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Life history parameters and predation capacities of *Nesidiocoris volucer*: a new biological control agent for tomato crop

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Research Paper

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Abstract

Whiteflies are one of the major pests of tomato under greenhouses, and their control partly relies on biocontrol strategies. Among those biocontrol agents, parasitoids or predators are widely used. However, the introduction of a biocontrol agent in a new area is not trivial. For that reason, we investigated the use of a tropical native mirid, *Nesidiocoris volucer* (Hemiptera: Miridae), for the biological control of whiteflies among other insect pests on tomato crops under greenhouses in the subtropical island of La Réunion, France. *Nesidiocoris volucer* life history traits and plant injury were examined. Nymphs developed and survived between 15 and 30°C and required on average 49.41 days at 15°C and on average 10.50 days at 30°C to develop (nymph survival >94%). At 25°C, each female produced on average 65 eggs. *Nesidiocoris volucer* was able to feed on several prey species, but performed better on whiteflies than on spider mites or thrips. No *N. volucer* feeding injury was observed on tomato. *Nesidiocoris volucer* has also been found in tropical countries of Africa, and we believe that the data presented on this natural enemy could be of great importance for the biocontrol of whiteflies in tropical areas.

Introduction

The use of invertebrate biological control agents to reduce the population of another organism considered as a pest has been widely adopted, and proved its efficiency, as an environmentally safe pest management method (Gurr and Wratten, 2012; Van Lenteren *et al.*, 2018). Mirids (Hemiptera: Miridae) have been studied and three main genus *Macrolophus*, *Dicyphus* and *Nesidiocoris* have been used as biological control agents (Van Lenteren, 2012; Van Lenteren *et al.*, 2018). These mirids are often considered both pests of major crops and natural predators of diverse invertebrates such as whitefly species, aphids, leafminers, thrips, mite, lepidopteran eggs, small larvae, etc. (Wheeler, 2001). Studies of these mirids have mostly focused on four species: *Dicyphus tamaninii* Wagner, *Dicyphus hesperus* Knight, *Macrolophus pygmaeus* Rambur and *Nesidiocoris tenuis* Reuter (Castañé *et al.*, 2011). Except for *D. tamaninii*, these species are currently being commercially mass reared as biological control agents (Van Lenteren, 2012). *Nesidiocoris tenuis* is used to control whiteflies (Hemiptera: Aleyrodidae), leafminers (Lepidoptera: Gelechiidae), thrips (Thysanoptera: Thripidae) and spider mites (Arachnida: Tetranychidae) mainly on tomato but also on eggplant and sweet pepper (Riudavets and Castañé, 1998; Ryckewaert and Alauzet, 2002; Urbaneja *et al.*, 2005, 2009). However, the beneficial status of *N. tenuis* is controversial (Pérez-Hedo and Urbaneja, 2016) because this mirid becomes a plant feeder that causes significant crop damage when prey numbers are low (Arnó *et al.*, 2006, 2010; Sanchez and Lacasa, 2008; Sanchez, 2009).

In Reunion, which is a subtropical island in the Indian Ocean, tomato is the main vegetable crop and is mostly produced in greenhouses, where whiteflies and spider mites are the main pests (Lange and Bronson, 1981). In addition to causing direct damage to plants, whiteflies vector plant viruses (Polston *et al.*, 2014). To help control whiteflies, farmers can release the parasitoids *Encarsia formosa* and *Eretmocerus eremicus* (Hymenoptera: Aphelinidae), both of which are mass reared by the company La Coccinelle© in Reunion (Saint-Pierre). Predators of whiteflies have not yet been reared in Reunion; however, farmers reported increasing problems to control whiteflies with only those parasitoids. Based on the lack of predators as biocontrol agents of tomato pests, we investigated potential indigenous candidates using literature records and direct observations. Among the different candidates, records of a predatory mirid, *Nesidiocoris volucer*, closely related to *N. tenuis*, described on the island in 1902 (Kirkaldy, 1902) caught our attention. Indeed, *N. volucer* was detected preying on the whitefly *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae) (authors' personal communication),

suggesting its potential as a biological control agent. This mirid had also been reported in other tropical countries of Africa such as Tanzania (Kilimanjaro), Cap Verde, Mozambique, Uganda and Sudan (Schuh, 2002–2013) and most recently Niger (Garba *et al*., 2020) showing its pantropical distribution.

Before considering an organism for use in biological control, thorough investigation of its biology and ecology is needed. The development and maintenance of sufficient numbers of the agent to protect the crop can be affected by temperature, food availability and many other factors (Bale *et al*., 2009; Gurr and Wratten, 2012). In this study, we investigated the life history and predation capacities of the indigenous *N. volucer*, as a potential new biocontrol agent of herbivorous pests under greenhouses conditions. We conducted experiments under controlled conditions to evaluate the influence of temperature on *N. volucer* development, survival of immature stages, and fecundity when feeding on *Ephestia kuehniella Zeller* (Lepidoptera: Pyralidae). We then determined the predation capacity of *N. volucer* on the following greenhouse pests: *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), *Tetranychus* sp. (Acari: Tetranychidae), *Thrips parvispinus* Karny (Thysanoptera: Thripidae) and *T. vaporariorum*. Finally, we determined whether *N. volucer* injures tomato plants.

Materials and methods

Insects used in this study

Tobacco whitefly

A laboratory population of the exotic invasive whitefly *B. tabaci* MEAM1 (formerly named B biotype) established from field-collected individuals in 2001 (Delatte *et al*., 2005) on cotton (*Gossypium* sp.) was used. This MEAM1 colony is kept in several ventilated Plexiglas containers (60 × 40 × 60 cm) in a climate (temperature and humidity controlled) room at 25°C, 70% relative humidity (RH), and a 16:8 (L:D) h photoperiod. For experiments, leaves with 4th–5th instar nymphs were collected and examined with a dissecting microscope to remove any drops of honeydew that are naturally produced by *B. tabaci* instars.

Greenhouse whitefly

A colony of *T. vaporariorum* initiated (from field-collected individuals) in 2010 on tobacco plants (*Nicotiana tabacum* L.) in the La Coccinelle© greenhouses was used. Leaves with 4th–5th-instar nymphs were collected for the different experiments.

Spider mite

Spider mite specimens of *Tetranychus* sp. group *desertorum* (probably *T. evansi* species, the only described species from this group in Reunion) were collected from a natural population infesting tomato plants (*Solanum lycopersicum* L.) at the La Coccinelle© facility. The remaining parts after morphological identification and paratypes were deposited as voucher specimens (no. LMAR00003_01) in the collection of CIRAD, UMR PVBMT in Saint-Pierre, La Réunion in ethanol tubes. For the experiments described below, individuals were collected on tomato leaves, examined with a dissecting microscope and transferred to young leaves of tomato seedlings that were not infested with other insects.

