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Effect of different foraging periods on the functional response of *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) at different densities of *Aphis craccivora*

Reza Jalalipour, Ahad Sahragard* and Azadeh Karimi-Malati

Department of Plant Protection, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran.

Abstract: Searching efficiency and handling time are two major components of functional response and are usually used to evaluate effectiveness of natural enemies. The effect of different foraging periods on the functional response of larval *Aphidoletes aphidimyza* (Rondani) (Dip.: Cecidomyiidae) feeding on third instar nymphs of *Aphis craccivora* was studied. The experiment was conducted in terms of time-specific (1, 2, 4, 6,12, 24 h.) functional response to varying densities (5, 10, 20, 40, 60 and 80) of third instar nymphs of *A.craccivora* at 23 ± 1 °C, 70 ± 5% of R.H., and a photoperiod of 16:8 h (L: D). Parameter estimates for logistic regressions showed a type II functional response for 4 day-old larvae of the predator at different foraging periods to varying densities of *A. craccivora*. The estimated searching efficiency (*a'*) and handling times (T_h), varied with foraging periods. The searching efficiency showed a decreasing trend as the foraging periods increased. The estimated maximum rates of predation (T/T_h) for the 4-day old larvae were directly related to the foraging periods increase but handling times (T_h), showed a decelerating trend. In conclusion it was found that searching efficiency was a variable parameter in different foraging periods of *A. aphidimyza* and was lowest at the foraging periods of 24 h. It was also suggested that *A. aphidimyza* with type II functional response in all foraging periods, could be considered as a highly effective biological agent in suppressing *A. craccivora* population.

Keywords: *Aphidoletes aphidimyza*, *Aphis craccivora*, foraging periods, functional response

Introduction

The cowpea aphid, *Aphis craccivora* (Koch) (Hemiptera: Aphididae) as a cosmopolitan pest feeds on several host plants especially Fabaceae. It is considered as a major pest of important economic crops such as alfalfa, beans and cowpea, *Vigna unguiculata* (L.) in Africa, Asia and Latin America (Singh and Jackai, 1985; Pettersson *et al*., 1998). It has been reported that this aphid can transmit some plant pathogenic viruses (Coceano and Peressini, 1989; Chen *et al*., 1999).

The aphidophagous, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) is an effective predator of many aphid species worldwide in glasshouses, on field crops, and fruit trees (Morse, 1981). It shows great promise as a biological control agent because of its high degree of density-dependency (El-Titi, 1973) and its tendency to kill more aphids than it consumes (Uygun, 1971).

The functional response also as a behavioral response is one of the most widely measured

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* **Corresponding author**, e-mail: sahragard@guilan.ac.ir
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attributes and the efficiency of predators and parasitoids (Trexler *et al*., 1988; De Clercq *et al*., 2000; Lester and Harmsen, 2002; Badii *et al*., 2004; Reis *et al*., 2003, 2007; Fathipour *et al*., 2006; Timms *et al*., 2008; Casas and Mccauley, 2012). Phenomenalistic descriptions of how predator attack rates differ with prey availability are basic components of consumer resource models. The application of these models typically assumes continuous foraging by individuals, along with stationary in their behavioral and physiological processes (Casas and Mccauley, 2012). However, most species display a diurnal cycle in foraging and resting, and the impact of this foraging pattern on the functional response is unknown (Casas and Mccauley, 2012). The state spaces for parasitoids and predators are the number of mature eggs, the egg load, and the satiation level, respectively (Casas and Mccauley, 2012). The corresponding rates are those of egg maturation and oviposition on one hand, and digestion and prey capture on the other (Casas and Mccauley, 2012).

