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Biological and Microbial Control

Biological traits of the zoophytophagous predatory mirid *Nesidiocoris poppiusi* (Heteroptera: Miridae), a candidate biocontrol agent in China

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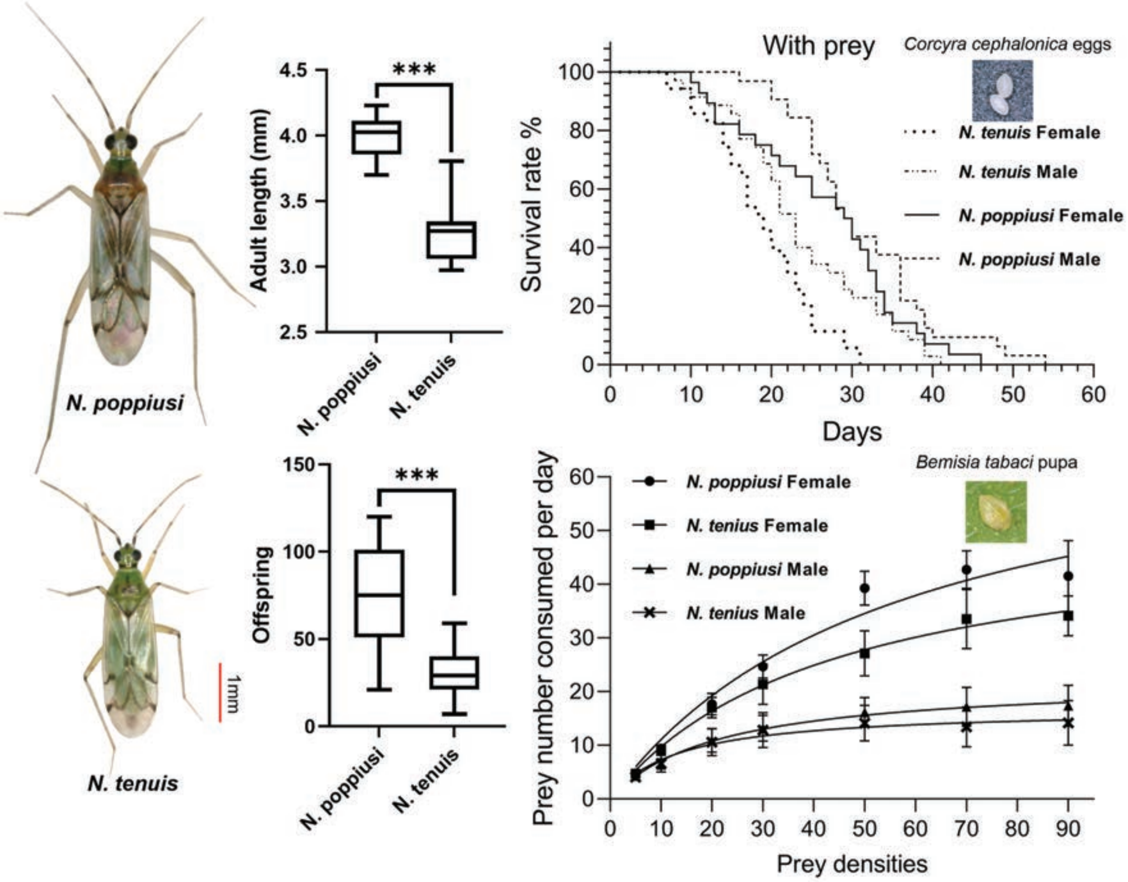
Mirid predators are increasingly used in biological control of multiple greenhouse crops pests. However, due to great morphological similarity and tiny body size, some mirid predators have been largely confused with their allied species. *Nesidiocoris tenuis* Reuter as a commercial mirid predator was confused largely with *Nesidiocoris poppiusi* Carvalho in China. To evaluate the biocontrol potential of *N. poppiusi*, its biological traits and the functional response to *Bemisia tabaci* Gennadius were studied compared with *N. tenuis* under laboratory conditions. The results showed that no significant differences of the developmental times from the first instar to adult stages between the 2 mirids fed on *Corcyra cephalonica* Stainton eggs were observed, while *N. poppiusi* had better population growth parameters than *N. tenuis.* Under the condition with prey, both female and male of *N. poppiusi* lived significantly longer than those of *N. tenuis*. It could lay 74.0 eggs, which was significantly higher than that of *N. tenuis* (30.2 eggs). Under the condition without prey, both *N. poppiusi* and *N. tenuis* couldn't complete development to adulthood on tomato, tobacco, muskmelon, and cabbage leaves, however, tobacco and tomato were more suitable than the other 2 plants. A type II functional response was observed for both males and females of the 2 predators. *Nesidiocoris poppiusi* females consumed significantly more *B. tabaci* pupae than *N. tenuis* when prey densities were large than 30. Our results indicated that *N. poppiusi* could be a promising candidate for biological control of *B. tabaci*.

