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EFFECT OF DIFFERENT DIETS ON THE DEVELOPMENT, MORTALITY, SURVIVAL, FOOD UPTAKE AND FECUNDITY OF *TUPIOCORIS CUCURBITACEUS* (HEMIPTERA: MIRIDAE)

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ABSTRACT

Several Miridae (Hemiptera) species have been identified as useful predators for biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). There is interest in determining the effects of different diets on *Tupiocoris cucurbitaceus* (Spinola) (Hemiptera: Miridae) in order to facilitate their breeding and use in biological control. Given that mirids can be both phytophagous and zoophytophagous, the developmental time, mortality, survival, feeding and fecundity of this species on tomato and tobacco leaves with and without the addition of *T. vaporariorum* or *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs were studied. To determine embryonic duration, *T. cucurbitaceus* was allowed to oviposit on tobacco plants for 24 h at 26 °C, 83% RH and a photoperiod of 16:8 h L:D. The time of onset of the first instar nymphs was recorded. Subsequently, these nymphs fed on different diets on 9 cm × 1.5 cm plates under the same environmental conditions. Results showed that diet influences the duration of development in *T. cucurbitaceus*, with nymphal stadia being shorter and the adult stadium being longer when fed prey than when not fed prey. With the addition of prey, nymphal mortality was generally lower and adult survival was higher. The high consumption of *T. vaporariorum* eggs by *T. cucurbitaceus* suggests the need for subsequent studies on the latter for inclusion of this species in biological control programs in greenhouses.

Key Words: predator, biology, diets, intraguild predation, *Trialeurodes vaporariorum*, *Ephestia kuehniella*

RESUMEN

Varios Miridae (Hemiptera) son reconocidos como depredadores útiles en programas de control biológico de la mosca blanca de los invernaderos, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). Existe interés en determinar los efectos de varias dietas sobre *Tupiocoris cucurbitaceus* (Spinola) de modo de facilitar su cría y utilización en control biológico. Dado que los miridos pueden ser tanto fitófagos como zoofitófagos se estudió el tiempo de desarrollo, la mortalidad, la sobrevivencia, el consumo y la fecundidad de esta especie sobre hojas de tomate y tabaco con y sin el agregado de huevos de *T. vaporariorum* o de *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). Para determinar la duración embrionaria se permitió oviponer a *T. cucurbitaceus* sobre una planta de tabaco durante 24 horas a 26°C, 83% de RH y un fotoperíodo 16:8 (L:O) y se registró el tiempo de aparición de las ninfas del primer estadio. Posteriormente, dichas ninfas se alimentaron con las diferentes dietas en placas de 9 x 1,5 cm a las mismas condiciones ambientales. Se comprobó que la dieta influyó en la duración de desarrollo de *T. cucurbitaceus*, siendo más breve el estado ninfal y más extensa la vida adulta cuando fue alimentado con presas que sin ellas. Con el agregado de presas la mortalidad de las ninfas resultó generalmente menor y la sobrevivencia de los adultos fue mayor. El alto nivel de consumo de huevos de *T. vaporariorum* sugiere la necesidad de continuar los estudios sobre *T. cucurbitaceus* para su inclusión en los programas de control biológico en los invernaderos.

Palabras Clave: depredador, biología, dietas, *Trialeurodes vaporariorum*, *Ephestia kuehniella*

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) and the sweetpotato whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) are serious pests in protected culture as well as in outdoor crops (Bi et al. 2002; Byrne & Bellows 1991; Ellsworth & Martinez-Carrillo 2001; Naranjo & Ellsworth 2001; Park et al. 2004, 1998; Stansly et al. 2004). These whiteflies cause economic damage to crops by feeding on phloem sap, contaminating leaves and fruits with honeydew, which supports the growth of sooty mold, and by transmitting plant viral diseases (Arnó et al. 2006; Bi et al. 2002; Byrne & Bellows 1991; Hodges & Evans 2005; Park et al. 1998; van Lenteren & Noldus 1990).

The use of Aphelinidae parasitoids (Hymenoptera) has yielded satisfactory results in numerous examples of biological control of whiteflies such as *Encarsia formosa* Gahan (Hoddle 2004; Pilkington et al. 2010; van Lenteren et al. 1996) and *Eretmocerus mundus* Mercet (De Barro et al. 2000; Stansly et al. 2005, 2004). Nonetheless, several pests are often present on crops at the same time and may survive due to the host specificity of some parasitoid species. To complement this effect it would be of interest to use a natural enemy that is not only attack whiteflies but also will attack other harmful species on the crop such as aphids, thrips, and mites (Fauvel et al. 1987).

Among the various generalist predators, Miridae (Hemiptera) species are being researched and commercialized to control whiteflies, especially the Palearctic species *Macrolophus pygmaeus* (Rambur) (Miridae), incorrectly identified as *M. caliginosus* Wagner (Faten Hamdi et al. 2012; Perdikis et al. 2003). This species has been successfully used in Europe against *T. vaporariorum* (Bonato et al. 2006; Gabarra et al. 2004; Lucas & Alomar 2002; Malézieux et al. 1995; Trottin-Caudal & Millot 1994; van Scheltema et al. 1995) and *B. tabaci* (Alomar et al. 2006; Bonato et al. 2006; Jazzar & Hammad 2004; Lucas & Alomar 2002; Pasini et al. 1998, Sampson & King 1996).

Spinola (1852) described the mirid *Tupiocoris cucurbitaceus* (Spinola) from Chile. It was identified in Uruguay by Carvalho (1947) and later reported in Colombia, Ecuador, Mexico, Brazil (Carvalho & Afonso 1977) and Argentina (Carpintero & Carvalho 1993). Like *M. caliginosus* (Bonato et al. 2006; Lucas & Alomar 2001), it is a zoophytophagous species (Bado et al. 2005; Ohashi & Urdampilleta 2003), which exploits both plant and animal food sources. The insects live in a competitive system, because the omnivore (predatory species) and its prey (whiteflies species) feed on the same plant. It is an apparent competitive system, because both plant and herbivore are consumed by the same omnivore. This case is a special (or "degenerate") case of intraguild predation (IGP), namely when a plant provides food to an intraguild (IG) predator (Arim & Marquet 2004; Coll &

Guershon 2002; Garay et al. 2012; Holt & Polis 1997; Polis & Holt 1992). IGP gained major interest in biological control, not only for conservation purposes but also for pest control in open-field and greenhouse crops (Brodeur & Boivin 2006).

