Predation of *Bradysia* sp. (Diptera: Sciaridae), *Liriomyza trifolii* (Diptera: Agromyzidae) and *Bemisia tabaci* (Hemiptera: Aleyrodidae) by *Coenosia attenuata* (Diptera: Muscidae) in greenhouse crops

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Abstract. We studied the predation behaviour of the "hunter fly" (*Coenosia attenuata* Stein) in the laboratory and greenhouse. In the laboratory, which was conducted at 25°C at 60–80% RH, with a 16L: 8D photoperiod, we examined the functional response of this species to three different pests, namely the sciarid fly (*Bradysia* sp.), the tobacco whitefly (*Bemisia tabaci*) and the leaf miner *Liriomyza trifolii*. In the greenhouse, we studied the population dynamics of the predator and its prey on pepper and water melon crops grown in southern Spain. Adult hunter flies were found to exhibit a type I functional response to adult sciarid flies and whiteflies, but a type II response to adult leaf miners. The type II response was a result of the greater difficulty in capturing and handling leaf miners compared to the other two species. The dynamics of the predator-prey interaction in the greenhouse revealed that the predator specializes mainly on adult sciarids and that the presence of the other prey can be supplemental, but is never essential for survival of the predator; this, however, is crop-dependent. The results on the dynamics of the predator-prey systems were obtained through a known population dynamics model with modifications.

INTRODUCTION

Coenosia attenuata Stein is a polyphagous predator occurring in the Palaearctic region (Henning, 1964). In the last decade this species, which is commonly known as the hunter fly, has been reported to have spontaneously colonized a number of crops outdoors and in greenhouses in Germany (Kühne, 1998), Spain (Rodriguez & Aguilera, 2002), Italy (Colombo & Eördegh, 1991), Portugal (Prieto et al., 2003), France (Martinez & Cocquempot, 2000), Turkey (Polh et al., 2003) and Egypt (Henning, 1964). The hunter fly has also been reported from the USA, where it was probably introduced accidentally (Hoebeke et al., 2003; Sensebach et al., 2004).

C. attenuata adults can feed on a wide variety of insects of their own or smaller size, including adults of the sciarid Bradysia sp., whiteflies [Bemisia tabaci (Gennadius) and Trialeurodes vaporariorum (Westwood)] and adult leaf miners (Liriomyza spp.). The larvae attack immature arthropods in the soil, particularly sciarid larvae (Kühne, 2000). The hunter fly exhibits a unique behaviour as regards capturing other insects. In greenhouses, it can be found standing on a framework tube, wire or plant until it detects a prey flying nearby. It takes flight, using its front legs to capture the prey in the air, and then returns to the starting point to handle and feed on the prey (Kühne, 1998).

This predator has been widely detected in greenhouses in southern Spain. Its abundance depends on the soil type and the type and frequency of pesticide treatments; thus the hunter fly is more commonly found on crops grown in sand than semi-hydroponically, and on crops grown using biological or integrated control rather than on conventionally controlled crops (Téllez & Tapia, 2005). *C. attenuata* is a potentially effective biological control agent for sciarids and whiteflies in greenhouses; however, the optimum conditions for mass rearing this species remain to be established (Kühne, 1998; Morechi & Colombo, 1999). This may restrict the potential of the predator for periodic releases, whether inundative or inoculative, though not for conservation biological control.

Tests to identify functional responses have been widely used to assess the potential of natural enemies for controlling pest species (Cabello & Vargas, 1988; Jervis & Kidd, 1996; Hawkins & Cornell, 1999; García-Martín et al., 2006) and for an overview of the biological significance of Holling' response curves see Cabello et al. (2007). The calculated estimates of the parameters of the curves can be used in combination with how feasible it is to mass rear the species concerned to assess whether it is possible to develop effective biological control strategy for greenhouse crops. The aims of this work were to elucidate, via laboratory tests, the functional responses of the predator to the density of most frequent pests present in the green-

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house crops studies and to assess the utility of the results for predicting the impact of the predator on the population dynamics of the pests under commercial greenhouse conditions.

MATERIAL AND METHODS

Functional response

We examined the functional response of the predator to three different prey species, namely: *B. tabaci, Liriomyza trifolii* (Burgess in Comstock) and *Bradysia* sp. To this end, we used a completely randomized design involving a single factor (viz. adult prey density). The initial number of prey supplied per 50.3 cm² (the area of a leaf disc, see below) was 5, 10, 15, 20, 25, 30, 45, 100 and 150 adult whiteflies; 5, 15, 30, 45 and 60 adult leaf miners and 5, 10, 20, 30 and 50 adult sciarids.