Key words: Nesidiocoris tenuis, biological trait, biocontrol agent, *Bemisia tabaci*

Graphical Abstract



Introduction

Generalist heteropteran predators are among the most commonly used predators in augmentative biological control, comprising about 8% of all arthropod natural enemies used in pest management worldwide (van Lenteren 2012, De Clercq et al. 2022). Particularly, predators of the family Miridae are used in biological control of Solanaceous pests, such as *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) and *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (Ingegno et al. 2013, Roda et al. 2020, Park et al. 2022). Predatory mirids are known as zoophytophagous predators, which are primarily predaceous but also feed on plants (Urbaneja et al. 2022). Their phytophagy allows them to survive in periods of prey scarcity and to establish before pest appearance (Pérez-Hedo and Urbaneja 2016). Many species in several genera of the subfamily Bryocorinae consume a wide range of prey, including aphids, lepidopterans, and other arthropod pests (Pérez-Hedo et al. 2021b). However, only 3 species from this subfamily, *Dicyphus hesperus* Knight, *Macrolophus pygmaeus* Rambur, and *Nesidiocoris tenuis* Reuter (Heteroptera: Miridae), are commercially produced recently and mainly used in tomato crops around the world (Pérez-Hedo et al. 2021b). And among them, *N. tenuis* is considered the only commercial mirid predator in China (Li et al. 2022).

Some mirid predators are tiny bugs and notoriously difficult to identify (Sanchez and Cassis 2018). For example, due to great morphological similarity, 2 commercially successful biocontrol agents *Macrolophus pygmaeus* Rambur and *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) had been largely confused with identification in the Mediterranean (van Lenteren 2003, Perdikis et al. 2011). Several studies using '*Macrolophus caliginosus*' may in fact have studied *M. pygmaeus* (De Clercq et al. 2022). This kind of messiness had affected both the mass rearing and the conservation of these species. In China, we found a similar situation that the commercial mirid predator labeled as '*Nesidiocoris tenuis*' was *Nesidiocoris poppiusi* in fact. *Nesidiocoris tenuis* is widely distributed in the Palaearctic and Mediterranean regions (Kerzhner and Josifov 1999, Sanchez et al. 2009).In many countries, this species has recently been used as a biological control agent in agro-ecosystems in order to control major greenhouses insect pests such as whiteflies and *Tuta absoluta* (Calvo et al. 2012, Urbaneja-Bernat et al. 2013, Pérez-Hedo and Urbaneja2016, Kandori et al. 2022). The commercial use of *N. tenuis* in China started in recent years (Li et al. 2022). *Nesidiocoris poppiusi* is a closely related species of *N. tenuis* and both 2 species are widely distributed in China and with similar morphology (Liu et al. 2022). The misidentification of these 2 species might cause the mass rearing of *N. poppiusi* instead of *N. tenuis*. In other words, the commercialized mirid predator in China may be *N. poppiusi*. Chinese researchers predicted *N. poppiusi* should have a higher predation ability than *N. tenuis* as it had bigger body size and higher displacement velocity (Xun 2016). However, no study has so far examined the role of *N. poppiusi* as predator of any pests, or the development and reproduction of this mirid.

Therefore, this study focused on the potential biocontrol ability of *N. poppiusi* and compared the difference of its biological traits with *N. tenuis*. Firstly, due to the similar morphology, we characterized the 2 mirids molecularly (see the Supplementary Material). Then the experiments were carried out to study the life history traits and the reproductive parameters of these 2 mirids with or without prey. To explore the predatory capacity, the functional response of *N. poppiusi* to *B. tabaci* was investigated. The results may explain the reason that the mass reared mirid is mainly *N. poppiusi* instead of *N. tenuis* in China, and to improve the mass rearing techniques and to guide the subsequent field application.

Materials and Methods

Insect Rearing and Plant Cultivation

To establish laboratory colonies of *N. poppiusi* and *N. tenuis*, mixed populations were collected from a tobacco field in Kunming City, Yunnan, China (Latitude 24.896, longitude 103.418). The mirids were reared in plastic box (29 cm × 23 cm × 10 cm) on fresh stems of tomato plants (*Lycopersicum esculentum*), as an oviposition substrate. The cut end of the stems was covered with cotton and placed in a 50-ml container with water to keep the tomato stems fresh for a few days. The food of the stock colony of the predators primarily consisted of frozen and irradiated eggs of *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) (Shangdong Lubao Co., Jinan, China) was given twice per week. The laboratory colonies of *B. tabaci* were collected from tomato field in Beijing, China. The whiteflies were reared on tobacco plants in cages (50 cm × 50 cm × 50 cm) and new tobacco plants were introduced regularly to the cage. Insect rearing and all of the experiments were carried out in a growth chamber under a LD 16:8 h photocycle maintained at 25 ± 1 °C and 60 ± 10% relative humidity.

Tomato (*L. esculentum*), tobacco (*Nicotiana tabacum*), cabbage (*Brassica chinensis*), and melon (*Cucumis melo*) plants were used in this study. Seedlings were cultured in plastic pots (0.5 liters), watered semiweekly, and fertilized weekly. About 45 days old plants would be used for experiments. All plants were cultivated in a growth room under a LD 16:8 h photocycle maintained at 25 ± 1 °C and 60 ± 10% relative humidity.

