Predatory functional response and fitness parameters of *Orius similis* when fed *Bemisia tabaci* and *Trialeurodes vaporariorum* as determined by age-stage, two-sex life table

Running Title: development and survival of *O. similis* fed on two whitefly species

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Abstract

Background: The polyphagous predatory bug *Orius similis* Zheng is an active predator used to control thrips and aphids. The whitefly species *Bemisia tabaci* and *Trialeurodes vaporariorum* are voracious pests of different economic agricultural crops and vegetables.

Method: In this study, Holling disc equation and age-stage, two-sex life table technique was used to investigate the functional response and biological traits of third instar nymphs and adult female *O. similis* when presented third instar nymphs of both whitefly species as prey.

Results: The results showed a type II functional response for each life stage of *O. similis* when fed each whitefly species. The calculated prey handling time for different *O. similis* life stages were shorter when fed *T. vaporariorum* than when fed *B. tabaci* nymphs. In contrast, the nymphal development of *O. similis* was significantly shorter when fed *B. tabaci* than *T. vaporariorum* nymphs. Additionally, the total pre-oviposition period of adult females was statistically shorter when fed *B. tabaci* nymphs than *T. vaporariorum* nymphs. Furthermore, the survival rates and total fecundity of *O. similis* were higher when fed *B. tabaci* than *T. vaporariorum*. There were no significant differences in any population parameters of *O. similis* when fed either whitefly species. These results show that *O. similis* could survive and maintain its populations on both species of whitefly and could therefore serve as a biological control agent in integrated pest management (IPM).

Key words: *Orius similis* (Anthocoridae), functional response, biological traits, predation, whitefly species, biological control.

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Introduction

Invasive insect pests can significantly disturb native insect communities and cause considerable damage to agriculture and forests (Pimentel et al. 2000). Among these pests, whiteflies (Hemiptera: Aleyrodidae) are the most damaging insect pests to agricultural crops globally, including China where more than 1450 species are known (Martin et al. 2000; Anderson et al. 2004; Lapidot et al. 2014~~; Martin et al. 2000~~). Included in these species are the silver-leaf whitefly (*Bemisia tabaci*) (Hemiptera: Aleyrodidae) and greenhouse whitefly (*Trialeurodes vaporariorum*) (Homoptera: Aleyrodidae), which are generally considered responsible for major economic losses. However, *B. tabaci* is thought to be a complex of morphologically indistinguishable sibling species, referred to as different biotypes (Wraight et al. 2017). ~~Bemisia tabaci~~They ~~is~~ considered to be one of the most significant plant pests and colonizes over 600 host plants, causing significant damage (Polston et al. 2014). ~~Bemisia tabaci~~This specie of whitefly is distributed globally (De Barro 1995; De Barro et al. 2000; De Barro et al. 2005~~; De Barro 1995; De Barro et al. 2000~~) and causes significant damage to crop yield and quality by feeding on plant phloem and secreting honeydew that stimulates the rapid growth of molds (Colvin et al. 2006; Prijović et al. 2013). However, the most significant problem associated with outbreaks of *B. tabaci* is the transmission of plant viruses (Navas-Castillo et al. 2011). *Bemisia tabaci* has been reported as the vector for the transmission of over 300 viral species in major economically important agricultural and vegetables crops (Gilbertson et al. 2015). Similarly, *Trialeurodes vaporariorum*, commonly known as greenhouse whitefly, is also considered an important pest of vegetable and agricultural crops but transmits fewer viruses than does *B. tabaci* (Wisler et al. 1998; Jones 2003; Brown 2007~~; Jones 2003~~; Navas-Castillo et al. 2011; López et al. 2012~~; Navas-Castillo et al. 2011; Wisler et al. 1998~~). However, because of its short life cycle, this species has been considered a more prevalent insect

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pest in greenhouse (Simmonds et al. 2002). *Trialeurodes vaporariorum* can also adapt to cold climates better than *B. tabaci* does and is common at high elevations (Barboza et al. 2019). Because of its resistance to insecticides such as neonicotinoids, *T. vaporariorum* has received much research attention (Gorman et al. 2007; Karatolos et al. 2011; Pym et al. 2019).

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Extensive use of pesticides not only causes environmental contamination and ozone layer depletion, but also creates serious health problems in mammals and creates toxic conditions for beneficial insect species (Shaaya et al. 1997; Yoza et al. 2005). Hence, to reduce insecticide use, biological control methods such as use of natural predators, resistant varieties, and plants extracts are important in controlling pests in modern integrated pest management (IPM) programs (Kageyama et al. 2010; Yazdani & Zarabi 2011; Yang et al. 2012; Asare-Bediako et al. 2014~~; Kageyama et al. 2010; Yang et al. 2012; Yazdani & Zarabi 2011~~).

