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FUNCTIONAL RESPONSES OF *Encarsia perniciosi* (TOWER) AND *Encarsia citrina* (CRAW.) TO *Quadraspidiotus perniciosus* (COMSTOCK) IN RESPONSE TO TEMPERATURE

Bayoumy, M. H.[1,2]; A. I. Abd El-Kareim[2]; A. H. Abdel-Salam[2]; N. F. Abdel-Baky[2] and A. Schopf[1]

1- Forest Pathology and Forest Protection (IFFF), Institute of Forest Entomology, Univ. of Natural Resources and Applied Life Sciences (BOKU), Vienna 1190, Austria.

2- Economic Entomology Dept., Fac. of Agric., Mansoura Univ., B. O. Box 35516, Mansoura, Egypt.

Corresponding author: marsamarium@yahoo.com

ABSTRACT

Prior to the field release of natural enemies in bio-control programs, it is essential to evaluate their efficiency under laboratory conditions. One informative method is the functional response of natural enemy to host density. Moreover, temperature is an important factor that affects the efficiency of bio-control agent. First, the effect of densities of the diaspidid host, *Quadraspidiotus perniciosus* (Comstock) on functional response types of the aphelinid parasitoids, *Encarsia perniciosi* (Tower) and *Encarsia citrina* (Craw.) was examined. Secondly, we examined the temperature-dependent functional response for the *E. perniciosi*. Three temperatures (15, 20, and 25°C) and five host densities (10, 15, 20, 25 and 30 scales) were used. At each temperature, 10 to 30 1st instars were exposed to a female *E. perniciosi* for a 24 h. In the first experiment, the decelerating rate of decrease in the parasitism rate of *E. perniciosi* indicated a type II response, whereas the absence of significant dependence on host density by *E. citrina* indicated a type I response. In the second experiment, *E. perniciosi* exhibited a type II response (inverse-density dependent parasitism rate) at all temperatures. Therefore, releasing the *E. perniciosi* in the beginning of growing season on low host populations can provide more control. The attack rate of *E. perniciosi* increased with increasing temperatures from 15 to 25°C, whereas the handling time decreased. 25°C seems to be the most suitable condition for *Encarsia* activity and reproduction. This implies that *E. perniciosi* is well adapted to relatively moderate temperature, which allows its implementation as a bio-control agent of *Q. perniciosus* during the growing season even in countries of higher latitudes.

Keywords: *Encarsia*, Functional response, Handling time, Instantaneous attack rate.

INTRODUCTION

The San Jose scale, *Quadraspidiotus peniciosus* (Comstock), is an important pest in several countries of the world (*e.g.*, Kozàr *et al.* 1982; Jahn and Polesny 1999; Abdel-Kareim *et al.* 2005). Since 2000, it has been recorded for the first time in Egypt infesting apricot trees (Abdel-Kareim *et al.* 2005), while the first record in Austria orchards goes back to 1931 (Jahn and Polesny 1999). It attacks at least 34 families of hosts (over 700 species) and can be particularly problematic in stone fruits, apple, pear, apricot, and cherry

trees (Kaiser and Sheard 2006). The cosmopolitan polyphagous aphelinid wasp, *Encarsia citrina* Craw. has a worldwide distribution (Malipatil *et al.* 2000). It is a primary, solitary, proovigenic, and thelytokous endoparasitoid (Malipatil *et al.* 2000). It is capable of parasitizing both male and female *Q. perniciosus* (Matadha *et al.* 2005). Baroffio (1997) describes the biology of *Encarsia perniciosi* (Tower), which was introduced for biological control of *Q. perniciosus* in 1949. *Encarsia perniciosi* can attack multiple scale species, but *Q. perniciosus* is the only common host available in our study area. Although successes and failures of *E. perniciosi* in classical biological control for *Q. perniciosus* have been mentioned in different studies (*e.g.*, Jolly 1962; Sahai and Joshi 1965; Neuffer 1990), this study is a first report that concentrates on the suitability of *E. perniciosi* for using it in management for *Q. perniciosus*.

Prior to the release of natural enemies in a biological control program, it is essential to evaluate their efficiency under laboratory conditions. One informative method for assessing the efficacy of natural enemies is the study of their foraging behavior including functional response (Fathipour *et al.* 2006; Bayoumy 2009). Functional response is the number of hosts successfully attacked per parasitoid as a function of host density (Solomon 1949). It is a commonly measured attribute of natural enemies. Practitioners of inundative biological control may use functional response to estimate the appropriate numbers of biological control agents to be released in order to bring about an immediate reduction in pest numbers (Mills and Lacan 2004). Holling (1965) proposed three types of functional responses: type I, a linear rise to a plateau; type II, a curvilinear rise to a plateau; and type III, a sigmoid curve rising to a plateau which then levels off under the influence of handling time or satiation (Hassell 2000). Among the types of functional responses, type II and III have received the most attention (Allahyari 2004). Holling (1961) divided the functional response into several basic and subsidiary components. The attack rate (a) can be considered to be a function of: (1) the reaction distance of the parasitoid, i.e., the maximum distance at which the parasitoid will react by attacking host; (2) the speed of movement of parasitoid and host; and (3) the proportion of attacks that are successful. The handling time (T_h) can be considered to be a function of: (1) the time spent pursuing an individual host; (2) the time spent investigating and probing each host; and (3) the time spent drilling each host. The time as host and parasitoid exposure (T) can be considered to be a function of: (1) time in non-ovipositing activities; and (2) time in ovipositing-related activities (*i.e.*, T_h).