Molecular Diagnosis using COI Barcoding

Genomic DNA was extracted from whole body of single mirid using the QIAamp DNA Mini Kit in accordance with the protocol of the manufacturer (Qiagen, China), after identification based on genital morphology. There were 4 replications for each species. Polymerase chain reactions were performed using the Premix Taq Version 2.0 plus dye (TaKaRa, China) with the primer pair LCO1490 GGTCAACAAATCATAAAGATATTGG and HCO2198 TAAACTTCAGGGTGACCAAAAAATCA (Folmer et al. 1994). The thermal cycling program consisted of an initial step of 95°C for 2 min followed by 35 cycles of 95°C for 20 s, 50°C for 50 s, and 72°C for 1 min, and then followed by a final extension step of 72°C for 5 min. The product yield was monitored by electrophoresis with 1.0% agarose gel. The amplified products were purified using QIA quick PCR Purification Kit (Qiagen, China), and were sequenced using an ABI PRISM 3730xl analyzer (serviced by Tsingke Biotechnology Co., Ltd, Beijing, China). All the sequences obtained were aligned with *N. tenuis* COI fragments using BLAST (National Center for Biotechnology Information) on the online server (https://blast.ncbi.nlm.nih.gov/Blast.cgi).

Development and Reproduction of *N. poppiusi* and *N. tenuis* Preying on *C. cephalonica* Eggs

Mated adults of both predators were kept with tomato stems covered with cotton and placed in a 50-ml container with water to keep the fresh for a few days. After 12 h, the adults were removed, and tomato stems were saved until nymphs of the predators emerged. The newly emerged first-instar nymphs of both predators were kept in a round plastic box (diameter 7 cm, height 5 cm), separately, the covers of which had a hole (diameter 5 cm) screened with muslin for ventilation. Each nymph was fed daily with about 100 irradiated eggs of *C. cephalonica*, placed on fresh tomato leaves. About 55 individuals of *N. poppiusi* and 59 individuals of *N. tenuis* were tested. The development time of each instar of *N. poppiusi* and *N. tenuis* was recorded. Upon emergence, adults were transferred to a new round box with tomato stems placed in a 5-ml container with water separately. The survival was recorded daily. The tomato stems were replaced with fresh ones every 5 days. The stems containing eggs of both predators were kept separately until the nymphs emerged. The number of first-instar nymphs appearing was recorded as a measure of fecundity. About 23 females of *N. poppiusi and* 25 females of *N. tenuis* were tested. To observe morphological characters, photographs of *N. poppiusi* and *N. tenuis* nymphs and adults were taken by a KEYENCE VHX-6000 microscope (KEYENCE Co., Ltd, China). Measurements were taken using an equipped software program with the same microscope.

The raw life-history data for *N. poppiusi* and *N. tenuis* were analyzed using an age-stage, 2-sex life table in the TWO-SEX-MSChart program (Chi and Liu 1985, Chi and Yang 2003, Chi 2022). Mean ± SE values of the life table parameters were estimated using a bootstrap technique. The life-history parameters (r, intrinsic rate of increase; λ, finite rate of increase, T, mean generation time; DT, generation doubling time; GRR, gross reproductive rate; R_0, net reproductive rate) were calculated accordingly.

Life-History Parameters of *N. poppiusi* and *N. tenuis*on Different Host Plant Without Prey

This experiment was performed as described for the previous experiment but without prey and with different plant leaves. Upon hatching, the first-instar nymphs of both predators were placed in round plastic boxes supplied only with fresh tomato, tobacco, Chinese rape, and melon leaves separately. About 40 individuals were tested for each treatment. The survival and the duration of different stages were recorded daily.

Female and Male Longevity of *N. poppiusi* and *N. tenuis* Reared With or Without Prey

The newly emerged *N. poppiusi* and *N. tenuis* adults were transferred in couples (1 female and 1 male) to a round plastic box with tomato stems placed in a 5 ml container with water separately. The adults were fed daily with about 200 fresh irradiated eggs of *C. cephalonica* or without. The tomato stems were replaced with fresh ones every 5 days. The survival was recorded daily. About 30 individuals were tested for each adult.

Functional Response of *N. poppiusi* and *N. tenuis* against *B. tabaci*

The experimental arena consisted of a single tobacco leaf disk (about 6 cm in diameter) placed upside down on moistened filter paper in a plastic Petri dish 9 cm in diameter. Seven different densities of whitefly pupae (5, 10, 20, 30, 50, 70, and 90 individuals per arena) were presented to each female or male, by transferring them to the leaf disks gently using a fine paint brush (Montserrat et al. 2000). The experiments were carried out in a growth chamber (60 ± 10% RH, LD 16:8 h photoperiod). Twenty-four hours after introducing the predator, the numbers of prey consumed were counted and recorded. About 10 individuals of each adult and 10 groups of prey were used