The genus *Orius* (Hemiptera: Anthocoridae) is the largest group of flower bugs, containing around eighty species globally. They are polyphagous predators of small and soft-bodied insects considered pests in agriculture and forestry, including spider mites, aphids, thrips, and whiteflies in protected and open-field crops within its native range of Asia (Herring 1966; Hernández 1999; Postle et al. 2001; Carpintero 2002; Arnó et al. 2008; ~~Carpintero 2002; Hernández 1999; Herring 1966; Postle et al. 2001;~~ Yamada et al. 2016; Zhao et al. 2017). The artificial introduction of *O. sauteri* as a biological control agent provides potential control against small insect pests on pepper and eggplant, especially under greenhouse conditions (Jiang et al. 2011; Yin et al. 2013). *Orius laevigatus* is an effective biological control species in Europe and is widely used in augmentative release programs (Van Lenteren & Bueno 2003). Studies have been conducted into predation by *O. albidipennis*, *O. insidiosus*, *O. majusculus*, and *O. niger* on different prey species (Fritsche & Tamo 2000; Tommasini et al. 2004; Rutledge & O'Neil 2005~~; Tommasini et al. 2004~~). ~~In a recent~~

~~study~~Similarly, *O. majusculus* and *O. laevigatus* were reported as potential natural enemies of *B. tabaci* eggs, nymphs, and adults (Arnó et al. 2008).

Orius similis Zheng is a common and effective natural enemy present in cultivated fields in China and is used as a biological control agent against many small pests of economically important agricultural crops (Zhang et al. 2012). Both pre-adult and adult stages prey on lepidopteran insects including eggs or newly hatched larvae of *Pectinophora gossypiella*, *Anomis flava*, and *Helicoverpa armigera* as well as *Frankliniella formosae*, *Aphis gossypii*, and *Tetranychus cinnabarinus*. Large populations of *O. similis* in cotton fields are useful as biological control agents (Zhou & Lei 2002). This Anthocorid species has many features that make it a good biological control agent, such as high searching efficiency, the ability to increase population levels with outbreaks coinciding with prey density, and an aptitude to aggregate in regions of high prey populations (Hodgson & Aveling 1988). Mass rearing of *O. similis* and the subsequent augmentative release into crop fields leads to the control of many insect pests, decreasing their populations and hence reducing the use of pesticides (~~Bonte & De Clercq 2011;~~ Tommasini et al. 2004; Bonte & De Clercq 2011). However, it is important to estimate the effectiveness of a predator before using it in an integrated pest program (Fathipour et al. 2006).

The potential of a predator to control a pest depends upon its functional response to different populations of prey (Butt & Xaaceph 2015). Therefore, the efficiency of a predator can be assessed by its functional response (i.e., changes in attack rate in response to variations of prey populations ~~and~~ x number of prey consumed per unit time in relation to prey density (Riechert & Harp 1987). Four types of functional response have been defined based on the predation rate of a predator as a function of prey density: type I (a linear increase), type II (an increase with a slowdown at high prey densities), type III (a sigmoidal increase) and type IV (a dome shape in

prey consumption increase (Holling 1961; Pervez 2005; Sakaki & Sahragard 2011). Similarly, the biological traits of a predator, influenced by changes in prey species, greatly affect its predation activity. Thus, this study aims to investigate the interaction of the predator *O. similis* with the prey species *B. tabaci* and *T. vaporariorum* under controlled conditions. The main aim is to evaluate the functional response parameters, fitness parameters, biological traits, and population parameters of *O. similis* when fed *B. tabaci* and *T. vaporariorum* nymphs separately.

Material and Methods

Insect rearing~~, Predator~~

Adults of *O. similis* were captured from vegetable and cotton fields of the Huazhong Agricultural University (Wuhan, China) and mass reared in an insectarium following the method described by Zhou et al. (2006) with slight modifications. The rearing arenas consisted of transparent boxes (23.5 × 22.0 × 5.5 cm) with ventilation in the lid. Nymphs and adults of *O. similis* were supplied black aphids (*Aphis fabae*). Small stems of *Vitex negundo* (3–4) wrapped with wet cotton over the end were provided as oviposition substrate. The environmental conditions of 28 ± 1 ºC temperature, 70 ± 5 % R.H and a photoperiod of 16 L: 8 D h at a light intensity of 1400–1725 lux.

~~Prey species~~

Adult *B. tabaci* were collected from vegetables grown in greenhouses and from other crops from open fields located in the campus of the Huazhong Agricultural University. They were then moved to insectaria and released on potted cotton (*Gossypium hirsutum*) plants (10 cm) to develop the stock culture for the experiments (Khan & Wan 2015; Tomar et al. 2017). The stock culture of *T. vaporariorum* was maintained from a few adults received from the Southwest University

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(Chongqing, China). Large screen cages (65 × 65 × 65 cm) were used as arenas for both whitefly species. The obtained *T. vaporariorum* individuals were released on tobacco (*Nicotiana tabacum*) plants (10 cm) for mass rearing (Haiyan et al. 2017; Wei et al. 2018). The following environmental conditions were maintained inside the insectaria: temperature 26 ± 1°C, RH 65 ± 5%, and a photoperiod of 16 L: 8 D h at a light intensity of 1400–1725 lux.