Adults of *C. attenuata* and *Bradysia* were collected from greenhouse crops in Almeria (southern Spain) using a hand-held battery-powered aspirator. Adult *B. tabaci* were supplied by Koppert Biological Systems and *L. trifolii* adults were reared on bean plants in pots under laboratory conditions, using the methodology of Téllez (2003).

The field-collected *C. attenuata* adults were transferred to the laboratory for sexing; only females were used in the tests. The individual females were isolated in glass vials 8 cm long and 8 cm in diameter, furnished with a metal cap having metal mesh covering a ventilation hole 3 cm in diameter. An 8 cm diameter leaf disc (i.e. 50.3 cm^2 in area) of *Phaseolus vulgaris* was placed on a 1-1.5 cm thick layer of 2% agar to maintain the turgidity of the leaf disc throughout the test. Experimental conditions of $25 \pm 1^{\circ}\text{C}$, 60-80% RH and a 16L: 8D photoperiod were maintained in a climatic cabinet. The specimens were kept unfed under such conditions for 24 h, after which the different prey were introduced in the vials for each studied density.

After 24 h, the prey were examined under a binocular microscope, and decapitation or the presence of a ventral incision in the prey were the criteria used to identify that predation had occurred.

The numbers of prey killed were subjected to analysis of variance. Means were compared by the LSD test (P = 0.05), using the software SPSS v. 15 (SPSS, 2006). The functional responses of *C. attenuata* to each prey species were fitted to the equations, without replacement, for the Holling type I, II and III functional response models taken from Hassell (1978):

Type I:
$$N_a = N_t (1 - \exp(-a'TP_t))$$

Type II: $N_a = N_t (1 - \exp(-a'P_t(T - T_h \frac{N_a}{P_t})))$
Type III: $N_a = N_t \{1 - \exp[-\frac{bN_tP_t}{1+cN_t}(T - \frac{T_hN_a}{P_t})]\}$ $a' = \frac{bN_t}{1+cN_t}$

where N_a is the number of prey killed, N_t the initial number of prey supplied, T the total test time (in days), a' the instantaneous search rate, T_h the handling time (as the proportion of one day) and P_t the number of predators studied. b and c in the type III equation are two fitting parameters.

Data were fitted with the software Tablecurve 2D v. 5.0 (Jandel Scientific, 1994). The coefficient of determination (R^2) was used to measure the goodness-of-fit of the data to each model, but for model comparison and to select the best one we used the Akaike's information criterion (AIC) which takes the number of parameters needed to achieve the goodness of fit obtained. Therefore, we regarded the best fitting model for each prey species as the one that resulted in the smallest value for the corrected Akaike's information criterion (AIC_C). We calculated the AICc values, evidence ratio (a high ratio indicates a better model) and its probability (W) by the procedure established by Motulsky & Christopoulos (2003).

Predator-prey dynamics under greenhouse conditions

This test was conducted from July 2004 to February 2005 in a commercial greenhouse in Dalias (Almeria, Spain). The greenhouse covered an area of 9000 m², with first a pepper crop and later one of watermelon. The crops were subjected to the usual agricultural practices in the area, and pest and disease control were maintained in accordance with IPM recommendations from the Plant Protection Services of the Andalusian Regional Government (Torres et al., 2002; Rodriguez et al., 2008). Briefly, no insecticide was applied to the watermelon crop, and for the pepper crop insecticide was applied only once (8 days after transplanting), when *Bacillus thurigiensis azawai* (Bacillus thurigiensis azawai 2,5% WP, Du Pont[©]) was used to control beet armyworm larvae [*Spodoptera exigua* (Hübner)].

Relative population size for the predator (*Bradysia* sp.) and its two prey (whitefly and sciarids) was evaluated by capturing individuals on 20 × 25 cm yellow coloured sticky traps (Takitramps® Koppert Biological Systems); a total of 8 traps were distributed 1.5 m above ground level and roughly uniformly in the greenhouse. The traps were visually inspected to count the number of adults captured and replaced at 7-day intervals. This system had previously been found to provide accurate relative estimates of population size in whitefly (Ekbon & Rumei,

Table 1. Mean number of prey killed by C. attenuata under laboratory conditions ($25 \pm 1^{\circ}$ C, 70% RH, 16L : 8D photoperiod, variable prey number).

