Bulletin of Insectology ***68*** *(2): 211-218, 2015*
ISSN 1721-8861

Effect of hunger level on prey consumption and functional response of the predator *Macrolophus pygmaeus*

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Abstract

A study was conducted to examine the influence of the hunger level on the prey consumption of *Macrolophus pygmaeus* Rambur (Hemiptera Miridae) at varying densities of *Myzus persicae* Sulzer (Hemiptera Aphididae) through laboratory functional response experiments. Newly emerged adult females of the predator were subjected to 24 or 48 h of prey deprivation on pepper plant, as well as to 48 h only on a wet layer of cotton wool. In all experiments, 2nd instars of the aphid were used as prey at densities of 2, 4, 8, 12, 16, 20, 24, 32 and 40 individuals. An adult female predator of each level of hunger was introduced into a dish with a pepper leaf with aphids, and the predation rate was recorded after a period of 24 and 48 h (after prey replacement). The predatory behaviour of insects was not altered with the hunger level. However, a significantly higher predation rate was recorded when predators were deprived of both prey and leaf for 48 h at the prey density of 20 prey items. The logistic regression showed that *M. pygmaeus* exhibited a Holling's Type II functional response in all treatments. Values of handling time and attack rate were not significantly different between the treatments regardless of the predator hunger level.

Key words: *Macrolophus pygmaeus*, hunger, predation, pepper plant, random predator equation.

Introduction

To understand the relationship between the consumption rate of a predator and its prey density, the number of food items consumed per time unit must be related to food abundance through a functional response curve (Solomon, 1949). According to Holling (1959) and Hassell (1978), the shape of this curve depends on two parameters, the attack rate that represents the rate of successful attack (searching efficiency of the predator) and the handling time that is the time required for a predator individual to handle a prey individual (pursuing, subduing, eating and digesting a prey individual). Holling (1959) has categorized functional responses into three main types: a linear functional response, when handling time is negligible and the proportion of prey captured of the total number offered remains constant and independent of prey density (Type I), a rectangular hyperbola when the consumption of prey is limited by satiation of predators, handling time and time spent hunting prey (Type II) or a sigmoid response (Type III), when learning behaviour occurs in the predator population with a consequent increase in the discovery rate as more encounters with prey occur.

Among the several factors that may affect functional response are predator's search mode (Akre and Johnson, 1979; Cloarec, 1991), development stage of predator and prey (Thompson, 1975), availability of prey refugees (Hildrew and Townsend, 1977) and prey quality (Holling *et al.*, 1976). Predators' hunger/satiation has also been reported to be an important component of foraging behaviour that could have a significant effect on the feeding rate by influencing the motivation to search (Holling, 1966; Jeschke *et al.*, 2002) and consequently functional responses (Nagamura, 1974; Thompson, 1975; McArdle and Lawton, 1979; Mills, 1982; Bailey, 1986; Jeschke *et al.*, 2002). Under a more intense level of hunger the predator may become more or less efficient to forage or handle the prey. Therefore, hunger may positively influence a predator's motivation to search for and consume food and thus significantly may reduce attack rate, foraging time and increase digestive pauses (Sabelis, 1990; van Gils *et al.*, 2003; Jeschke and Tollrian, 2005). According to Jeschke *et al.* (2002) predators can be divided to those that digestion limits their predation ability (digestion limited predators) and those that their limitation is the time they handle the prey (handling limited predators).