Attack rate or searching efficiency (a') and handling time (T_h) are the two major components of functional response to assess the effectiveness of predators and parasitoids (Hassell and Waage, 1984).The rate of these parameters are affected by different factors such as: age of a predator (Ding-Xu *et al*., 2007) and a parasitoid (Sahragard, 1989; Asadi *et al*., 2012), developmental stages of predator (Yaşar and Özger, 2005a; Farhadi *et al*., 2010), sex of predator (Rocha and Redaelli, 2004; Farhadi *et al*., 2010), parasitoid density (Tahriri *et al*., 2007), prey and host developmental stages (De Jong and van Alphen, 1989; Godfray, 1994; Joyce *et al*., 2001; Gonza´lez-Herna´ndez *et al*., 2005; Chong and Oetting, 2006 a; Taleb and Sardar, 2007), prey size, availability and density (Laing and Osborn, 1974; Cogni *et al*., 2002; Pervez and Omkar, 2005; Varone *et al*., 2007), host age and density (Chen *et al*., 2006; Chong and Oetting, 2006 b), host plant and plant architecture (De Clercq *et al*., 2000; Garcia and O'Neil, 2000; Madadi *et al*., 2007; Timms *et al*., 2008), and the size of arenas (Yaşar and Özger, 2005b; Sabaghi *et al*., 2011b). Casas and McCauley (2012) on the other hand, showed that temporal variation in foraging activity may have high influence on the estimate of interaction rates for predator–prey dynamics. They also stated that the simple approach that is most commonly used implicitly assumes that the functional response is time-invariant, and hence that all underlying behavioral and physiological processes are constant.

The functional response of *A. aphidimyza* has only been studied at its larval stage to different densities of *Aphis pomi* (Degeer) in 24 h. experiment that was a type II (Morse and Croft, 1987). The larval age-specific searching efficiency of *A. aphidimyza* has also been studied during its larval stage (Madahi, 2012). However, the objectives of this research were to evaluate the effect of different foraging periods on searching efficiency and functional responses of *A. aphidimyza* larvae at different densities of *A. craccivora* as prey.

Materials and Methods

The nymphs of *A. craccivora* were collected from *Robinia pseudoacacia* L. and reared on black eyed bean, *Vigna unguiculata* (L.). The larvae of *A. aphidimyza* were collected from the colony of *A. craccivora* in an infested black eyed bean field at the College of Agriculture in the University of Guilan (Northern Iran). The predators were reared for two generations on different instars of *A. craccivora* before starting the functional response experiments. All aphids and predator stocks were kept in a growth chamber at 23 ± 1 °C, 70 ± 5% relative humidity (R. H.), and a photoperiod of 16:8h (L: D).

Functional response

In order to evaluate the searching efficiency and handling time of *A. aphidimyza*, the functional response of *A. aphidimyza* was studied at six time periods (1, 2, 4, 6, 12, 24 h) to different densities of third instar nymphs of *A. craccivora* as prey at (23 ± 1 °C, 70 ± 5% relative humidity (R. H.) and a photoperiod of 16:8h (L: D). Since it was very difficult to separate larval instars of the predator,

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the experiments were done with4-day old larvae of *A. aphidimyza*. They were exposed to different densities (5, 10, 20, 40, 60 and 80) of third instar nymphs of *A. craccivora* separately on a black eyed bean leaf in a transparent plastic container (15 × 13 × 3 cm). Aphids were gently transferred with a fine brush from the host plant to the leaves in experimental arenas. After different foraging periods (1, 2,4,6,12,24 h), the number of aphids eaten by the larvae of *A. aphidimyza* was recorded. Each foraging periods and prey density was replicated 10 times.

Data analysis

The type of the functional response was determined by logistic regression analysis [SAS/STAT, CATMOD procedure (SAS version 9.1)] of the proportion of prey killed (*Na*) in relation to initial prey density (N_0) (Trexler and Travis, 1993). The data were fitted to the logistic regression which describes the relationship between N_a / N_0 and N_0 (Juliano, 1993):

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

Where P_0, P_1, P_2, and P_3 are the intercept of linear, quadratic and cubic coefficients, respectively, and estimated using the method of maximum likelihood. If the linear parameter P_1 is negative, a type II functional response is obtained, whereas a positive linear parameter indicates density-dependent predation and thus a type III functional response (Juliano, 1993).

The Rogers' type II random predator model is:

$$N_a = N_0\left(1 - \exp\left[-a\left(T - T_h N_a\right)\right]\right)$$

Where N_0 is initial prey density, N_a, number of prey consumed, T is the total time (different foraging periods), a is the attack rate (h^{-1}), and T_h is handling time in hours.

Statistical analysis of the functional response was performed using the SAS software (SAS Institute, 2001). A nonlinear regression was used (the least square technique with DUD initialization) to estimate parameters. Curves were drawn using the Excel software.