The capacity of *M. pygmaeus* to go in and out of greenhouses may regulate the density of the predator on the crop which would explain why this facultative predator does not cause damage in the open Mediterranean greenhouses in comparison with that reported for northern latitudes (Sampson & Jacobson 1999), where the use of *M. pygmaeus* for biological control is considered risky because of its capacity to damage certain ornamental and tomato varieties (Gabarra et al. 2004). Greenhouses in Uruguay, and in many other South American countries (Argentina, Brazil, Chile, Colombia), are open like in the Mediterranean, so the predatory activity of *T. cucurbitaceus* could be of great importance in the implementation of biological control.

In the case of Miridae, many studies have focused on the advantages and limitations of a strictly phytophagous diet (Perdikis & Lykouressis 1997, 2000, 2004; Lykouressis et al. 2008; Ingegno et al. 2011; Portillo et al. 2012) or, alternatively, a strictly zoophagous diet (Iriarte & Castané 2001; Castané & Zapata 2005; Castané et al. 2011). It is observed in omnivore predators that when the usual prey diet is supplemented with plant food, their development rate generally increases and so do the other biological parameters such as survive rate, longevity and/or fecundity of adults (Eubanks & Styrsky 2005). These observations confirm that, the food intake has a strong effect on the growth rate of omnivore and its prey.

The aim of the current study is to determine the developmental times of the immature instars, longevity, fecundity, nymphal mortality, adult survival and prey consumption of *T. cucurbitaceus* on different host plants in the presence and absence of insect prey. Given the limited knowledge available about this predator, characterizing the effect of different trophic regimes on its biology could contribute both to the knowledge of trophic connections, a central element in the structure of ecosystems, and also to improved management of these pests and the utilization of this species as a biological control agent.

MATERIALS AND METHODS

Insect Colony and Experimental Conditions

Specimens of *Tupiocoris cucurbitaceus*, *T. vaporariorum* and *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) used in the experiments were mass-reared in the Faculty of Agronomy (Montevideo, Uruguay) laboratory. *Tupiocoris cucurbitaceus* was collected in 2008 at the Faculty of

Agronomy park (S34° 54' -W 56° 12') on yacon (*Smallanthus connatus* (Spreng.) H. Robinson) (Asterales: Asteraceae) and mass-reared on tobacco (*Nicotiana tabacum* L, Virginia, cv. K-326; Solanales: Solanaceae). Experiments were carried out in controlled environmental conditions (26 ± 1 °C, $83 \pm 10\%$ RH and a photoperiod of 16:8 h L:D).

Determination of Embryonic Development

Twenty-five fertilized *T. cucurbitaceus* females were placed for 24 h on a tobacco plant 'sprinkled' with eggs of *E. kuehniella* as a food supplement. This plant was placed in a 35 × 15 × 30 cm (length × width × height) glass box covered by fine muslin to prevent high humidity accumulation (Perdikis & Lykouressis 2000). Given the difficulty of observing the eggs, because, as in other Miridae species, the females insert these into the plant tissue leaving only the operculum visible (Fauvel et al. 1987; Gemeno et al. 2007), once the mirids were placed on the plants, daily observations were conducted to determine the occurrence of first nymphal instars in order to determine the duration of embryo development.

Effect of Diet on Nymphal Development

First nymphal instars individuals of *Tupiocoris cucurbitaceus* were placed individually in 9 × 1.5 cm (diam × height) plastic dishes and fed on host plants of tomato or tobacco in presence or absence of prey (*T. vaporariorum* or *E. kuehniella*), resulting in 6 experimental treatments: 1) one piece of tobacco leaf 1 × 8 cm, 2) one piece of tobacco leaf 1 × 8 cm + *E. kuehniella* eggs (ad libitum), 3) one tomato leaflet, 4) one tomato leaflet + *E. kuehniella* eggs (ad libitum), 5) one piece of tobacco leaf 1 × 8 cm + *T. vaporariorum* eggs (ad libitum) and 6) one tomato leaflet + *T. vaporariorum* eggs (ad libitum).

A ball of wet paper towel was placed on each dish to keep the vegetable material hydrated and as water source for the mirids. The paper towel was wetted daily. The plates were placed in a glass cage 21 × 34 × 14 cm (length × width × height) that held a container with salt-saturated water in order to maintain moisture conditions ($65 \pm 5\%$ RH). Food was offered on a daily basis and the presence of exuvia from molting was looked for at the same time.

Effect of Diet on Adult Longevity

The effect of diet on longevity (length of adult life) of *T. cucurbitaceus* was determined from individuals that reached the adult stage for each of the 6 diets detailed above. The adults were kept on the same diet which they had been given

during preimaginal development, and the number of days which the mirids lived as adults were counted.

Effect of Diet on *T. cucurbitaceus* Nymph Mortality and Adult Survival

Mirid nymph mortality was determined in each of the 6 treatments as the percentage of individuals that did not reach the adult stage. The mortality of adult mirids was daily verified in all 6 treatments, in order to establish the number of surviving individuals. Observations were finished when all individuals died.

Adult Fecundity of *T. cucurbitaceus*

Ten fertilized *T. cucurbitaceus* females from a mass breeding facility were placed on tobacco plants 'sprinkled' with *E. kuehniella* eggs. One hundred *T. cucurbitaceus* nymphs were raised to the fifth instar, which is when mirids exhibit sexual dimorphism (Yonke 1991). Then, thirty pairs were formed (1♂ + 1♀) and placed individually on tobacco plants with *E. kuehniella* eggs. Following Fauvel et al. (1987), the pairs were changed to a different plant every 7 days. The plants were isolated in transparent plastic tubes covered by fine muslin. Fertility was determined from daily observations of the number of nymphs found on plants. All observations were made using an optical microscope (Nikon SMZ-1B x 35) and a hand lens (Carl Zeiss Jena x 8).

