

Development, consumption rates and reproductive biology of *Orius albidipennis* reared on various prey

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Abstract The predatory bug *Orius albidipennis* (Reuter) (Hemiptera: Anthocoridae) has tremendous potential as a biological control agent, especially in its native range around the Mediterranean Basin and East Africa. The need to exploit native biological control agents is growing in importance as concerns over the introduction of non-native species continue to increase. However, little is known of the effects of different prey on development and reproduction of *O. albidipennis* compared with other species of *Orius*. Therefore, we compared the development, survival, reproductive biology, and prey consumption of *O. albidipennis* when fed eggs of *Ephestia kuehniella* Zeller, *Tetranychus urticae* Koch, and *Trialeurodes vaporariorum* (Westwood), and larvae of *Gynaikothrips ficorum* (Marchal), under laboratory of $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH and 16L:8D photoperiod. Individuals

were reared from the neonate stage until death on one of the four prey types. The type of prey had profound effects on all measured performance traits. The highest survival rate was recorded for nymphs that were fed on *E. kuehniella* eggs, while the lowest survival rate was observed for those fed on *T. vaporariorum* eggs. The shortest nymphal period was recorded for nymphs fed on *E. kuehniella* eggs, while the longest was measured for those fed on *T. urticae* eggs. During the nymphal period, *O. albidipennis* consumed significantly more eggs of *T. urticae* than other prey types, whereas the lowest number of consumed prey were eggs of *E. kuehniella*. Adult females and males consumed significantly more *T. urticae* eggs than other types of prey. However, *Orius albidipennis* females showed the highest fecundity when fed on *E. kuehniella* eggs, and the lowest when fed on *T. vaporariorum* eggs. Adult females and males that fed on *G. ficorum* larvae had significantly longer life spans compared with those fed other prey. Because of their relatively rapid development and high fecundity, *O. albidipennis* fed *E. kuehniella* eggs had a significantly higher net reproductive rate (R_0) and intrinsic rate of increase (r_m) than *O. albidipennis* fed other prey types. Overall, eggs of *E. kuehniella* were the most suitable diet for nymphs and adults of *O. albidipennis*. Although less suitable, *O. albidipennis* could survive and reproduce on the other prey types, which is a favourable attribute in biological control agents. These results on the effect of different prey types on development and reproduction of *O. albidipennis* will also contribute to

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the development of mass rearing programs for biological control agents in developing countries, such as Egypt.

Keywords *Orius albidipennis* (Hemiptera: Anthocoridae) · Reproductive biology · Feeding consumption · Life table

Introduction

Generalist predatory insects are capable of attacking a diverse spectrum of prey species (Eubanks and Denno 2000) because they have the necessary phenotypical plasticity to adjust their biology to different food sources (Mendes et al. 2002). However different types of prey can substantially alter the development and reproduction of predators, which in turn affect population dynamics. Species in the genus *Orius* (Hemiptera: Anthocoridae) are generalist predators that attack eggs and immature stages of various arthropods, or small soft-bodied adult arthropods, including numerous important agricultural pest species (Bush et al. 1993; Riudavets 1995; Lee et al. 1996; Reitz et al. 2006; Butler and O'Neil 2007). Although they are polyphagous, *Orius* spp. show a preference for attacking larval and adult thrips (Thysanoptera) over other available prey (Kakimoto et al. 2006; Arnò et al. 2008; Xu and Enkegaard 2009). Consequently, they are considered promising and effective as biological control agents and have been used successfully in biological control programs in greenhouse and open-field cropping systems against various thysanopteran pests. In particular, *Orius insidiosus* (Say) has been released into sweet pepper and cucumber greenhouses in Europe to successfully control *Thrips tabaci* (Lindeman) and the invasive *Frankliniella occidentalis* (Pergande) (van den Meiracker and Ramakers 1991; Dissevelt et al. 1995; Sabelis and van Rijn 1997; Perdakis et al. 2008). In its area of origin, conservation of *O. insidiosus* is a key component of integrated pest management (IPM) programs for thrips in field grown crops (Funderburk 2009). *Orius laevigatus* (Fieber) is another species that has been widely employed in successful biological control programs in Europe (Chambers et al. 1993; Sanchez and Lacasa 2002; Coll et al. 2007). For these reasons, a number of *Orius* spp.,

in particular *O. laevigatus* and *O. insidiosus*, are mass produced for augmentative release by various commercial insectaries in Europe and North America (Cranshaw et al. 1996; van Lenteren et al. 1997; Lattin 1999), where they are routinely reared on eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller (Arijs and De Clercq 2004; Bonte and De Clercq 2008). However, mass production of *Orius* spp. has not been realized in most developing countries (van Lenteren et al. 1997).