Functional Response of *O. similis*

The third instar nymphs and three-day old adult females of *O. similis* were collected from the insectaria and fed third instar nymphs of *B. tabaci* and *T. vaporariorum* for 48 h separately and starved for 24 h. The predatory bugs were then individually transferred to small petri dishes (9 cm in diameter and 2 cm in depth) and supplied separately with third instar nymphs of *B. tabaci* and *T. vaporariorum* with different densities (4, 6, 8, 10, 12, and 14) per predator. After 24 h, predators were removed, and the prey consumed by both life stages of *O. similis* counted under stereomicroscope (Liu Pingping, et al., 2018). Bugs were used once only. All the dead/empty nymphs of both whitefly species were assumed killed by the predator as preliminary study indicated 100% survival of bugs in the absence of whitefly nymphs. Thirty replications of the experiments involving the third instar nymphs and adult females of *O. similis* were made for each treatment/density with both prey species separately.

Life table study

Nymphal development

Approximately sixty freshly laid healthy eggs of *O. similis* were isolated from the insectaria and incubated until hatched. All collected eggs of *O. similis* were equally distributed to feed on *B. tabaci* and *T. vaporariorum* third instar nymphs separately. After hatching, *O. similis* neonates (≤

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24 h) were isolated in small Petri dishes (diameter: 9 cm; depth: 2 cm) firmed with filter paper. From the results of functional responses, we supplied fifteen third instar nymphs of *B. tabaci* and *T. vaporariorum* separately to each individual of the predatory bug as food. Dead/empty nymphs of whitefly were replaced every day. A stem of *V. negundo* was placed in each Petri dish to provide shelter and moisture to the predatory bugs. The end of each stem was wrapped with wet cotton to keep them moist. Thirty nymphs were used in the experiment with three biological replicates for each prey species. Developmental time for each nymphal instar was measured. Individuals that died before reaching the adult stage were also recorded. Sex was confirmed as soon as the adults emerged.

Adult longevity and fecundity

Newly emerged male and female *O. similis* adults were paired for mating. Females that mated for more than 1.5 min were considered to have been mated (Butler and O'Neil, 2006). Each mated female was placed separately in a new cylindrical translucent vial (2.5 × 14 cm diameter and length respectively) enclosed with an adequate mesh nylon screen. A small section of *Vitex negundo* stem was offered to each *O. similis* female as an oviposition substrate. Each stem was wrapped with moist cotton at the end to provide moisture to the stem as well as the bugs using the method of Zhou et al. (2006). *Bemisia tabaci* and *T. vaporariorum* nymphs (N = 15) were supplied into each vial as a source of food for female *O. similis*. Stems of *Vitex negundo* were examined under a stereomicroscope (15×) to confirm egg laying. The stem was changed every day after the female laid the first egg. The total number of eggs laid by each female was counted under a stereomicroscope (15×). All predatory bugs were observed until they died. Development period, survival rate, pre-oviposition and oviposition period, fecundity, and longevity of female and male adults of *O. similis* were recorded.

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Data analysis

Functional response

The shape of the curve was determined using the polynomial logistic regression following the method describe by Pervez, 2005; Butt and Xaaceph, 2015 and Varshney et al. 2018. ~~To find the functional response type, all the data collected from the experiment were fitted to polynomial function.~~ The polynomial function described the relationship between the proportion of prey consumed (N_a) in relation to the density of prey offered (N_0) (Holling, 1959a; Holling, 1959b). Hence, a cubic model was applied in a logistic regression analysis (Juliano, 2001).

$$\frac{N_a}{N_0} = \frac{\exp(P_o + P_1N_o + P_2N_o^2 + P_3N_o^3)}{1 + \exp(P_o + P_1N_o + P_2N_o^2 + P_3N_o^3)}$$

~~(Juliano, 2001):~~

~~$N_a/N_0 = \exp((P_0 + P_1N_0 + P_2N^2_0 + P_3N^3_0) / [1 + \exp(P_0 + P_1N_0 + P_2N^2_0 + P_3N^3_0)])$~~

In this equation, P_0, P_1, P_2, and P_3 represent the intercept, linear, quadric, and cubic coefficients, respectively. The negative and positive values of linear coefficient (P_1) define type II and III functional responses, respectively. The cubic expression will often provide a good fit to a type II and III responses and will provide a good starting point for fitting a logistic regression (Trexler et al. 1988; Trexler and Travis 1993; Juliano, 2001). Modifying the Holling disc equation through reciprocal linear transformation, handling time (T_h) and the attack rate (a) ~~functional response parameters (T_h and a)~~ were calculated (Livdahl & Stiven 1983). This method is famous because of its simplicity and accuracy (Veeravel and Baskaran 1997; Pervez and Omkar 2003; Omkar and Pervez 2004). The modified Holling equation, after reciprocal linear transformation is as follows:

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~~The equation for the linear regression was y = ax + b. Hence, the modified equation obtained was:~~

~~$1/N_a = 1/a \cdot 1/TN_e + T_h/T$~~ $1 / N_a = 1 / aTN_0 + T_h / T + \varepsilon$