Effect of Diet on Prey Consumption

The number of prey consumed (*T. vaporariorum* and *E. kuehniella* eggs) in zoophytophagous diets was recorded daily during the nymphal and adult stage mirids. New prey were added daily.

Statistical Analysis

A Factorial arrangement analysis of variance (ANOVA) was performed to determine differences in embryonic and nymphal development time, and longevity. The separation of means was analyzed using a Tukey-Kramer test with $\alpha = 0.05$ as the threshold for significance differences. Comparison of prey consumption and fecundity was performed using a t-test for comparison of two means ($\alpha = 0.05$). Nymph mortality was analyzed using a Generalized Linear Model, assuming a binomial distribution for the variable 'number of dead nymphs of the total number of nymphs studied'. The Genmod procedure of the SAS/STAT package, version 9.1.3 was used (SAS/STAT 2005). Adult survival was analyzed using the product limit estimator (Kaplan – Meier). The

curves were compared using the generalized Wilcoxon test by Gehan ($\alpha = 0.05$).

RESULTS

Duration of Development (Eggs, Nymph and Adult Stages)

The duration of *T. cucurbitaceus* egg development on tobacco plants was 10.90 days [10.82; 10.98] (IC 95%). The duration of the nymphal stage of *T. cucurbitaceus* was affected by both the diet being consumed and by the plant it was living on ($F = 19.04$, $df = 1$, 94 , $P < 0.0001$) as well as by the presence or absence of prey ($F = 124.62$, $df = 2$, 94 , $P < 0.0001$), with a significant plant*prey interaction ($F = 3.18$, $df = 1$, 94 , $P = 0.0460$). The nymphs which were fed plants and prey showed a lesser development time compared to those fed only on plants ($P < 0.0001$). The prey type (*T. vaporariorum* or *E. kuehniella*) had not an effect on development time (considering $P < 0.05$), but the type of plant (tomato or tobacco) did have an effect when the diet of the nymphs did not include prey. The duration of the nymphal stage for individuals which were only fed plants varied from 20.8 days on tobacco plants to 18.3 days for tomato plants ($P < 0.0001$) (Table 1).

When the duration of each of the nymphal instars was analyzed separately, it was proven that plant type affected development at the second instar ($P = 0.0141$), third instar ($P = 0.0401$) and fourth instar ($P = 0.0468$), but not the other instars (first and fifth instars) (considering $P < 0.05$), whereas that prey influenced development times of all instars ($P < 0.0001$). Plant*prey interaction was not significant at 95% in any of the cases.

First instar nymphs molted sooner when they were fed *T. vaporariorum* eggs than when no prey was provided, both on tomato ($P = 0.0100$) and on tobacco ($P = 0.0464$). This effect was not found when *E. kuehniella* eggs were provided, on either on tomato or tobacco (considering $P < 0.05$). Second instar nymphs fed with only tobacco had a longer development time than if the diet was supplemented with *T. vaporariorum* eggs ($P = 0.0028$) or *E. kuehniella* eggs ($P = 0.0468$). There was no change in the duration of the second nymphal instar on tomato plants through the addition of *E. kuehniella* eggs ($P = 0.1180$) or *T. vaporariorum* eggs ($P = 0.2180$). The development time of third instar nymphs on tobacco was reduced with the addition of *T. vaporariorum* eggs ($P = 0.0022$) or *E. kuehniella* eggs ($P < 0.0001$). By contrast, third instar nymphs which fed only on tomato had a longer development time than those which received *E. kuehniella* eggs ($P = 0.0025$), but no difference was found in their development time when compared with those fed *T. vaporariorum* eggs ($P = 0.1627$). Fourth instar nymphs

TABLE 1. DURATION (DAYS) OF TUPIOCORIS CUCURBITACEUS DEVELOPMENT EXPOSED TO DIFFERENT DIETS.

Treatment	1 st. instar		2 nd instar		3 rd instar		4th instar		5th instar		Total Development		Total Life span	
	Prey	D (days)	N	D (days)	N	D (days)	N	D (days)	N	D (days)	N	D (days)	N	D (days)
Tob	—	4.08 b	36	3.46 b	17	3.59 c	11	4.82 c	9	4.20 ab	9	20.78 c	9	25.3 a
Tob	Ek	3.57 ab	23	2.43 a	21	2.24 a	18	3.33 ab	18	3.83 a	18	14.22 a	15	28.1 abc
Tom	—	3.98 b	45	2.69 ab	29	3.00 ab	22	4.23 bc	15	5.13 b	10	18.30 b	10	25.5 ab
Tom	Ek	3.23 ab	22	1.99 a	18	2.06 a	18	2.61 a	17	3.33 a	17	12.94 a	15	34.1 abc
Tob	Tv	3.16 ab	25	2.22 a	24	2.58 ab	24	2.50 a	24	3.50 a	24	13.67 a	21	34.5 abc
Tom	Tv	2.96 a	27	2.10 a	24	2.46 ab	23	2.43 a	22	3.43 a	22	13.23 a	22	36.4 c

D = duration, Tob = Tobacco, Tom = Tomato, Ek = *E. kuehniella* eggs, Tv = *T. vaporariorum* eggs. Means followed vertically by the same letter are not significantly different ($P < 0.05$) in the Tukey-Kramer test.

fed only with tobacco had a longer duration compared to those fed with *T. vaporariorum* eggs ($P < 0.0001$) or *E. kuehniella* eggs ($P = 0.0179$). This was also observed in mirids of the same instar fed on tomato; the duration was reduced when *T. vaporariorum* ($P < 0.0001$) or *E. kuehniella* eggs ($P = 0.0006$) were added. Fifth instar nymphs on tobacco showed no differences in the duration of development with or without the addition of eggs, both for *T. vaporariorum* ($P = 0.6135$) or *E. kuehniella* ($P = 0.9705$). However, their development on tomato plants was slower when no prey was added than with *T. vaporariorum* or *E. kuehniella* eggs ($P = 0.0002$ in both cases). None of the durations of development time of any nymphal instars varied depending on the type of prey offered (considering $P < 0.05$) (Table 1).