Climatic adaptation is an important criterion for selecting potential biological control agents (van Lenteren 1986). Although field-testing of natural enemies for the selection for climatic adaptation can be very time consuming, especially if several candidates are involved, laboratory and greenhouse studies are useful for choosing a suitable candidate (Pak and van Lenteren 1988). Ambient temperature is an important factor influenced the functional response of a natural enemy (Pakyari *et al.* 2009). Lack of success in biological control programs has often been caused by high mortality of natural enemies due to climatic extremes (van Driesche and Bellows 1996). Bayoumy *et al.* (2009) studied the influence of temperature on the searching rate of *E. citrina*, while no detailed information has been reported on *E.*

perniciosi. Up to now, the role of natural enemies in the management of *Q. perniciosus* in Egypt is low due to the influence of temperature on the synchronization between developmental cycles of *Q. perniciosus* and its parasitoids (Abdel-Kareim *et al.* 2005), resulting in high dispersal of the insect to other hosts and regions (Moursi *et al.* 2008). The best way to judge the quality of a natural enemy for the future biocontrol programs is evaluating its efficiency against the pest in one of the native homelands prior to its introduction in a new area (like Egypt). Through the comprehensive evaluation for parasitoids of *Q. perniciosus* in Egypt and followed in Austria for selecting the parasitoid which could be provide more control, functional response in response to temperature was used to determine the most suitable temperature for the efficient parasitoid, *E. perniciosi*. First, an experiment was conducted to determine the functional response type of *E. perniciosi* and *E. citrina*. Next, based on the data of the first study, the temperature-dependent functional response of *E. perniciosi* to *Q. perniciosus* was evaluated. The results from this study might be contribute in the understanding of the response of *E. perniciosi* to *Q. perniciosus* under different environmental conditions, and thus this will useful be in development of future mass rearing and bio-control programs.

MATERIALS AND METHODS

1. Source of parasitoids and colony maintenance

Laboratory colonies of *E. perniciosi* and *E. citrina* were started by obtaining individuals from *Q. perniciosus* infested apple trees, located in the university farm and from euonymus scale, *Unaspis euonymi* (Comstock)-infested Japanese euonymus, *Euonymus japonicus* (L.), located in the home gardens of Vienna, respectively. Small colonies of the parasitoid species were reared on infested green apple fruits with *Q. perniciosus* in plastic boxes (10×5×10 cm) in temperature controlled cabinets at 20±1°C and 16:8 (L:D photoperiod). Each box contained one apple fruit. To rear each parasitoid species, 10 apple fruits harbored 5–10-day-old scales were exposed to wasp oviposition by 20 females (2 female/fruit) of *E. perniciosi* and 100 females (10 female/fruit) of *E. citrina* every three days to maintain a constant colony source. Water was provided in 5-ml plastic cups with cotton wicks and honey streaked on small self-adhesive paper strips to serve as a food source for the parasitoids. Parasitoids were obtained by isolating them in the pupal stage within the host body from apple fruits bearing parasitized scales using a pin and a small camel's- hair brush. Because *Encarsia* is an endoparasitoid, pupae within host body could be isolated from host plant material without disrupting their development. Scale covers were lifted with an insect hand pin, and when a parasitoid pupa was found, it was picked up with a small camel's hair brush and placed in small plastic tubes (3 cm in height and 0.5 cm in diameter) provided with honey on its cover. The tubes were marked and kept in the laboratory until adult emergence.

2. Functional response type of *E. perniciosi* and *E. citrina*

Through the peak of crawler (*i.e.*, 1st instar) emergence, unknown numbers of *Q. perniciosus* crawlers were transferred to non-infested green

apple fruits using a small hand pin in the same day of their emergence. Two days later, the fruits were investigated to determine the numbers of settled 1st instar. Scales in excess of the specified densities (5, 10, 15, 20 and 25 scales/fruit) were removed.