Where ~~$1/N_a$ represents y, 1/a represents a, $1/TN_e$ represents x, and T_h/T represents b.~~ N_a is the number of prey killed by predators during time (T: 24 h ~~in our experiment~~). ~~N_e~~ N_0 is the density of prey, ~~a~~ α is the attack ~~and~~rate and T_h is the predator handling time for one prey item. Hence, the variables used in the regression were $y = ax + b + \varepsilon$. The inverse mathematical function for curve estimation was used to estimate the values of ~~a~~ α and T_h (Ali et al., 2011). For each prey density we calculated total handling time ($Th_{total} = T_h \times N_a$), search time ($Ts = T - T_{h\ total}$), attack rate (~~$a$~~ $\alpha = N_a/(N_e N_0 \times Ts)$), and search efficiency ($E = N_a/N_e N_0$) (Hassell 2000; Rocha & Redaelli 2004). All statistical analyses were performed in MINITAB ~~17~~19.

Life table analysis

The data obtained from experiments were analyzes based on the age-stage, two-sex life table theory using Twosex-MSChart, a computer program (Chi, 1988; Chi and Liu, 1985; Huang and Chi 2011; Qi Chen et al 2017; Farooq et al. 2018). The different biological traits and demographic parameters such as eggs, nymphs and adult development, oviposition, pre-oviposition, fecundity and *r*, *λ*, R_0, *GRR* and *T* were calculated by following the methodology of Chi (2015).

In the age-stage, two-sex life table, the age-specific survival rate (l_x) and fecundity (m_x) were calculated using the equation (1) and (2) respectively.

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$$l_x = \sum_{j=1}^{k} s_{xj} \quad (1)$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj}\, f_{xj}}{\sum_{j=1}^{k} s_{xj}} \quad (2)$$

In this equation, S_{xj} is the age-stage specific survival rate of *O. similis* (x = age which is in days and j = stage) which describe the probability of survival of neonate to age x and stage j, meanwhile, f_{xj} describe age-stage specific fecundity of adult female (Chi and Liu, 1985). The Euler–Lotka equation was used to estimate the intrinsic rate of increase (r) following the method of iterative division with the age index from 0 using equation (3) (Goodman, 1982).

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (3)$$

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The values of (R_0) which described the ability of the female to produce a mean number of offspring in his lifetime, was calculated as

$$\sum_{x=0}^{\infty} l_x m_x = R_0 \quad (4)$$

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The relation between female and R_0 can describe as

$$R_0 = F \frac{N_f}{N} \quad (5)$$

Here N and N_f represent the total number of *O. similis* used in the experiment and the number of female adults respectively (Chi, 1988). The gross reproduction rate GRR and rate of increase (λ) were estimated as

$$GRR = \sum_{x=0}^{\infty} m_x \quad (6)$$

$$\lambda = er \quad (7)$$

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The mean generation time (T) that a population required to rise to R_0-fold of its size i.e. $e^{rT} = R_0$ or $\lambda^T = R_0$ at the stable age-stage distribution was intended using the equation

$$T = \frac{\ln R_0}{r} \quad (8)$$

The bootstrap test method (100,000 bootstrap) was used to estimate the standard errors of developmental time of each stage, fecundity, adult longevity and population parameters (Akca et al., 2015; Akköprü et al., 2015; Tuan et al., 2015). To compare the values, a pair bootstrap test based on the confidence of the interval of difference was used (Chi, 2015; Pru et al., 2015). To obtain the curves of survival rate, fecundity, life expectancy and reproductive vales, Sigma Plot 12.0 was used. ~~All the raw data for the life table of *O. similis* were analyzed based on the age-stage, two-sex life table theory (Chi 1988; Chi & Liu 1985). The developmental period, fecundity of female adults, and male and female longevity/survival of *O. similis* were evaluated using the computer program two-sex MS-Chart (Akca et al. 2015). To calculate the standard error of pre-adult stage, adult male and female longevity, female fecundity, and population parameters (rate of increase [r], [γ], the highest net reproductive rate [R_0], gross reproduction rate [GRR], and mean generation time of individuals [T]), 100,000 bootstrap replicates were run (Akca et al. 2015; Akköprü et al. 2015; Tuan et al. 2016). Based on the confidence intervals of differences, paired bootstrap tests were also used to compare the results of different treatments using two-sex MS-Chart (Akca et al. 2015; PRU et al. 2015). Equations used in the age-stage, two-sex life tables are listed in Table 1. Sigma Plot 12.0 was used to create graphs of survival rates, fecundity, life expectancy, and reproductive value.~~

~~In Table 1, S_{xj} represents the age-stage specific survival rate, based on the probability that newly hatched individuals will survive to age x and j (Chi & Liu 1985). The l_x and m_x were estimated using equation 1 and 2 respectively. The intrinsic rate of increase (r) was calculated from~~

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~~the Euler–Lotka equation with age indexed from 0 (Goodman 1982), equation 3. Equation 4 was used to calculate the R_0 (mean number of siblings that an individual can produce in its lifespan). The gross reproduction rate (GRR) was estimated using equation 5. The time a population required to rise to R_0 fold of its size as it acquired a stable age-stage distribution (T) was determined with equation 6. To estimate the rate of increase (λ), Equation 7 was used.~~

Results

Functional response of *O. similis*

The results of the logistic regression analysis for third instar nymphs of *O. similis* were highly significant ($P < 0.05$) suggesting a type II functional response as the linear coefficient (P1) was negative against nymphs of both *B. tabaci* and *T. vaporariorum* (Table ~~2~~1). Similarly, the adult females also showed a type II functional response against both prey species, although the parameters were not significant.