While certain species of *Orius* are mass produced for augmentative biological control, growing concerns over the introduction of non-native species limits where any particular species may be deployed (van Lenteren et al. 2003; Louda et al. 2003). As a result there is increased interest in other species of *Orius* that could be deployed as biological control agents in their native ranges. This interest is reinforced by the recognition that biological control agents also must be well acclimatized to environments where they would be deployed (Cocuzza et al. 1997a).

One species of *Orius* of particular interest as a biological control agent is *O. albidipennis* (Reuter), which is frequently found in large numbers in various agricultural habitats throughout the Mediterranean basin, the Atlantic zone of Western Europe, and East Africa (Salim et al. 1987; Chyzik et al. 1995b; Cocuzza et al. 1997b; Hernandez and Stonedahl 1999; Fritsche and Tamò 2000). Chyzik and Ucko (2002) reported that *O. albidipennis* could control thrips in pepper fields in Israel. In Egypt, *O. albidipennis* is very common throughout much of the country, south to Wadi Halfa, in the desert, and in cultivated areas, especially in corn and cotton fields. It is usually found in flowers of plants infested with thrips, lepidopteran eggs or other small arthropods (Tawfik and Ata 1973; Zaki 1989).

Orius albidipennis is well adapted to high temperatures (Cocuzza et al. 1997a) and does not have a photoperiod induced reproductive diapause (Chyzik et al. 1995a) as do other species of *Orius* (van den Meiracker 1994). Rather, its abundance and activity is only limited by low temperatures (Chyzik et al. 1995a). On the basis of our observations in Egypt, *O. albidipennis* does not occur in the field before March, but its activity increases from April until the end of November. Because of its heat tolerance and lack of photoperiod induced diapause, it could be an

ideal candidate for mass rearing and augmentative releases in subtropical and tropical areas. However, its use as a biological control agent has been hindered by a relative lack of information on its interactions with different prey and in determining the suitability of different prey diets for *O. albidipennis* is an obstacle in its mass production. Therefore, the aim of the current study was to determine the effect of a range of different prey types (i.e. eggs of *E. kuehniella*, *Tetranychus urticae* Koch and *Trialeurodes vaporariorum* [Westwood], and 2nd instars of *Gynaikothrips ficorum* [Marchal]) on the development, reproduction, longevity, and prey consumption of this predator. These types of data can provide important information for understanding predator population dynamics and estimating population level effects of predators on prey species.

Materials and methods

Rearing of *O. albidipennis*

A colony of *O. albidipennis* was established from nymphs and adults collected on sunflower plants (*Helianthus annuus* L.) at the Experimental Farm, Faculty of Agriculture, Suez Canal University at Ismailia Governorate, Egypt. Adults and nymphs were maintained in one litre plastic jars (10 cm diameter × 20 cm height), which were covered with muslin that was held in place by rubber bands. Each jar was provided with sufficient quantities of loose *E. kuehniella* eggs as a food supply for the enclosed predators (Cocuzza et al. 1997b) and a piece of cotton that had been soaked in a 10% honey solution. A part of bean pod (*Phaseolus vulgaris* L.) was provided in each jar as an oviposition substrate (Isenhour and Yeargan 1981). Bean pods with newly deposited eggs were removed and replaced daily, and kept in the previously described plastic jars. Jars were examined daily for emergence of *O. albidipennis* nymphs. Soon after hatching, nymphs were carefully transferred to new plastic jars provisioned with *E. kuehniella* eggs and small styrofoam balls to offer hiding places and reduce cannibalism (Sobhy et al. 2005). Field collected adults and nymphs were added on a regular basis to refresh the colony and to increase its genetic variation. Upon eclosion, adults were sexed and placed in new plastic jars, provisioned with the same

type of prey and oviposition substrates. Colonies were maintained at $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH and 16L:8D photoperiod (Sobhy et al. 2006).

Rearing of prey species

Ephestia kuehniella: Eggs of *E. kuehniella* were taken from the mass rearing line in the Public Service Centre of Biological Control, Faculty of Agriculture, Suez Canal University, Ismailia, Egypt. *Ephestia kuehniella* larvae were reared on a wheat germ based diet.

Trialeurodes vaporariorum: The stock culture was maintained on eggplant seedlings (*Solanum melongena* L.) reared in a glasshouse under controlled conditions of $25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH.

Tetranychus urticae: The stock culture was maintained on sweetpotato plants (*Ipomoea batatas* [L.] Lam.) in a glasshouse under controlled conditions of $25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH.

Gynaikothrips ficorum: Large populations of *G. ficorum* infest Ficus trees (*Ficus nitida* Thunb.) in Egypt, causing immense damage (Tawfik 1967; Ragab 1991). Thus, large numbers of larvae of *G. ficorum* were collected directly from Ficus trees cultivated on the Experimental farm for use in experiments. Second instars were used in all experiments.