The female wasps (48 h old) were released on fruits infested with *Q. perniciosus*. *E. perniciosi* was released when the host was 3-8 days- old (Sahai and Joshi 1965) and *E. citrina* was released when the host was 10 days old (Matadha *et al.* 2005; Bayoumy *et al.* 2009). Five densities of scale insect (5, 10, 15, 20, and 25) were chosen for determining the functional response of the two parasitoid species. Each parasitoid female was released on each host density in plastic boxes (10×10×20 cm) for 24 h at room temperature (23/14°C Max.:Man.). Each box contained one fruit infested with the required numbers of host. Each treatment was replicated ten times. To measure the parasitism, following the removal of the female parasitoids, the exposed scales were incubated at 25±1°C and 16L: 8D photoperiod until the pupal stage (≈17 d) of the parasitoid. Each parasitoid selected for the experiment was used only once. Only replicates with the parasitoid surviving within 24 hr. were used to determine the functional response. In this experiment, we sought to select the wasp has an effective type of response to study its temperature-dependent functional response in the next step.

3. Temperature-dependent functional response of *E. perniciosi*

Influence of three temperatures (15, 20, and 25°C) and host densities (10, 15, 20, 25, and 30 individuals) on progeny distributions for females of *E. perniciosi* was evaluated. One active female (48 h old) was transferred to each density of *Q. perniciosus* at each temperature in the above mentioned boxes for 24 hr ovipositing period. Each box contained one apple fruit and each treatment was replicated five times. Following the removal of the female parasitoids, the exposed scales were incubated at 25±1°C and 18:6 h (L: D photoperiod) until the parasitoid's egg developed to the pupal stage.

4. Data processing and analysis

To determine the type of functional response, the data were fitted to a linear model ln [p/(1-p)] $\alpha + \beta N_0/P$ (i) using SPSS 15.0 for windows (SPSS 2006) to establish the relationship between the proportion of host scales attacked ($p=N_a/P$) to scale density per parasitoid (N_0/P) (Trexler *et al.* 1988; Mills and Lacan 2004). The absence of a significant dependence of p on N_0/P is attributed to a type I response, a significant negative dependence to a type II, and a positive dependence to a type III response (Mills and Lacan 2004).

Type I (Nicholson and Bailey 1935): $N_a /P= N_0/P \{1-\exp(-aP)\}$ (ii) for $N_0 \leq bP/a$ and $N_a/P=b$ for $N_0>bP/a$ and type II (Holling 1959): $N_a=aTN_0/1+aT_hN_0$ (iii), where N_a is the number of scale insects attacked, N_0 is host scale density available, P is parasitoid density, a is instantaneous attack rate or area covered by a parasitoid in a given amount of time (1day), and b is the maximum number of scales that can be attacked in the given time. For type I functional response (for $N \leq bP/a$), the parameter *a* was estimated by nonlinear least square regression by fitting the type I model to data between 5 and 20 hosts and the parameter *b* (for $N>bP/a$) was estimated from the mean numbers of scale insects attacked (N_a) at host

density of 30 (Mills and Lacan 2004). The handling time of *E. citrina* could be estimated using the relationship $b = T/T_h$ (Getz and Mills 1996).

Data analysis for studying the influence of temperature on functional response of *E. perniciosi* includes two steps (Juliano 2001; Mohaghegh *et al.* 2001): (1) the shape (*i.e.*, the type) of functional response must be determined. Usually, it is difficult to discriminate between type II and III functional responses (Trexler *et al.* 1988). Trexler *et al.* (1988) showed that logistic regressions of proportion of hosts parasitized (N_a) against the number of hosts offered (N_0) provided a more powerful and accurate means of distinguishing between type II or III functional responses compared to analysis of the typical functional response curve (*i.e.*, N_a against N_0). Briefly, to determine the shape of functional response, a polynomial regression (Juliano 2001) is fitted to observed proportions of scales parasitized N_a against N_0 at each temperature, and the shape of this polynomial fit is determined. If the proportion parasitized initially increases with the number of hosts, this is sufficient to identify a type III functional response. If, on the other hand, the proportion parasitized declines monotonically with the number of hosts, this is sufficient to identify a type II response. The polynomial function was fitted to the data on the proportion of scale attacked as.

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

Where the parameters P_0, P_1, P_2, and P_3 are the constant, linear, quadratic, and cubic parameters, respectively, related to the slope of the curve. The sign of P_1 and P_2 can used to distinguish the shape of the curves (Juliano 2001). The slope of P_1 for type III is accelerating [*i.e.*, a significant positive linear parameter (P_1) and a negative quadratic parameter (P_2)] and the type II is declining [*i.e.*, a significant negative linear parameter (P_1)]. (2) after the determination of the shape of the curve (*i.e.*, type), the parameters a (the coefficient of attack rate), T_h (handling time), and b (the asymptote of functional response curve or the maximum number of hosts parasitized) of type II response were estimated using the disc equation (the most widely used model for describing the functional response of parasitoid / predator) given by Holling (1959) as mentioned above and using SPSS procedure.