Results

The prey consumption rate of 4-day- old larvae of *A. aphidimyza* at different prey densities and different foraging periods were all significantly different (1 hour: $F_{2, 60} = 221.30$, $p < 0.0001$; 2 hours: $F_{2, 60} = 266.20$, $p < 0.0001$; 4 hours: $F_{2, 60} = 237.19$, $p < 0.0001$; 6 hours: $F_{2, 60} = 582.88$, $p < 0.0001$; 12 hours: $F_{2, 60} = 640.37$, $p < 0.0001$; 24 hour: $F_{2, 60} = 774.59$, $p < 0.0001$).

Parameter estimates for logistic regressions of proportion of prey killed (Na/N0) against number of prey offered (N_0) showed that the linear parameter P1was negative, resulting in a type II functional response (Table 1). Therefore, the 4-day-old larvae of *A. aphidimyza* showed a type II functional response at all different foraging periods to varying densities of *A. craccivora* (Fig. 1)

Table 1 Maximum likelihood estimate from logistic regression of proportion of third instar *Aphis craccivora* eaten as a function of initial prey densities by *Aphidoletes aphidimyza* 4-day- old larvae at different foraging periods.

Time interval (h)	Parameters	Estimate	SE	p
1	Constant	-1.3244	0.2970	< 0.0001
	Linear	-0.0504	0.0161	0.0017
	Quadratic	0.00034	0.00017	0.0512
2	Constant	-0.6254	0.2485	0.0119
	Linear	-0.0655	0.0134	< 0.0001
	Quadratic	0.0005	0.00014	0.0004
4	Constant	-0.2302	0.2273	0.3113
	Linear	-0.0718	0.0120	< 0.0001
	Quadratic	0.0006	0.0001	< 0.0001
6	Constant	-0.2022	0.2097	0.3352
	Linear	-0.0407	0.0104	< 0.0001
	Quadratic	0.0002	0.0001	0.0253
12	Constant	0.1419	0.1972	0.4719
	Linear	-0.0362	0.0093	0.0001
	Quadratic	0.00025	0.00009	0.0101
24	Constant	1.2269	0.2145	< 0.0001
	Linear	-0.0160	0.00936	0.0868
	Quadratic	-0.00001	0.00009	0.8885

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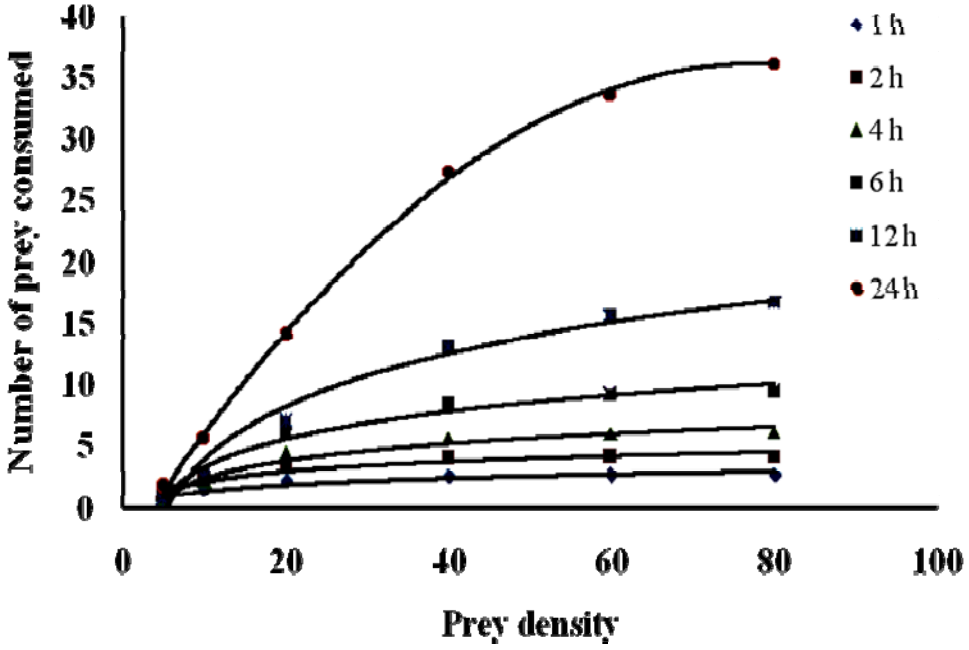

Figure 1 Type II functional response of *Aphidoletes aphidimyza* 4-day-old larvae to varying densities of third instar *Aphis craccivora* at different foraging periods (hours).