Effect of different prey on the immature stages of *O. albidipennis*

The effect of prey type on nymphal development, survival and predation was determined at $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH and 16L:8D photoperiod. Newly eclosed nymphs (0–6 h old) were separated individually into small petri dishes (9 cm diameter × 1.5 cm height) by using a small fine-hair brush. There were 47–49 replicates for each prey treatment.

Each nymph was provided with one of the four investigated prey (eggs of *E. kuehniella*, *T. urticae*, *T. vaporariorum*, or 2nd instars of *G. ficorum*). Eggs of *E. kuehniella* were glued onto pieces of filter paper with a diluted solution of Arabic gum (Tommasini et al. 2004) and placed on moistened filter paper discs, which provided additional moisture in the dishes. The other prey were provided to the predators on small leaf discs cut from host plants used in their colony's maintenance.

Each container was inspected daily to determine *O. albidipennis* development stage and the number of prey consumed. Predation was determined by visual examination of prey under a binocular microscope (20 \times), after removal from the petri dish arenas. New prey were provided on a daily basis until the *O. albidipennis* completed development or died, according to the schedule shown in Table 1. The amount of prey provided was based on preliminary experiments to ensure that more prey were available to predators than they would consume within one day. Therefore, immature development would not be affected by prey limitation.

Data were recorded in the form of developmental time, mortality, and prey consumption for each instar (El-Husseini et al. 1993). After adult eclosion, the sex ratio of *O. albidipennis* reared on each of the four prey types was determined and expressed as percent female.

Effect of different prey on the longevity and female fecundity of *O. albidipennis*

Fecundity and longevity were determined for adults emerging from the immature development tests. Newly emerged adults of *O. albidipennis* for the four prey treatments were paired (one female with one male), and these pairs were placed separately in petri dishes (9 cm diameter \times 1.5 cm height) for copulation. To stimulate mating, no prey were added at this time (Ortigosa and Rowe 2002). Twelve hours later, males were removed and separated to other petri dishes so that responses of individual predators could be determined.

The females were supplied daily with fresh excess prey on new plant leaves or paper discs, and bean pods as oviposition sites until death. In a manner similar to females, males were also provided with fresh excess prey, and bean pods, as *Orius* spp. will obtain moisture and nutrients from feeding on plant

material (Salas-Aguilar and Ehler 1977). The number of consumed prey and deposited eggs were counted daily, under a binocular microscope (20X). Experiments were conducted under the same laboratory conditions as for the experiment with nymphs (26 \pm 1 $^{\circ}$ C, 60 \pm 10% RH and 16L:8D photoperiod).

Statistical analyses

The data on nymph development and nymph prey consumption were analyzed by one-way ANOVA's, with Tukey's post-hoc comparison of treatment means. If assumptions for normally distributed data with homogeneous variances could not be fulfilled, we used the non-parametric Kruskal–Wallis ANOVA on ranks and compared treatment effects using Dunn's test. These analyses were performed with Sigmastat 2.03 (SPSS Inc, Chicago, IL, USA). Survival data and sex ratios were examined with a generalized linear model (GLM) fitted by maximum quasi-binomial estimation in the software package R (R: A Language and Environment for Statistical Computing, version 2.10.1, Zurich, Switzerland, 2009, <http://www.R-project.org>).

Adult prey consumption and adult longevity were analyzed by two-way ANOVA, with diet type and predator sex as treatment factors. In the event of a significant interaction, separate one-way ANOVA's for diet type were conducted for each sex. If assumptions for normally distributed data with homogeneous variances could not be fulfilled, we used the non-parametric Kruskal–Wallis ANOVA on ranks and compared treatment effects using Dunn's test. Female fecundity was analyzed using one-way ANOVA and Tukey's post-hoc comparison of treatment means when the data were normally distributed and the variances were homogeneous. These analyses were performed with Sigmastat 2.03.

Life table parameters were estimated for *O. albidipennis* fed on each prey diet. Parameter estimates and

Table 1 Number of prey provided per day for each nymphal instar of *Orius albidipennis* during development

Prey	<i>O. albidipennis</i> instars				
	1st instar	2nd instar	3rd instar	4th instar	5th instar
<i>E. kuehniella</i> eggs	10	10	20	20	30
<i>G. ficorum</i> larvae	35	45	55	65	75
<i>T. urticae</i> eggs	30	50	70	90	110
<i>T. vaporariorum</i> eggs	25	35	45	55	65

their 95% confidence limits were calculated for the net reproductive rate (R_0), the mean generation time (T), the doubling time (DT), the intrinsic rate of natural increase (r_m), and the finite capacity of increase (λ), using the jackknife technique developed by Maia et al. (2000). This technique allows for statistical comparisons to be made among the parameters for the different prey diet treatments. Data for the egg stage used in these calculations were obtained from Sobhy et al. (2006) for similar environmental conditions.

