not change significantly amongst different ages of *N. arcuatus* with similar functional response type (II or III). The attack rate determines how steeply the functional response of a predator curve rises with increasing different density of a prey (Pervez and Omkar, 2005). Thus, the results revealed that the steepness did not differ among different ages of *N. arcuatus*, and that the females with different ages had similar abilities to respond to higher density of prey population. In contrast, the prey handling time initially increases in older predators, and then increases. Handling time is a general term that reflects the cumulative effect of the time taken during capturing, killing, subduing, and digesting prey (Veeravel and Baskaran, 1997). Thus, in contrast to older female, the younger female of *N. arcuatus* spends less time for subduing and consuming, and digest more prey. Mukerjia and LeRoux (1965) reported that for both adult males and females of *Podisus maculiventris* (Say) the attack rate and the time of handling rise gradually up to the 50th day by feeding on *Galleria mellonlla* L. Ding-Xu *et al.* (2007) observed that the attack rates of *S. takahashii* females at various ages are similar, but handling time increases as females age increased.

In addition, a reduction in handling time with higher age of females indicates an elevation in the response level of predator, which is determined by the maximum attack rate (T/T_h). The maximum predation rate per day (T/T_h) and the lowest handling time occurred during the 17th to 20th days of female’s life. Female’s coccinellid requires abundant nutrition for egg production and oviposition (Seagraves, 2009).

Notably, the quantity of prey as food can influence the rate of development, reproductive output, and the fitness of predator (Dixon and Guo, 1993; Dixon and Agarwala, 2002; Omkar and Bind, 2004; Mirhosseini et al., 2015). Hence, the higher rate of consumption among adult females at early ages of 116.5 days (Zarghami et al., 2014a) may be related to their high energy requirements for gonadal development and sexual maturation. Therefore, the adult females increase their digestive capabilities in order to satisfy growing nutritional needs. Zarghami et al. (2014a) reported that at 30°C, female oviposition began at the 4^{th} day, and the maximum peak of reproductive occurred at the 24^{th} day, while reproduction decreased gradually after this day. A reduction is likewise noticeable in predation and increasing handling times at ages after the 25^{th} day. Therefore, probably the process of senescence leads to decline in consumption by *N. arcuatus* females, characterized by a decline in fecundity, fertility, assimilation and speed of locomotion with age (Dixon and Agarwala, 2002). Farhdi et al. (2017) introduced *H. polita* to have the potential for biological control of *N. viridis*. In their research, the maximum number of predation of 10-year-old adult female of *H. polita* on *N. viridis* egg was 150.57 prey. As illustrated in Table 2, despite smaller size of *N. arcuatus,* it has a higher consumption rate, compared to *H. polita* as arch rivals in controlling mealybug in orchards.

Our results show that functional response of *N. arcuatus* could be affected by predator age and prey density. With respect to the types of functional responses observed, the parameters estimated and voracity for 33 days of females' age of *N. arcuatus,* the best time to use females of this predator in an inoculative bio-control is the first 25 days of female's age, especially in early field infestations with *N. viridis* eggs. Obviously, empirical data obtained under laboratory conditions cannot be directly associated to field conditions, with different behavior in numerical response, intra and interspecific predator competition, long-term predation capacity and mealybug population suppression. Therefore, further studies are needed to evaluate the possibilities for using *N. arcuatus* in inoculative/inundative biological control strategies.

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واکنش تابعی وابسته به عمر کفشدوزک *Nephus arcuatus* (Col.: Coccinellidae)، شکارگر شپشک آردآلود جنوب *Nipaecoccus viridis* (Hem.: Pseudococcidae)

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چکیده

چکیده: در این پژوهش واکنش تابعی وابسته به عمر ماده بالغ کفشدوزک *Nephus arcuatus* Kapur، مهم‌ترین شکارگر *Nipaecoccus viridis* (Newstead) در شرایط آزمایشگاهی (دمای ۱±۳۰ درجه سلسیوس، رطوبت نسبی ٥±٦٥ درصد و دوره نوری به تاریکی ١٤:١٠ ساعت) مورد ارزیابی قرار گرفت. ابتدا تراکم‌های مختلف تخم شپشک (۲، ٤، ۸، ۱٥، ٤۰، ٦٥، ۹۰ و ۱۱٥ عدد) در اختیار ماده‌های بالغ ۳ روزه قرار گرفت و تا ۳۳ روزگی ادامه یافت. نتایج نشان داد سن ماده بالغ روی نوع واکنش تابعی، پارامترهای حاصل از آن شامل زمان دست‌یابی (T_h) و نرخ شکارگری (a) موثر است. ماده‌های بالغ در روزهای ١٦، ٢٤ و ۲۸ام واکنش تابعی نوع سوم و در بقیه ۳۰ روز عمر خود واکنش تابعی نوع دوم نشان دادند. با افزایش سن ماده‌های بالغ از ٤ تا ١٧ روزگی زمان دست‌یابی کاهش و پس از آن افزایش یافت. اگرچه قدرت جست‌وجوگری تحت تاثیر ماده‌ها قرار نگرفت. حداکثر نرخ شکارگری تحت تاثیر سن ماده‌ها بود و حداکثر نرخ شکارگری در روزهای ۱۲، ١٤، ۱٥، ۱۷، ۱۸، ۲۰ و ۲٥ ام از عمر ماده بالغ مشاهده شد. میانگین حداکثر نرخ شکارگری ١٥٦/٦ تخم در روزهای ١٧ و ۱۸ام برآورد شد. براساس نتایج بدست آمده بهترین زمان استفاده از این کفشدوزک در یک کنترل بیولوژیک اشباعی، به ویژه هنگامی که شپشک در مرحله تخم بوده، ۲٥ روز ابتدایی عمر ماده‌ها می‌باشد زیرا در این زمان قادرند به طعمه بیش‌تری حمله کنند.

کلید واژه ها: کنترل بیولوژیک، واکنش رفتاری، زمان دست‌یابی، قدرت جست‌وجوگری

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