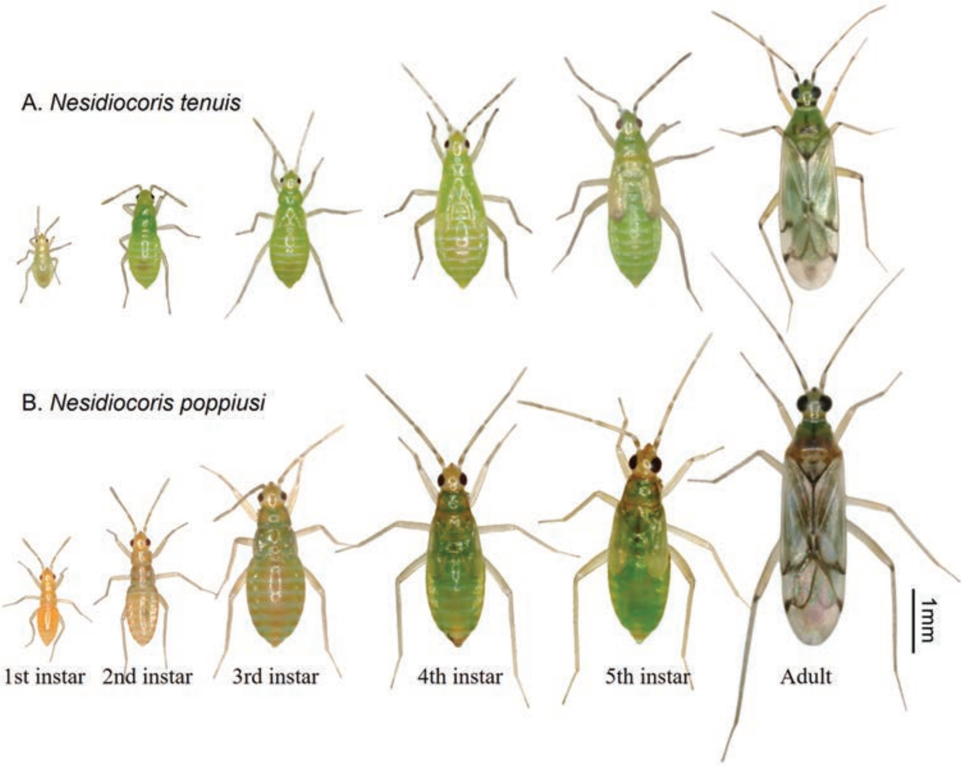


Fig. 1. Photos of nymphal instars and adults of *Nesidiocoris tenuis* and *Nesidiocoris poppiusi*. From left to right: first instar, second instar, third instar, fourth instar, fifth instar, adult.

for each prey density treatment. Moreover, we estimated predator voracity on pupae by fitting the Holling II functional response model. The parameters are calculated as the following equation:

$$N_a a' \; NT/(1a'T_bN)$$

where N_a is the net prey consumption rate by the predator during selected time period, a' is the instantaneous attack rate, N is the density of *B. tabaci* pupae, T is the predatory time of the predator (1 day), and T_b is the time required to prey on a pupa (handling time). The potential maximum Na (Na-max) was estimated by dividing handling time by the predatory time (T/T_b) (Holling 1959).

Statistical Analysis

The data collected in the experiments and the calculated residuals were tested for normality using the Kolmogorov–Smirnov test (all $P > 0.05$). The effect of the predator species on the life history traits (development time from eggs to adult and per each nymphal stage) was analyzed using student's *t*-test. The effect of the predator species and sex on the number of consumed *B. tabaci* pupae per prey density were analyzed using one-way analysis of variance (Tukey's test). The adult survival curve was compared among groups using the log-rank test with Bonferroni correction. Differences were considered significant at $P < 0.05$. All statistical analyses were performed using SPSS 20 and GraphPad Prism 9 (IBM Corp. 2011, GraphPad Software. 2021)

Results

The Morphology and Developmental Times of *N. poppiusi* and *N. tenuis* Preying on *C. cephalonica* Eggs

The morphology of nymphal stages and adults of *N. poppiusi* and *N. tenuis* is shown in Fig. 1. It is difficult to identify *N. tenuis* from *N. poppiusi* during nymphal stages under the naked eye as 2 mirid nymphs are tiny and with similar bodily form and similar coloration. *N. tenuis* adult is generally greenish brown, while *N. poppiusi* is generally yellowish brown. The length of *N. poppiusi* adult is significantly higher than *N. tenuis* (Supplementary Figure S1).

The developmental time of different stages of *N. poppiusi* and *N. tenuis* preying on *C. cephalonica* eggs is shown in Table 1. All instars successfully completed their life cycle reared on tomato leaves with eggs of *C. cephalonica*. The result showed no significant differences among the developmental times from first instar to adult stages of the 2 mirids. The duration of egg incubation period of *N. poppiusi* (7.24 ± 0.06) was significantly longer than that of *N. tenuis* (6.78 ± 0.05). The preadult developmental time (from egg to adult) had no significant difference between *N. poppiusi* and *N. tenuis*. The developmental time (mean ± SE) from the newly emerged first-instar nymph to adult ranged from 19.09 ± 0.11 d to19.2 ± 0.10 d in females of *N. poppiusi* and *N. tenuis*, respectively, and from 19.05 ± 0.11 d to 19.21 ± 0.16 d in males of *N. poppiusi* and *N. tenuis*, respectively. The mortality rates of the 2 mirids showed similar trends during preadult time according to the survival numbers. And the highest mortality occurred at the first instar stage.

The Developmental Time and Survival Rate Reared on Different Host Plants Without Prey

The developmental time of different stages of *N. poppiusi* and *N. tenuis* reared on different host plant without *C. cephalonica* eggs is shown in Table 2. The results demonstrated that both *N. poppiusi* and *N. tenuis* couldn't complete development to adulthood on tomato, tobacco, muskmelon, and cabbage leaves without supplemental prey. Both *N. poppiusi* and *N. tenuis* could develop to the second instar on cabbage leaves and the third instar on muskmelon leaves. *N. poppiusi* and *N. tenuis* showed different survivability on tomato and tobacco leaves. Tomato leaves proved to be the most suitable plant food for *N. tenuis*, allowing up one-third instar nymphs through to the fourth instar. However, *N. poppiusi* just developed to the third instar on tomato leaves but to the fourth instar on tobacco leaves.