Initial	Number of killed prey								
prey number		Adult sciarids		Whiteflies	Adult leaf miners flies				
	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)			
5	10	2.90 (0.17) a	10	4.00 (0.21) a	10	4.50 (0.17) a			
10	10	3.60 (0.48) a	3	6.33 (0.67) ab		_			
15		_	10	8.90 (0.95) ab	9	8.44 (0.69) b			
20	10	8.40 (0.72) b	3	10.00 (1.53) ab		_			
25		_	3	11.67 (0.88) ab		_			
30	10	11.50 (0.91) b	10	13.80 (1.14) b	5	10.20 (0.92) b			
45		_	10	23.80 (1.10) c	3	16.33 (0.33) c			
50	5	12.00 (0.71) b		_		_			
60		_		_	4	17.25 (0.48) c			
100		_	10	20.40 (1.61) c		_			
150		_	10	21.64 (1.30) c		_			

Values in the same column followed by a different letter (a, b or c) are significantly different at P < 0.01.

Table 2. Significance values for the fit of the functional responses of the predator to the t	hree hrey species

	Function	Eit manamatans				Statistical parameters				
Prey		Fit parameters			Regression			AICc		
		a'	T_h	b	c	R^2 (d.f.)	P	Value	W (%)	Evidence Ratio
	Type I	0.5033	_	_	_	0.979 (4)	< 0.01	36.589	99.82	_
Sciarids	Type II	0.9357	0.0540	_	_	0.943 (3)	< 0.05	49.295	0.17	540.07
	Type III	_	0.0759	0.3634	3.3136	0.940(2)	n.s.	55.437	0.01	12,378.30
	Type I	0.7136	_	_	_	0.970 (7)	< 0.01	24.073	99.73	_
Whiteflies	Type II	1.6184	0.0396	_	_	0.886 (6)	< 0.05	35.894	0.27	168,805.09
	Type III	_	0.0447	0.1217	0.4727	0.886 (5)	< 0.05	65.947	≈ 0	$1.238.10^9$
	Type I	0.4697	_	_	_	0.857 (5)	< 0.05	46.457	2.95	32.87
Leaf miners	Type II	1.0372	0.0392	_	_	0.936 (4)	< 0.01	39.472	97.05	_
	Type III	_	0.0575	1.6524	18.932	0.769(3)	n.s.	69.126	≈ 0	$2.75.10^6$

1990), hunter flies (Prieto et al., 2003; Téllez & Tapia, 2005), sciarids (Ciampolini et al., 2005) and adult leaf miners (Chandler, 1987).

The mean numbers (as relative density) of hunter flies and sciarid flies trapped in the pepper and watermelon crops, converted to numbers per m² of greenhouse, were fitted to a modified version of the model of Kindlmann & Dixon (2003) including the functional response, as a second positive term in the predator dynamics, to describe the positive effect of predator-prey interaction, namely:

$$\frac{dh}{dt} = ax, \quad h(0) = 0$$

$$\frac{dh}{dt} = (r - h)x - \frac{v.e.x.y}{b + e.x + y}, \quad x(0) = x_0$$

$$\frac{dh}{dt} = -\frac{v.y^2}{b + e.x + y} + (e + v)^2 .x.y + n.y, \quad y(0) = y_0$$

where h(t) is the cumulative prey density, x(t) the prey density, a a constant multiplier of h(t), r the maximum potential growth rate for the prey, y(t) the predator density, v the predator voracity (an estimate of the instantaneous search rate a' under field conditions), b the predator functional response, e the predator preference for the prey [a constant obtained from the fitted equation (1)], and n the predator intrinsic growth rate. The modified model was fitted to the results for the pepper and water melon crops by using the software SIMFIT v. 5.7.2 (Bardsley, 2007).

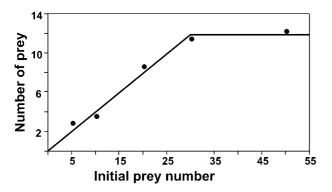


Fig. 1. Type I functional response of *C. attenuata* to adult sciarids (*Bradysia* sp.) under laboratory conditions ($25 \pm 1^{\circ}$ C, 70 % RH, 16L : 8D photoperiod).