To study the effect of temperature and host densities (*i.e.*, second experiment) and their interaction on proportion of scale parasitized per female and day by *E. perniciosi*, two-way followed by one-way ANOVA was performed. Both ANOVA were followed by least significant difference at α=0.05 comparisons using Duncan's Multiple Range test. Statistics were conducted using CoStat 6.3 software for windows (CoStat 2005).

RESULTS

1. Functional response type of *E. perniciosi* and *E. citrina*

The analysis of the proportion of San Jose scales attacked (p) by *E. citrina* at different scale density (N_0/P) showed no significant dependence ($F_{1,4}$=7.84; P>0.05) (Fig. 1a) indicating a type I functional response by the parasitoid (Fig. 1b). On the other hand, *E. perniciosi* showed a significant negative dependence ($F_{1,4}$=81.4; P<0.001) of the proportion of scales

attacked on scale density (Fig. 1a) indicating a type II response (Fig 1b). With increasing host density, *E. perniciosi* significantly parasitized higher proportions of *Q. perniciosus* than *E. citrina* (Fig. 1; $P<0.001$). On average, *E. perniciosi* parasitized 43% of *Q. perniciosus* compared to 18% by *E. citrina*.

The estimated values of instantaneous attack rate (a) and handling time (T_h), and maximum number of parasitized scales using Nicholson and Bailey (*i.e*, type I) and Holling (*i.e.*, type II) equations were 0.19±0.01, 6.08±0.51 hr., and 3.95±0.51scales ($r^2=0.93$) for *E. citrina* and 1.56±0.41, 3.81±0.39 hr, and 6.31±0.64 scales ($F_{1,24}=15.86$; $P=0.03$; $r^2=0.84$) for *E. perniciosi*, respectively.

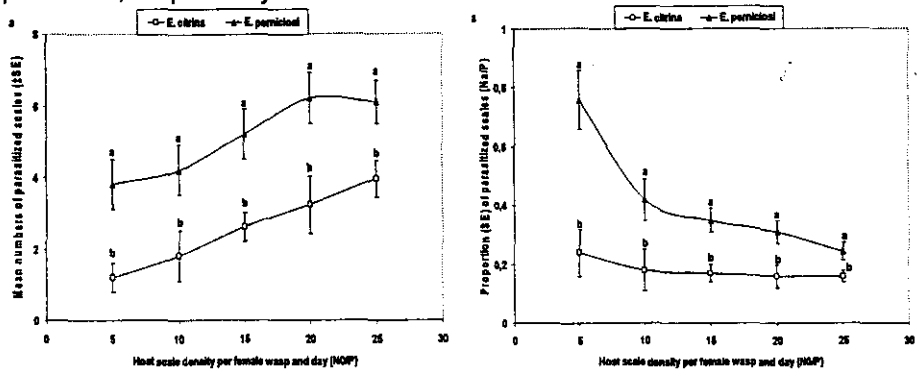

Fig. 1. Functional response curves (a) and proportion of parasitized scales (b) by *E. citrina* (type I) and *E. perniciosi* (type II) at various host density of *Q. perniciosus*. Comparisons labeled with the diverse letters are significantly different (P<0.001).

2. Temperature-dependent functional response of *E. perniciosi*

By increasing temperature and host density, the number of scales parasitized by *E. perniciosi* increased (Fig. 2a-c). Correspondingly, the proportion of scales parasitized decreased as the number of available scales increased (Fig. 2d-f). The accelerated decrease in the proportion of *Q. perniciosus* scales parasitized in relation to the host density and temperature best-fitted the description of a type II functional response. At the three tested temperatures, the significant negative parameter of P_1 suggested that the slopes of the functional response curves were declining, which is characteristics of a type II functional response (Table 1). By plotting a type II functional response model to the number and proportion of scales parasitized at each tested temperature, the lines fitted well the data (Fig. 2). Therefore, the Holling's model was fitted separately for each experimental temperature in order to measure the attack rate and handling time.

The daily rate of oviposition per female of *E. perniciosi* was significantly increased when temperature and host density increased ($P<0.001$). Moreover, there was significant effect of temperature by host density interaction on numbers of progeny was performed ($P<0.05$). The rate of oviposition by *E. perniciosi* was higher at 25°C than those at 15 and 20°C

(Fig. 3a). At 25°C, by increasing host density, the oviposition rates significantly increased (P<0.001; Fig. 3b).

The instantaneous attack rate (a) and the estimated maximum number of scales parasitized (b) by *E. perniciosi* increased with increasing temperature from 15 to 25°C. Correspondingly, the handling time (T_h) for *E. perniciosi* tended to decrease as temperature increased (Table 2).