The searching efficiency (a') and handling time (T_h) (estimated by Rogers' random attack equation) for *A. aphidimyza* 4-day-old larvae feeding on different densities of third instar *A. craccivora* nymphs at different foraging periods are presented in Table 2. The searching efficiency decreased as the foraging periods increased (Fig. 2). However, the handling time had a decelerating trend as the foraging periods increased (Fig. 3).The estimated maximum attack rates of predation (T/T_h) was directly related to foraging periods (Fig. 4).

Discussion

Many studies have been devoted to the functional response of insect predators (Sarmento *et al*., 2007; Sekoand Miura, 2008; Xiao and Fadamiro, 2010; Sabaghi *et al*., 2011a; Heidarian *et al*., 2012) in foraging periods of 24 h., but the time specific functional response has received little attention. This is the first study on the functional response of *A. aphidimyza* to varying densities of third instar nymphs of *A. craccivora* at different foraging periods. According to Morozov (2010) individual predators often forage over landscapes or in environments where there is significant spatial variation in quantities of prey, and recent work has shown how this spatial variability alters the functional response and hence the interaction rates between predators and prey in space. Dunlap *et al*. (2009) state that although spatial variation has received much attention, there is surprisingly little research on the effects of temporal changes in prey density on the functional response. This temporal variation can arise in a variety of ways. Indeed, many predators possess diurnal foraging patterns, and several other chronobiological rhythms which are of great importance in the life of many organisms.

This study showed that the time-specific functional response of 4-day old larvae of *A. aphidimyza* was a type II response at all foraging periods. It seems that the functional response studies at different foraging periods

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provide us better insights into the behavior of an insect's natural enemy. Predators which exhibit the type II functional response are commonly regarded as efficient biological control agents (Fernández-Arhexand Corley, 2003; Pervez and Omkar, 2005).The type II functional response has also been found on other insect natural enemies (Ryoo, 1986; De Clercq *et al*., 2000; Reis *et al*., 2003; Badii *et al*., 2004; Timms *et al*., 2008).Therefore, 4-day- old larvae of *A. aphidimyza* showing type II response to varying densities of *A. craccivora* at different foraging periods can be considered as an effective biocontrol agent in suppressing aphid populations especially *A.craccivora*. The searching efficiency showed a decreasing trend as the foraging periods increased. However, in contrast, the handling time had a decelerating trend as the foraging periods increased.

Casas and McCauley (2012) showed that the length of the foraging period altered both the shape of the functional response and the magnitude of attack rates, compared to a daily functional response proportional to the time spent foraging. However, it was concluded here that although the values of functional response parameters of *A. aphidimyza* changed at different foraging periods, the type of functional response did not vary.

Table 2 Coefficient of searching efficiency (a') and handling time (T_h) (estimated by Rogers random attack equation) of *Aphidoletes aphidimyza* 4-day- old larvae fed on third instar *Aphis craccivora* at different foraging periods.

Foraging periods (hour)	Parameters	Estimate	SE	95% CI[1]	
				Lower	Upper
1	a'	0.0339	0.0106	0.0127	0.0551
	T_h	0.3699	0.0212	0.3275	0.4123
2	a'	0.0261	0.0076	0.0110	0.0412
	T_h	0.4781	0.0250	0.4280	0.5283
4	a'	0.0098	0.0029	0.00412	0.0155
	T_h	0.6401	0.0376	0.5648	0.7154
6	a'	0.0077	0.00142	0.00484	0.0105
	T_h	0.6153	0.0241	0.5672	0.6635
12	a'	0.0029	0.0005	0.00192	0.00389
	T_h	0.6539	0.0307	0.5924	0.7155
24	a'	0.0039	0.00074	0.00243	0.00539
	T_h	0.601	0.0279	0.5539	0.6658

[1] CI indicates confidence intervals.