Results

Effect of different prey on the immature stages of *O. albidipennis*

As shown in Table 2, the type of prey had profound effects on the duration of all nymphal instars of *O. albidipennis*. Total developmental time was significantly faster for *O. albidipennis* that fed on *E. kuehniella* eggs or *G. ficorum* larvae compared with the other investigated prey ($F = 175.822$; $df = 3,126$; $P < 0.001$). Significant differences were found in development time for all instars *O. albidipennis* among the different prey diets (first instar: $H = 54.083$; $df = 3$; $P < 0.001$; second: $H = 105.410$; $df = 3$; $P < 0.001$; third: $H = 31.709$; $df = 3$; $P < 0.001$; fourth: $H = 77.004$; $df = 3$; $P < 0.001$; and fifth: $H = 93.102$; $df = 3$; $P < 0.001$), with proportionately greater differences in development time occurring in the later stadia.

Orius albidipennis nymphs were able to complete their development on all tested diets, although there were significant differences in survivorship ($\chi^2 = 18.90$, $df = 3$, $P = 0.004$; Table 2). The lowest overall survival rates to adulthood were recorded for nymphs that fed on *T. vaporariorum* eggs (51.06%) and on *T. urticae* eggs (59.57%), while the highest survival rate (87.75%) was recorded for those fed on *E. kuehniella* eggs. Intermediate rates for survivorship were reported for those fed on *G. ficorum* (72.91%) (Table 2).

The type of prey also had a significant effect on the number of prey consumed by *O. albidipennis* nymphs ($H = 124.540$; $df = 3$; $P < 0.001$ for the 1st instar; $H = 116.103$; $df = 3$; $P < 0.001$ for the 2nd instar; $H = 115.231$; $df = 3$; $P < 0.001$ for the 3rd instar; $H = 107.952$; $df = 3$; $P < 0.001$ for the 4th instar and

Table 2 Effect of four different prey on the survival and development of nymphs, and resulting sex ratio of *Orius albidipennis*

Prey ¹	Survival rate %	Developmental time ^{2,3} (Days)					Total nymphal development time (Days)	Sex Ratio (% female)
		1st instar	2nd instar	3rd instar	4th instar	5th instar		
<i>E. kuehniella</i> (n = 49)	87.75 ± 0.05 ^a	2.43 ± 0.07 ^c (47)	1.21 ± 0.03 ^c (46)	2.65 ± 0.13 ^a (45)	2.02 ± 0.12 ^b (43)	2.23 ± 0.12 ^c (43)	10.51 ± 0.25 ^c	58.13 ± 0.08 ^a
<i>G. ficorum</i> (n = 48)	72.91 ± 0.06 ^{ab}	2.96 ± 0.06 ^b (46)	1.73 ± 0.04 ^b (44)	1.81 ± 0.05 ^c (41)	1.18 ± 0.06 ^c (37)	3.17 ± 0.07 ^b (35)	10.90 ± 0.14 ^c	62.85 ± 0.08 ^a
<i>T. urticae</i> (n = 47)	59.57 ± 0.07 ^{bc}	3.65 ± 0.12 ^a (40)	2.78 ± 0.06 ^a (38)	2.19 ± 0.07 ^a (33)	2.48 ± 0.11 ^{ab} (30)	5.39 ± 0.12 ^a (28)	16.71 ± 0.18 ^a	53.57 ± 0.09 ^a
<i>T. vaporariorum</i> (n = 47)	51.06 ± 0.07 ^c	2.76 ± 0.09 ^{bc} (39)	1.71 ± 0.09 ^b (37)	2.24 ± 0.08 ^b (31)	3.41 ± 0.18 ^a (28)	4.77 ± 0.24 ^a (24)	15.12 ± 0.28 ^b	54.16 ± 0.10 ^a

¹ Initial number of replicates for each treatment are in parentheses

² Means ± SE within each column followed by the same letter are not significantly different according to Dunn's or Tukey's test ($P > 0.05$)

³ Numbers in parentheses for each instar are the number of survivors for that stage

$F = 857.467$; $df = 3,126$; $P < 0.001$ for the 5th instar). The prey consumption increased notably as *O. albidipennis* aged. The greatest total prey consumption was 209.85 eggs of *T. urticae* and the lowest was 62.25 eggs of *E. kuehniella* (Fig 1).