The Longevity of *N. poppiusi* and *N. tenuis* Adult Reared With or Without *C. cephalonica* Eggs

The survival rate changed with time of newly emerged female and male of 2 predators reared with *C. cephalonica* eggs on tomato leaves (Fig. 2A). The female and male longevity of *N. poppiusi* and *N. tenuis* was 26.9 d, 31.4 d, 18.9 d, 23.7 d, respectively. Both female and male of *N. poppiusi* lived significantly longer than those of *N. tenuis* (female $\chi^2 = 17.44$, df = 1, $P < 0.0001$; male $\chi^2 = 8.59$, df = 1, $P = 0.0034$). At the 30th day, half of both females and males of *N. poppiusi* were alive, while 88.6% females and 80.0% males of *N. tenuis* had died. *Nesidiocoris tenuis* male lived significantly longer than female when reared with *C. cephalonica* eggs ($\chi^2 = 7.764$, df = 1, $P = 0.0053$). *Nesidiocoris poppiusi* male also lived longer than female but without significant differences ($\chi^2 = 2.495$, df = 1, $P = 0.1142$).

The survival rate changed with time of newly emerged female and male of 2 predators reared without *C. cephalonica* eggs on tomato leaves (Fig. 2B). The female and male longevity of *N. poppiusi* and *N. tenuis* was 8.6 d, 6.4 d, 8.3 d, 6.0 d, respectively. Females of both *N. tenuis* and *N. poppiusi* lived significantly longer than males (*N. tenuis* $\chi^2 = 8.847$, df = 1, $P = 0.0029$; *N. poppiusi* $\chi^2 = 10.97$, df = 1, $P = 0.0009$). The survival rates of both female and male had no significant difference between *N. tenuis* and *N. poppiusi* (female $\chi^2 = 0.032$, df = 1, $P = 0.8576$; male $\chi^2 = 0.105$, df = 1, $P = 0.7460$). The median survival of *N. tenuis* female and male, and *N. poppiusi* female and male happened at the 8th, 5th, 7th, 6th day, respectively.

Reproductive Parameters of *N. poppiusi* and *N. tenuis* Preying on *C. cephalonica* Eggs

The population growth parameters showed some differences between *N. poppiusi* and *N. tenuis* (Table 3). *Nesidiocoris poppiusi* female could lay 74.0 eggs, significantly higher than that of *N. tenuis* (30.2 eggs). The net reproductive rate (R_0) followed the same order as total fecundity. The intrinsic rate of increase (r_m)

Table 1. Developmental time (days) of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* preying on eggs of *Corcyra cephalonica*

Predator		Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Nymphal development	Preadult
All	*N. poppiusi*	7.24 ± 0.06a	4.22 ± 0.06a	3.87 ± 0.05a	3.69 ± 0.07a	3.27 ± 0.07a	4.02 ± 0.06a	19.07 ± 0.08a	26.28 ± 0.10a
	N	55	50	47	45	44	43	43	43
	N. tenuis	6.78 ± 0.05b	4.36 ± 0.07a	3.94 ± 0.06a	3.53 ± 0.07a	3.22 ± 0.06a	4.11 ± 0.05a	19.14 ± 0.15a	25.98 ± 0.11a
	N	59	53	49	47	45	44	44	44
Female	*N. poppiusi*	7.22 ± 0.09a	4.13 ± 0.07a	3.87 ± 0.07a	3.74 ± 0.09a	3.26 ± 0.09a	4.09 ± 0.09a	19.09 ± 0.11a	26.30 ± 0.13a
	N	23	23	23	23	23	23	23	23
	N. tenuis	6.80 ± 0.08b	4.36 ± 0.10a	3.92 ± 0.08a	3.52 ± 0.10a	3.24 ± 0.09a	4.16 ± 0.07a	19.2 ± 0.10a	26.00 ± 0.13a
	N	25	25	25	25	25	25	25	25
Male	*N. poppiusi*	7.20 ± 0.09a	4.25 ± 0.10a	3.85 ± 0.08a	3.70 ± 0.11a	3.30 ± 0.11a	3.95 ± 0.09a	19.05 ± 0.11a	26.25 ± 0.16a
	N	20	20	20	20	20	20	20	20
	N. tenuis	6.74 ± 0.10b	4.37 ± 0.11a	4.00 ± 0.11a	3.58 ± 0.12a	3.21 ± 0.10a	4.05 ± 0.05a	19.21 ± 0.16a	25.95 ± 0.21a
	N	19	19	19	19	19	19	19	19

Values (mean ± SE) in each section between *N. poppiusi* and *N. tenuis* followed by the same lowercase letter indicate not significantly different ($P > 0.05$); *N* means the number of individuals survived during each development stage.