Thrips

Specimens of *T. parvispinus* (Karny) were collected from a population infesting sweet pepper (*Capsicum annum* L.) in a greenhouse (ARMEFLHOR, Saint Pierre). To determine the species, DNA was extracted from four individuals and a portion of the gene encoding cytochrome oxidase I (COI) was used for DNA barcoding. Paratypes in ethanol-preserved tubes are available in the insect collection of CIRAD, UMR PVBMT in Saint-Pierre, La Réunion, voucher no. MTEN00002_0201. Larvae and adults were transferred to young cotton leaves obtained from insect-free plants that had been grown in a climate room at 25°C, 70% RH and a 16:8 (L:D) h photoperiod.

Predatory bug

A wild population of the predatory bug *N. volucer* was collected in 2010 from weeds in Saint Paul, La Réunion and further maintained on a *T. vaporariorum* colony in the La Coccinelle© facility. Since then, the *N. volucer* population has been maintained on *T. vaporariorum* on tobacco in a greenhouse at the company. Specimens of this *N. volucer* population were examined by a mirid specialist (JC Streito, INRA, CBGP, France) who confirmed their identity. In addition, DNA was extracted from four specimens, and a portion of the gene that encodes COI was used for DNA barcoding of the *N. volucer* population. Paratypes are available in the insect collection of CIRAD, UMR PVBMT in Saint-Pierre, La Réunion, vouchers no. MATI00012_0101 and MATI00035_0101; GenBank accession numbers KT201360 and KT201350. All *N. volucer* specimens used in this study originated from the same population at the La Coccinelle© facility.

Data analysis

All statistical analyses were performed with the statistical program R 4.1.1 (R Development Core Team, 2021). Different statistical approaches were used, as detailed below in each experimental section: Fisher's exact tests or χ^2 tests, pairwise Wilcoxon rank-sum tests, and the generalized linear mixed model [GLMM, package lme4 (Bates *et al*., 2014)], with deviance tests on fixed effects (based on a χ^2 test) and, if necessary, Tukey's all pair comparison tests [package multcomp (Hothorn *et al*., 2008)]. A Bonferroni-like correction was applied for pairwise tests. The *P*-values of significance level are indicated for all tests.

Experimental design

Climate chambers description

All experiments were conducted in five climate chambers (Sanyo, MLR-350) that enabled control of temperature. Each of the five climate chambers was set with a temperature according to the experimental design (15, 20, 25, 30 and 35°C). A data logger (HOBO U12-013, Onset®, USA) was inserted in each chamber to confirm temperature and RH during all experiments.

Plastic cups design used throughout the study

All of the laboratory experiments used plastic cups (48 mm diameter, 23 mm high). Each cup contained a leaf disc of the tested plant, which was placed on a 5 mm layer of agar (1%). A sharp round plastic shape of 46 mm of diameter was used to obtain each leaf disc. Each cup also had a lid with a ventilation hole covered with fine-mesh gauze.

Development of nymphs

The developmental times for *N. volucer* nymphs were studied at 15, 20, 25, 30 and 35°C, with 76 ± 9% RH and a 12:12 (L:D) h photoperiod (Sanyo, MLR-350). For doing so, 120 *N. volucer*

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Table 1. Mean (SEM) development time (in days) for eggs and nymphs of *Nesidiocoris volucer* at various temperatures (in °C)

	Egg			Nymphs						
Temp (°C)	*N*	Hatching time	Sex	*N*	1st instar	2nd Instar	3rd instar	4th instar	5th instar	1st instar to adult*
15	150	27.59 (0.06)		70	9.78 (0.14)	7.81 (0.08)	8.26 (0.07)	9.57 (0.09)	14.06 (0.08)	49.41 (0.25)
			F	33	9.79 (0.26)	7.67 (0.11)	8.18 (0.09)	9.36 (0.1)	13.88 (0.11)	48.88 (0.4)a
			M	33	9.73 (0.14)	7.94 (0.11)	8.33 (0.11)	9.70 (0.14)	14.24 (0.12)	49.94 (0.29)a
20	51	13.94 (0.10)		67	4.72 (0.08)	3.67 (0.06)	3.79 (0.06)	4.58 (0.06)	7.43 (0.07)	24.19 (0.15)
			F	35	4.74 (0.14)	3.75 (0.08)	3.71 (0.1)	4.49 (0.09)	7.17 (0.08)	23.71 (0.22)c
			M	32	4.69 (0.08)	3.6 (0.09)	3.88 (0.07)	4.69 (0.08)	7.72 (0.10)	24.72 (0.18)b
25	49	8.18 (0.06)		60	3.12 (0.06)	2.17 (0.05)	2.31 (0.06)	2.56 (0.07)	3.98 (0.06)	14.12 (0.11)
			F	29	3.14 (0.08)	2.28 (0.1)	2.21 (0.08)	2.69 (0.09)	3.79 (0.08)	14.10 (0.18)d
			M	30	3.07 (0.08)	2.07 (0.05)	2.4 (0.09)	2.43 (0.09)	4.17 (0.07)	14.13 (0.14)d
30	87	6.14 (0.04)		72	2.07 (0.03)	1.93 (0.03)	1.49 (0.06)	1.92 (0.03)	3.09 (0.04)	10.50 (0.07)
			F	34	2.03 (0.03)	1.91 (0.05)	1.50 (0.09)	1.91 (0.05)	3.0 (0.04)	10.35 (0.09)e
			M	36	2.11 (0.05)	1.94 (0.04)	1.50 (0.08)	1.92 (0.05)	3.17 (0.06)	10.64 (0.11)e
35	88	6.10 (0.03)		45	2.69 (0.14)	2.00 (0.17)	2.50 (0.50)	nd	nd	nd

nd, no development.
N, number of individuals. For nymphs, we considered the individuals that completed their cycle from egg to adult, or at 35°C, individuals that achieved their 3rd instar (see table 2 for *N* at each stage).
*Means followed by the same letter do not differ significantly from pairwise Wilcoxon rank test with Bonferroni-like correction ($P < 0.01$).

adults (60 males and 60 females) were collected from the La Coccinelle© greenhouse and transferred to mesh cages (50 × 50 × 50 cm) containing a 30 cm-tall tobacco plant, on which they mated and laid eggs. Adults were removed 4 h later, and the tobacco plant was transferred to a climate chamber (Sanyo, MLR-350) at 25°C and with 60 ± 10% RH and a 12:12 (L:D) h photoperiod. Hatched nymphs were collected daily and individually caged in plastic cups (48 mm diameter, 23 mm high) with a tobacco leaf disc on agar and with *E. kuehniella* (Biobest©) eggs provided *ad libitum* at each of the five temperatures. Development and survival of nymphs were recorded daily, and the sex of newly emerged adults was determined. For each temperature, 61–72 individual nymphs were monitored, as a whole the development of 330 nymphs were individually followed (tables 1 and 2). This set up allowed us to follow individually each of nymphs until their adult stage.