The longevity of *T. cucurbitaceus* adults, when *T. vaporariorum* eggs were available, was 20.8 days on tobacco and 23.2 days on tomato plants. These periods were longer compared with those of individuals fed exclusively on plants (4.5 days on tobacco and 7.0 days on tomato respectively) ($P < 0.0001$). Adults fed with *E. kuehniella* lived an average of 21.3 days on tomato plants and 13.9 days on tobacco, differing from those without prey on tomato ($P < 0.0001$) and tobacco ($P = 0.0062$) respectively. The total duration of the lifetime of the mirid (nymph plus adult stage) was not affected by plant type ($P = 0.1528$) but it was affected by the addition of prey ($P = 0.0002$). However, no difference was noted between adding *E. kuehniella* or *T. vaporariorum* eggs ($P = 0.0825$). An increase in the total life duration of *T. cucurbitaceus* compared with individuals without added prey was only evident when *T. vaporariorum* was added to tomato plants ($P = 0.0128$) (Table 1).

Effect of Diet on *T. cucurbitaceus* Nymph Mortality and Adult Survival

Diet influenced the mortality of nymphs ($F = 10.26$, $df = 5, 181$, $P < 0.0001$). Nymphs fed with *T. vaporariorum* eggs on tobacco or tomato plants had lower mortality than those not fed prey on either tobacco ($P = 0.0007$) or tomato ($P < 0.0001$). When *E. kuehniella* eggs were added to tomato leaves, nymph mortality was lower than when no prey was provided ($P = 0.0007$). However, the addition of eggs did not affect mortality if the nymphs were on tobacco leaves, compared to when no prey was provided ($P = 0.0631$) (Table 2).

The assessed diets affected the survival of adult mirids (generalized Wilcoxon test by Gehan, $\chi^2 = 55.98$, $P = 0.000$). In pairwise comparison of treatments (Kaplan – Meier method) no significant differences were found when mirids fed only on tobacco or tomato. Though survival increased either on one plant or the other when prey were added (both *E. kuehniella* or *T. vaporariorum*). No differences were reported adding one prey or the

TABLE 2. MORTALITY (MEAN ± SE) OF *T. CUCURBITACEUS* DURING NYMPHAL DEVELOPMENT.

Plant	Prey	Mortality
Tob	—	0.71 ± 0.07 ab
Tob	Ek	0.35 ± 0.10 bc
Tom	—	0.79 ± 0.06 a
Tom	Ek	0.19 ± 0.09 c
Tob	Tv	0.12 ± 0.07 c
Tom	Tv	0.11 ± 0.06 c

Tob =Tobacco, Tom =Tomato, Ek = *E. kuehniella* eggs, Tv = *T. vaporariorum* eggs. Means followed by the same letter are not significantly different ($P < 0.05$) in the Tukey-Kramer test.

other on each one of the plants. Individuals on tomato with prey added (both *E. kuehniella* or *T. vaporariorum*), had a greater survival than those fed on tobacco with *E. kuehniella*, whereas that no differences were registered with mirids fed on tobacco with *T. vaporariorum* (Table 3) (Fig. 1).

Prey Consumption

The average number and range of *E. kuehniella* eggs consumed by *T. cucurbitaceus* during its life was 137 (114-160) on tomato and 149 (81-218) on tobacco ($P = 0.7004$). When the diet included *T.*

TABLE 3. PAIRWISE COMPARISON OF TWO SURVIVAL CURVES OF *TUPIUCORIS CUCURBITACEOUS* ADULTS ON DIFFERENT FOOD DIETS (T1 TO T6). SURVIVAL WAS ANALYZED USING THE PRODUCT LIMIT ESTIMATOR (KAPLAN – MEIER). T1 = ONE PIECE OF TOBACCO LEAF, T2 = ONE PIECE OF TOBACCO LEAF + *E. KUEHNIELLA* EGGS, T3 = ONE TOMATO LEAFLET, T4 = ONE TOMATO LEAFLET + *E. KUEHNIELLA* EGGS, T5 = ONE PIECE OF TOBACCO LEAF + *T. VAPORARIORUM* EGGS AND T6 = ONE TOMATO LEAFLET + *T. VAPORARIORUM* EGGS.

Comparison	dl	F	P
T1-T2	22-41	1.76	0.012
T1-T3	46-41	1.08	0.356
T1-T4	18-41	2.84	0.000
T1-T5	23-41	3.38	0.000
T1-T6	24-41	3.53	0.000
T2-T3	46-22	1.75	0.011
T2-T4	18-22	1.68	0.045
T2-T5	23-22	1.61	0.053
T2-T6	24-22	2.18	0.004
T3-T4	18-46	2.83	0.000
T3-T5	23-46	3.38	0.000
T3-T6	24-46	3.49	0.000
T4-T5	23-18	1.02	0.468
T4-T6	24-18	1.08	0.398
T5-T6	24-23	1.36	0.140