However, because of the differences in development times for predators reared on the different prey, the mean daily predation rates (prey/day) were higher with *G. ficorum* as the prey than for the other types of prey, especially for the younger instars of *O. albidipennis*.

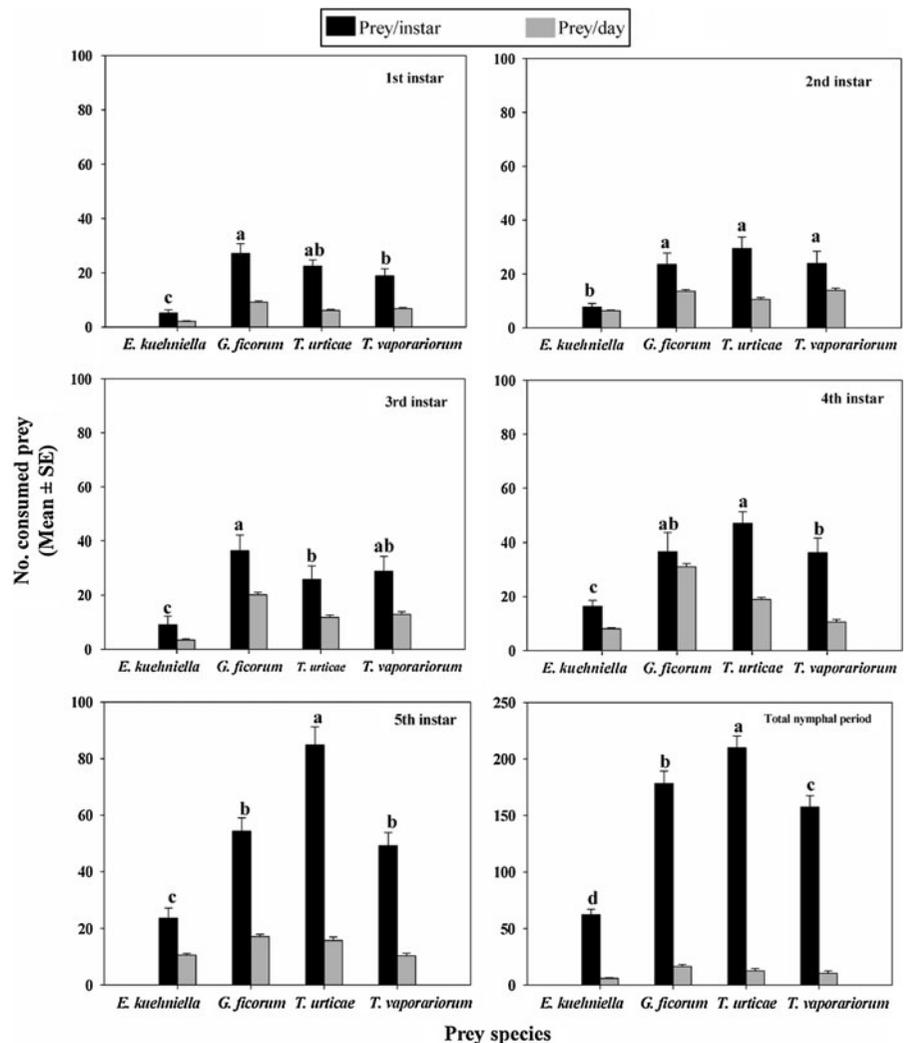
Females outnumbered males, with slightly female biased sex ratios occurring in all treatments, although these were not significantly different (Table 2). The lowest proportions of females occurred among *O. albidipennis* reared on eggs of *T. urticae* and *T. vaporariorum*, whereas the highest proportion of

females was 62.85% when *G. ficorum* larvae were supplied as prey.

Effect of different prey on the longevity and fecundity of *O. albidipennis*

Longevity of adult *O. albidipennis* was dependent on both prey type and predator sex, with females living considerably longer than males. There was a significant interaction between prey type and predator sex ($F = 14.53$; $df = 3,122$; $P < 0.0001$), which was a result of the comparatively short longevity of males fed *E. kuehniella* eggs. Because of the significant interaction, separate analyses were conducted for females and males. Significant differences in adult longevity were observed among the different prey

Fig. 1 Prey consumption (Means \pm SE) of different nymphal stages of *Orius albidipennis* fed one of four different prey (*Ephestia kuehniella*; *Gynaikothrips ficorum*; *Tetranychus urticae*; *Trialeurodes vaporariorum*). For each instar, different letters above the bars indicate a significant difference between tested prey ($P < 0.05$), based on a post-hoc Dunn's test



diets ($H = 42.834$; $df = 3$; $P < 0.001$ for females; $H = 39.191$; $df = 3$; $P < 0.001$ for males). The shortest longevity for females (14.33 days) was for those fed *T. urticae* eggs whereas the longest (26.86 days) was recorded for those fed *G. ficorum* larvae. The longest longevity for males was for those fed *G. ficorum* larvae (8.76 days), and the shortest longevity (3.97 days) was for those fed *E. kuehniella* eggs.