The functional response curves of different life stages of *O. similis* to third instar nymphs of *B. tabaci* and *T. vaporariorum* at different densities are show in Fig. 1. The number of nymphs of both prey species consumed by third instar nymphs and adult females of *O. similis* increased with increases in the prey density from 4 to 8 nymphs per predator, but plateaued with no significant increase in prey consumption with densities of more than 8 nymphs per predator. When only four nymphs of *B. tabaci* and *T. vaporariorum* were provided, the third instar nymphs of *O. similis* consumed a mean of 3.8 ± 0.097 and 3.3 ± 0.128 nymphs per predator per day, respectively, indicating that the predator is more efficient at finding whitefly nymphs at low prey densities.

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~~Similarly, the mean consumption of whitefly nymphs by adult female *O. similis* was higher at lower prey densities (Fig. 1).~~ When provided with third instar nymphs of *B. tabaci* and *T. vaporariorum*, the maximum and minimum prey consumption levels of third instar nymphs of *O. similis* were (95% and 46.4%) and (82.5% and 44%), respectively. However, there were no significant differences found in maximum prey consumption by adult female *O. similis* (92% and 92.5%) when preying on nymphs of *B. tabaci* and *T. vaporariorum*, respectively. The minimum percentage of *B. tabaci* and *T. vaporariorum* nymphs killed by adult female *O. similis* was 48% and 51%, respectively.

Functional response parameters

The parameters of functional response (handling time (T_h), attack rate (a), and maximum predation rate) of different stages of *O. similis* against whitefly species are listed in Table ~~3~~2. There were no differences estimated in the T_h of third instar nymphs of *O. similis* against both whitefly species. However, adult females undertook shorter handling times (1.75 h) when pursuing, subduing, and consuming *T. vaporariorum* third instar nymphs when compared with the handling times for *B. tabaci* (2.45 h).

In contrast, the coefficient of attack rate was higher, ranging from 0.05 to 0.06, when third instar nymphs and adult females of *O. similis* were fed nymphs of *B. tabaci* compared to *T. vaporariorum* (Table 3). However, there were no significant difference noted for different life stages of *O. similis* in attack rate. The maximum predation rate (T/T_h) of third instar nymphs of *O. similis* per individual was higher (9.82 d^{-1}) for *T. vaporariorum* nymphs compared to *B. tabaci* (9.78 d^{-1}). Similarly, the maximum predation rate of adult females was (13.70 d^{-1}) and (11.12 d^{-1})

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for *T. vaporariorum* and *B. tabaci* nymphs, respectively. The functional response parameters of different life stages of *O. similis* to different densities of whitefly species are given in Table 43. The T_h for third instar nymphs and adult females of *O. similis* increased with increasing prey densities. However, the searching time and searching efficiency show an inverse relationship with both prey densities. The attack rates of both life stages of *O. similis* were similar with no significant differences at different densities of both prey species.

Growth, development, and longevity of *O. similis*

Developmental characteristics of *O. similis* ~~against~~ when fed of whitefly species (*B. tabaci* and *T. vaporariorum*) are listed in Table 4 ~~4~~. The ~~nymphal~~ development time for nymphal instar of N1–N4 of *O. similis* took statistically longer ~~from N1–N4~~ when fed *T. vaporariorum* than when fed *B. tabaci*.

However, there were no significant differences in development of fifth instar *O. similis* nymphs against both whitefly species. In addition, higher mortality rates were observed in the fifth instar when fed *T. vaporariorum* nymphs than when fed *B. tabaci*. The results also showed that longevity of both male and female *O. similis* was statistically similar when *B. tabaci* and *T. vaporariorum* were provided as prey (Table 4). ~~The highest longevity of adult females was recorded when they were fed *B. tabaci* nymphs (15.47 days), while when presented with *T. vaporariorum* nymphs, it was comparatively shorter (13.82 days).~~ It was also observed that more individuals of the predatory bug survived and successfully reached the adult stage when fed *B. tabaci* nymphs (86.66%) than when fed *T. vaporariorum* nymphs (56.70%).

Fecundity and oviposition of female adults

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No significant effects of the presence of the two whitefly species were observed on adult pre-ovipositional period (APOP) of *O. similis* (2.35 days for *B. tabaci* and 2.4 days for *T. vaporariorum*~~, respectively~~; Table ~~5~~5**)**. However, the total pre-ovipositional period (TPOP) of *O. similis* was significantly longer when offered *T. vaporariorum* nymphs (20.5 days) compared to *B. tabaci* (19.82 days, Table 5).~~)~~.