Effects of sex and rearing temperature on the duration of *N. volucer* nymph development were analysed using a pairwise Wilcoxon rank test with a Bonferroni-like correction. The effect of rearing temperature on overall survival was analysed with a Fisher's exact test on a contingency table containing the total number of dead nymphs and living adults at each temperature. For each temperature, the comparison of instar survival was done by a Fisher's exact test using a contingency table containing the number of dead and living nymphs at each instar. Differences in the sex ratio between rearing temperatures were tested with a χ^2 test.

Development of eggs

To determine the developmental time of eggs, eggs were obtained using the same protocol that was used to obtain hatched nymphs but the tobacco plants with eggs were directly transferred into a climate chamber at each of the five temperatures. *Ephestia kuehniella* eggs were sprinkled on the leaves, and the newly hatched nymphs were counted daily. For each temperature, 49–150 eggs were studied (tables 1 and 2). A pairwise Wilcoxon rank test was done with a Bonferroni-like correction to compare egg developmental durations between the five rearing temperatures.

Fecundity

The fecundity of 33 *N. volucer* females was investigated at 25 ± 1°C and with 89 ± 6% RH and a 16:8 (L:D) h photoperiod (in a climate chamber Sanyo, MLR-350). To obtain newly emerged adult to conduct this experiment, over hundreds of 4th–5th-instar nymphs of *N. volucer* were collected from the greenhouse rearing and maintained in plastic cups described above with a tobacco leaf disc placed on a 5 mm layer of agar (1%) sprinkled with an *ad libitum* quantity of *E. kuehniella* eggs. Newly emerged adults were collected each day for use in this experiment. Then, one female with two males, newly emerged, were transferred to a ventilated cylinder plastic cage (88 mm diameter, 255 mm high) with a mature tomato leaflet sprinkled with *E. kuehniella* eggs. In total, 33 cups, containing one female and two males were used. All leaflets were kept at 25°C (in a climate chamber Sanyo, MLR-350) and were inspected daily. In order to always keep fresh leaves for egg laying, adults were transferred to a new ventilated cylinder plastic cage with a mature tomato leaflet sprinkled with *E. kuehniella* eggs twice each week. Dead males were replaced until the female died. All leaflets kept at 25°C (for each female cylinder plastic cage) were inspected daily for hatched nymphs during 2 weeks after adult removal. Whenever hatched nymphs were observed, they were removed from the leaflets and counted to assess fecundity for each of the 33 females. This set up allowed us to follow individually the fecundity of each of the female until their death. *Nesidiocoris volucer* fecundity (as indicated by the number of hatched nymphs) was statistically analysed by a GLMM with a Poisson distribution, with weeks as a fixed effect and with each individual female as a random effect. A pairwise

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Table 2. Survival (S) in percentage at each stage of the nymph development, sex ratio in percentage (with binomial standard deviation), of *Nesidiocoris volucer*

Temp (°C)	1st instar		2nd instar		3rd instar		4th instar		5th instar		Overall survival (95% CI)*	Sex ratio (95% CI)**
	N	*S* (95% CI)	*N*	*S* (95% CI)	*N*	*S* (95% CI)	*N*	*S* (95% CI)	*N*	*S* (95% CI)		
15	70	98.6 (92.3–99.9)	69	100 (94.8–100.0)	69	100 (94.8–100.0)	69	100 (94.8–100.0)	69	95.7 (87.8–99.1)	94.3a (86.01–98.4)	50 (37.4–62.6)
20	67	100 (94.6–100.0)	67	100 (94.6–100.0)	67	100 (94.6–100.0)	67	100 (94.6–100.0)	67	100 (94.6–100.0)	100a (94.6–100.0)	52.2 (39.7–64.6)
25	60	100 (94.0–100.0)	60	98.3 (91.1–99.9)	59	100 (93.9–100.0)	59	100 (93.9–100.0)	59	100 (93.9–100.0)	98.3a (91.1–99.9)	49.2 (35.9–62.5)
30	72	100 (95.0–100.0)	72	98.6 (92.5–99.9)	71	100 (94.9–100.0)	71	100 (94.9–100.0)	71	98.6 (92.4–99.9)	97.2a (90.3–99.7)	48.6 (36.4–60.8)
35	61	73.8 (60.9–84.2)	45	46.7 (31.7–62.1)	21	9.5 (1.8–30.4)	2	0.0 (0.0–84.2)	0	–	0.0b (0.0–5.9)	–

N, number of individuals; –, no data.
*Overall survival with the same letter are not significantly different (pairwise χ^2 test, all $P > 0.05$ except for 35°C where $P < 0.001$ vs. all other temperatures).
**No significant differences between temperature (χ^2 test, $P = 0.976$).

Tukey test with Bonferroni-like correction was used to compare weekly fecundity.

Predation

Predation by *N. volucer* adults was assessed on adult thrips (*T. parvispinus*), adult spider mites (*Tetranychus* sp.) and nymphs of two whitefly species (*B. tabaci* and *T. vaporariorum*), see insects section to have more details on each of the mentioned prey used in this section. Newly emerged adults of *N. volucer* were placed individually in plastic cups containing one leaf disc of the host plant but no prey (cotton, tomato, sweet pepper or tobacco, according to the prey rearing material). After 12 h for males and 24 h for female, each *N. volucer* adult was transferred in a similar plastic cup with *ad libitum* prey, and each adult was observed individually for 20 min with a dissecting microscope. The number of prey killed and predation behaviours (probing a prey and feeding on a prey) were recorded (Supplementary fig. S1: *N. volucer* feeding on *T. vaporariorum* nymphs). The following behaviours were also recorded and gathered in different classes: (i) the class 'other feedings' was gathering several behaviours: probing of the agar, probing of the leaf disc, probing of water droplets or probing on honeydew (produced by whiteflies); (ii) the class 'contact' was represented by behaviours of a contact made by the predator without feeding on the leaf disc; (iii) the class 'other behaviours' was represented by behaviours of resting, grooming and moving without probing; (iv) the last behaviour class was defined as 'prey feeding' including attack and consumption of the prey. The probing behaviour was referred here as the action of tasting different media by the predator. Each combination of prey species and *N. volucer* sex was represented by 14–20 replicate cups. The number of killed prey by *N. volucer* adults was analysed with a GLMM with a Poisson distribution, with the type of prey, the sex of the predator and their interaction as fixed effects and the experiment as a random effect. Because the interaction between sex and type of prey was significant, the effect of sex was tested for each type of prey and *vice versa* by a pairwise Tukey test with a Bonferroni-like correction.