Prey species had a significant effect on the fecundity of *O. albidipennis*. ($F = 534.991$; $df = 3,71$; $P < 0.001$). The greatest lifetime fecundity (147.88 eggs/female) was recorded for females fed *E. kuehniella* eggs (Table 3). When females fed on *G. ficorum* larvae, fecundity dropped to 93.36 eggs/female, but fecundity was even significantly lower for females fed eggs of *T. urticae* or eggs of *T. vaporariorum*. Females on those diets produced only 42.77–36.67% of the eggs, respectively, produced by females that fed on *E. kuehniella* eggs.

The greatest mean daily fecundity, averaged over female lifetime, (7.71 eggs/female/day) was also recorded for females that were fed *E. kuehniella* eggs (Table 3). Females fed the other prey diets produced only 37.35–54.73% of the eggs produced daily by females fed *E. kuehniella* eggs ($H = 66.827$; $df = 3$; $P < 0.001$). Oviposition was not constant over time. Oviposition patterns for each prey type showed an initial increase early in adulthood followed by declines as females aged. Although oviposition declined over time, most females were able to continue egg laying almost until death (Fig. 2). Peak daily oviposition occurred on day 7 of adulthood for females fed *E. kuehniella* eggs, with these females laying 15.64 ± 1.08 eggs (mean \pm SE). This amount was over twice the maximum daily oviposition recorded for females reared on the other prey types (6.50 ± 0.40) eggs laid on day 10 for *G. ficorum* as prey; 7.07 ± 0.41 eggs laid on day 6 for *T. urticae* eggs as prey; 5.00 ± 0.23 eggs laid on day 8 for *T. vaporariorum* eggs as prey).

Prey type had a significant effect on prey consumption by *O. albidipennis* adults. There was a significant prey type by predator sex interaction for total prey consumption ($F = 21.74$; $df = 3,122$; $P < 0.0001$), but overall, female predators did consume significantly more total prey than male predators ($F = 3677$; $df = 1,122$; $P < 0.0001$). Part of this difference is attributable to differences in longevity

Table 3 Effect of four different prey on longevity, fecundity and prey consumption of *Orius albidipennis* adults

Prey	♀				♂			
	Fecundity ¹ (eggs/female)	Oviposition rate (eggs/female/day)	Longevity (days)	Prey consumption	Daily prey consumption	Longevity (days)	Prey consumption	Daily prey consumption
<i>E. kuehniella</i>	147.88 \pm 2.21 ^a	7.71 \pm 0.19 ^a	18.72 \pm 1.38 ^b	123.96 \pm 2.09 ^a	7.19 \pm 0.28 ^b	3.97 \pm 0.21 ^{bc}	24.61 \pm 1.29 ^c	6.22 \pm 0.28 ^a
<i>G. ficorum</i>	93.36 \pm 1.49 ^b	3.48 \pm 0.05 ^{bc}	26.86 \pm 0.97 ^a	113.95 \pm 1.97 ^b	4.39 \pm 0.30 ^d	8.76 \pm 0.37 ^a	31.53 \pm 1.34 ^b	3.69 \pm 0.33 ^b
<i>T. urticae</i>	63.26 \pm 1.18 ^c	4.22 \pm 0.09 ^b	14.33 \pm 0.62 ^c	127.53 \pm 1.76 ^a	9.14 \pm 0.36 ^a	7.57 \pm 0.51 ^{ab}	42.15 \pm 1.45 ^a	5.86 \pm 0.33 ^a
<i>T. vaporariorum</i>	54.23 \pm 1.59 ^d	2.88 \pm 0.06 ^c	18.61 \pm 0.70 ^b	98.23 \pm 2.13 ^c	5.35 \pm 0.39 ^c	5.54 \pm 0.35 ^b	29.63 \pm 1.08 ^{bc}	5.55 \pm 0.36 ^a

¹ Means \pm SE within each column followed by the same letter are not significantly different according to Dunn's or Tukey's test ($P > 0.05$)