It was also observed that the total reproductive days of female adult *O. similis* were statistically similar with no significant difference for both whitefly species (8.29 and 7.80 days when fed *B. tabaci* and *T. vaporariorum*, respectively, Table 5). Furthermore, no significant difference was recorded in total female fecundity against both prey species; however, more eggs were laid by adult females when fed *B. tabaci* nymphs (54.18 eggs) than *T. vaporariorum* (49.82 eggs). More females were produced when fed *B. tabaci* than *T. vaporariorum*.

Population parameters of *O. similis*

The influence of the two prey species on the population parameters of *O. similis* are listed in Table ~~6~~6. No significant differences were found in *O. similis* population parameters when fed *B. tabaci* and *T. vaporariorum* separately. The intrinsic rate of increase (r) and finite rate of increase (λ) for *O. similis* were (0.13 d^{-1} and 1.14 d^{-1}, respectively) when fed nymphs of *B. tabaci* and (0.11 d^{-1} and 1.12 d^{-1}) when fed *T. vaporariorum*. However, the highest net reproductive rate (R_0) occurred when *O. similis* was fed *B. tabaci* (30.70 offspring per female) than when fed *T. vaporariorum* (18.27). Furthermore, the mean generation time of individuals (T) and the values of *GRR* were higher when *B. tabaci* was offered as prey (25.46 d and 54.62) compared to *T. vaporariorum* (26.61 d and 61.57; Table ~~6~~6).

Age-stage and age-specific survival of *O. similis*

The Fig. 2 explains the age-stage specific survival rate (S_{xj}; the possibility a newly hatched individual that will successfully survive to age x and stage j) of *O. similis* when fed *B. tabaci* and *T. vaporariorum*. Overlap occurs between stages as a result of variations in the developmental rate of individuals. When fed nymphs of *B. tabaci*, 86.66% of *O. similis* eggs successfully survived and reached to the adult stage. However, the survival rate was significantly lower (56.7%) when *O. similis* were fed *T. vaporariorum* nymphs.

Age-specific survival rate (l_x; a simplified form of S_{xj}), age-stage specific fecundity (f_x), age-specific total fecundity of the whole population (m_x), and age-specific maternity ($l_x m_x$; formed on the basis of f_x and m_x) of *O. similis* when fed *B. tabaci* and *T. vaporariorum* are presented in Fig. 3. As age increased, the l_x of *O. similis* decreased and showed an inverse relationship for both prey species. The peak of the m_x curve was at 26.98 days (5.14 eggs) and 31.09 days (5.72 eggs) when *O. similis* fed on *B. tabaci* and *T. vaporariorum*, respectively. The peak of f_x was at 24.90 days (8.45 eggs) and 30.88 days (7.80 eggs) for *B. tabaci* and *T. vaporariorum* nymphs respectively.

Life expectancy and reproductive values

The curves for life expectancy (e_{xj}) of *O. similis* at each stage when presented with *B. tabaci* and *T. vaporariorum* are shown in Fig. 4. It describes the estimated survival of an individual of age x and stage j at a later age x. The life expectancy of a newly hatched egg of ~~born~~ *O. similis* ~~egg~~

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was ~~greater when fed nymphs of *B. tabaci* (~~28.57 and 24.91 d on *B. tabaci* and *T. vaporariorum* respectively. ~~days) than those of *T. vaporariorum* (24.91 days).~~

The age-stage reproductive values (v_{xj}) of adult female *O. similis* when exposed to different species of whitefly are shown in Fig. 5. Age-stage specific reproductive value is a measure of the contribution of an individual (from age *x* and stage *j*) to a future population. When adult female *O. similis* fed on *B. tabaci*, the highest peak was observed at 21 days, which was greater than when offered *T. vaporariorum* (19.79 days). The Age-stage specific reproductive curve (V_{xj}) indicated that the presence of *B. tabaci* had a more positive effect on *O. similis* reproduction than *T. vaporariorum*.

Discussion

To quantify the ability of a predator to combat agricultural pests, the Holling functional response model has been used for several years (Ganjisaffar & Perring 2015; Yazdani & Keller 2016). Handling time (T_h) and attack rate (*a*) are considered key parameters in explaining oscillations in predator and prey interactions (Wang et al. 2019). A predator's functional response to its prey plays a significant role in the effect it has on a prey population (Begon et al. 1986). Similarly, life table studies enable us to understand the ecology of an organism and supply some crucial tools to study vital biological functions such as growth, survival, and reproductive rate when an organism is in a diverse environment. Some drawbacks have been found in Jackknife methods; therefore, a bootstrap method using 100,000 resamples was developed to calculate population parameters with more accurate results (Huang & Chi 2012; Huang & Chi 2013). Numerous studies have investigated *Orius* spp. as a predator of *B. tabaci*, (Arnó et al. 2008; Adly

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2016; ~~Arnó et al. 2008;~~ Banihashemi et al. 2017; Zandi-Sohani et al. 2018; Shahpouri et al. 2019~~;~~ ~~Zandi-Sohani et al. 2018~~). ~~However, to our knowledge, functional response and age-stage life table traits (age-specific survival, age-stage survival, female reproductive values and life expectancy) have not been investigated for *O. similis* when preying on *B. tabaci* and *T. vaporariorum*. Thus, our study was designed to determine the predatory potential of *O. similis* against both whitefly species.~~