Effect of prey on development and longevity

We determined the effect of prey species on the duration of *N. volucer* nymph development and the longevity of adults. The prey included larvae and adult thrips (*T. parvispinus*), adult spider mites (*Tetranychus sp.*), nymphs of two whitefly species (*B. tabaci* and *T. vaporariorum*) and *E. kuehniella* eggs. This experiment used newly *N. volucer* hatched nymphs and newly emerged adults that were placed individually in plastic cups (as described above) with the tested prey on a leaf disc of the host plant of the prey (see above insects section). The cups were kept at 25°C (in a climate chamber Sanyo, MLR-350), and tested prey and leaf discs were replaced twice each week. Leaf discs without prey were used as a control in each of the combination tested. The mortality of nymphs and adults was recorded daily. Each prey species was represented by 24–128 replicate cups for nymphs and by 25–88 replicate cups for adults (see table 3). The longevity of *N. volucer* adults according to each prey was each analysed with a GLMM with a Poisson distribution, with the type of prey, the sex of the predator and their interaction as fixed effects and the experiment as a random effect. Because the interaction between sex and type of prey was significant, the effect of sex was tested for each type of prey and *vice versa* by a pairwise Tukey tests with a Bonferroni-like correction. The survival of *N. volucer* nymphs

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Table 3. Mean (SEM) nymph development time (in days), survival of nymphs and longevity of adults (in days) of *Nesidiocoris volucer* feeding on several prey

		Nymph stage			Adult stage				
					Female		Male		
Prey species	Stage of prey	*N*	Survival (95% CI)	Development time	*N*	Longevity	*N*	Longevity	*P*
B. tabaci	Nymph	49	61.2b (46.2–74.8)	12.70 (0.18)c	25	16.32 (1.34)a	24	11.38 (0.73)ab	$<1 \times 10^{-4}$
E. kuehniella	Egg	105	87.6c (79.8–93.2)	11.19 (0.07)a	41	15.73 (1.19)a	48	9.52 (0.52)bc	$<1 \times 10^{-4}$
Tetranychus sp.	Adult	41	0.0a (0.0–8.6)	nd	55	8.89 (0.38)c	56	7.75 (0.40)c	0.200
T. parvispinus	Larva	24	66.7b (44.7–84.4)	14.94 (0.35)d	–	–	–	–	
T. parvispinus	Adult	34	0.0a (0.0–10.3)	nd	25	5.72 (0.45)e	25	4.76 (0.33)d	0.591
T. vaporariorum	Nymph	107	77.6bc (68.5–85.1)	11.53 (0.10)b	76	12.46 (0.77)b	72	12.10 (0.75)a	0.989
No prey		128	0.0a (0.0–2.8)	nd	98	6.52 (0.31)d	91	5.60 (0.27)d	0.068

N, number of individuals; nd, no development; –, no data.
For nymph survival, survival within a column followed by the same letter does not differ significantly from a pairwise χ^2 test with a Bonferroni-like correction ($P = 0.05$).
For nymph development time, means within a column followed by the same letter do not differ significantly from a pairwise Wilcoxon rank test with a Bonferroni-like correction ($P < 0.0001$).
For adult longevity, means within a column followed by the same letter do not differ significantly from a pairwise Tukey test ($P = 0.05$). The last column '*P*' shows *P*-value of the effect of the predator sex on his longevity for each prey from pairwise Tukey test.

was analysed with a pairwise χ^2 test with a Bonferroni-like correction. A pairwise Wilcoxon rank test was done with a Bonferroni-like correction to compare nymph developmental time, according to sex and the type of prey.

Injury of plants by N. volucer *feeding*

Feeding injury to plants caused by *N. volucer* was assessed under controlled conditions (i.e. constant number of insect per plant). The experiment was made on potted tomato plants in a greenhouse. Twelve newly emerged *N. volucer* females and 12 *N. volucer* males were collected (already mating) in the *N. volucer* rearing greenhouse and transferred in couple – in plastic cups. After 48 h, time considered as enough for the end of mating, the males and females were placed individually in a large insect-proof cap that enclosed the apical part of a 20 cm-tall tomato plant (one cap with one insect per plant). Twelve other tomato plants with no insect in the cap were used as blank controls. After 11 days (average time where adults of *N. volucer* died without prey nor leaf, results obtained in a preliminary test in lab conditions at 25°C), the caps and still alive *N. volucer* individuals were removed, and the plants were examined for damage. Damage looked for were as follows: number of brown rings and scars on the stem, petioles of leaves and leaflets. Each plant was grown for an additional 4 weeks during which it was examined for damage twice each week as described in Arnó *et al.* (2010) and compared to the growth development of the control plants.

Results

Development of eggs and nymphs

The mean (SEM) developmental time of *N. volucer* eggs ranged from 27.59 (0.06) days at 15°C to 6.10 (0.03) days at 35°C (table 1). Mean egg developmental time significantly differed between all temperatures tested (all $P < 0.0001$), except between 30 and 35°C ($P = 0.75$). At 35°C, no nymphs survived beyond the 4th instar, and data from rearing at 35°C were only used to compare the survival of instars. The mean (SEM) duration of the entire developmental period for nymphs ranged from 49.41 (0.25) days at 15°C to 10.50 (0.07) days at 30°C (table 1). Pairwise comparisons of nymph development indicated significant differences between all temperatures, whatever the sex (all $P < 0.0001$, table 1). There was no difference between male and female at 25°C ($P = 0.85$), but a very slightly significant difference at 30°C ($P = 0.049$) was observed. A significant difference at 15 and 20°C ($P = 0.015$ and $P < 0.001$, respectively) was also observed.

The sex ratio was not significantly affected by temperature ($P = 0.976$). Overall survival of nymphs ranged from 94 to 100% (table 2) and did not depend on the temperature. Survival of instars was not significantly affected by temperatures between 15 and 30°C (all $P > 0.106$) but was significantly reduced ($P < 0.0001$) at 35°C (table 2).