Extensive literature reports that hunger level may mediate prey searching behaviour traits and prey digestion, and ultimately affects the prey consumption rates as reported for the predator *Poecilus cupreus* L. (Coleoptera Carabidae) and for *Dicyphus hesperus* Knight (Hemiptera Miridae) that increased the number of prey consumed (Lövei *et al.*, 1985; Gillespie *et al.*, 2012), or for *Deraeocoris lutescens* Schilling (Hemiptera Miridae), *Orius majusculus* (Reuter) (Hemiptera Anthocoridae), and *Phytoseiulus persimilis* (Athias-Henriot) (Acarina Phytoseiidae) that altered their search path of the predator with starvation period (Alauzet *et al.*, 1992; Lamine *et al.*, 2005; Nachappa *et al.*, 2006). Recently Papanikolaou *et al.* (2014) provided evidence that density dependent predation rate of *Propylea quatuordecimpunctata* (L.) (Coleoptera Coccinellidae), was limited by its digestion process. However, these studies have been performed under a narrow range of prey availability rates and thus variability of the effects due to low or high prey densities has not been searched. This variability would be most appropriately investigated and quantified by the functional response of predators when acting under various levels of hunger.

Omnivorous predators have been considered to have the ability to survive longer periods of prey scarcity or even absence (Coll and Guershon, 2002; Eubanks and

Styrsky, 2005; Perdikis *et al.*, 2011). However, little is known about prey consumption rate in response to starvation level for omnivorous predatory heteropteran species. Evidence can be derived from the study of Gillespie *et al.* (2012) for *D. hesperus*, though, in their experiments a fictitious prey (eggs of *Ephestia kuehniella* Zeller, Lepidoptera Pyralidae) was used. Additionally, variable starvation periods may be particularly important for the efficacy of beneficials considering that they are sometimes released after a period of prey deprivation (Henaut *et al.*, 2002).

Macrolophus pygmaeus (Rambur) (Hemiptera Miridae) is a generalist predator of whiteflies, aphids, mites and several lepidopteran species including *Tuta absoluta* Meyrick (Lepidoptera Gelechiidae), and it is commonly used in pest management (Gemeno *et al.*, 2007; Urbaneja *et al.*, 2009; van Lenteren, 2012). This species naturally occurs in the agroecosystems on non-cultivated host plants (Ingegno *et al.*, 2009; Urbaneja *et al.*, 2009; Lambion, 2013), it can survive in the absence of prey by feeding on plant sap (Perdikis and Lykouressis 2000; 2004a), whereas pollen has been reported to favour its development and fecundity (Maleki *et al.*, 2006). Perdikis *et al.* (1999) reported that the voracity of 5th instar nymphs of the predator is higher compared to other instars and similar to that of adult females on nymphs of *Myzus persicae* (Sulzer) (Hemiptera Aphididae). Moreover, Fantinou *et al.* (2008; 2009) showed that *M. pygmaeus* exhibited a Type II functional response on each of the nymphal instars of *M. persicae*, and reported higher predation rate and preference for younger than older instars at all tested prey densities. Recently, Lykouressis *et al.* (2014) showed that similar predation rates of *M. persicae* were recorded on plants of either lower or higher suitability for the development of *M. pygmaeus*, whereas studies have indicated that the presence of floral resources reduced the plateau of its functional response on aphids (Maselou *et al.*, 2014). The aims of this study were i) to investigate the effect of different starvation periods of the omnivorous predator *M. pygmaeus* on its prey consumption and ii) to explore the functional response and its parameters at different foraging time and hunger level. Our hypotheses were: a) a more intense hunger level of the predator should result in an increase of prey consumption and b) a negative effect of hunger on prey consumption might coincide with predator's prey handling, and digestion process. To test these hypotheses predation rates were recorded in two subsequent days using predators from 3 different levels of hunger. The functional response experiments were run separately for each hunger level and foraging time.

Materials and methods

Study organisms

M. pygmaeus rearing was initiated from adults and nymphs collected from a tomato field in Boeotia region, central Greece. Insects were reared on potted sweet pepper (cv. Vidi) plants supplied with *E. kuehniella* eggs *ad libitum* (Entofood, Koppert BV, The Netherlands). Nymphs of first or second instars were transferred from potted caged pepper plants with eggs of *E. kuehniella* into wood-framed rearing cages at 25 °C, 65 ± 5% RH and 16 h photophase. Rearing of the aphids *M. persicae* was established on pepper plants. Cultures of plants and rearing of all insect species were maintained in wood-framed cages (length 80 × height 70 cm), in a greenhouse kept at 22.5 ± 2.5 °C under natural lighting conditions.

