

Functional response of *Anisopteromalus calandrae*, a parasitoid of cowpea weevil *Callosobruchus maculatus*: effects of the host plant and patch complexity

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Abstract

The functional response of ectoparasitoid wasp *Anisopteromalus calandrae* parasitizing the 4th instar larvae of the cowpea weevil, *Callosobruchus maculatus* was investigated over host plant and complex patch treatments in the laboratory. In the first group of experiments, the effect of two different host plants including cowpea *Vigna unguiculata* L. and chickpea *Cicer arietinum* was studied on the functional response of the parasitoid wasp. In the second series of tests, the influence of patch complexity was investigated using chickpea as the host plant. According to the results of the logistic regression, the functional response for *A. calandrae* when attacking 4th instar larvae of *C. maculatus* on both chickpea and cowpea, and also in the complex patches of the host was type II. The search rates of the parasitoid were estimated 0.0488 and 0.0378 h⁻¹, and the handling times were calculated to be 2.0962 and 2.1804 h in chickpea and cowpea treatments, respectively. In the complex patch using chickpea seeds as host plant, the estimated search rate value for *A. calandrae* (0.0269 h⁻¹) decreased in comparison with a simple patch (0.0488 h⁻¹); however, the difference was not significant. These results can provide useful information for the biological control of the cowpea weevil in silos and store places.

Keywords: Cowpea weevil, Handling time, Pteromalidae, Search rate

واکنش تابعی زنبور *Anisopteromalus calandrae*، پارازیتوئید سوسک چهارنقطه‌ای حبوبات *Callosobruchus maculatus*:

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چکیده

واکنش تابعی زنبور پارازیتوئید *Anisopteromalus calandrae* که لاروهای سن چهارم سوسک چهارنقطه‌ای حبوبات *Callosobruchus maculatus* را پارازیت می‌کند، روی میزبان‌های گیاهی مختلف و لکه‌های با پیچیدگی متفاوت در شرایط آزمایشگاهی مورد بررسی قرار گرفت. در آزمایش اول، اثر دو میزبان گیاهی مختلف شامل لوبیا چشم بلبلی *Vigna unguiculata* و نخود *Cicer arietinum* روی واکنش تابعی زنبور پارازیتوئید بررسی شد. در آزمایش دوم، تأثیر پیچیدگی لکه بر واکنش تابعی زنبور با استفاده از لوبیا چشم بلبلی به عنوان میزبان گیاهی مورد بررسی قرار گرفت. براساس نتایج رگرسیون لجستیک، واکنش تابعی زنبور پارازیتوئید *A. calandrae* روی لارو سن چهارم سوسک چهارنقطه‌ای حبوبات، در آزمایش‌های انجام شده روی هر دو میزبان لوبیا چشم بلبلی و نخود و همچنین در لکه‌های پیچیده میزبان از نوع دوم بود. نرخ جستجوی پارازیتوئید در تیمار لوبیا چشم بلبلی و نخود به ترتیب ۰/۰۳۷۸ و ۰/۰۴۸۸ بر ساعت و زمان دستیابی در این تیمارها به ترتیب ۲/۰۹۶۲ و ۲/۱۸۰۴ ساعت محاسبه شد. نرخ جستجوی زنبور پارازیتوئید *A. calandrae* در لکه پیچیده با استفاده از دانه لوبیا چشم‌بلبلی به عنوان میزبان گیاهی، (۰/۰۲۶۹ بر ساعت) در مقایسه با لکه ساده (۰/۰۴۸۸ بر ساعت) کاهش یافت، هر چند این اختلاف معنی دار نبود. این نتایج می‌تواند اطلاعات مفیدی جهت کنترل بیولوژیکی سوسک چهارنقطه‌ای حبوبات در سیلوها و مکان‌های بسته در اختیار محققین قرار دهد.