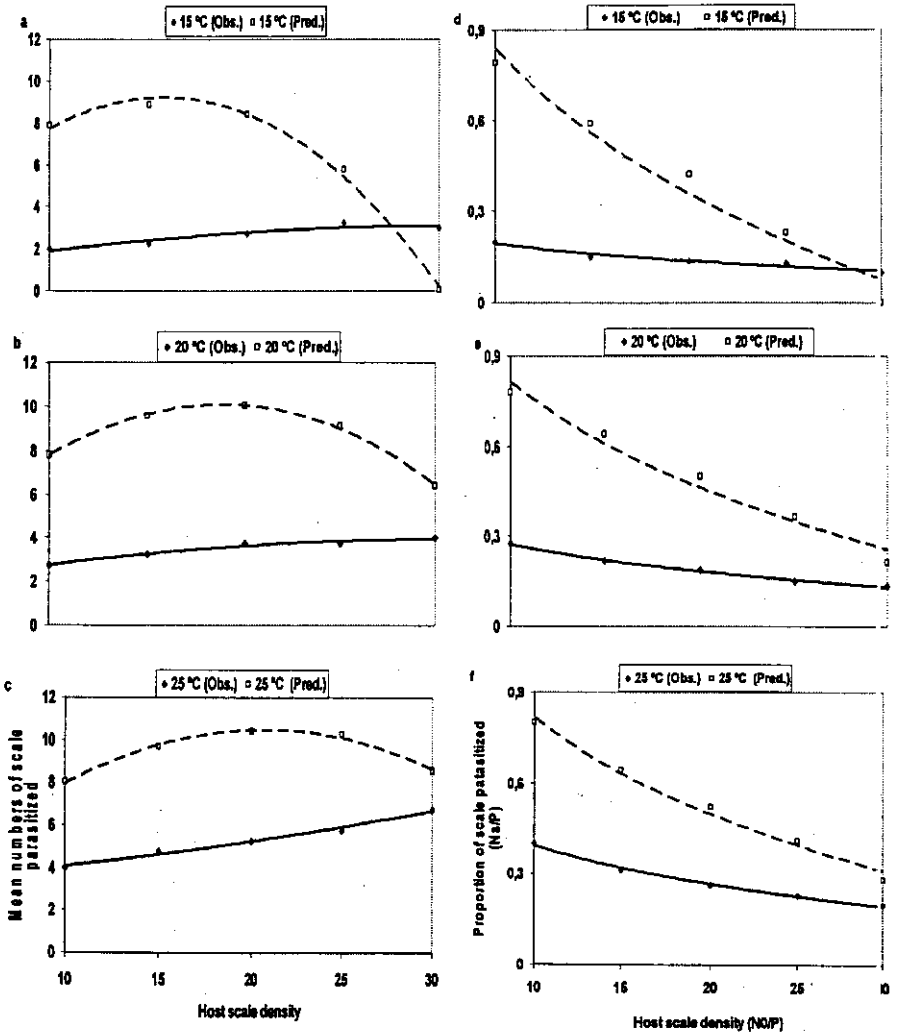

Fig. 2. Mean numbers (a-c) and proportion (d-f) of *Q. perniciosus* scales parasitized by *E. perniciosi* (N_a/P) in relation to different host densities (N_0/P) and temperatures. The solid (observed) and dashed (predicated) lines represent the best-fitted type II functional response curves (a) and logistic regression models (b) for parasitoids attacking *Q. perniciosus* at different experimental temperatures.

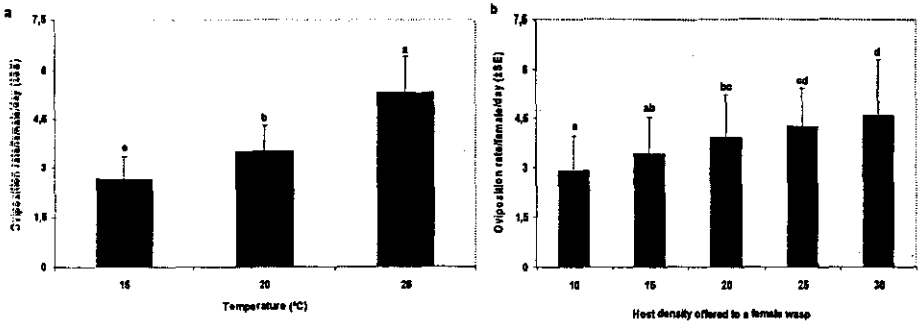

Fig. 3. Daily oviposition rate by *E. perniciosi* female at different temperatures (a) and host densities (b) at 25 °C. Values labeled with the diverse letters are significantly different (P<0.05).

Table 1: Polynomial regression analysis between proportion of *Q. perniciosus* scales parasitized by *E. perniciosi* (N_a) and the initial numbers of hosts (N_0) at different tested temperatures.