Experimental procedure

The experimental set-up consisted of Petri dishes (⌀ 9 cm, 1.5 cm height) with a mesh-covered hole in the lid (⌀ 3 cm) to reduce the accumulation of humidity. A leaf of sweet pepper (cv. Vidi) was placed, abaxial surface up, on a layer of water-moistened cotton wool on the bottom of each Petri dish. In all the experiments, less than 24 hr of age adult females of *M. pygmaeus* were used and assigned to different hunger levels (treatments). The food deprivation periods began when we transferred individuals to dishes without food at designated times before the experiments. Periods of food deprivation were selected according to preliminary experiments, where water was only provided to newly emerged females of *M. pygmaeus* and their longevity was found to be lasted 5.3 ± 0.5 days (10 replicates). Thus, two starvation periods were classified i) a low hunger level corresponded to 24 h and ii) a high hunger level corresponded to 48 h without prey on pepper plant leaf. Because of the predator's ability to survive and reproduce even in periods of prey scarcity by feeding on plants, a third hunger treatment was also applied, where adults were placed only on a wet layer of cotton wool in plastic Petri dishes for 48 h without prey or leaf. Each starved predator was individually introduced into a Petri dish with a leaf of sweet pepper on which 2nd instar *M. persicae* nymphs had been gently placed to create various densities. We used aphids of this instar because it has been reported that *M. pygmaeus* would occasionally abandon without consuming a killed prey individual and this behaviour was more frequent on larger aphid instars (Fantinou *et al.*, 2008). Prey were offered at densities of 2, 4, 8, 12, 16, 20, 24, 32 and 40 individuals per dish. For each predator, prey consumption was recorded after a foraging period of 24 or 48 h thereafter indexes as 1st and 2nd day of observation. Predators were allowed to forage freely for 24 h, after which prey consumption was recorded under a binocular stereoscope (1st day of observation). After recording, consumed prey were removed and the constant number of prey was maintained by adding new ones. After 24 h prey consumption was also recorded (total foraging period 48 h, 2nd day of observation). The completely consumed aphids were totally shrivelled and their skin remained after the predators feeding. For each density treatment at each hunger level 10 replications were performed. Controls without predators (five replicates) were also included to evaluate aphid mortality or moving at each prey density due to the experimental manipulations.

Statistics

The data of the predation rates were compared among prey densities at each starvation level both in the first and in the second day of foraging, using a one-way

ANOVA. The data of the three starvation levels (24 or 48 h on pepper leaf and 48 h only on cotton) were compared between the first and the second day of foraging using a repeated measures analysis, at each prey density. Analyses were conducted on log-transformed data. Comparisons among means were performed using the HSD test. Analyses were conducted with the JMP 10.0 statistical package (SAS, 2012).

The relationship between the predation rate of each predator and the prey density was investigated by fitting functional response curves in each plant for each treatment in a dish. The shape of the curve was determined by the polynomial function from Juliano (1993):

$$\frac{Ne}{No} = \frac{\exp(Po + P_1No + P_2No^2 + P_3No^3)}{1 + \exp(Po + P_1No + P_2No^2 + P_3No^3)} \qquad (1)$$

where *Ne* is the number of prey consumed, N_0 is the initial prey number available, and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic and cubic coefficients, respectively estimated using maximum likelihood. Estimates of the parameters P_0 to P_3 were obtained by applying logistic regression. Each term was different from zero if its 95% confidence interval did not include zero. Once the functional response type was determined, the parameters for the type model were estimated using iterative non-linear least squares regression to the random equation (Rogers, 1972). Since prey were depleted during the experiment, Rogers' model, which does not assume constant prey density, is appropriate for this experiment (Rogers, 1972; Juliano, 1993). Holling's disc equation, in contrast, is based on an assumption of unchanging prey density, and is thus inappropriate for this experiment (Juliano, 1993). Therefore, the random attack equation (Royama, 1971; Rogers, 1972) was used to estimate handling time (T_h) and attack rate (*a*) of the predator modified by Livdahl and Stiven (1983). This modification removes the statistical problems related to the transformation of Royama (1971) and Rogers (1972) and increases the explanation degree of the independent variable in the regression. This modified equation is:

$$\frac{1}{N_a} = \frac{1}{\alpha T N_0} + \frac{T_h}{T} \qquad (2)$$

where *Na* is the number of prey attacked, N_0 is the initial prey density and *T* is the total time that prey was exposed to predator (24 h, or 1 day in this study). The parameter α is the attack rate and the parameter T_h is the time required to handle a prey individual. Analyses were conducted with the SPSS 19.0.0 statistical package (SPSS, 2010). The performance in terms of α and T_h of the predator were compared between and within the hunger treatments with the use of 95% Confidence Interval. In addition, the maximum attack rate, that is, the maximum number of prey which can be attacked by a predator during the time interval under consideration (T/T_h) was calculated using the mean estimate of T_h.

Results

The natural mortality of aphids in dishes due to the experimental manipulations was negligible and found to be 0 ± 0, 0 ± 0, 0.8 ± 0.37, 2.5 ± 0.4, 2.0 ± 0.32, 2.5 ± 0.24, 2.5 ± 0.24, 2.4 ± 0.4 and 2.5 ± 0.24 (mean ± SE) for densities of 2, 4, 8, 12, 16, 20, 24, 32 and 40 prey individuals per dish respectively. The predation rates for each hunger level, prey density and day of observation, are given in table 1.

The analysis of the results revealed a significant effect of hunger level on prey consumption at the prey density of 20 individuals (table 2). Therefore, when the predator was provided only with water for 48 h on cotton, the prey consumption was significantly higher than that when predators were deprived for prey for 24 or 48 h on a leaf. In the other prey densities significant effects of the treatment and the day of observation were not recorded.

The logistic regression showed that *M. pygmaeus* exhibited a Holling's type II functional response (figure 1) at all hunger levels both at the 1st and 2nd day of foraging. This is justified by the parameters showed in table 3 where the linear term of estimated parameter is negative and significantly different from zero along with a non significant quadratic and cubic term (Trexler *et al.*, 1988).

Table 1. Number (mean ± S.E.) of 2nd instar *M. persicae* nymphs consumed by *M. pygmaeus* at three hunger levels (24 and 48 h on leaf and 48 h on cotton) foraging for 1 and 2 days (10 replicates per density).

Prey	24 hours on leaf				48 hours on leaf				48 hours on cotton			
density	1st Day		2nd Day		1st Day		2nd Day		1st Day		2nd Day	
2	1.9 ± 0.1	A	1.9 ± 0.1	A	1.9 ± 0.1	A	1.9 ± 0.10	A	1.8± 0.13	A	2.0 ± 0.00	A
4	3.7 ± 0.15	B	3.8 ± 0.2	B	3.9 ± 0.1	B	3.8 ± 0.13	B	3.3 ± 0.26	B	3.6 ± 0.84	B
8	6.9 ± 0.43	C	7.0 ± 0.3	C	6.1 ± 0.4	C	7.0 ± 0.30	C	6.9 ± 0.28	C	7.5 ± 0.22	C
12	10.7 ± 0.37	D	10.5 ± 0.78	D	10.6 ± 0.52	D	10.7 ± 0.42	D	10.3 ± 0.26	D	10.4 ± 0.54	D
16	13.5 ± 0.45	E	12.2 ± 0.66	D	11.8 ± 0.85	D	12.5 ± 0.64	E	13.0 ± 0.49	E	13.3 ± 0.72	E
20	15.0 ± 0.7	E	15.3 ± 1.27	E	16.5 ± 0.60	E	15.8 ± 0.65	F	18.2 ± 0.63	FG	18.2 ± 0.44	F
24	19.0 ± 0.83	F	19.4 ± 0.85	F	18.1 ± 0.88	EF	19.6 ± 0.72	G	17.2 ± 1.30	F	18.1 ± 0.99	F
32	21.8 ± 0.87	G	21.3 ± 1.22	F	20.8 ± 1.27	F	22.9 ± 1.16	H	21.4 ± 1.97	GH	23.3 ± 1.41	G
40	25.9 ± 1.52	H	26.1 ± 2.15	G	27.6 ± 1.38	G	28.9 ± 1.39	I	23.5 ± 1.57	H	26.1 ± 1.75	G
$F_{(8, 81)}$	295.21		115.38		224.41		334.53		163.95		224.57	
P	< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001	