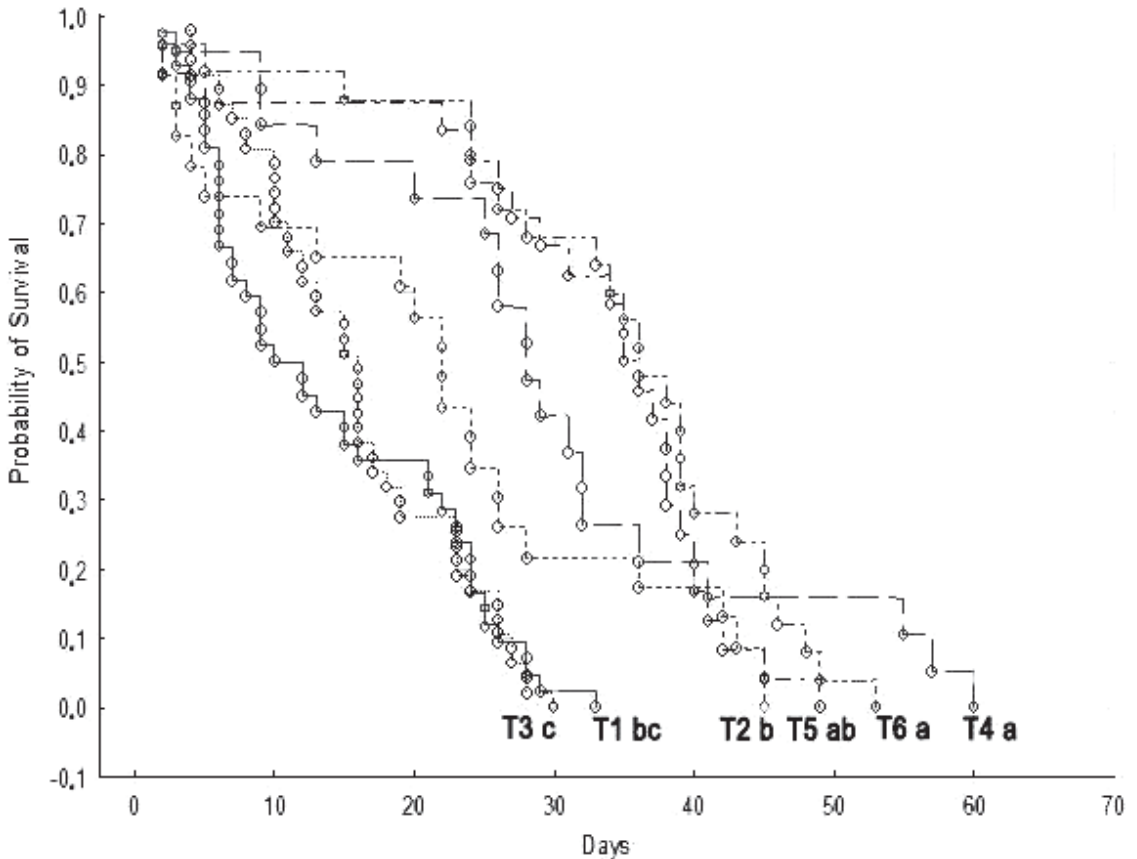


Fig. 1. Survival curves of *Tupiocoris cucurbitaceus* under different food diets (T1 to T6). T1 = one piece of tobacco leaf, T2 = one piece of tobacco leaf + *E. kuehniella* eggs, T3 = one tomato leaflet, T4 = one tomato leaflet + *E. kuehniella* eggs, T5 = one piece of tobacco leaf + *T. vaporariorum* eggs and T6 = one tomato leaflet + *T. vaporariorum* eggs. Survival was analyzed using the product limit estimator (Kaplan – Meier). Different letters indicate significant difference ($P < 0.05$).

vaporariorum eggs consumption ranged from 732 eggs (603-828) on tobacco and 712 eggs (600-824) on tomato ($P = 0.8184$) (Fig. 2).

and the 11.8 days for *Dicyphus tamaninii* Wanger on tobacco at 25 ± 1 °C, $70 \pm 10\%$ RH and 16:8 h L:D reported by Iriarte & Castañé (2001)

Adult Fecundity of *T. cucurbitaceus*

In the first week of oviposition fecundity of *T. cucurbitaceus* females reached an average of 37.7 eggs. In the second week fecundity was 39.7 eggs, in the third week it was 38.7 eggs and in the fourth week it was 23.6 eggs (Table 4). In summary, females deposited between 74 and 205 eggs in adulthood, and between 3 and 7 eggs per day.

DISCUSSION

The duration of *T. cucurbitaceus* embryonic development observed in this study (10.9 days) was lower but close to the 11.4 days reported by Fauvel et al. (1987) for *M. pygmaeus* on tomato plants at 25 °C, 60% RH and a photoperiod of 16:8 h L:D

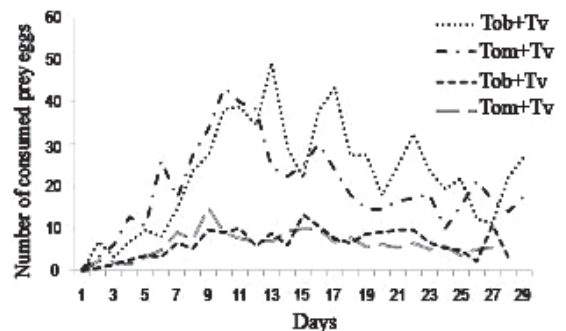


Fig. 2. Number of eggs (*E. kuehniella* or *T. vaporariorum*) consumed by *T. cucurbitaceus* during its life on tomato and tobacco leaves.

TABLE 4. FERTILITY OF *TUPIUCORIS CUCURBITACEUS* ON TOBACCO PLANTS.

Oviposition period	N pairs	N nymphs	IC 95%	Nymphs/day
Week 1	19	37.7	[27.3; 48.1]	3.9-6.9
Week 2	17	39.7	[26.7; 52.7]	3.8-7.5
Week 3	9	38.7	[10.8; 66.6]	1.5-9.5
Week 4	10	23.6	[9.7; 37.5]	1.4-5.4

A shorter preimaginal developmental time with the addition of *T. vaporariorum* to the diet was observed for the mirid *M. pygmaeus* on egg-plant plants, and a host plant effect was observed in the absence of prey, as duration was less on tomato plants than on beans or tobacco (Perdikis & Lykouressis 2000). Meanwhile, Fauvel et al. (1987) indicated that *M. pygmaeus* presented a shorter preimaginal developmental time when *E. kuehniella* eggs were provided as prey than when *T. vaporariorum* eggs were supplied. In the case of *T. cucurbitaceus*, there are no previous studies and our study found no differences in the duration of the nymph development depending on the type of prey added.