Temperature (°C)	Parameters	Estimates± SE	*P*
15	Constant (P_0)	0.53±0.01	0.02
	Linear (P_1)	-0.054±0.002	0.01
	Quadratic (P_2)	0.003±0.0	0.07
	Cubic (P_3)	-4.0E-005±0.0	0.02
20	Constant (P_0)	0.43±0.11	0.16
	Linear (P_1)	-0.04±0.002	0.003
	Quadratic (P_2)	0.0±0.0	0.005
	Cubic (P_3)	-2.7E-006±0.0	0.09
25	Constant (P_0)	0.33±0.03	0.11
	Linear (P_1)	-0.034±0.006	0.014
	Quadratic (P_2)	0.001±0.0	0.001
	Cubic (P_3)	-4.7E-005±0.0	0.02

The significant negative estimate for the parameter of P_1 indicates that the slope of the functional response curve is declining for *E. perniciosi*, thus a type II functional response at different temperatures (Mills and Lacan 2004).

Table 2: Estimates (±SE) of instantaneous attack rate (a), handling time (T_h), and maximum number of scale parasitized (b) for type II response of *E. perniciosi* parasitizing *Q. perniciosus* as host derived from Holling's model (T=1 day).

Temperature (°C)	A	T_h, hr.	$b=T/T_h$	*F*	*P*	R^2
15	0.32±0.06	4.08±1.57	5.46±1.88	22.15	0.02	0.88
20	0.56±0.32	3.52±1.4	6.24±2.6	67.43	0.004	0.92
25	1.13±0.39	3.33±0.31	7.29±0.64	43.19	0.007	0.94

DISCUSSION

1. Functional response type of *E. perniciosi* and *E. citrina*

A type II functional response is the most common type reported for most parasitoids (Matadha *et al.* 2005). In the current study, *E. perniciosi* exhibited a type II functional response, whereas *E. citrina* exhibited a type I response. The present results for *E. perniciosi* and *E. citrina* are similar to those reporting type I and II responses for the lab strain of *Enarsia* sp. nr.

diaspidicola (Silvestri) and for the field strain of *E. citrina* (Matadha *et al.* 2005). Our results are the first to show a type II functional response for *E. perniciosi* which attacking *Q. perniciosus*. Although a parasitoid with a linear response does not exhibit the theoretical potential for control of the host required for classical biological control, the presence of a linear response is important for the continued interaction of the host and parasitoid (Hassell 1978). Parasitoids or predators that impose positively density dependence host mortality (*i.e.*, type III) are supposed to manage the host population (Murdoch and Oaten 1975; Fernández-Arhex and Corley 2003). However, certain parasitoids and predators exhibiting type II response (*i.e.*, inversely density dependent mortality) have been successfully established and managed host populations (Fernández-Arhex and Corley 2003). Hassell (1985) modeled the situation where parasitism rates are inversely density dependent in space. This pattern is thought to arise from a combination of little or no aggregation to high patch densities and handling time or egg limitation constraints. Provided the inverse density dependence is strong enough, this mechanism can stabilize host-parasitoid models.

In the current study, host density significantly influenced the proportion of scales parasitized by *Encarsia* spp. Previous studies reported that *Aphytis* species are highly dependent on climate and less on the host scale, whereas the reverse applies to *Encarsia* species (Rosen and Huffaker 1983). An attempt to determine the most efficient parasitoid of *E. perniciosi* and *E. citrina* was conducted using the functional response. We found that *E. perniciosi* is more effective than *E. citrina* in attacking greater proportions of scales as scale density increased. In average, the proportion of scales parasitized by *E. perniciosi* was more than double that of *E. citrina*. Jahn and Polesny (1999) in Austria reported that *E. perniciosi* is a more effective parasitoid of *Q. perniciosus* than *Aphytis* sp. under field conditions.

2. Temperature-dependent functional response of *E. perniciosi*

The information about the maximum daily rate of oviposition by *E. perniciosi* is lacking. Therefore, in the first experiment (*i.e.*, effect of host density on functional response type), we used densities like those used by Matadha *et al.* (2005). However, based on the data obtained from the first experiment, we changed the host densities in the second experiment (*i.e.*, effect of temperature on functional response of *E. perniciosi*) because we found that a female *E. perniciosi* parasitized more than 75% of hosts at 5 scales/fruit. Accordingly, we increased the tested densities of *Q. perniciosus* to 10, 15, 20, and 30 scales/fruit. Moreover, we used 15, 20 and 25°C like the average temperatures during seasons of activity for *E. perniciosi* under Austrian field conditions (*i.e.*, autumn, spring, and summer, respectively).