Female longevity and fecundity

The average (SEM) female longevity was 27.12 (1.58) days, and the maximum longevity was 49 days. Fecundity in terms of numbers of nymphs that hatched ranged from 8 to 142 per female. The mean (SEM) number of total offspring produced per female was 65.0 (5.89) with a significant effect on the week ($P < 0.0001$). Nevertheless, no significant differences between the first 3 weeks were found (all $P > 0.820$) (fig. 1). The first 3 weeks accounted for 81.9% of the total number of hatched nymphs, and these 3 weeks were each significantly different from the other weeks ($P < 0.001$ with weeks 4–6). Week 4 was significantly different from weeks 5 and 6 ($P < 0.001$). There was only one female laying eggs on week 7.

Predation and the effect of prey species and stage on N. volucer *development and longevity*

When the prey was *B. tabaci*, *Tetranychus* sp., *T. parvispinus* or *T. vaporariorum*, the average time spent exhibiting predatory behaviour (contact and prey feeding, fig. 2) was 64.1, 80.4, 41.8 and 85.6%, respectively, for *N. volucer* females and 54.5, 56.1,

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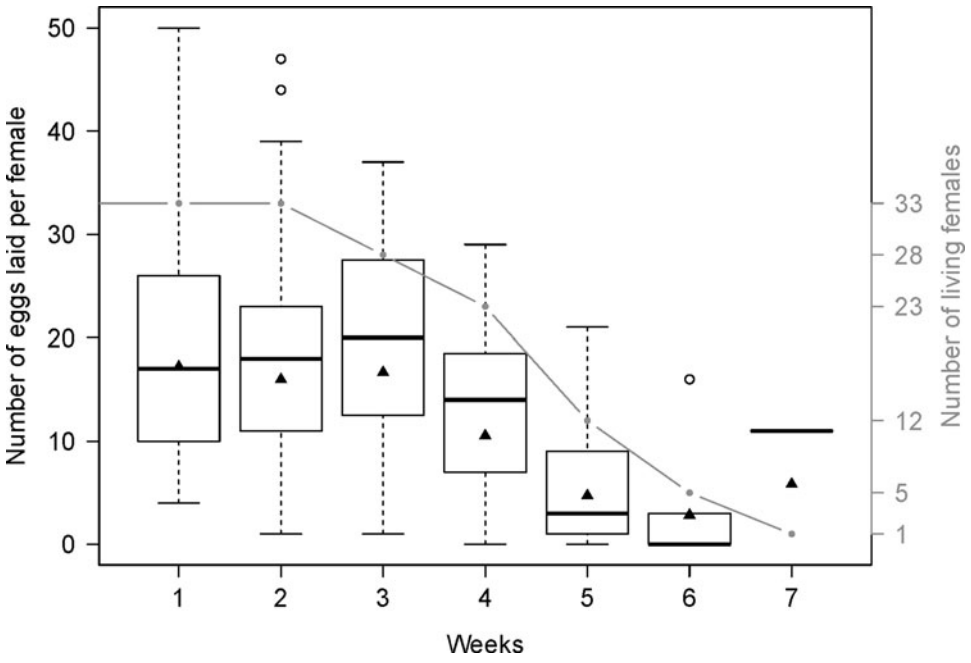

Figure 1. Weekly number of eggs laid (hatched nymphs) by an initial number of 33 females of *Nesidiocoris volucer* followed until their death. The number of eggs is presented by a boxplot displaying the distribution of data based on a five number summary: minimum, first quartile, median, third quartile and maximum of values observed. Whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. ▲ indicates the absolute mean number of eggs per female each week (values given by the model prediction, including no random effect).

24.6 and 75.8%, respectively, for *N. volucer* males (fig. 2). A significant interaction between sex and type of prey ($P = 0.014$) on the number of prey killed was observed. For each prey, the mean number killed did not significantly differ between *N. volucer* males and females (all $P > 0.221$), except that significantly more *Tetranychus* sp. were killed by females than males ($P < 0.0001$) (fig. 2). Significantly fewer *T. parvispinus* than other prey were killed by females ($P < 0.007$) and males ($P < 0.007$). Probing of the leaf disc and agar was observed regardless of prey type.

Nesidiocoris volucer nymphs died before reaching the adult stage when fed on adults of *Tetranychus* sp. or adults of *T. parvispinus*, and obviously with no prey (table 3). For the four other feedings, nymph survival was 61.2, 66.7, 77.6 and 87.6% for nymph fed with *B. tabaci*, instars of *T. parvispinus*, *T. vaporariorum* or *E. kuehniella*, respectively. Mean developmental time did not significantly differ between male and female nymphs whatever the feeding (all $P > 0.254$). Mean development duration significantly differs for *N. volucer* nymphs fed with *E. kuehniella* eggs, *T. vaporariorum* nymphs, *B. tabaci* nymphs and *T. parvispinus* larvae (all $P < 0.0001$). For *N. volucer* nymphs, the longest development times corresponded with the lowest survival rates (table 3).

The longevity of *N. volucer* adults was significantly affected by the interaction between sex and the type of prey ($P < 0.0001$). *Nesidiocoris volucer* females lived significantly longer when fed with *E. kuehniella*, *or B. tabaci*, than when fed with the other species tested ($P < 0.0001$), and males fed with *T. vaporariorum* ($P < 0.0001$). Longevity was shorter for males and females that were not fed with prey or that were fed with *T. parvispinus* ($P < 0.0001$). Females lived significantly longer than males when fed with *B. tabaci* ($P < 0.001$) or with *E. kuehniella* ($P < 0.0001$) (table 3).

Plant injury caused by N. volucer

After 11 days, when the adults were removed, zero of 12 males were alive and four of 12 females were alive, and no damage to the plant were recorded. After the plants had grown an additional 4 weeks, the damage was still not observed. Damage was also absent on the 12 control plants (i.e. those without *N. volucer* adults).

Discussion

The results of this study suggest that the native mirid *N. volucer* may be an effective predator of insect pests in greenhouses in La Réunion and might probably be in other tropical areas such as it was observed in the field in Niger (Garba *et al.*, 2020). The establishment and performance of biological control agents are greatly affected by temperature (Bale *et al.*, 2009; Hughes *et al.*, 2009), and we found that temperature significantly influenced the developmental time of the immature stages of *N. volucer*. Development from egg to adult required only 17 days at 30°C but 77 days at 15°C. However, neither sex ratio nor nymph survival was influenced by temperature (except nymphs failed to develop at 35°C); nymph mortality was <6% at temperatures between 15 and 30°C. Reunion is known for its multitude of climates and its significant temperature changes, which are greatly affected by altitude (Robert, 2003). Our results suggest that this indigenous insect might be well adapted to the multiple environmental conditions found on the island. On the other hand, the rate of development was much greater at 30°C than at 15°C (the lower temperature tested), suggesting that *N. volucer* populations might be more effective as biological control agents in the warmer, low altitude parts of the island.