The reduction of *T. cucurbitaceus* nymphal mortality with the addition of prey coincides with reports by Perdikis & Lykouressis (2000) and Lykouressis et al. (2001) who indicated that the survival of *M. pygmaeus* was greater when prey were provided than when none was available. Meanwhile, Lucas & Alomar (2001) indicated that *D. tamaninii* individuals fed exclusively on tomato leaves failed to complete their development. Fauvel et al (1987) reported a total fecundity of 122 eggs per female for *M. pygmaeus* and daily fecundity of 3 eggs per day when fed with *E. kuehniella* eggs on *Pelargonium peltatum* L. (Geraniaceae) at 25 °C. At the same temperature, Castañe & Zapata (2005) obtained a fecundity of 7.03 eggs per day with the same species fed on tobacco leaves and *E. kuehniella* eggs. Iriarte & Castañe (2001) reported a fecundity of 4.45 eggs per day for the same mirid with a meat diet prepared according to De Clercq et al. (1998). Our results showed that the quality of the diet influences the development period and longevity of *T. cucurbitaceus*, with nymphal instar being shortest and the adult stage being the longest when *T. vaporariorum* or *E. kuehniella* eggs were provided, on tomato or tobacco leaves, than when the leaves were the only available food source. Meanwhile, predator nymphal mortality was less and adult survival was greater when prey were provided.

When using biological control, it is observed that an omnivore agent feeding only on a plant species reaches a lower population density than when it is living on a mixed diet (with prey) (Garay et al. 2012). That result is also found in cases when plants provide food for natural enemies of phytophagous insects (Wäckers 2005; Young et al.

1997). In this kind of mutualism it is an important point for the plant that the cost of defense is less than its benefit (Szilágyi et al. 2009). Here, the cost for the plant is its biomass consumed by the omnivore (with or without the presence of the herbivore), and its benefit is the biomass the herbivore would have consumed in absence of the predator. Garay et al. (2012) formulated the hypothesis that the food provided by the plant for its mutual omnivore is poor at least in one of the essential nutrients, and the pest of the plant is rich in this nutrient. This hypothesis might be chemically tested.

As one of the elements of a complex system, *T. cucurbitaceus* could be a promising candidate for complementing more specialized parasitoids in whitefly biological control programs. Or, taking into account that this species is present in nature, facilitating the colonization of greenhouse crops from vegetation, as has been done with *M. pygmaeus* (Albajes & Alomar 1999). Applied studies would be necessary to establish the population level reached by the pests under such conditions and also the stability of the system. The present study is one of the very few conducted on *T. cucurbitaceus* up to the present and it is hoped that it will prompt further complementary research.

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REFERENCES CITED

- ALBAJES, R., AND ALOMAR, O. 1999. Current and potential uses of polyphagous predators, pp. 265-275 In R. Albajes, M. L. Gullino, J. C. van Lenteren and Y. Elad [eds.], Integrated Pest and Disease Management in Greenhouse Crops. Kluwer Academic Publishers, Dordrecht, The Netherlands. 545 pp.
- ALOMAR, O., RIUDAVETS, J., AND CASTAÑE, C. 2006. *Macrolophus caliginosus* in the biological control of *Bemisia tabaci* on greenhouse melons. Biol. Control 36: 154-162.
- ARIM, M., AND MARQUET, P. A. 2004. Intraguild predation: a widespread interaction related to species biology. Ecol. Lett. 7: 557-564.
- ARNÓ, J., ALBAJES, R., AND GABARRA, R. 2006. Within-plant distribution and sampling of single and mixed