کلمات کلیدی: نرخ جستجو، زمان دستیابی، سوسک چهارنقطه‌ای حبوبات، Pteromalidae

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Introduction

The cowpea weevil, *Callosobruchus maculatus*, Fabricius (coleopteran: Chrysomelidae) is the most important post-harvest pest of the cowpea and other legumes especially in tropical regions of the world. The pest is able to infest both pods in the field and seeds in the storage. Their larvae penetrate into the seeds and feed from the inside (Kpoviessi *et al.* 2019).

Anisopteromalus calandrae Howard (Hymenoptera: Pteromalidae) is a well-known and cosmopolitan ectoparasitoid wasp that parasitizes the larvae and pupae of several species of coleopteran pests. The hosts of *A. calandrae* usually hide within the host food (Ghimire & Phillips 2014). Most of the host species are stored-product pests. Therefore, *A. calandrae* is considered as a potential biological control agent in stores and silos (Kasamatsu & Abe 2015). Some characteristics such as high fecundity and strong flying ability make the wasp as one of the promising candidates for biological control (Ghimire & Phillips 2014). Several species of stored grain pests for example *Sitophilus granarius* (L.), *Trogoderma granarium* Everts, *Sitophilus oryzae* L., *Sitophilus zeamais* Motsch., *Rhyzopertha dominica* (Fab.), and *Callosobruchus* species are attacked by the parasitoid (Ahmed 1996; Ngamo *et al.* 2007). During parasitism, *A. calandrae* paralyzes the host larva and lays a single egg on or near the larva. Only one parasitoid grows on each host

larva which consumes the body fluid of the host for its development (Belda & Riudavets 2010).

A parasitoid's functional response describes the relationship between the number of hosts parasitized and initial host density (Solomon 1949). The assumptions made are the parasitoid search is random and the host population is distributed at random and is homogenous. Two parameters of the coefficient of instantaneous search rate and handling time are among the criteria used for assessing the potential of a parasitoid (Holling 1959). Three different types of functional response have been defined, types I, II, and III. In type I functional response a linear increase in host numbers attacked occurs with an increase in host population density. In type II response, the correlation between the attack rate and host population density is curvilinear and in type III, the form of the curve is sigmoid (Hassell 1978). Functional response plays an important role in understanding the behavior of biological control agents and is considered as a measure in selecting appropriate agents for biological control programs (Lester & Harmsen 2002; Madadi *et al.* 2007).

Several biotic and abiotic factors including temperature, humidity, host species, host plant cultivar, and the age of parasitoid have been reported that affect the type and parameters of functional response of a parasitoid (Allahyari *et al.* 2004; Moezipour *et al.* 2008; Cetintas & McAuslane 2009; Asadi *et al.* 2012; Joodaki *et al.* 2018). The effect of temperature on the

functional response of *A. calandrae* has been investigated in some previous studies (Smith 1994; Menon *et al.* 2002). There are also some previous reports related to the role of the host plant or habitat complicity on the other parasitoid wasps (Gols *et al.* 2005; Soler *et al.* 2007; Grieshop *et al.* 2008; Gibb & Parr 2010; Kruidhof *et al.* 2015). For example, in a study on the parasitoid wasp *Cotesia glomerata* (L.) (Hymenoptera: Braconidae), natural vegetation surrounding *Pieris brassica* infested plants had a negative influence on the foraging efficiency of the parasitoid under semi-field conditions (Kruidhof *et al.* 2015). The searching efficiency of *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae) reduced under habitat complexity conditions (Gols *et al.* 2005). Studies on the effects of microhabitat complexity on host foraging by three species of *Trichogramma* spp. showed the potential negative effects of fine-grain habitat complexity (Grieshop *et al.* 2008). To the best of our knowledge, there is no information about the effect of other factors except temperature on the searching efficiency and functional response of *A. calandrae*. The current study aimed to determine the effect of different host plants and patch complexity on the functional response of *A. calandrae* to different densities of *C. maculatus*.

Materials and Methods

The study was carried out in the Entomology laboratory of Agricultural Sciences and Natural

Sciences University of Khuzestan in the south-west of Iran. The experiments were performed at $30 \pm 1^\circ\text{C}$, $65 \pm 5\%$ R.H. and dark condition.