Our results reveal that the type of response for *E. perniciosi* (*i.e.*, type II) did not alter with changing temperature. No study has been conducted on the functional response of *E. perniciosi* to *Q. perniciosus* at a range of temperatures. Temperature and host density significantly affected the daily reproductive rate of *E. perniciosi*. The highest oviposition rate was obtained at 25°C, and thus this condition seems to be more suitable for its activity and reproduction. The lowest rate was obtained at 15°C. This implies that this condition not optimal for its searching and activity and appears to be near

lower temperature thresholds for its oviposition. Danne *et al.* (2004) found that the lower and upper developmental threshold for *E. perniciosi* was 13 and 33°C, respectively. The estimation of a temperature threshold for development and oviposition is essential for understanding the effectiveness of *E. perniciosi* in controlling *Q. perniciosus* populations under cooler temperature conditions. Our study in addition to Danne's study (Danne *et al.* 2004) confirms that *E. perniciosi* is unable to reproduce at temperatures below 15°C. Although *E. perniciosi* can parasitize at 15°C, such temperature may not be favorable for egg maturation and oviposition. Likewise, 15°C was not optimal condition for *E. citrina* reproduction on *Hemiberlesia rapax* (Comst.) (Logan and Thompson 2002). *E. citrina* females survived for longer durations at 15°C (34 d), but they did not contribute significantly toward scale parasitism because of their proovigenic condition (Huffaker 1990).

The exactness of functional response in several previous studies is highly related to models and data analysis; the use of inappropriate models and methods of analysis may result in an incorrect estimation. Although the logistic model (Juliano 2001) easily illuminates the subtle differences in the type II and III responses, it fails to discriminate them from type I. Hence, efforts are needed to make a similar logistic model to differentiate type I from II and III. Ecologists normally face difficulties in determining functional response when the curve lies between type II and III. Hence, a suitable analysis that can best determine the functional response is highly needed, as it is of great practical relevance in estimating the bio-efficacy of natural enemy (Trexler *et al.* 1988). *E. perniciosi* has a type II response in the first experiment, and thus in the second experiment we directly used a logistic regression model using polynomial function to determine the correctness of the shapes (*i.e.*, type) of *E. perniciosi* at different temperatures. For a type II response, there should be a decline in the proportion of parasitized hosts as the density increases, so that the linear term should be negative. The significant negative values for the linear parameter obtained in this study at different temperatures confirm the type II response for *E. perniciosi*.

Although Holling's disc equation (1959) is widely used to estimate parameters of type II functional response, some authors emphasize on the limitation of Holling's disc equation, and suggest Roger's random parasitoid/predator equation (1972) as an alternative, which is more appropriate when prey depletion (for a predator) or re-encounter (for a parasitoid) may be occurs during the experiment (Juliano 2001). Holling's disc equation can be used only when Roger's model does not enable the researcher to estimate valid parameters. For example, Mohaghegh *et al.* (2001) used Holling's model because Rogers's model provides invalid parameters for their data set. Similarly, Holling's model adequately described the decrease in parasitism rate with increasing host density at all experimental temperatures, and thus provided valid parameters for our data set. Holling's model is really designed for predators, however it is appreciate for proovigenic parasitoids (Chong, JH., personal communication).

The instantaneous attack rate and handling time were defining parameters of type II responses for *E. perniciosi* at different temperatures. The values of instantaneous attack rate and handling time differed when

exposed to different temperatures, which indicated that they have different abilities to respond to increase host densities at different temperatures. This indicates that parasitoids exhibiting similar functional response curves (i.e., type) under different conditions cannot be deemed to respond similarly *E. perniciosi* has the highest instantaneous attack rate and the shortest handling time at 25°C. This reveals that the parasitoid will spend a larger amount of time with non-searching activities (*e.g.*, resting) at lower temperatures, while more searching and activity would be expected at higher temperatures. As consequence, *E. perniciosi* parasitized more hosts at 25°C, and thus *E. perniciosi* seemed to be an effective candidate to control *Q. perniciosus* from late spring to early summer in Austria and Egypt, where the temperature is frequently around 25°C. Handling time is a general term that includes time for killing a prey or antennating and parasitizing a host, time for resting, preening and time for water ingestion (or sap feeding in parasitoids). We cannot determine how *E. perniciosi* allocates time to different non-foraging activities.

The handling time derived from the first experiment for *E. perniciosi* was similar to that measured from second experiment at 25°C. However, the instantaneous attack rate was differed. The difference may be the influence of rh% or the differences in host densities between both experiments. It appeared that the parasitoids' handling times derived from the functional response models for *E. perniciosi* tended to be overestimated because the parasitoids did not spend all the available time in foraging but often engage in other activities (*e.g.*, searching, feeding, grooming, and resting). Thus, it is essential to obtain actual handling time through behavioral observation. Direct observations showed a female usually took about 32-37s (n=10) to oviposit in a host; this value was much lower than that obtained from the experimental data at each temperature. This was the case, because the estimated time not included the time of non-searching activities.