- infestations of *Bemisia tabaci* and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) in winter tomato crops. *J. Econ. Entomol.* 99: 331-340.
- BADO, S. G., CERRI, A. M., AND VILELLA, F. 2005. Fauna insectil asociada a cultivos de dos especies de *Physalis* (Solonaceae) en Argentina. *Bol. Sanid. Veg., Plagas* 31: 321-333.
- BI, J. L., TOSCANO, N. C., AND BALLMER, G. R. 2002. Greenhouse and field evaluation of six novel insecticides against the greenhouse whitefly *Trialeurodes vaporariorum* on strawberries. *Crop Prot.* 21: 49-55.
- BONATO, O., COUTON, L., AND FARGUES, J. 2006. Feeding preference of *Macrolophus caliginosus* on *Bemisia tabaci* and *Trialeurodes vaporariorum*. *J. Econ. Entomol.* 99: 1143-1151.
- BRODEUR, J., AND BOIVIN, G. 2006. Trophic and guild interaction in biological control. Springer, Dordrecht, The Netherlands. pp. 239.
- BYRNE, D. N., AND BELLOWS, T. S. 1991. Whitefly biology. *Annu. Rev. Entomol.* 6: 431-457.
- CASTAÑÉ, C., AND ZAPATA, R. 2005. Rearing the predatory bug *Macrolophus caliginosus* on a meat-based diet. *Biol. Control* 34: 66-72.
- CASTANÉ, C., ARNO, J., GABARRA, R., AND ALOMAR, O. 2011. Plant damage to vegetable crops by zoophytophagous mired predators. *Biol. Control* 59: 22-29.
- CARPINTERO D. L., AND CARVALHO J. M. C. 1993. An annotated list of the miridae of the Argentine Republic (Hemiptera). *Rev. Brasileira Biol.* 53: 397-420.
- CARVALHO, J. C. M. 1947. Mirídeos Neotropicais; XXVIII. Géneros Propomiris Berg. Lampethusa Distant, Cyrtopeltis Fieber e Dicyphus Fieber (Hemiptera). *Bol. Mus. Nacl. Rio de Janeiro* 77: 1-40.
- CARVALHO, J. C. M., AND AFONSO, C. R. S. 1977. Mirídeos Neotropicais, CCVIII: Sobre uma coleção enviada para estudo pela academia de ciências da Califórnia (Hemiptera). *Rev. Brasileira Biol.* 37: 7-16.
- COLL, M., AND GUERSHON, M. 2002. Omnivory in terrestrial arthropods: Mixing plant and prey diets. *Annu. Rev. Entomol.* 47: 267-297.
- DE BARRO, P. J., HART, P. J., AND MORTON, R. 2000. The biology of two *Eretmocerus* spp. (Haldeman) and three *Encarsia* spp. Forster and their potential as biological control agents of *Bemisia tabaci* biotype B in Australia. *Entomol. Exp. Appl.* 94: 93-102.
- DE CLERCQ, P., MERLEVEDE, F., AND TIRRY, L. 1998. Unnatural prey and artificial diets for rearing *Podisus maculiventris* (Heteroptera: Pentatomidae). *Biol. Control* 12: 137-142.
- ELLSWORTH, P. C., AND MARTINEZ-CARRILLO, J. L. 2001. IPM of *Bemisia tabaci*: a case study from North America. *Crop Prot.* 20: 853-869.
- EUBANKS, M. D., AND STYRSKY, J. D. 2005. Effects of plant feeding on the performance of omnivorous "predator" pp. 148-177 *In* F. L. Wäckers, P. C. J. van Rijn, and J. Bruin [eds.], Plant-provided food for carnivorous insects: A protected mutualism and its applications. Cambridge University Press, Cambridge. UK. pp. 256.
- FATEN HAMDI, F., CLOUET, C., STREITO, J.-C., BONATO, O., AND GAUTHIER, N. 2012. Isolation and characterisation of 9 polymorphic microsatellite loci in the predatory bug *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) using pyrosequencing technology. *Permanent Genetic Resources Note* 12: 972-974.
- FAUVEL, G., MALAUSA, J. C., AND KASPAR, B. 1987. Etude en laboratoire des principales caractéristiques biologiques de *Macrolophus caliginosus* (Heteroptera: Miridae). *Entomophaga* 32: 529-543.
- GABARRA, R., ALOMAR, O., CASTAÑÉ, C., GOULA, M., AND ALBAJES, R. 2004. Movement of greenhouse whitefly and its predators between in- and outside of Mediterranean greenhouses. *Agric. Ecosyst. Environ.* 102: 341-348.
- GARAY, J., VARGA, Z., CABELLO, T., AND GÁMEZ, M. 2012. Optimal nutrient foraging strategy of an omnivore: Liebig's law determining numerical response. *J. Theor. Biol.* 310: 31-42.
- GEMENO, C., ALOMAR, O., RIUDAVETS, J., AND CASTAÑÉ, C. 2007. Mating periodicity and post-mating refractory period in the zoophytophagous plant bug *Macrolophus caliginosus* (Heteroptera: Miridae). *Eur. J. Entomol.* 104: 715-720.
- HODDLE, M. S. 2004. Biological control of whiteflies on ornamental crops, pp. 149-170 *In* K. M. Heinz, R. G. Van Driesche, M. P. Parrella [eds.], Biocontrol in protected culture. Ball Publishing, Batavia, Illinois, USA. pp. 552.
- HODGES, G. S., AND EVANS, G. A. 2005. An identification guide to the whiteflies (Hemiptera: Aleyrodidae) of the Southeastern United States. *Florida Entomol.* 88: 518-534.
- HOLT, R. D., AND POLIS, G. A. 1997. A theoretical framework for intraguild predation. *American Nat.* 149: 745-764.
- INGEGNO, L. B., PANSÀ, M. G., AND TAVELLA, L. 2011. Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus* (Heteroptera: Miridae). *Biol. Control* 58: 174-181.
- IRIARTE, J., AND CASTAÑÉ, C. 2001. Artificial rearing of *Dicyphus tamaninii* (Heteroptera: Miridae) on a meat-based diet. *Biol. Control* 22: 98-102.
- JAZZAR, C., AND HAMMAD, E. A. F. 2004. Efficacy of multiple biocontrol agents against the sweet potato whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on tomato. *J. Appl. Entomol.* 128: 188-194.
- LUCAS, E., AND ALOMAR, O. 2001. *Macrolophus caliginosus* (Wagner) as an intraguild prey for the zoophytophagous *Dicyphus tamaninii* Wagner (Heteroptera: Miridae). *Biol. Control* 20: 147-152.
- LUCAS, E., AND ALOMAR, O. 2002. Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). *Biol. Control* 25: 123-128.
- LYKOURESSIS, D., GIATROPOULOS, A., PERDIKIS, D., AND FAVAS C. 2008. Assessing the suitability of non cultivated plants and associated insect prey as food sources for the omnivorous predator *Macrolophus pygmaeus* (Hemiptera: Miridae). *Biol. Control* 44: 142-148.
- LYKOURESSIS, D., PERDIKIS, D., AND MICHALAKI, M. 2001. Nymphal development and survival of *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) on two eggplant varieties as affected by temperature and presence/absence of prey. *Biol. Control* 20: 222-227.
- MALÉZIEUX, S., GIRARDET, C., NAVEZ, B., AND CHEYRIAS, J. 1995. Contre l'aleurode des serres en cultures de tomates sous abris utilisation et développement de *Macrolophus caliginosus* associé à *Encarsia formosa*. *Phytoma* 471: 29-32.
- NARANJO, S. E., AND ELLSWORTH, P. C. 2001. Special issue: Challenges and opportunities for pest man-