Table 2. Developmental time (days) and survival rate of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* nymphs fed on different host plants without prey

Host plant	Predator	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Tomato	*N. poppiusi*	4.93 ± 0.12	4.67 ± 0.33	3.00 ± 0.52	/	/
	Survival rate	33.33%	20.00%	0		
	N. tenius	4.70 ± 0.15	4.70 ± 0.21	5.00 ± 0.00	3.50 ± 0.50	/
	Survival rate	53.33%	36.11%	15.38%	0	
Tobacco	*N. poppiusi*	4.35 ± 0.18	6.00 ± 0.31	14.50 ± 1.50	6.00 ± 1.00	/
	Survival rate	55.56%	50.00%	13.33%	0	
	N. tenius	4.97 ± 0.18	4.67 ± 0.21	4.33 ± 0.67	/	/
	Survival rate	52.78%	31.58%	0		
Melon	*N. poppiusi*	4.86 ± 0.16	5.50 ± 0.50	2.50 ± 0.50	/	/
	Survival rate	58.33%	9.53%	0		
	N. tenius	5.12 ± 0.15	5.00 ± 0.41	3.00 ± 0.41	/	/
	Survival rate	47.22%	23.53%	0		
Cabbage	*N. poppiusi*	4.79 ± 0.45	4.86 ± 0.73	/	/	/
	Survival rate	38.89%	0			
	N. tenius	4.87 ± 0.19	3.87 ± 0.45	/	/	/
	Survival rate	41.67%	0			

"/" means no individual develops to the corresponding stage.

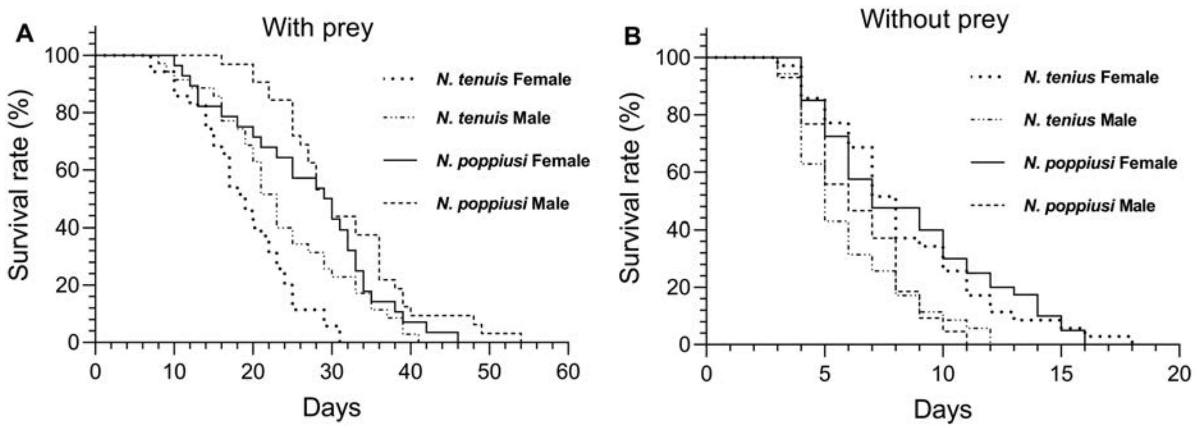


Fig. 2. Survival rate of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* newly emerged female and male reared with or without *Corcyra cephalonica* eggs on tomato leaves.

Table 3. Reproduction parameters and life-history parameters of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* fed on eggs of *Corcyra cephalonica*

	N. poppiusi	*N. tenuis*	*P-value*
Total fecundity (mean ± SE)	73.954 ± 6.251	30.239 ± 2.847	<0.01
Net reproductive rate (R_0)	30.929 ± 5.57	12.806 ± 2.29	<0.01
Intrinsic rate of natural (days) increase/day (r_m)	0.116 ± 0.006	0.066 ± 0.005	<0.01
The finite rate of increase (λ)	1.123 ± 0.007	1.068 ± 0.005	<0.01
Mean generation time (T)	29.373 ± 0.181	38.246 ± 0.529	<0.01
The doubling time (DT)	5.979 ± 0.331	10.514 ± 0.767	<0.01

of *N. poppiusi* was 0.116, more than about 0.76 times that of *N. tenuis*. The mean generation time (T) of *N. poppiusi* showed shorter than that of *N. tenuis*. The generation doubling time (DT) indicated that *N. poppiusi* had faster rate of population growth than *N. tenuis*. According to the DT values, a population of *N. poppiusi* increases 13.1 times, and *N. tenuis* increases 7.4 times over 30 days.

Functional Response of *N. poppiusi* and *N. tenuis* With *B. tabaci* Pupa as Prey

The logistic regression for both predatory species had a significant linear parameter and the proportion of prey whiteflies eaten by the 2 predators decreased with increasing prey density that suggested type II functional responses (Fig. 3). The values of the correlation coefficient R^2 of the functional response were greater than 0.9 (Table 4), revealing a significant correlation between the observed and the predicted predated-prey number. There was significant difference in observed predated-prey numbers between 2 predator females. *Nesidiocoris poppiusi* female consumed significantly more *B. tabaci* pupae than *N. tenuis* when prey numbers were large than 30 (Supplementary Table S1). The maximum theoretical number (Na-max) of *B. tabaci* pupae that could be eaten by *N. poppiusi* and *N. tenuis* female over a day ($1/T_h$) is 73.5 and 52.0, respectively. Although there was no significant difference in observed predated-prey numbers between 2 predator males except the number was 70, *N. poppiusi* male consumed more *B. tabaci* pupae than *N. tenuis* when prey numbers were large than 10. Both *N. poppiusi* and *N. tenuis* females consumed more preys than males when prey numbers were large than 10. Female predators exhibited shorter T_h for *B. tabaci* pupae than males.