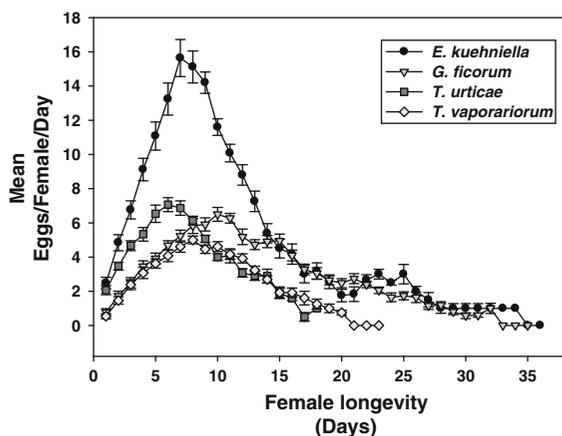


Fig. 2 Mean (\pm SE) daily oviposition for *Orius albidipennis* females when fed one of four different prey (*Ephesthia kuehniella*; *Gynaikothrips ficorum*; *Tetranychus urticae*; *Trialeurodes vaporariorum*). The end data point for each line denotes when the last female in each prey treatment died

between males and females. Although females did consume more eggs of *E. kuehniella* or *T. urticae* per day than did corresponding males, daily predation rates were similar between males and females fed either *G. ficorum* or *T. vaporariorum*. These differences produced a significant interaction for predator sex by prey type ($F = 8.52$; $df = 3,122$; $P < 0.0001$; Table 3).

When considering the sexes separately, *O. albidipennis* females differed significantly in their lifetime consumption of the four tested prey ($F = 31.143$; $df = 3,71$; $P < 0.001$). Lifetime prey consumption was greatest when females were given *T. urticae* eggs (127.53) or *E. kuehniella* eggs (123.96) and lowest (98.23) when given *T. vaporariorum* eggs (Table 3).

When accounting for differences in longevity, females consumed more *T. urticae* eggs per day than other types of prey. Significant differences also existed among the tested prey in lifetime prey consumption by male *O. albidipennis* ($F = 32.204$; $df = 3,51$; $P < 0.001$). The lowest daily prey consumption was for males given *G. ficorum* larvae as prey, although these males did have the greatest mean longevity (Table 3).

In terms of the number of eggs females laid per prey item, *E. kuehniella* fed females produce over 1.2 eggs per prey item. Females fed *G. ficorum* produced 0.8 eggs per prey item. In contrast, females fed either *T. urticae* or *T. vaporariorum* produced less than

50% of the eggs per prey item that females fed *E. kuehniella* did.

Life table parameters

Life table parameter estimates (Table 4) reinforce that *E. kuehniella* eggs were a superior diet for *O. albidipennis* compared with the other prey tested. Because of the rapid nymphal development time and high fecundity early in adulthood, *O. albidipennis* fed *E. kuehniella* eggs had a significantly greater net reproductive rate (R_0), intrinsic rate of natural increase (r_m), and finite rate of increase (λ) than those fed other prey (Table 4). The mean generation time and population doubling time were also significantly shorter when *E. kuehniella* eggs were prey compared with other prey types. Although *O. albidipennis* reared on *G. ficorum* larvae had a rapid development, the length of time to reach their peak oviposition resulted in relatively long generation and doubling times.

Discussion

Although generalist predatory insects are capable of attacking a diverse spectrum of prey species, the results of our study show that the type of prey can substantially impact a wide range of characteristics related to the performance of *O. albidipennis*, including development, survival and fecundity, which have important implications for population dynamics. Because the quality of food for predatory insects can be measured by growth and oviposition (Arijs and De Clercq 2004), it is important to consider effects of prey across both immature and adult stages. Our results from rearing *O. albidipennis* from neonate first instars until adult death on specific diets indicate that eggs of *E. kuehniella* were the most suitable for rearing *O. albidipennis* among the different arthropod prey tested. These results are in agreement with studies of other species of *Orius* (Kiman and Yeargan 1985; Bush et al. 1993; Richards and Schmidt 1996; Nagai et al. 1998; Mendes et al. 2002; Bonte and De Clercq 2008). However, some comparative studies have found that thrips, including *G. ficorum*, are more suitable than other arthropod prey, including Lepidoptera eggs for *O. albidipennis* (Tawfik and Ata 1973; Chyzik et al. 1995b). Thrips are generally

Table 4 Life table parameter estimates and 95% confidence limits for *Orius albidipennis* reared on each of four different types of prey

Prey diet	Parameter estimates ¹ (95% confidence limits)				
	Net reproductive rate (R_0)	Mean generation time (T) (days)	Doubling time (DT) (days)	Intrinsic rate of natural increase (r_m)	Finite rate of increase (λ) (days ⁻¹)
<i>E. kuehniella</i>	75.43 ^a (73.10–77.77)	19.76 ^a (19.03–20.49)	3.16 ^a (3.06–3.28)	0.2187 ^a (0.2109–0.2265)	1.244 ^a (1.235–1.254)
<i>G. ficorum</i>	42.78 ^b (41.36–44.20)	22.82 ^b (22.04–23.61)	4.21 ^b (4.06–4.36)	0.1645 ^b (0.1587–0.1704)	1.179 ^b (1.172–1.186)
<i>T. urticae</i>	20.19 ^c (19.38–21.00)	23.49 ^b (22.97–24.01)	5.42 ^c (5.31–5.53)	0.1279 ^c (0.1252–0.1306)	1.136 ^c (1.133–1.139)
<i>T. vaporariorum</i>	15.00 ^d (14.03–15.96)	23.55 ^b (22.87–24.23)	6.02 ^d (5.83–6.22)	0.1150 ^d (0.113–0.1187)	1.122 ^d (1.118–1.126)