Values followed by the same upper case letters were not significantly different among rows.

Table 2. ANOVA results of the consumption rate of 2^{nd} instar *M. persicae* nymphs by *M. pygmaeus* as affected by the hunger level (24 and 48 h on leaf; 48 h on cotton) and the time of observations (1 or 2 days).

Factor	df	Prey density																	
		2		4		8		12		16		20		24		32		40	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Hunger	2, 54	0.03	0.97	2.41	0.099	2.09	0.13	0.10	0.89	1.31	0.27	7.99	0.0009	1.75	0.18	0.04	0.95	1.89	0.16
Time	1, 54	0.64	0.43	0.26	0.61	4.26	0.04	0.05	0.81	0.03	0.85	0.13	0.71	1.61	0.21	1.19	0.28	0.49	0.48
Hunger × time	2, 54	0.64	0.53	0.43	0.65	0.72	0.49	0.16	0.85	1.42	0.25	0.13	0.87	0.17	0.83	0.73	0.48	0.35	0.70

Table 3. Estimated parameters of the logistic regression of the proportion of 2^{nd} instar of *M. persicae* consumed by *M. pygmaeus* as a function of 3 hunger levels (24 and 48 h on leaf; 48 h on cotton), foraging for 1 and 2 days.

Hunger levels	Parameter	1^{st} Day			2^{nd} Day		
		Estimate	S.E.	P	Estimate	S.E.	P
24 hours on leaf	Intercept (P_0)	−1.103	0.049	0.004	−1.065	0.072	0.009
	Linear (P_1)	−0.141	0.008		−0.149	0.012	
	Quadratic (P_2)	0.004	0.0001		0.004	0.001	
	Cubic (P_3)	$-3.930e^{-5}$	0.0001		$-4.492e^{-5}$	0.0001	
48 hours on leaf	Intercept (P_0)	−1.113	0.062	0.007	−1.075	0.047	0.004
	Linear (P_1)	−0.142	0.010		−0.146	0.008	
	Quadratic (P_2)	0.004	0.001		0.004	0.0001	
	Cubic (P_3)	$-3.880e^{-5}$	0.0001		$-4.182e^{-5}$	0.0001	
48 hours on cotton	Intercept (P_0)	−1.221	0.067	0.008	−1.090	0.057	0.006
	Linear (P_1)	−0.123	0.011		−0.142	0.009	
	Quadratic (P_2)	0.003	0.0001		0.004	0.0001	
	Cubic (P_3)	$-3.013e^{-5}$	0.0001		$-4.091e^{-5}$	0.0001	

Table 4. Mean (± S.E.) estimates of the attack constant (a) and handling time (T_h) of *M. pygmaeus* when feeding on 2^{nd} instar *M. persicae* at different hunger levels (24 and 48 h on leaf; 48 h on cotton) and foraging for 1 and 2 days.