Host and Parasitoid rearing

A stock culture of *C. maculatus* was maintained on three different plant hosts of cowpea *Vigna unguiculata* L., chickpea *Cicer arietinum* L., and mung bean *V. radiata* (L.) R. Wilczek, in separate plastic containers (8 cm diameter \times 20 cm height) with proper ventilation. Uninfested beans were used as food for insect pest and they were reared for several generations at laboratory. The maintenance conditions of colonies were similar to those mentioned above for the experiments. The colony of the wasp, *A. calandrae*, was reared on 4th instar larvae of *C. maculatus* on cowpea, the preferred host of the pest, at the same condition of the *C. maculatus*.

Experimental design

Effect of different host plants on functional response: Kernels of cowpea, chickpea, and mung bean were infested by allowing *C. maculatus* adult females (1-3 days-old) to oviposit for 48 h in three different containers. For oviposition 500 g of kernels was offered to females in a 1000 ml plastic container with ventilation. Then, the cowpea seeds were examined for *C. maculatus* eggs and after assurance of oviposition the females were removed. One egg was maintained on each seed and the extra eggs were removed by an insect pin.

The seeds were kept in the containers for 18 days at 30°C until the larvae reached the 4th instar (the preferred age for *A. calandreae*) before starting the experiments.

To evaluate the functional response of *A. calandreae*, different densities of 2, 4, 8, 16, 30, 40, and 50 fourth instar larvae of *C. maculatus* were offered to mated females of the parasitoid (48 hours old) at the experimental condition. Separate tests were carried out on each type of seed. The test arena was a cylindrical transparent container (7 × 9 cm) with proper ventilation. The parasitoids were allowed to find and parasitize the host larvae for 24h and then they were removed. Afterward, *C. maculatus* larvae placed in incubators with constant temperature until the adult parasitoids emergence. The number of the emerged wasps was recorded. Ten replications were considered for each host density and each treatment.

Effect of patch complexity on functional response: In another series of functional response tests, the effect of patch complexity was investigated in the laboratory. In this experiment, chickpea was used as a host plant to feed the larvae of *C. maculatus*. In each density of *C. maculatus* larvae offered to *A. calandreae* females (2, 4, 8, 16, 30, 40, and 50) equal numbers of uninfested kernels were added to make the searching arena of parasitoid more complicated. For example, at the density of 2 larvae, two uninfested kernels were added to the experiment.

The rest of the test conditions were similar to those mentioned above.

Statistical analysis: Two separate stages of analysis were conducted to determine the effects of different host plants and patch complexity on the functional responses of parasitoids. In the first step, logistic regression analysis of the proportion of parasitized larvae as a function of initial density indicated the type of functional response (Juliano 2001). This is done by fitting a polynomial function:

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

Where N_a is the number of parasitized hosts, N_0 is the initial number of hosts offered, and $P_0, P_1, P_2,$ and P_3 are the parameters to be estimated. These parameters were calculated using the method of maximum likelihood (PROC CATMOD, SAS Institute 2001). The type of functional response was determined by examining the signs of P_1 and P_2 . If P_1 is positive and P_2 is negative, the data describe a type III of functional response, but if P_1 is negative and P_2 is positive, the type of functional response is II (Juliano 2001). In the second step, for calculation of the functional response parameters, nonlinear least-squares regression (PROC NLIN; SAS Institute Inc., 2001) was used to fit Roger's random attack model, which describes a type II or III functional response (Rogers 1972; Juliano 2001). Roger's random attack model is an appropriate choice for analysis as host density

was depleted during the experiments and it was not constant (Juliano 2001).

The data from the above test fitted the type II functional response; thus, Roger's type II equation was used to determine the parameters as follows:

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

Where N_a is the number of parasitized hosts, N_0 is the initial number of hosts, a is the instantaneous searching efficiency (attack rate), T is the total amount time available for searching (24h), and T_h is the handling time.

The maximum parasitism rate (T/T_h), describes the maximum number of hosts that can be parasitized by a single parasitoid during 24h, was calculated using the estimated T_h (Hassell, 2000).