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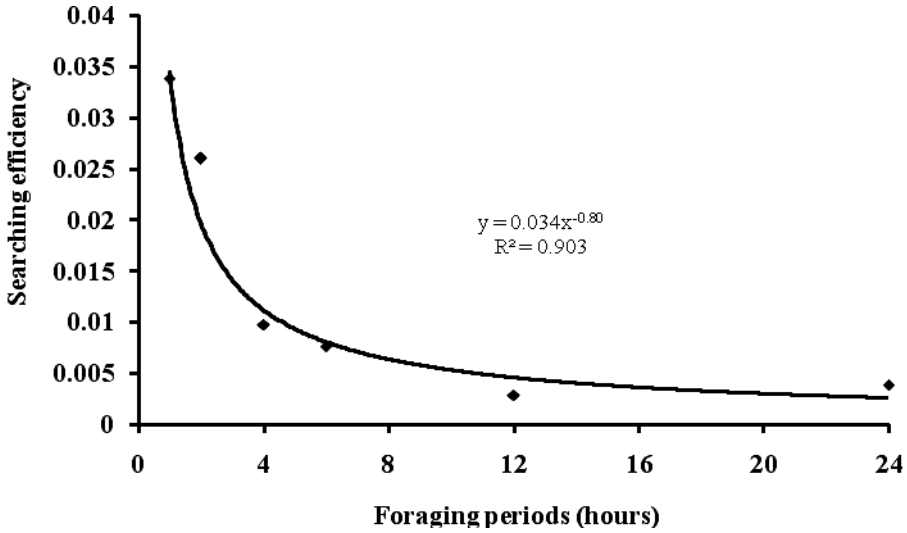

Figure 2 Searching efficiency (a') of *Aphidoletes aphidimyza* 4-day-old larvae feeding on third instar *Aphis craccivora* at different foraging periods.

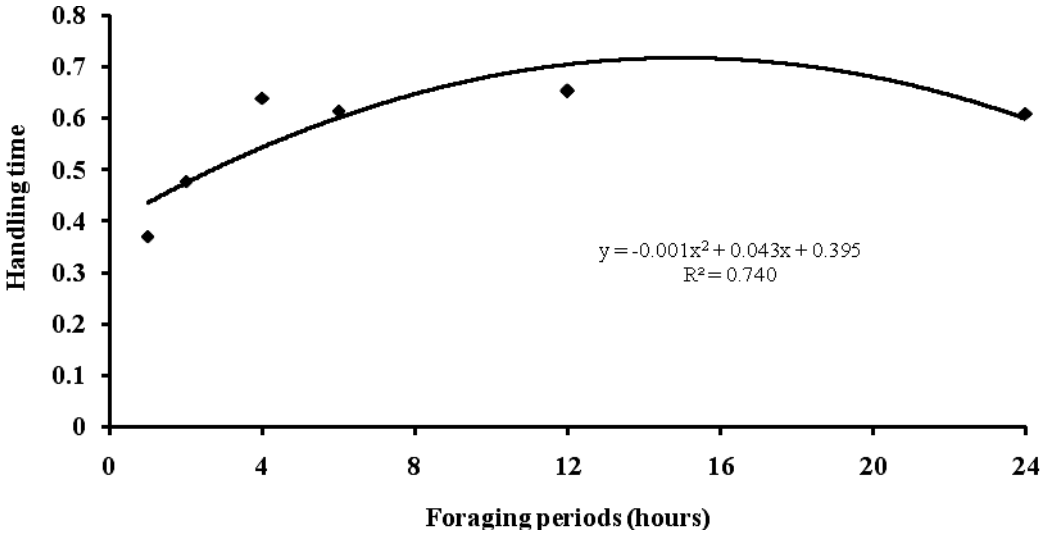

Figure 3 Handling times of *Aphidoletes aphidimyza* 4-day-old larvae feeding on third instar *Aphis craccivora* at different foraging periods.