RESULTS

Functional response

Prey consumptions were strongly dependent on prey density. Sciarids were consumed in significantly different numbers at densities from 5 to 20 individuals (the number of killed flies changed from 2.90 to 8.4, respectively, Table 1). However, increasing prey availability beyond 20 individuals resulted in no substantial increase in predation. Similar results were obtained with whiteflies and leaf miner flies, albeit at prey densities above 45 individuals per vial.

The lowest AIC_C values and highest regression coefficients (Table 2) were obtained by fitting the results for *Bradysia* sp. and *Bemisia tabaci* to a type I equation (Figs 1 and 2), and those for *L. trifolii* (Fig. 3) to a type II equation. Therefore, the predator response was dependent on the species of prey.

Predator-prey dynamics under greenhouse conditions

Figs 4 and 5 show the population fluctuations of hunter flies and their prey (sciarid flies, whiteflies and leaf miner flies) in the pepper and water melon crops grown in the greenhouse. The population data for hunter flies and sciarids were fitted by using the modified model of Kindlmann & Dixon [equation (1) above]; the results are

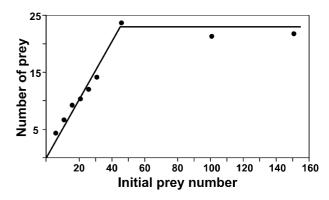


Fig. 2. Type I functional response of *C. attenuata* to tobacco whiteflies (*Bemisia tabaci*) under laboratory conditions (25 \pm 1°C, 70% RH, 16L : 8D photoperiod).

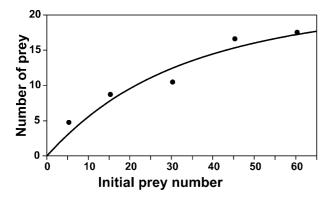


Fig. 3. Type II functional response of *C. attenuata* to adult leaf miners (*Liriomyza trifolii*) under laboratory conditions (25 \pm 1°C, 70% RH, 16L : 8D photoperiod).

shown in Figs 6 and 7, and the goodness of fit is given in Table 3. However, the populations of the other two prey species (whiteflies and leaf miner flies) did not fit this model.

Seemingly, the population of sciarid flies was driven to extinction by the action of the predator in the pepper crop (Fig. 6), consistent with the very strong specialization of immature *C. attenuate* to immature stages of sciarids (Kühne, 2000). However, the height of the peak in the predator population is not well reflected by the model; this suggests that the predator population had to feed on other prey than sciarids at some time (Fig. 4). On the other hand, no similar effect was observed in the water melon crop, which exhibited a fairly substantial increase in the sciarid fly population and in the populations of whiteflies and leaf miner flies (Fig. 5), but no increase in the predator population (Fig. 7). Therefore it was not possible to adjust the mathematical model to fit the whitefly and leaf miner prey data.

DISCUSSION

The type I functional response of *C. attenuata* to whiteflies and sciarids observed in this work is typical of

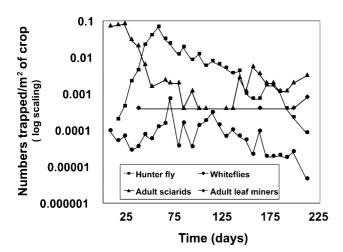


Fig. 4. Numbers of *C. attenuata* and its prey (sciarid flies, whiteflies and leafminer flies) captured on yellow sticky traps in a greenhouse pepper crop.

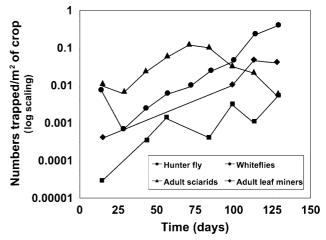


Fig. 5. Numbers of *C. attenuata* and its prey (sciarid flies, whiteflies and leafminer flies) captured on yellow sticky traps in a greenhouse watermelon crop.

many other predators and parasitoids; however, our predator exhibited a type II response to adult leaf miners. The principal difference between the two response types was the presence of a handling time T_h with leaf miners, which hindered predation of this species; this was not the case with the type I response, which depends exclusively on the search rate, a'. The change of functional response to the leaf miner from type I to II suggests greater adaptability to different prey species in C. attenuata than has previously been observed in other entomophagous species, both predators and parasitoids (Tostowaryk, 1972; Wang & Ferro, 1998; Skirvin & Fenlon, 2001; Pekár, 2005; Garcia-Martin et al., 2006, 2008).