Results

The preliminary experiments showed that the mung bean, *V. radiata*, was not a proper host for

A. calandrae development and no parasitoid wasp emerged from the *C. maculatus* larvae parasitized on the kernel. Therefore, the functional response experiments continued on chickpea and cowpea.

Effect of different host plants on functional response

The results of the logistic regression revealed a type II functional response for *A. calandrae* when attacking 4th instar larvae of *C. maculatus* on both chickpea and cowpea according to the negative sign of the linear term of the equation (Table 1). The mean number of parasitized larvae of *C. maculatus* increased with increasing the number of host individuals offered in both treatments; however, the proportion of host parasitized to the initial number of hosts decreased with increasing the number of hosts offered (Figure 1).

Table 1. Results of logistic regression analysis of the proportion of 4th instar larvae of *Callosobruchus maculatus* parasitized by *Anisopteromalus calandrae* on two host plants.

Host plant	Parameters	Estimate	SE	P value
Chickpea	Constant	0.9917	0.3617	0.0076
	Linear	-0.1240	0.0549	0.0240
	Quadratic	0.00249	0.00218	0.2537
	Cubic	-0.00002	0.000025	0.4313
Cowpea	Constant	0.2638	0.3575	0.4606
	Linear	-0.0721	0.0542	0.1833
	Quadratic	0.00134	0.00217	0.5372
	Cubic	-0.00001	0.000025	0.6021

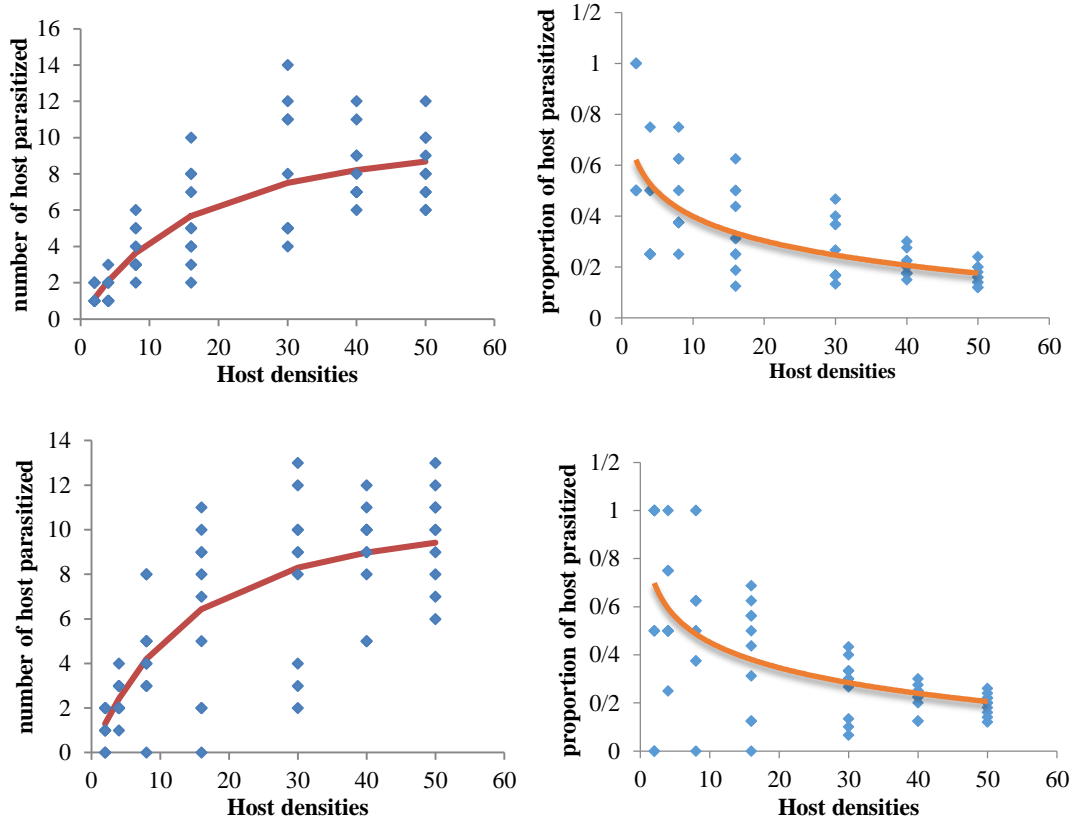


Figure 1. Functional responses of *Anisoteromlus calandreae* females on different densities of 4th instar larvae of *Callosobruchus maculatus* on cowpea (Up) and chickpea (down); Symbols are observed data and lines were predicted by model (equation 2).