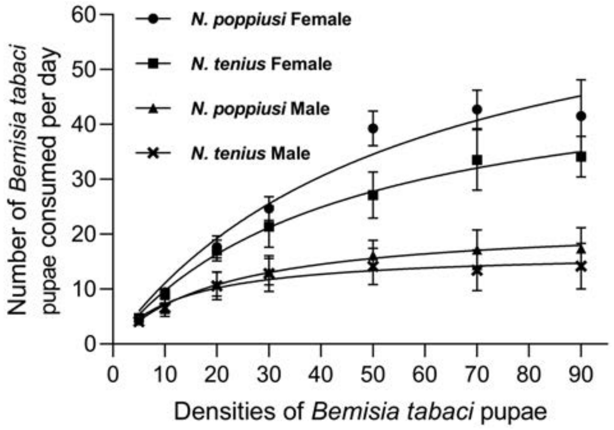


Fig. 3. Functional response curves of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* preying on pupae of *Bemisia tabaci.* Vertical bars show mean number (±SD) of *Bemisia tabaci* eaten per day in different densities.

Discussion

Nesidiocoris tenuis is a famous product mainly for the biological control of whitefly and leaf miner. *Nesidiocoris poppiusi* was proposed as a junior synonym of *N. tenuis* (Yasunaga 2017), however, they were 2 different species confirmed by Chinese researchers' studies (Xun 2016, Liu et al. 2022). *Nesidiocoris poppiusi* is generally found in Chinese tropical and subtropical zone, such as Sichuang, Guizhou, Henan provinces (Liu et al. 2022). It is difficult to distinguish these 2 species only according to the description of their morphological characteristics. Therefore, DNA barcoding, a molecular method for identification of certain animal groups was used, and the cytochrome c oxidase subunit I (*COI*) gene could be used to identify *N. tenuis* and its allied species effectively (Kim et al. 2016). Firstly, we characterized the 2 *N.* mirids molecularly using *COI* gene and confirmed the specific names of the 2 colonies of mirids used in the study. The percent identify between *N. tenuis* and *N. poppiusi* was only about 81% (Supplementary Figure S2), keeping in line with the report that the average interspecific genetic distance between *N.*

Table 4. Parameters of the functional response of *Nesidiocoris poppiusi* and *Nesidiocoris tenuis* preying on pupae of *Bemisia tabaci*

Sex	Predator	Predatory functional response equation	R^2	a'	T_h	Na-max	χ2	*P*
Female	*N. poppiusi*	Na = 1.304 × *N*/(1 + 0.018 × *N*)	0.968	1.304	0.0136	73.529	3.081	0.799
	N. tenuis	Na = 1.194 × *N*/(1 + 0.023 × *N*)	0.994	1.194	0.0192	51.975	0.969	0.987
Male	*N. poppiusi*	Na = 1.184 × *N*/(1 + 0.027 × *N*)	0.994	1.046	0.0450	22.217	0.457	0.998
	N. tenuis	Na = 1.129 × *N*/(1 + 0.058 × *N*)	0.963	1.287	0.0593	16.855	0.844	0.991

Na means the net prey consumption rate by the predator during selected time period. *N* means the density of *B. tabaci* pupae.

tenuis and its allied species was reported to be 111 times higher than the average intraspecific genetic distance (Kim et al. 2016).

We firstly compared the developmental durations of *N. poppiusi* and *N. tenuis* preying on *C. cephalonica* eggs, one of the most efficient surrogate hosts for rearing a wide range of biological control agents (Vincent et al. 2021, Wang et al. 2021, Di et al. 2022). The hatching time for *N. poppiusi* was significantly slower than that for *N. tenuis* at 25°C in this study, which was similar to the several previous studies (Fauvel et al. 1987, Perdikis and Lykouressis 2002, Sanchez et al. 2009). The nymphal development time of mirid was also significantly affected by food and the different geographical populations may have different related biological parameters. For example, *N. tenuis* nymphs developed slower when fed on dry *Artemia* cysts than on *Ephestia kuehniella* eggs and nymphs from Spain developed much faster than those from Japan (Nakaishi et al. 2011, Urbaneja-Bernat et al. 2013, Owashi et al. 2020). In this study, the nymphal period of *N. tenuis* kept for about 19.14 d, close to that of Japanese strain (about 17.5 d), but much longer than that of European strain (12.8~14.7 d) under similar environmental condition (De Puysseleyr et al. 2013, Urbaneja-Bernat et al. 2013, Mollá et al. 2014, Owashi et al. 2020). The nymphal and total preadult periods of *N. poppiusi* were no significant difference with those of *N. tenuis* which means we couldn't separate the 2 mirids by the development rate. The 2 mirids showed immature survival rates higher than 70%, suggesting that *C. cephalonica* eggs as prey and tomato as host plant provide a suitable environment for development compared to the similar nymphal survival rate of *N. tenuis* fed on *E. kuehniella* eggs as prey (Urbaneja et al. 2005, Mollá et al. 2014).