One important physical factor affecting predator responses is prey size (Sabeli, 1992). Also, characteristics of the cuticle or the presence of wax can alter the response of the predator to a potential prey (Hagen, 1987). In addition, the chemical, morphological and behavioural defence mechanisms of a prey can lead to acceptance or rejection by the predator (Sih, 1987; Sabeli, 1992). With the response of *C. attenuata* to leaf miners, the switch to a type II response due to the increased handling time involved does not seem to have been the result

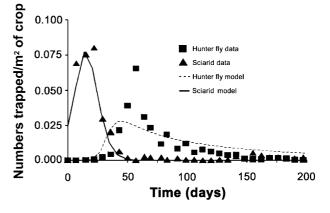


Fig. 6. Model for the predator (*C. attenuata*)-prey (*Bradysia* sp.) population dynamics in a greenhouse pepper crop.

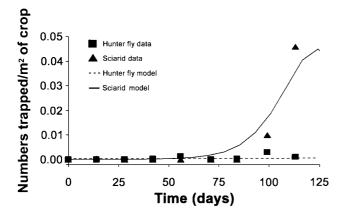


Fig. 7. Model for the predator (*C. attenuata*)-prey (*Bradysia* sp.) population dynamics in a greenhouse water melon crop.

of prey size; in fact, adult sciarids are larger than adult leaf miners (2.5–3.0 mm versus 1.4–2.3 mm). Therefore, the adoption of a different functional response must have had a different, as yet undetermined origin.

Our results for leaf miners are consistent with those obtained in the only previous study we have found on the functional response of *C. attenuata* (Gillioli et al., 2005), where the predator was found to exhibit a type II response to *Drosophila melanogaster* Meigen.

The dynamics of the hunter fly population in the pepper crop in a commercial greenhouse can be ascribed to the predator's type I functional response to its prey (the sciarid), which led to the suppression of the latter. As cited before for the case of parasitoids, their capacity to attack above a threshold value of the host population, is one of the most important factors in the suppression of the host (Mills, 2001). However, the capacity to attack or instantaneous search rate (a'), as has recently has been established by Cabello et al. (2007), depends only on the mortality of the prey/host caused by the type I response function; while in the other types (type II and type III) this mortality is divided by the handling time (T_h) . Therefore, if other conditions are the same, a biological control agent displaying a type I response will have a higher capacity to attack and will therefore perform better in an inundative release programme. This observation has indeed been confirmed in practice, with the use of Trichogramma species, which show a type I response function, as biological control agents (Elzen et al., 2003). In our experiments, the adult predator population also declined after it had reduced the sciarid to a negligible population, albeit somewhat more slowly as it was able to feed on other prey present in the greenhouse (adult whiteflies). Eventually, however, it extinguished as the likely result of the absence of immature sciarids in the soil, which constitute the target prey of immature hunter flies. No similar phenomenon was observed in the water melon crop. Here, although the sciarid population was relatively large, it failed to increase further, possibly as a result of the architecture of the crop used (the creeping habit of water melons in contrast to the staking of peppers). This may have led to the predator having fewer high resting points available from which to launch its captures. The particular cropping periods (summer-winter for peppers and summer for water melon) may also have had some effect, i.e. the high temperatures of summer may have affected the predatory activity of C. attenuata or the development of its immature stages in the soil.

In conclusion, the hunter fly can be an effective predator for sciarids depending, to a great extent, on the particular cropping conditions. Its action on other pests present in greenhouse crops may be supplemental to, but will never be the sole agent of, their control.

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Table 3. Fit of the model for the dynamics of *C. attenuata* and its sciarid prey in pepper and water melon crops in a greenhouse.

Cuon	Fit parameters						Statistical parameters (species)	
Crop	a r v e		e	b n		R^2	P	
		0.146	0.620	2.000	0.918		C. attenuata	
Pepper	0.142					-0.005 -	0.917	< 0.05
						-0.003	sciarids	
							0.727	< 0.05
		0.089	0.220	0.300	0.322		C. at	tenuata
Water melon	0.092					0.004 -	0.939	< 0.05
water meion						0.004 -	sc	iarids
						_	0.717	< 0.05

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