The effects of temperature on the duration of *N. volucer* immature stages reported here are similar to those previously reported for *N. tenuis* (Hughes *et al.*, 2009; Sanchez, 2009). The latter authors, however, reported much higher mortality for immature stages of *N. tenuis* than we recorded for *N. volucer*, i.e. *N. tenuis* mortality was 48% at 15.5°C and 37% at 15°C. The thermophilic nature of *N. tenuis* means that it is unlikely to establish in cooler areas (Hughes *et al.*, 2009, 2010; Sanchez, 2009), and about 50% of its nymphs were able to mature to the adult stage at 35°C (Sanchez, 2009), which was not the case for *N. volucer* in the

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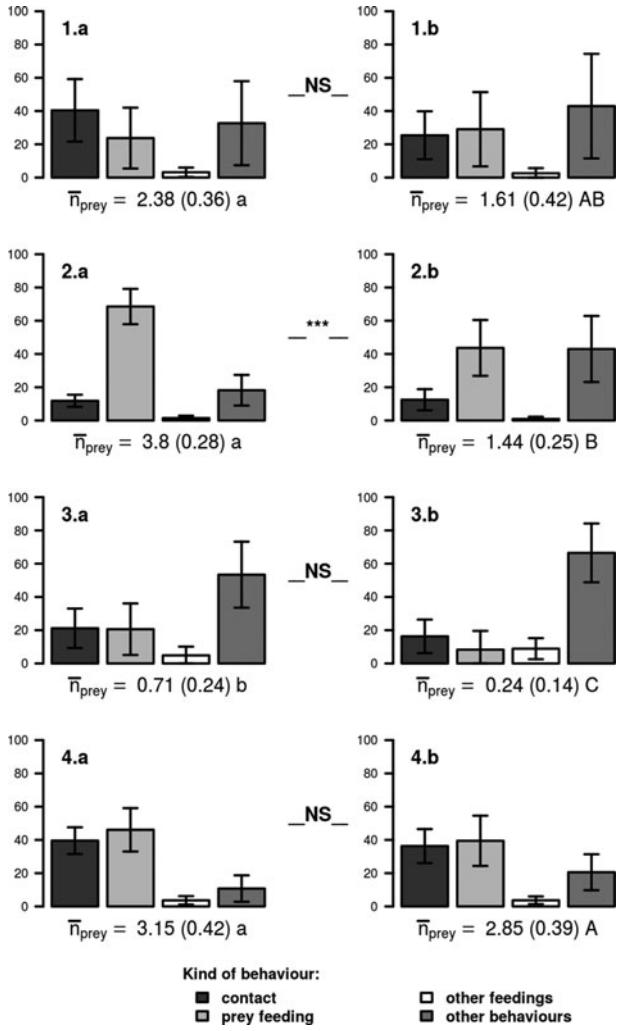

Figure 2. Percentage of elapsed time recorded during 20 min for each behaviour of females (1) and males (2) of *Nesidiocoris volucer* feeding on (a) *Bemisia tabaci* 4th–5th instar nymphs (n_{female} = 16; n_{male} = 18), (b) *Tetranychus* sp. adults (n_{female} = 20; n_{male} = 18), (c) *Thrips parvispinus* adults (n_{female} = 14; n_{male} = 17) and (d) *Trialeurodes vaporariorum* 4th–5th instar nymphs (n_{female} = 20; n_{male} = 20). The mean number of prey killed $\bar{n}_{prey}$ (SEM) is indicated under each graph. For numbers of killed prey (transformed data), means within a column followed by the same letter are not significantly different from Tukey's all pair comparison test with Bonferroni-like correction (P = 0.05). For each prey tested, within a row, the symbol between the two graphs indicates if the mean number of killed prey by sex differ significantly (***) or not (NS) from deviance test (P = 0.05). Recorded behaviours were separated into four different classes, see material and methods section for more details.

current study. Nevertheless, the high survival of *N. volucer* immature stages on a large range of temperature could make it as effective as or more effective than *N. tenuis* in greenhouses in tropical area.

To be effective, a biological control agent should have a high reproductive potential (Hastings, 1997; Uneke, 2007). *Nesidiocoris volucer* females produced an average of 65 viable eggs (as indicated by the numbers of nymphs that hatched) at 25°C, and the maximum recorded in our study was 142. More than 80% of the eggs were laid during the first 3 weeks of the female's adult life. Sanchez *et al.* (2009) found a similar fecundity for *N. tenuis* at 25°C, with a mean (SEM) of 60.0 (5.00) eggs per female deposited during the first 3 weeks of the female's adult life. At 20 and 30°C, *N. tenuis* produced 79.5 (5.50) and 68.0 (4.99) eggs per female, respectively (Sanchez *et al.*, 2009). Additional research is needed to determine how *N. volucer* fecundity is affected by temperatures other than 25°C and especially at lower temperatures. Given that *N. tenuis* is successfully mass reared and given the *N. volucer* fecundity recorded here, we suspect that fecundity will not be a limiting factor for the mass rearing of *N. volucer*.

In the current study, we investigated *N. volucer* predation on a local range of prey, among the main insect pest of greenhouse-produced tomatoes in La Réunion (Delatte *et al.*, 2007). Although our observations indicate that *N. volucer* males and females fed on each of the four prey, the prey type and stage significantly influenced the duration of *N. volucer* nymph instars and the longevity of *N. volucer* adults. However, nymph development was fastest when *N. volucer* females fed on *E. kuehniella* eggs. This food has often been used to feed predacious insects because of its high protein content (Morales-Ramos *et al.*, 2014). However, *E. kuehniella* eggs are expensive and cannot be used for the mass rearing of predators. Still, *E. kuehniella* eggs could be useful to help establish an *N. volucer* population in a greenhouse or as a complementary food (Urbaneja-Bernat *et al.*, 2015).

Among all pests tested as prey for *N. volucer*, the whiteflies *B. tabaci* and *T. vaporariorum* supported the fastest nymph development, one of the highest survival rate, and the greatest adult longevity. Similar results were observed for *N. tenuis* (Perdikis and Arvaniti, 2016). Although numbers of *Tetranychus* sp., *B. tabaci* and *T. vaporariorum* killed by *N. volucer* adult predators were not significantly different in the current study, *N. volucer* nymphs could not complete their development and adults had shorter lifespans when fed with *Tetranychus* sp. This suggests that *Tetranychus* sp. might not provide sufficient nutrients for the development and maximal survival of *N. volucer*. Other studies have demonstrated that the type of prey can greatly affect predator development and reproduction (Bonte *et al.*, 2015; Ugine *et al.*, 2018). In the current study, *N. volucer* nymphs developed on *T. parvispinus* larvae but not on *T. parvispinus* adults, which are more mobile than the larvae. Although *N. volucer* was able to predate *Tetranychus* sp. and adults of *T. parvispinus*, our results suggest that the complete development of nymphs on these prey would require complementary food like *E. kuehniella*.