It was indicated that there were no significant differences in the calculated amounts of instantaneous search rate and handling time of *A. calandreae* between chickpea and cowpea treatments according to asymptotic 95%

confidence intervals (Table 2). The search rates of parasitoid were estimated 0.0488 and 0.0378h⁻¹, and the handling times were calculated to be 2.0962 and 2.1804 h in chickpea and cowpea treatments, respectively.

Table 2. Parameters for type II functional response model for *Anisopteromalus calandreae* females parasitize 4th instar larvae of *Callosobruchus maculatus* on two host plants.

Host plant	Parameter	Estimate	SE	Asymptotic 95% CI		T/T _h	R ²
				Lower	Upper		
Chickpea	a	0.0488	0.00140	0.0209	0.0768	11.45	0.88
	T _h	2.0962	0.2387	1.6199	2.5725		
Cowpea	a	0.0378	0.00908	0.0169	0.0559	11.00	0.61
	T _h	2.1804	0.2436	1.6942	2.666		

Effect of patch complexity on functional response

According to the logistic regression, type II functional response was determined for *A.*

calandrae when it searched for *C. maculatus* larvae in a complex patch of chickpea (Table 3).

Table 3. Results of logistic regression analysis of the proportion of 4th instar larvae of *Callosobruchus maculatus* parasitized by *Anisopteromalus calandrae* in a complex patch of chickpea.

Parameter	Estimate	SE	P value
Constant	0.3937	0.3593	0.2732
Linear	-0.1171	0.0548	0.0327
Quadratic	0.00308	0.00210	0.1611
Cubic	-0.00003	0.000025	0.2338

The functional response curve showed that the average number of hosts parasitized increased at

first by increasing the host densities and then reached a constant level (Figure 2).

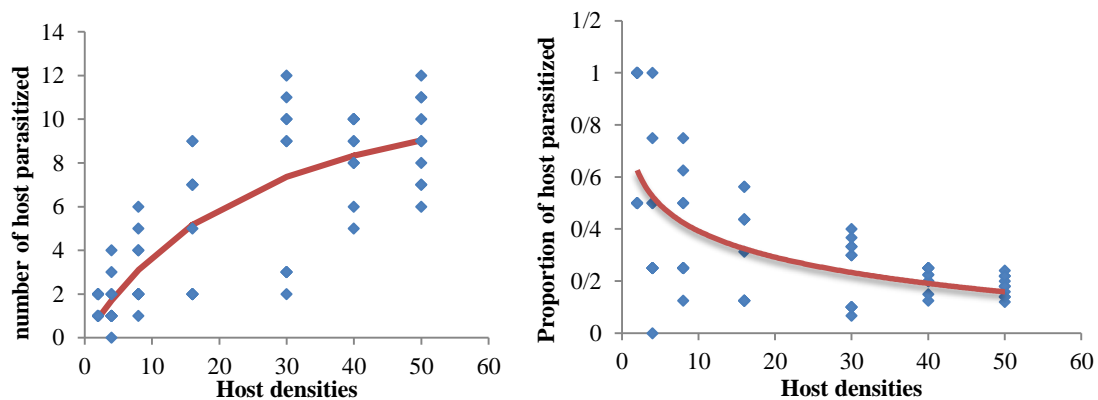


Figure 2. Functional responses of female *Anisoteromlus calandrae* on different densities of 4th instar larvae of *Callosobruchus maculatus* on chickpea in a complex patch; Symbols are observed data and lines were predicted by model (equation 2).