Hunger level	Parameter	1^{st} day					2^{nd} day				
		Estimate	S.E.	95% C.I.	R^2	P	Estimate	S.E.	95% C.I.	R^2	P
24 h on leaf	T_h	0.630	0.008	0.613-0.646	0.959	0.004	0.637	0.013	0.612-0.663	0.909	0.009
	a	0.325	0.140	0.297-0.353			0.327	0.022	0.284-0.371		
48 h on leaf	T_h	0.628	0.011	0.606-0.649	0.935	0.007	0.615	0.009	0.598-0.632	0.957	0.004
	a	0.310	0.017	0.277-0.344			0.313	0.014	0.286-0.341		
48 h on cotton	T_h	0.633	0.011	0.611-0.655	0.935	0.007	0.624	0.009	0.606-0.643	0.947	0.005
	a	0.314	0.018	0.279-0.349			0.331	0.016	0.298-0.363		

The values of the functional response parameters are shown in table 4. When the predator was exhibited for 48 h to deprivation of prey either on a leaf or a cotton layer a reduction of a was recorded whereas T_h values were kept at the same level. However according to the comparisons of the confidence intervals, the values of a and T_h did not differ significantly between the various treatments regardless of the hunger level, even when the consumption was recorded after one or after 2 days (table 3).

The maximum theoretical predation rate (T/T_h) estimated by the model for the 1st day of observation was 38.1, 38.2, 37.9 aphids /24 h for all the three hunger levels tested (24 h, 48h and 48 h on cotton). For the 2nd of observation the predicted maximum number of aphids eaten by a single predator was 37.7, 39, 38.5 aphids /24 h for the three hunger levels respectively.

Discussion

According to our results the prey consumption rates of *M. pygmaeus* females were not affected by the level of hunger applied in almost all cases. Therefore, the starvation period, corresponded to half of the time that females can withstand, had not a significant influence on their predatory efficiency. Although plant feeding has been well known as a major factor to support the survival of this predator in the field, where prey may be absent or scarce (Albajes and Alomar, 1999; Perdikis and Lykouressis, 2000), potential effects of starvation on its predation rates have not been reported. While Lykouressis *et al.* (2014) showed that the predation effect of this predator was not mediated by the host plant, Maselou *et al.* (2014) indicated that there is a prey density above which the prey consumption may be replaced by utilizing nutrient-rich plant resources such as pollen or flowers. Therefore, it seems that the leaf feeding by