Several studies have found that biological control tended to be stronger when agents were generalists rather than specialists (Symondson *et al.*, 2002; Stiling and Cornelissen, 2005). *Nesidiocoris tenuis* is mostly used against whiteflies on tomato, but can be considered as a generalist predator, i.e. it can contribute to the control of thrips, leafminers, spider mites and other lepidopterans in the greenhouse (Riudavets and Castañé, 1998; Schaefer and Panizzi, 2000; Calvo *et al.*, 2009; Hassanpour *et al.*, 2016). This generalist predator is closely related to *N. volucer*, and (i) regarding the current results, (ii) the recent field study conducted in Niger that has detected *N. volucer* in tomato fields infested with *Tuta absoluta* (Lepidoptera: Gelechiidae) (Garba *et al.*, 2020) and (iii) previous studies on *N. tenuis*, it tends to indicate that the prey range is similar for the two species, placing *N. volucer* as a potential efficient generalist predator.

A biological control agent should control the pest without detrimental side effects (Gurr and Wratten, 2012; Van Lenteren *et al.*, 2018). Many mirids are zoophytophagous and can cause economically significant damage to crops (Wheeler, 2001; Castañé *et al.*, 2011). *Nesidiocoris tenuis*, for example, causes necrotic rings, flower abortion, reduced growth and small fruits (Sanchez and Lacasa, 2008; Calvo *et al.*, 2009; Arnó *et al.*, 2010). Some predators

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use plant material to complement or supplement their diet in order to enhance their fitness (Maleki *et al*., 2006; Ugine *et al*., 2018). In our study, *N. volucer* nymphs could not complete their development without prey, and adult longevity was quite reduced in the absence of prey even when plant tissue was available. These results demonstrate that *N. volucer* requires animal prey as a component of its diet. We observed that *N. volucer* punctured the leaf discs even when prey were present. Perhaps *N. volucer* obtains supplemental food or water from plants. We suspect that water may be important because predaceous heteroptera use extra-oral digestion and therefore require a substantial amount of water to feed on their prey (Cohen, 1995). They also need water to maintain their physiological status. This required water is mainly obtained from plant tissues (Castañé *et al*., 2011). When *N. volucer* adults were contained on the top of tomato plants without prey, they did not cause visible damage to the plants even after 6 weeks. However, this experiment did not allow us to test for all possible damage on tomato plants (i.e. flower abortion). Mirids could injure different parts of the plant (stems, leaves, fruits, flowers), and the injury might differ among mirid stages. Additional observations of a *N. volucer* population in a tomato greenhouse during the entire 6-month growing cycle were made (authors' personal communication) and indicated that *N. volucer* did not damage any plant, even though the numbers of *N. volucer* nymphs sometimes exceeded 100 per plant. Arnó *et al*. (2006) observed that the zoophytophagous *N. tenuis* caused necrotic rings on tomato, and that the damage was positively correlated with the number of adult mirids. Although *N. tenuis* and *N. volucer* are closely related, our observations suggest that they differ in their direct effects on plants. If *N. volucer* is able to regulate pest numbers without damaging host plants, it could be a very useful biological control agent. Additional research is still needed on how *N. volucer* affects pest numbers and crop yields.

This study has shown that *N. volucer* has thermal plasticity, can reproduce and develop in tomato greenhouses, does not damage the plants supporting its prey, and is a generalist predator that feeds on *T. vaporariorum*, *B. tabaci*, *T. parvispinus* and *Tetranychus* sp. The results suggest that *N. volucer* could be useful for the biological control of insect pests in tomato greenhouses of La Réunion and a candidate could be tested in other tropical environments where it is also present (Schuh, 2002–2013). The effectiveness of *N. volucer* could be increased by applying it with other biological control agents. Based on a meta-analysis, Stiling and Cornelissen (2005) found that the addition of two or more biological control agents would increase mortality by 12.97% and decrease pest abundance by 27.17% compared to the addition of one biological control agent. Only two parasitoids, *E. formosa* and *E. eremicus*, are currently mass reared to control whiteflies on La Réunion; biological control of whiteflies might be increased by complementing these parasitoids with *N. volucer*. Rearing of this mirid, in small quantity, is already successful on tobacco and it has been efficiently established in a tomato greenhouse for 6 months, revealing our ability to raise it. As a whole, all those results have shown to present this mirid as a new generalist predator for tomato pests under greenhouse (with great suitability for tropical and subtropical climates), its development in mass-rearing facilities has started in La Réunion.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485321001164

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Conflict of interest. None.

References

Arnó J, Castañé C, Riudavets J and Gabarra R (2006) Characterization of damage to tomato plants produced by the zoophytophagous predator *Nesidiocoris tenuis*. *IOBC WPRS Bulletin* **29**, 249.

Arnó J, Castañé C, Riudavets J and Gabarra R (2010) Risk of damage to tomato crops by the generalist zoophytophagous predator *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae). *Bulletin of Entomological Research* **100**, 105–115.

Bale J, Allen C and Hughes G (2009) Thermal ecology of invertebrate biological control agents: establishment and activity. In *Proceedings of the Third International Symposium on Biological Control of Arthropods (ISBCA)*, pp. 57–65.

Bates D, Mächler M, Bolker B and Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Bonte J, De Hauwere L, Conlong D and De Clercq P (2015) Predation capacity, development and reproduction of the southern African flower bugs *Orius thripoborus and Orius naivashae* (Hemiptera: Anthocoridae) on various prey. *Biological Control* **86**, 52–59.

Calvo J, Bolckmans K, Stansly PA and Urbaneja A (2009) Predation by *Nesidiocoris tenuis* on *Bemisia tabaci* and injury to tomato. *Biocontrol* **54**, 237–246.

Castañé C, Arnó J, Gabarra R and Alomar O (2011) Plant damage to vegetable crops by zoophytophagous mirid predators. *Biocontrol* **59**, 22–29.

Cohen AC (1995) Extra-oral digestion in predaceous terrestrial Arthropoda. *Annual Review of Entomology* **40**, 85–103.

Delatte H, Reynaud B, Granier M, Thornary L, Lett JM, Goldbach R and Peterschmitt M (2005) A new silverleaf-inducing biotype Ms of *Bemisia tabaci* (Hemiptera: Aleyrodidae) indigenous of the islands of the south-west Indian Ocean. *Bulletin of Entomological Research* **95**, 29–35.