The patch complexity did not affect the type of functional response of *A. calandrae*. The estimated search rate value for *A. calandrae* showed that in the complex patch this parameter decreased (0.0269 h^{-1}) in comparison with a simple patch (0.0488 h^{-1}). However, the

difference was not significant according to 95% confidence intervals (Tables 2 and 4). The values of *A. calandrae* handling time were 1.8379 h in the complex patch and 2.0962 h in the simple patch and no significant difference was observed (Tables 2 and 4).

Table 4. Parameters for type II functional response model for *Anisopteromalus calandrae* females parasitize 4th instar larvae of *Callosobruchus maculatus* on chickpea in a complex patch of chickpea.

Parameters	Estimate	Asymptotic SE	Asymptotic 95% CI		T/T _h	r ²
			Lower	Upper		
a	0.0269	0.00657	0.0138	0.0400	13.05	0.78
T _h	1.8379	0.3055	1.2283	2.4475		

Discussion

It is believed that functional response is an important element in decision making for the most suitable biocontrol agents (Fernandez-Arhex & Corely 2003). In this study, type II functional response was reported for *A. calandrae* and it was not affected by different host plants and patch complexity. This type of functional response has been previously reported for the parasitoids from the family Pteromalidae; e.g. *A. calandrae* (Smith 1994; Menon *et al.* 2002) and *Theocolax elegans* (Westwood) (Flinn & Hagstrum 2002) at different temperature treatments when offered various host species from stored product pests. According to previous studies more than three-quarters of insect parasitoids showed type II functional response (Fernandez-Arhex & Corely 2003). The scarcity of the type III functional response in parasitoids may be due to the experimental artifact particularly experimental conditions; when parasitoids are kept in a small arena with their hosts for a fixed period and in such situations,

parasitoids usually exhibit type II functional response (Van Lenteren & Bakker 1978).

In the current study, the search rate of *A. calandrae* on two different host plants indicated a minor decrease in the cowpea treatment when compared to the chickpea treatment. The reason may be due to the various odors that emerged from the two different kernels upon damage by the insect pest. After injured by herbivores, plants expand their volatile production, and modify the odor constituents, and release a new composition which is called herbivore-induced plant volatiles (McCormick *et al.* 2012). This new compound is effortlessly perceptible by parasitoids and can attract them from long distances (Braasch & Kaplan 2012). Since there is considerable variation in volatile composition among plant species and other taxonomic levels, the parasitoids' innate response to the herbivore-induced plant volatiles is different and they may prefer blends of certain host-infested plants species (Knudsen *et al.* 2006). Comparing the search rate and handling time of *A. calandrae* in two different host plant treatments in the current

study with previous reports showed a difference at the same temperature. At 30°C, the search rate and handling time of *A. calandrae* was 0.136 h⁻¹ and 1.27h (Menon *et al.* 2002), respectively. There may be several reasons for these differences such as alteration in experimental conditions, host species, the age of the parasitoid, and the host plant (Byeon *et al.* 2011; Asadi *et al.* 2012).

In the current study, although the difference between attack rates in a simple and complex patch was not significant, a distinct decrease was observed in the complex patch. When the patch was simple it was easy for parasitoids to find the host. However, in the case of the complex patch, the attack rate decreased because the *C. maculatus* larvae dispersed in the patch and it was difficult to find them. These findings are in line with Khan *et al.* (2016) who reported that *Aphelinus asychis* Walker (Hemiptera: Aphididae) in small plant canopies consumes less energy and attacks more aphids easily but in dense canopies, it expends more energy and due to this reason the attack rate was less in dense canopies. Hauzy *et al.* (2010) believe that plants with more branches provided more obstacles to predators, leading to decreasing attack rates. Moreover, host aggregation levels affect the foraging behavior of parasitoids and it seems that in females experiencing a higher level of host

aggregation, the foraging passion is more powerful (Louâpre *et al.* 2019).

Information from this study showed that the functional response of *A. calandrae* did not vary significantly by alteration of the host plant and patch complexity. These facts help develop biological control programs for stored grains.

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