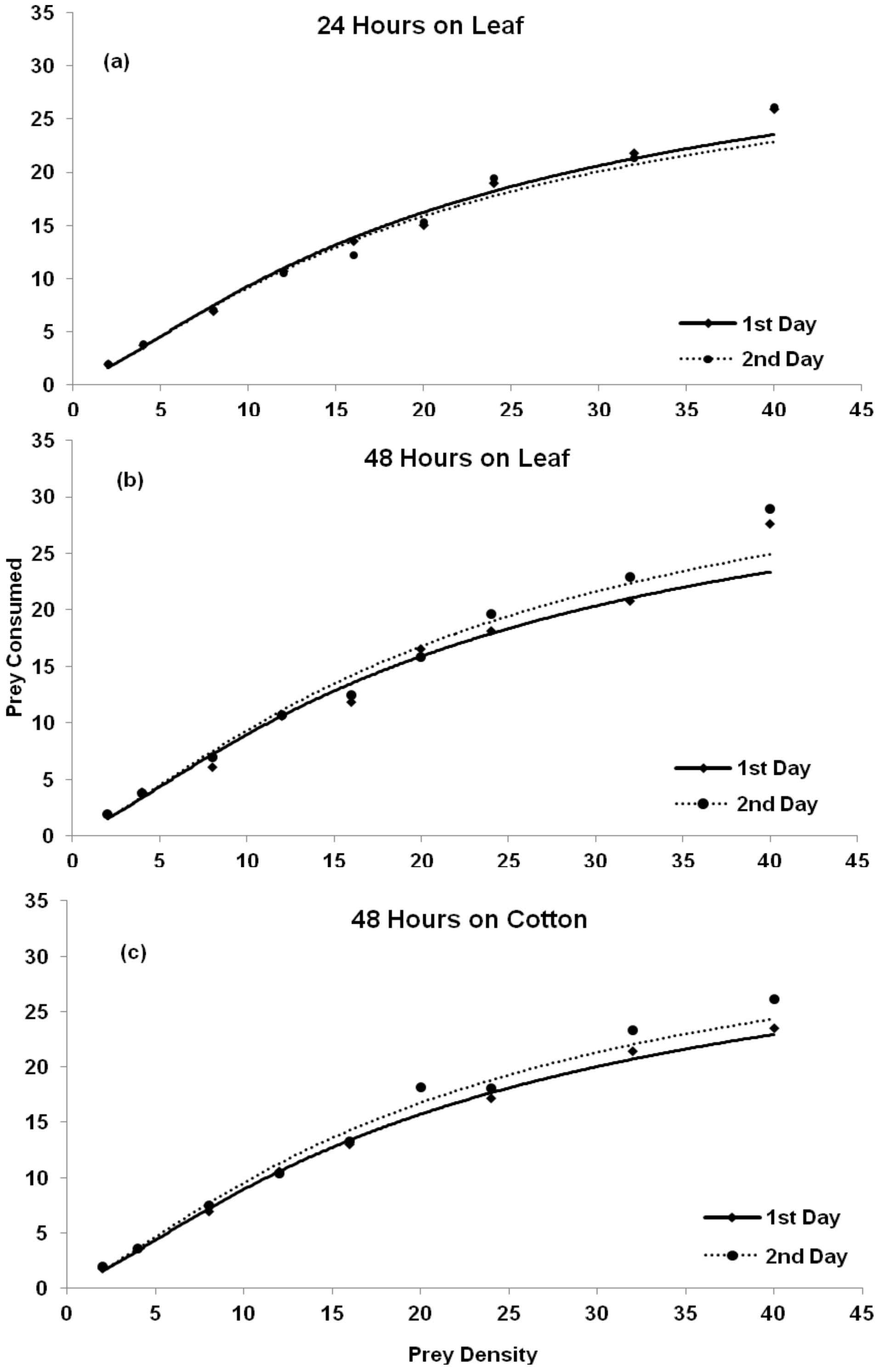

Figure 1. Functional response curves of *M. pygmaeus* when feeding on 2nd instar nymphs of *M. persicae* at different hunger levels (24 and 48 h on leaf; 48 h on cotton) foraging for 1 and 2 days.

the predator did not affect prey consumption and our results further support the potential use of this species as an effective predator since its predatory capacity is not reduced even under conditions of prior intense starvation.

Generally, heteropteran predators can survive without food however specific research on their predatory efficacy at various hunger levels is limited. Gillespie *et al.* (2012) investigated the prey consumption of *D. hesperus* females starved for a period of 1 to 7 days on different plants. Generally, they found that the prey consumption increased with the starvation period however, this was dependent on the plant species. In particular, on pepper, the predation was found almost 2-fold increased with the increase of the starvation period from 1 to 2 days. Plant preference of *M. pygmaeus* was measured by multi-choice host plant selection and pepper appeared rather attractive for *M. pygmaeus*, especially in leaf multi-choice experiments (Ingegno *et al.*, 2011). Additionally pepper has been found the least suitable plant, for this predator survival and reproduction in absence of prey (Perdikis and Lykouressis, 2000; 2004a; 2004b). As in the case of *M. pygmaeus*, pepper was not a suitable plant for *D. hesperus* development. It has been reported that survivorship of nymphs was high but nymphal development time without the presence of prey on pepper plants was low compared with other plants (Sanchez *et al.*, 2004). Moreover, females did not lay any eggs on pepper and consequently this plant was included in the non-host plant group tested. Furthermore, the high increase of prey consumption observed for *D. hesperus* may indicate a stronger effect of hunger on this species than *M. pygmaeus*. Similar results have been reported also by other studies on different predator groups. Starvation had a much more strong effect on prey consumption in the carabid predator *P. cupreus* and larvae after one day starvation consumed nearly twice as much prey compared to unstarved ones (Lovei *et al.*, 1995). *Podisus maculiventris* (Say) (Hemiptera Pentatomidae) also nymphs starved for 9 h showed a higher predation than the satiated ones (Torres *et al.*, 2002). Therefore, it seems that the effect of hunger level is less important for the actual consumption of *M. pygmaeus* compared to other predators. In addition, it may be hypothesized that the common practice of exposing *M. pygmaeus* individuals to starvation for 24 h prior to predation experiments, aiming to standardize their hunger level, may not be required at least on pepper plants, since individuals that starved for 24 h, exhibited similar predation rate to those starved for 48 h on leaf.