- agement of *Bemisia tabaci* in the new century. *Crop Prot.* 20: 707-869.
- OHASHI, D. V., AND URDANILLETEA, J. D. 2003. Interacción entre insectos perjudiciales y benéficos en el cultivo de tabaco de Misiones, Argentina. *Rev. Investig. Agrop.* 32: 113-124.
- PARK, J. D., KIM, D. I., AND PARK, U. 1998. Occurrence and within-plant distribution of *Trialeurodes vaporariorum* (Westwood) and *Encarsia formosa* (Gahan) in greenhouse. *Korean J. Appl. Entomol.* 37: 117-121.
- PARK, J. J., SHIN, K. I., AND CHO, K. 2004. Evaluation of data transformations and validation of a spatial model for spatial dependency of *Trialeurodes vaporariorum* populations in a cherry tomato greenhouse. *J. Asia-Pacific Entomol.* 7: 289-295.
- PASINI, C., D'AQUILA, F., GANDOLFO, M., COSTANZI, M., AND MIRTO, L. 1998. *Macrolophus caliginosus* in biological control. *Crop Prot.* 27: 43-46.
- PERDIKIS, D., AND LYKOURESSIS, D. 1997. Rate of development and mortality of nymphal stages of the predator *Macrolophus pygmaeus* Rambur feeding on various preys and host plants. *IOBC/WPRS Bull.* 20: 241-248.
- PERDIKIS, D., AND LYKOURESSIS, D. 2000. Effects of various items, host plants, and temperatures on the development and survival of *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae). *Biol. Control* 17: 55-60.
- PERDIKIS, D., AND LYKOURESSIS, D. 2004. *Macrolophus pygmaeus* (Hemiptera: Miridae) population parameters and biological characteristics when feeding on eggplant and tomato without prey. *J. Econ. Entomol.* 97: 1291-1298.
- PERDIKIS, D., MARGARITPOULOS, J. T., STAMATIS, C., MAMURIS, Z., LYKOURESSIS, D. P., TSITSIPIS, J. A., AND PEKAS, A. 2003. Discrimination of the closely related biocontrol agents *Macrolophus melanotoma* (Hemiptera: Miridae) and *M. pygmaeus* using mitochondrial DNA analysis. *Bull. Entomol. Res.* 93: 507-514.
- PILKINGTON, L. J., MESSELINK, G., VAN LENTEREN, J. C., LE MOTTEE, K. 2010. "Protected Biological Control" - Biological pest management in the greenhouse industry. *Biol. Control* 52: 216-220.
- POLIS, G. A., AND HOLT, R. D. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7: 151-154.
- PORTILLO, N., ALOMAR, O., AND WÄCKERS, F. 2012. Nectarivory by the plant-tissue feeding predator *Macrolophus pygmaeus* Rambur (Heteroptera: Miridae): Nutritional redundancy or nutritional benefit? *J. Insect Physiol.* 58: 397-401.
- SAMPSON, C., AND JACOBSON, R. J. 1999. *Macrolophus caliginosus* Wagner (Heteroptera: Miridae): a predator causing damage to UK tomatoes. *IOBC/WPRS Bull.* 22: 213-216.
- SAMPSON, C., AND KING V. J. 1996. *Macrolophus caliginosus*, field establishment and pest control effect in protected tomatoes. *IOBC/WPRS Bull.* 19: 143-146.
- SAS/STAT 2005. SAS Institute Inc., Cary, North Carolina, USA. pp. 220.
- SPINOLA, M. 1852. Fauna chilena; Miridae. v. 7, pp. 183-199 In C. Gay [ed.] Historia física y política de Chile; zoología. Casa del autor, Paris, Francia. pp. 541.
- STANSLY, P. A., CALVO, J., AND URBANEJA, A. 2005. Release rates for control of *Bemisia tabaci* (Homoptera: Aleyrodidae) biotype "Q" with *Eretmocerus mundus* (Hymenoptera: Aphelinidae) in greenhouse tomato and pepper. *Biol. Control* 35: 124-133
- STANSLY, P. A., SÁNCHEZ, P. A., RODRÍGUEZ, J. M., CAÑIZARES, F., NIETO, A., LÓPEZ LEYVA, M. J., FAJARDO, M., SUÁREZ, V., AND URBANEJA, A. 2004. Prospects for biological control of *Bemisia tabaci* (Homoptera, Aleyrodidae) in greenhouse tomatoes of southern Spain. *Crop Prot.* 23: 701-712.
- SZILÁGYI, A., SCHEURING, I., EDWARDS, D. P., ORIVER, J., AND YU, D. W. 2009. The evolution of intermediate castration virulence and ant coexistence in spatially structured environment. *Ecol. Lett.* 12, 1-11.
- TROTTIN-CAUDAL, Y., AND MILLOT, P. 1994. Lutte intégrée contre les ravageurs sur tomate sous abri, situation et perspectives en France. *IOBC/WPRS Bull.* 17: 5-13.
- VAN LENTEREN, J. C., AND NOLDUS, L. P. J. J. 1990. Whitefly-plant relationships: behavioural and ecological aspects. pp. 47-89 In D. Gerling [ed.], Whiteflies: their bionomics, pest status and management. Intercept Ltd, Andover, UK. 348 pp.
- VAN LENTEREN, J. C., VAN ROERMUND, H. J. W., SUETTERLIN, S. 1996. Biological control of greenhouse whitefly (*Trialeurodes vaporariorum*): how does it work? *Biol. Control* 6: 1-10.
- VAN SCHELT, J., LETARD, M., AND AUCOUTURIER, C. 1995. The use of *Macrolophus caliginosus* as a whitefly predator in protected crops, pp. 515-521 In D. Gerling, and R. T. Mayer [eds.], *Bemisia*: Taxonomy, biology, damage, control and management, Intercept Ltd, Andover, UK. 702 pp.
- WÄCKERS, F. L. 2005. Suitability of (extra-) floral nectar, pollen, and honeydew as insect food source pp. 17-74 In F. L. Wäckers, P. C. J. van Rijn, and J. Bruin [eds.], Plant-provided food for carnivorous insects: A protected mutualism and its applications. Cambridge University Press, Cambridge, UK, 256 pp.
- YONKE, T. R. 1991. Order Hemiptera pp. 22-65 In F. W. Stehr [ed.] *Immature Insects*, vol 2. Kendall/Hunt publishing, Dubuque, Iowa, USA. 975 pp.
- YOUNG, T. P., STUBBLEFIELD, C. H., AND ISBELL, L. A. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 109: 98-107.