The efficiency of a parasitoid from laboratory-derived functional response data reflects the potential of *E. perniciosi* as a bio-control candidate. Pak and van Lenteren (1988) mentioned that strains that showed a high potential in the laboratory also have the ability to perform well in the field. However, we caution that because the observed pattern may be an experimental artifact, i.e. unnatural (Kareiva 1990) due to the differences in the size of the area parasitoids have to search to find hosts (O'Neil 1989), and thus not reflecting the true effect of parasitoid on its host population in the field (van Lenteren and Bakker 1978). Such studies are, however, useful in providing the first step for comparing the efficiency of different species/strains (Overholt and Smith, 1990) and also provide a valid means of comparing host finding abilities of candidate natural enemies (Munyaneza and Obrycki, 1997).

Due to the inversely density-dependent parasitism for *E. perniciosi* in response at 25°C, it seems to be more effective in low host densities and relatively moderate temperature and this result has to be considered in future bio-control and mass rearing programs. Hence, releasing the parasitoid in the beginning of growing season on low host populations or using the chemical pesticides to reduce the host population before its release might provide more control. The data obtained here at constant temperatures will provide a

direction for future research on evaluating the impact of *E. perniciosi* in infested fruit orchards under variable environment conditions. Further studies are highly needed to determine the effect of host stage and parasitoid's age on response of *E. perniciosi* under laboratory conditions. Moreover, under field conditions, factors such as large searching arenas (Wiedenmann and O'Neil 1991), effect of common predators like as ants and spiders, and spatial complexity (Kareiva 1990) may adversely influence the effectiveness of natural enemies. By understanding these interactions, we will be able to develop suitable strategies for the future bio-control of *Q. perniciosus*.

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الإستجابات الوظيفية لطفيل *Encarsia citrine* و *Encarsia erniciosi* لحشرة سان جوزيه القشرية *Quadraspidiotus perniciosus* مع التركيز على درجة الحرارة

محمد حسن بيومي[1،2]، عبد الستار ابراهيم عبد الكريم[2]، عادل حسن عبد السلام[2]، نجدى فاروق عبد الباقى[2] و Axel Schopf[1]

١- معهد حشرات وأمراض ووقاية الغابات - جامعة المصادر الطبيعية و علوم الحياة التطبيقية - فيينا ١١٩٠- النمسا

٢- قسم الحشرات الإقتصادية - كلية الزراعة - جامعة المنصورة - مصر

من الضرورى قبل استخدام الأعداء الطبيعية فى برامج المكافحة البيولوجية تقييم فاعليتها تحت الظروف المعملية. تعتبر الاستجابة الوظيفية للعدو الطبيعى تجاه كثافة العائل من الطرق الهامة فى التقييم. كذلك تعتبر الحرارة من أهم العوامل التى تؤثر على فاعلية العدو الطبيعى. أولا تم دراسة تأثير كثافة حشرة سان جوزيه القشرية على نموذج الاستجابة الوظيفية لطفيل *Encarsia perniciosi* و *Encarsia citrina*. ثانيا تم دراسة تأثير الحرارة على الاستجابة الوظيفية لطفيل *E. perniciosi* وذلك باستخدام ثلاث درجات حرارة (١٥ و ٢٠ و ٢٥م°) وخمس كثافات للعائل (١٠ و ١٥و ٢٠و ٢٥و ٣٠ فرد/طفيل). على كل درجة حرارة تم تعريض ١٠-٣٠ فرد عمر أول لأنثى الطفيل لمدة ٢٤ ساعة. فى التجربة الأولى كان الانخفاض البطئ فى معدل التطفل بـ *E. perniciosi* يشير إلى نموذج الاستجابة من النوع الثانى (II)، فى حين أن غياب الاعتماد المعنوى على كثافة العائل لطفيل *E. citrina* يشير إلى النموذج من النوع الأول (I). فى التجربة الثانية أبدى طفيل *E. perniciosi* استجابة من النوع الثانى على كل درجات الحرارة المختبرة. ولذلك فأن أطلاق الطفيل فى بداية موسم النمو على تعدادات العائل المنخفضة ربما تعطى مكافحة أعلى. لوحظ زيادة معدل الهجوم لطفيل *E. perniciosi* مع زيادة درجة الحرارة من ١٥ إلى ٢٥ م°، فى حين أن وقت الأداء أنخفض. لذلك فأن ٢٥ م° تبدو أنها الأكثر ملائمة لنشاط وإنتاج الطفيل. وهذا يشير هذا إلى أن الطفيل أكثر تأقلما فى درجات الحرارة المتوسطة نسبيا والتى تسمح باستخدامه كعامل مكافحة بيولوجية ضد الحشرة خلال موسم النمو حتى فى البلاد ذات خطوط العرض العالية.