Our results indicate that the third instar nymphs and adult female of *O. similis* show type II functional responses when fed separately on six different densities of *B. tabaci* and *T. vaporariorum* third instar nymphs. With increases in prey density, the net prey consumption of both life stages of *O. similis* increased until a plateau was reached. Predators with type II and III functional responses have a probability of being a stabilizing force in biological control programs (Fernández-arhex & Corley 2003). *Orius* spp. have shown a type II functional response in numerous other studies (Holling 1965). A type II functional response was reported for *O. albidipennis* when it was fed *T. tabaci* (Madadi et al. 2007), *Megalurothrips sjostedti* (Thysanoptera: Thripidae) larvae (Gitonga et al. 2002), and *Tetranychus turkestani* (Acari: Tetranychidae)~~;~~ (Hasanzadeh et al. 2015). In contrast to our results, the adult female *O. albidipennis* showed a type III functional response when fed *B. tabaci* third instar nymphs (Shahpouri et al. 2019). Similarly, *M. caliginosus* showed a type III functional response when presented with nymphs of *T. vaporariorum* (Enkegaard et al. 2001). These contradictory results may be related to changes in predator species and differences in body size. Supporting our results, *O. majusculus* and *O. laevigatus* exhibited a type II functional response when fed nymphs of *T. vaporariorum* (Montserrat et al. 2000). Predator functional response is influenced by several

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420 factors, such size and density of predators and preys (Aljetlawi et al. 2004), temperature (Gitonga
421 et al. 2002; Zamani et al. 2006), occurrence of alternative prey (Abrams 1990), and internal state
422 of the predator (Hassell et al. 1976). In our study, the arena consisted of small Petri dishes. This
423 small experimental arena accelerated the searching efficiency of the predatory bugs and enabled
424 them to repeatedly attack prey that initially escaped (Wiedenmann & O'Neil 1991). The optimal
425 foraging theory of predator-prey relationships has helped reveal the influence of different prey
426 densities on predator handling time, searching time, and predation rate (Cook & Cockrell 1978;
427 Stephens & Krebs 1986). In our study, searching time decreased with increases in prey density for
428 both third instar nymphs and adult female of *O. similis*.

429 To estimate the effectiveness of a predator in relation to its prey, handling time is thought
430 to be a key parameter because it shows how long a predator takes to capture, subdue, kill, and
431 digest a single prey item (Atlıhan et al. 2010). In our study, the handling time was shortest when
432 adult female *O. similis* were offered *T. vaporariorum* nymphs. In contrast to our study, the
433 handling time was higher when adult female *O. albidipennis* fed on nymphs of *B. tabaci*
434 (Shahpouri et al. 2019). However, long handling time enables increased nutrient consumption from
435 prey and hence increases the persistence of predators (Montserrat et al. 2000). Recent studies have
436 shown that handling time is higher when *O. albidipennis* preys on *B. tabaci* nymphs than eggs
437 (Shahpouri et al. 2019). Similarly, handling time of *O. laevigatus* was longer than that for other
438 *Orius* species when tested again different densities of thrips (Montserrat et al. 2000). Maximum
439 prey consumption enhances the possibility of gaining optimal ratios between predators and pests.
440 Hence it can be useful to accelerate the application of inoculative releases (Wang et al. 2019). Our
441 results show that maximum predation occurred when adult female *O. similis* fed on *T.*
442 *vaporariorum*. Meanwhile, more nymphs were eaten by third instar nymphs of *O. similis* when fed

on *T. vaporariorum*. Higher prey densities (and thus greater prey availability) or decreases in searching area accelerate predator attack rates while reducing handling time (Hassell et al. 1976). In a previous study (Opit et al. 1997), lower prey densities induced reduction in predator searching activity to reduce the use of energy. In our study, no significant differences in attack rate were observed when both life stages of *O. similis* preyed on nymphs of *B. tabaci* and *T. vaporariorum* separately, even with six different densities. The attack rate did not therefore depend on prey densities (Holling 1959). However, our results showed higher attack rates with *B. tabaci* than *T. vaporariorum* for both third instar nymphs and adult females of *O. similis*. In contrast to our results, previous work resulted in different values for handling time and attack rate when *O. majuscules* and *O. laevigatus* were fed *T. vaporariorum* (Montserrat et al. 2000). This may be due to changes in experimental design, environment, or predator species (Van Alphen & Jervis 1996). The polyphagous predatory species of *Orius* prey on a broad range of arthropods. Additionally, prey type can significantly alter the activity of their predators (Bonte et al. 2015). The developmental and reproductive performance and fitness of predators in relation to particular prey types highlights their potential as active biological control agents (Grenier & De Clercq 2003).