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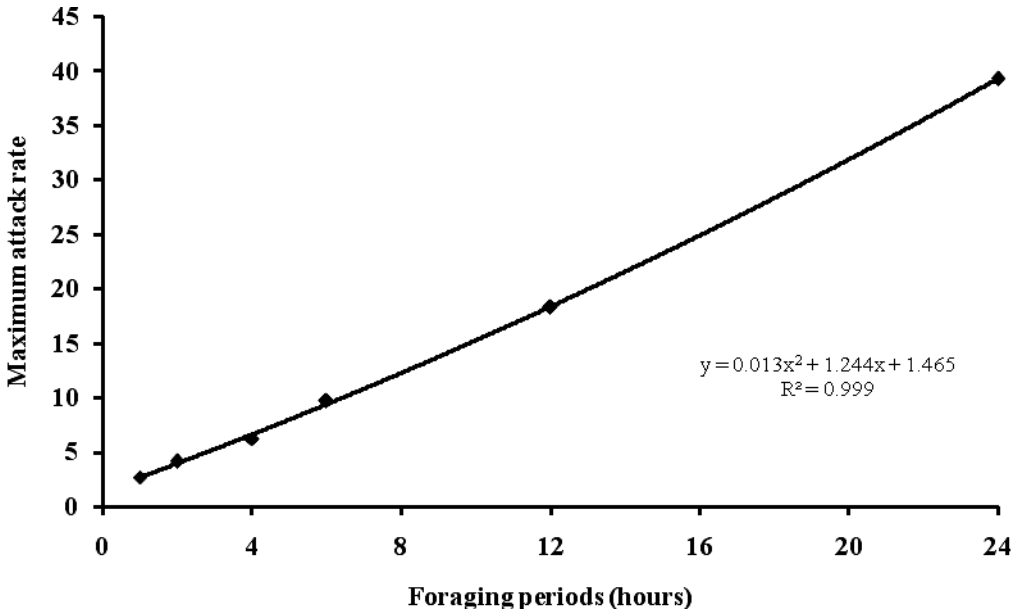

Figure 4 Maximum attack rate of *Aphidoletes aphidimyza* 4-day-old larvae feeding on third instar *Aphis craccivora* at different foraging periods.

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تأثیر دوره‌های زمانی مختلف جستجوگری روی واکنش تابعی *Aphidoletes aphidimyza* در تراکم‌های مختلف شته اقاقیا *Aphis craccivora*

رضا جلالی‌پور، احد صحراگرد* و آزاده کریمی-ملاطی

گروه گیاه پزشکی، دانشکده علوم کشاورزی، دانشگاه گیلان، رشت.
* پست الکترونیکی نویسنده مسئول مکاتبه: Sahragard@guilan.ac.ir
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چکیده: قدرت جستجو (a') و زمان دستیابی دو جزء مهم واکنش تابعی دشمنان طبیعی هستند و به‌طور معمول برای ارزیابی کارایی آن‌ها استفاده می‌شوند. تأثیر دوره‌های زمانی مختلف جستجوگری روی واکنش تابعی لارو *Aphidoletes aphidimyza* با تغذیه از پوره‌های سن سوم شته اقاقیا *Aphis craccivora* مورد مطالعه قرار گرفت. آزمایش براساس واکنش تابعی وابسته به زمان در دوره‌های (۱، ۲، ۴، ۶، ۱۲و ۲۴) ساعت به تراکم‌های مختلف (۵، ۱۰، ۲۰، ۴۰، ۶۰ و ۸۰) پوره‌های سن سوم شته اقاقیا *A. craccivora* در شرایط کنترل شده (در شرایط۱ ± ۲۳ درجه سلسیوس، ۵ ± ۷۰ درصد رطوبت نسبی و دوره نوری-تاریکی ۱۶: ۸ ساعت) انجام شد. برآورد پارامترها با استفاده از رگرسیون لوجستیک، واکنش تابعی نوع دوم را برای لارو چهار روزه شکارگر در دوره‌های زمانی مختلف را در تراکم‌های مختلف شته اقاقیا *A. craccivora* نشان داد. قدرت جستجو (a') و زمان دستیابی (T_h) با زمان‌های مختلف تغییر کرد. قدرت جستجو روند کاهشی با دوره‌های زمانی نشان داد. برآورد حداکثر نرخ شکارگری (T/T_h) برای لارو چهار روزه به‌طور مستقیم با افزایش دوره‌های زمانی رابطه داشت اما زمان دستیابی (T_h)، روند کم شونده ای را نشان داد. درنتیجه مشخص شد که قدرت جستجو پارامتر متغیر دوره‌های زمانی مختلف جستجوگری *A. aphidimyza* است. همچنین پیشنهاد شد که *A. aphidimyza* با دارا بودن واکنش تابعی نوع دوم در دوره‌های زمانی مختلف می‌تواند به‌عنوان عامل کنترل بیولوژیک بسیار مؤثر در کاهش جمعیت *A. craccivora* درنظر گرفته شود.

واژگان کلیدی: واکنش تابعی، دوره‌های جستجوگری، *Aphidoletes aphidimyza*، *Aphis craccivora*

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