In the present study, we determined the development time and survival of 2 kinds of mirids on 4 host plant species in the absence of prey, and none of them was able to complete development. This result agreed with the similar mortality of *N. tenuis* fed on pepper, eggplant, tomato, and daisy (Urbanejaet al. 2005, Biondi et al. 2016) but disagreed with several studies fed on tomato, eggplant, cucumber (Nakaishi et al. 2011, Nakano et al. 2021). These controversial results may indicate a genetic basis for variation in feeding behavior (both zoophagy and phytophagy) (Chinchilla-Ramírez et al. 2020). Mirids showed different phytophagy in different host plants, in this study, although the 2 different mirid species were collected from tobacco filed, *N. poppiusi* nymphs were more adapted to tobacco, while *N. tenuis* nymphs were more adapted to tomato in the absence of prey. This may be the reason why these bugs are also called as ‘tomato bug’ in world but ‘tobacco bug’ in China. *Nesidiocoris poppiusi* showed very strong survival ability on tobacco leaves and some nymphs could survive for up to 30 days without any prey in this study. We also observed that some *N. poppiusi* nymphs could developed to adulthood fed on tobacco plant with flowers, but not on tomato plants with flowers in our cage experiments. When fed on tomato without prey, *N. poppiusi* nymphs showed lower survival rate and viability than *N. tenuis*, but similar with *D. maroccanus* (Abbas et al. 2014). These results suggested that *N. poppiusi* may generate lower risk than *N. tenuis* on tomato plants when prey was scarce. Zoophytophagous mirid predators had been reported with different phytophagy ability, for example, on tomato, the American native species *M. praeclarus* caused less damage on the plant than *N. tenuis*, but *D. cerastii* could cause floral abortion (Roda et al. 2020, Pérez-Hedo et al. 2021a). Whether *N. poppiusi* was safer for tomato plants than *N. tenuis* would be studied in the future.

Besides, the longevity of *N. tenuis* female was similar with those preying on *E. kuehniella* eggs, but much shorter than those fed on nature prey such as *B. tabaci* and *Thrips palmi* (e.g., Mollá et al. 2014, Yano et al. 2020). However, *N. poppiusi* adults survived much longer than *N. tenuis* adults fed on tomato leaves with prey. Similar results can be found on another mirid predator *M. pygmaeus*, which also showed longer female longevity than *N. tenuis* when preying on *T. absoluta* and *E. kuehniella* eggs on tomato plants (Mollá et al. 2014). The difference of adult longevity of different mirid predators between female and male was inconsistent. For example, *N. tenuis* males survived for longer time than females, while *M. basicornis* females had higher longevity. In contrary, the longevity of adult *N. poppiusi* had no remarkable difference between female and male, in keeping with *Engytatus varians* and *Campyloneuropsis infumatus* (Silva et al. 2016).

Meanwhile, *N. poppiusi* adults had similar survival ability compared with *N. tenuis*, more than 80% of both species` adults died within 12 days on tomato leaves without prey. In general, prey and host plant species have an important effect on mirid adult survival, for example, *N. tenuis* female was reported to survive for less than 9 days on tomato plant, but up to 48 days on *Sesamum indicum* in the absence of prey (Biondi et al. 2016); the addition of an alternative diet of *Artemia* cysts could increase *N. tenuis* adult longevity compared to treatment without prey (Owashi et al. 2020). How to improve mirids predator's survival would be an interesting research topic and should be paid more attention by entomologists in the future.

Fecundity is an important indicator for the potential control ability of the mirid predator population. The studies on the fecundity of *N. tenuis* showed that the Spanish and Japanese strains could lay more than 60 eggs per female (Sanchez et al. 2009, Yano et al. 2020), while the Chinese strain of *N. tenuis* was reported to have a lower fecundity of 10.7 eggs laid per female (Hu 2010). In this study, *N. poppiusi* showed better reproduction parameters and a faster population growth rate than *N. tenuis* in the laboratory. The cost of production of *N. poppiusi* would be more economical based on the fact that *N. poppiusi* had higher fertility and longevity than *N. tenuis*. This may be the main reason why *N. tenuis* produced by manufacturer in China was in fact *N. poppiusi*.

The type II functional response was recorded for *N. poppiusi* in this study. It was in accordance with other mirid predators (Martinou et al. 2015, Sharifian et al. 2015, van Lenteren et al. 2016, Madbouni et al. 2017, Ingegno et al. 2019). Our results showed that *N. poppiusi* female could consume more *B. tabaci* pupae than *N. tenuis* at high prey densities (≥30), which was similar to the reports of another mirid *D. cerastii* female also consumed more *B. tabaci* pupae than *N. tenuis* female (Madbouni et al. 2017, Abraços-Duarte et al. 2021). These similar results may be due to the body sizes as both *N. poppiusi* and *D. cerastii* are larger than *N. tenuis*. Therefore, we proposed that *N. poppiusi* could have a higher predatory capacity than *N. tenuis*. Body size is considered fundamental in ecological and physiological functioning of any organism and having a substantial impact on overall fitness (Kingsolver and Huey 2008). For example, *Orius laevigatus* as a predator, the strain with a larger body size was considered to exhibit a better performance based on the laboratory evaluation (Mendoza et al. 2020).

In conclusion, *N. poppiusi* showed better population growth parameters than *N. tenuis* when fed on *C. cephalonica* eggs, which may be the main reason why *N. tenuis* produced by manufacturer in China was in fact *N. poppiusi*. The results that *N. poppiusi* nymphs showed lower survival rate and viability than *N. tenuis* rearing on tomato leaves in the absence of any prey suggested that using *N. poppiusi* may be less risky than *N. tenuis* on tomato plants when prey was scarce. The higher predation amount of *B. tabaci* pupae by *N. poppiusi* indicated that *N. poppiusi* could be a promising candidate for biological controls of *B. tabaci*.

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Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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