The results obtained from the age-stage two-sex life table analysis indicate that *O. similis* can survive and build strong populations when feeding on different species of whiteflies (*B. tabaci* and *T. vaporariorum*). However, we found that the nymphal developmental durations of the predator were significantly longer when praying on nymphs of *T. vaporariorum* than on nymphs of *B. tabaci*. Moreover, adult male and female longevity was longer when presented *B. tabaci* relative to *T. vaporariorum*, but a significant difference was not observed. Our results agree with previous reports indicating that the developmental period of *O. similis* pre-adults is greater when they prey on *A. cracivora* than on *C. cephalonica* eggs (Amer et al. 2018). The same interaction

466 was documented in numerous studies where the prey species strongly alter the developmental
467 duration of pre-adults of *O. similis* (Kim 1997; Kim 1999; Ohta 2001; Sengonca et al. 2008).
468 Consequently, these fluctuations in the developmental period show that a prey species can strongly
469 influence the developmental time of the pre-adult stages of *O. similis* (Sengonca et al. 2008). The
470 survival of *O. similis* individuals was higher when fed on *B. tabaci* nymphs than *T. vaporariorum*.
471 Amer et al. (2018) documented that higher mortality rates occurred in the pre-adult stages of *O.*
472 *similis* when they fed on *C. cephalonica* eggs compared to *A. cracivora*. Similarly, the survival
473 rate of *O. laevigatus*, *O. niger*, and *O. majusculus* individuals during development was very low
474 (i.e., high mortality rates) when fed eggs of *E. kuehniella* than those of *F. occidentalis* (Kiman &
475 Yeargan 1985; Tommasini et al. 2004). Based on our results and those of Arnó et al. (2008), the
476 total developmental duration and survival of *O. similis* nymphs, when fed *B. tabaci* nymphs, were
477 similar to those ~~of O~~of *O. majusculus* and *O. laevigatus*. Arnó et al. (2008) also reported results
478 similar to those reported by Riudavets & Castañé (1998), suggesting that whitefly species could
479 be considered suitable prey analogous to *F. occidentalis* larvae predated upon by *Orius* spp.
480 Furthermore, our results showed no significant difference in adult-pre-oviposition period for both
481 whitefly species. In contrast to our study, Zhang et al. (2012) found that after mating, the
482 development of the reproductive system of adult female *O. similis* took longer (5–6 days)
483 compared to our results. Similarly, the number of eggs laid by adult female *O. similis* were
484 comparatively higher for both whitefly species than that of *Tetranychus cinnabarinus* (Zhang et
485 al. 2012).

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486 Chen et al. (2017) found that intrinsic rate of increase (r) is a key population parameter in
487 determining the development, growth, and survival of an organism. Southwood & Henderson
488 (2009) also documented that greater values of (r) i.e., $r > 0$ highlight the fit of a prey with its host.

Comparing our result with these studies shows that the intrinsic rate of increase was more than (0) and similar for both prey species ~~Table 4~~. The net reproductive rate (R_0) is also considered an important demographic life table parameter. Values of R_0 of more than 1 indicate an increase in the mean population of an insect (Southwood & Henderson 2009; Chen et al. 2017~~; Southwood & Henderson 2009~~). Our results agree with this theory, as the highest R_0 was when *O. similis* was fed *B. tabaci* relative to *T. vaporariorum*. In contrast to our study, low reproductive rates have been observed when *O. similis* is fed *T. cinnabarinus* (Zhang et al. 2012). The gross reproduction rate (*GRR*) is thought to be a symbol of a rapid increase of population, which is directly related to adult eclosion and the number of eggs laid and hatched. All of these parameters can be significantly influenced by prey species (Cocuzza et al. 1997; Huang & Chi 2013). In our results, the highest *GRR* and greatest generation time (*T*) occurred when *O. similis* fed on *T. vaporariorum* when compared to *B. tabaci*. However, in their study, Zhang et al. (2012) observed longer generation times at three constant temperatures when individuals of *O. similis* preyed on *T. cinnabarinus*.

The survival of a predator from the neonate to the adult stage when presented specific prey species highlights its role as an effective biological control agent (Van Lenteren & Woets 1988). Similarly, the searching ability and concomitance of predators and prey in space and time, are thought to be a crucial factor~~s~~ in successful biological control of a pest (Arnó et al. 2008). Trottin-Caudal et al. (1991) and Montserrat (2001) ~~and Trottin-Caudal et al. (1991)~~ both reported large populations of *Orius* spp. on vegetable crops where thrips and whiteflies coexist. Thus, it can be assumed that if *O. similis* remains on the crop after suppression of the population of their desired prey, they can play a vital role in suppression of both whitefly species and could serve as an effective biological control agent. Supporting our hypothesis, Riudavets (2001) reported more than

20 *Orius* per cucumber plant when the population of *F. occidentalis* was very low, which may have been due to the presence of other pests.

In summary, our results suggest that the predatory bug *O. similis* has the potential to actively maintain strong populations when in the presence of species of whitefly such as *B. tabaci* and *T. vaporariorum* and could serve as a biological control agent in cotton fields and other vegetable crops, as well as in greenhouses where the populations of these species are destructive pests. The results obtained from laboratory experiments should be useful in understanding the biology of *O. similis* when in association with whitefly species, but field experiments will be required to validate them.

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