Delatte H, Lett JM, Lefeuvre P, Reynaud B and Peterschmitt M (2007) An insular environment before and after TYLCV introduction. In Czosnek H (ed.), *Tomato Yellow Leaf Curl Virus Disease, Management, Molecular Biology, Breeding for Resistance*. Dordrecht, The Netherlands: Springer, pp. 13–23.

Garba M, Streito J and Gauthier N (2020) First report of three predatory bugs (Heteroptera: Miridae) in tomato fields infested by the invasive South American tomato pinworm, *Tuta absoluta* in Niger: an opportunity for biological control? *Phytoparasitica* **48**, 215–229.

Gurr G and Wratten S (2012) *Biological Control: Measures of Success*. Dordrecht, The Netherlands: Springer Science & Business Media.

Hassanpour M, Bagheri M, Golizadeh A and Farrokhi S (2016) Functional response of Nesidiocoris tenuis (Hemiptera: Miridae) to *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae): effect of different host plants. *Biocontrol Science and Technology* **26**, 1489–1503.

Hastings A (1997) *Population Biology: Concepts and Models*. New York, NY, USA: Springer Science & Business Media.

Hothorn T, Bretz F and Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* **50**, 346–363.

Hughes GE, Bale JS and Sterk G (2009) Thermal biology and establishment potential in temperate climates of the predatory mirid *Nesidiocoris tenuis*. *Biocontrol* **54**, 785.

Hughes GE, Alford L, Sterk G and Bale JS (2010) Thermal activity thresholds of the predatory mirid *Nesidiocoris tenuis*: implications for its efficacy as a biological control agent. *Biocontrol* **55**, 493–501.

Kirkaldy GW (1902) XIV. Memoir upon the Rhynchotal family CapsidæAuctt. *The Royal Entomological Society* **50**, 243–272.

Lange WH and Bronson L (1981) Insect pests of tomatoes. *Annual Review of Entomology* **26**, 345–371.

Maleki F, Ashouri A, Mohaghegh J and Bandani A (2006) Effect of some diets on *Macrolophus pygmaeus rambur* (Hemiptera: Miridae) fitness under laboratory conditions. *Communications in Agricultural Applied Biological Sciences* **71**, 393–397.

Morales-Ramos JA, Rojas MG and Coudron TA (2014) Artificial diet development for entomophagous arthropods. In Morales-Ramos JA, Rojas MG and Shapiro-Ilan D (eds), *Mass Production of Beneficial Organisms*. Academic Press, Elsevier, pp. 203–240. doi: 10.1016/B978-0-12-391453-8.00007-8.

Perdikis D and Arvaniti K (2016) Nymphal development on plant vs. leaf with and without prey for two omnivorous predators: *Nesidiocoris tenuis* (Reuter, 1895) (Hemiptera: Miridae) and *Dicyphus errans* (Wolff, 1804) (Hemiptera: Miridae). *Entomologia Generalis* **35**, 297–306.

Pérez-Hedo M and Urbaneja A (2016) The zoophytophagous predator *Nesidiocoris tenuis*: a successful but controversial biocontrol agent in tomato crops. In Horowitz A and Ishaaya I (eds), *Advances in Insect Control and Resistance Management*. Cham: Springer, pp. 121–138.

Polston JE, De Barro P and Boykin LM (2014) Transmission specificities of plant viruses with the newly identified species of the *Bemisia tabaci* species complex. *Pest Management Science* **70**, 1547–1552.

R Development Core Team (2021) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at http://www.R-project.org/.

Riudavets J and Castañé C (1998) Identification and evaluation of native predators of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in the Mediterranean. *Environmental Entomology* **27**, 86–93.

Robert R (2003) *Les régions climatiques de l'île de la Réunion: évolution des connaissances depuis quarante ans, 1958–1998*. Saint-Denis, France: Université de la Réunion.

Ryckewaert P and Alauzet C (2002) The natural enemies of *Bemisia argentifolii* in Martinique. *Biocontrol* **47**, 115–126.

Sanchez JA (2009) Density thresholds for *Nesidiocoris tenuis* (Heteroptera: Miridae) in tomato crops. *Biological Control* **51**, 493–498.

Sanchez J and Lacasa A (2008) Impact of the zoophytophagous plant bug *Nesidiocoris tenuis* (Heteroptera: Miridae) on tomato yield. *Journal of Economic Entomology* **101**, 1864–1871.

Sanchez J, Lacasa A, Arnó J, Castane C and Alomar O (2009) Life history parameters for *Nesidiocoris tenuis* (Reuter) (Het., Miridae) under different temperature regimes. *Journal of Applied Entomology* **133**, 125–132.

Schaefer CW and Panizzi AR (2000) *Heteroptera of Economic Importance*. Boca Raton, FL, USA: CRC Press LLC.

Schuh RT (2002–2013) On-line systematic catalog of plant bugs (Insecta: Heteroptera: Miridae) Available at: http://research.amnh.org/pbi/catalog.

Stiling P and Cornelissen T (2005) What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biological Control* **34**, 236–246.

Symondson W, Sunderland K and Greenstone M (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**, 561–594.

Ugine TA, Krasnoff SB, Grebenok RJ, Behmer ST and Losey JE (2018) Prey nutrient content creates omnivores out of predators. *Ecology Letters* **22**, 275–283.

Uneke CJ (2007) *Integrated Pest Management for Developing Countries: A Systemic Overview*. New York, NY, USA: Nova Publishers, Inc.

Urbaneja-Bernat P, Mollá O, Alonso M, Bolkcmans K, Urbaneja A and Tena A (2015) Sugars as complementary alternative food for the establishment of *Nesidiocoris tenuis* in greenhouse tomato. *Journal of Applied Entomology* **139**, 161–167.

Urbaneja A, Tapia G and Stansly P (2005) Influence of host plant and prey availability on developmental time and survivorship of *Nesidiocoris tenius* (Het.: Miridae). *Biocontrol Science and Technology* **15**, 513–518.

Urbaneja A, Montón H and Mollá O (2009) Suitability of the tomato borer *Tuta absoluta* as prey for *Macrolophus pygmaeus* and *Nesidiocoris tenuis*. *Journal of Applied Entomology* **133**, 292–296.

Van Lenteren JC (2012) The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *Biocontrol* **57**, 1–20.

Van Lenteren JC, Bolckmans K, Köhl J, Ravensberg WJ and Urbaneja A (2018) Biological control using invertebrates and microorganisms: plenty of new opportunities. *Biocontrol* **63**, 39–59.

Wheeler AG (2001) *Biology of the Plant Bugs (Hemiptera: Miridae): Pests, Predators, Opportunists*. New York, NY, USA: Cornell University Press.

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