It has been shown that functional traits of predators such as the handling time (including searching) and prey digestion influence prey rate capture (Jeschke *et al.*, 2002; Papanikolaou *et al.*, 2014). Since a significantly higher predation was recorded when the predator had deprived of prey and leaf tissue for 48 h, at the prey density of 20 individuals it seems that these attributes are most likely differentially affected by prey density. Likely, at an intermediate prey density such as 20 prey individuals and at the intense hunger level, either each of these traits or both may have been affected leading to this significant effect in predation. These results indicate that discriminating how interacting behavioural attributes are related to the predation rate, is essential information to scale individual feeding process. However more complicated approaches may be explicitly considered when quantifying the effects of hunger level on the predation rates at low and intermediate prey densities.

The female adults of *M. pygmaeus* exhibited a Type II functional response in all the treatments, supporting the findings of previous studies for 5th instar nymphs of this species (Fantinou *et al.*, 2008). The Type II of functional responses are common among predatory heteropterans from varying densities of different prey species and have been reported for *Dicyphus tamaninii* Wagner (Hemiptera Miridae) and *M. pygmaeus* on *Trialeurodes vaporariorum* Westwood (Hemiptera Aleyrodidae) and *Frankliniella occidentalis* (Pergande) (Thysanoptera Thripidae) (Montserrat *et al.*, 2000; Enkegaard *et al.*, 2001; Hamdan, 2006; Lampropoulos *et al.*, 2013), *Aphis gossypii* Glover (Hemiptera Aphididae) (Alvarado *et al.*, 1997), *M. persicae* (Foglar *et al.*, 1990) as well as *Tetranychus urticae* Koch (Acari Tetranychidae) (Foglar *et al.,* 1990), A Type III functional responses have also been reported for *M. pygmaeus* when feeding on first instars or eggs of *T. vaporariorum* (Enkegaard *et al.*, 2001; Hamdan, 2006). The fact that the response type of this predator remained unchanged irrespectively of the hunger levels indicates that the predator foraging mode was not affected by the hunger level and consequently that this predator is well adapted to overcome possible adverse effects of starvation. Therefore, this predator may withstand the stress of prey-non availability at least for the tested periods and reserves may be restored when essential prey becomes available again. According to Messelink *et al.* (2014) this predator species could successfully reduce aphid populations when released prior to an artificially introduced aphid infestation on sweet pepper plants. However, such changes in hunger may alter the energy management (storage and expenditure) of this predator and may have long term physiological effects. Future studies, using more intense levels of hunger, may deliver further valuable results in the effects of hunger level on the prey consumption of this predator.

In conclusion, predation rates and functional responses of *M. pygmaeus* remained unaffected by its hunger level. Thus, according to our results, *M. pygmaeus* can effectively overcome adverse effects of starvation. However, predators conditioned under the most intense hunger level showed significantly lower predation rate at an intermediate prey density, indicating that the level of hunger may affect handling and/or digestion in a manner that interacts with prey density. These outcomes have implications for the potential of a predator to withstand hunger and for its field effectiveness but also for a better understanding of complexities in the effects of hunger on functional responses of predators.

Acknowledgements

This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

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Received June 9, 2015. Accepted September 15, 2015.