¹ Life table parameter estimates were calculated using a jackknife technique, with an SAS program written by Maia et al. (2000). Parameter estimates marked with the same letter within columns are not significantly different ($P > 0.05$)

considered a key component of natural diets of *Orius* spp. (Lattin 1999), and *Orius* spp. typically demonstrate a preference for thrips over other types of prey in choice situations (Kakimoto et al. 2006; Arnò et al. 2008; Xu and Enkegaard 2009).

Although *O. albidipennis* nymphs completed their development on all of the four tested prey, not all of the prey were equally suitable for development. Nymphal development time was shortest and survivorship was greatest when *E. kuehniella* eggs were provided as prey. Nymphs given *E. kuehniella* eggs had relatively high survivorship throughout all stadia (>95% survived each stadium). Mortality was highest for 4th instars reared on *G. ficorum* larvae. For predators reared on eggs of *T. urticae* or *T. vaporariorum*, the greatest mortality occurred during the first stadium. These results are similar to most other studies comparing the development of *Orius* spp. on Lepidoptera eggs versus thrips (Kiman and Yeargan 1985; Nagai et al 1998; Richards and Schmidt 1996), in which developmental rates and survival were lower with thrips as prey. In one notable exception, Mendes et al. (2002) found that development of *O. insidiosus* was longer with eggs of *E. kuehniella* as prey than with adults of *Caliothrips phaseoli* (Hood) as prey.

The order of suitability of the different prey for adults was similar to the order of suitabilities for nymphs. Female *O. albidipennis* had the highest fecundity when fed eggs of *E. kuehniella*. Although thrips larvae are considered a preferred prey for *Orius* spp. (Nagai 1991; Yano 1996; Kohono and Kashio 1998; Mendes et al. 2002; Baez et al. 2004), *G. ficorum* larvae were not the most suitable prey for *O. albidipennis* in our study. Larvae of *G. ficorum* were a more suitable prey than eggs of *T. urticae* or *T. vaporariorum*, which produced females with significantly shorter longevities and lower fecundities. Yet, despite longevity being the longest for females fed *G. ficorum* larvae, these females had much lower reproductive rates and lifetime fecundity than those fed eggs of *E. kuehniella*. This increase in fecundity with *E. kuehniella* eggs as prey was not just a reflection of differences in longevity of *O. albidipennis*, as daily oviposition was 1.8–2.6 times higher for females fed on *E. kuehniella* than on other prey diets. Total fecundity was 1.6–2.7 times higher with *E. kuehniella* than with the other prey. Interestingly, although we found that it took relatively few eggs of *E. kuehniella* for *O. albidipennis* to complete

development, adult female predators consumed as many or more *E. kuehniella* eggs as any other prey.

Eggs of *T. urticae* and *T. vaporariorum* may be poor quality prey because they lack certain essential nutrients, which may slow development, increase mortality, or hinder ovigeny. Because we gave immature and adult *O. albidipennis* an excess of fresh prey each day, the differential response to prey type is likely the result of differences in the nutritional value of the prey rather than a scarcity of food or differences in searching times. Hagler et al. (2004) concluded that sweetpotato whitefly, *Bemisia tabaci* (Gennadius), eggs are a non preferred prey for *O. tristicolor* (White). Arnò et al. (2008) found that the different life stages of *B. tabaci* could support development of *Orius majusculus* (Reuter) and *O. laevigatus*, but these predators ultimately preferred the thrips *F. occidentalis* over *B. tabaci*. For all instars of *O. albidipennis* fed on eggs of *T. urticae*, there was a tendency towards an increased development time and relatively low survival rates. Paik et al. (2003) found that *O. sauteri* (Poppius) was also able to complete development on eggs of *T. urticae*, but this prey resulted in slower development and lower survivorship than prey such as thrips larvae.

The high quality of Lepidoptera eggs is likely related to their relatively high nitrogen content. Ferkovich et al. (2007) found that *E. kuehniella* eggs had the highest protein concentrations among five Lepidoptera species tested. It is also possible that the fat content is higher in *E. kuehniella* eggs than in other prey, which could contribute to the greater development rate and reproduction on that diet (De Clercq et al 2005). Indeed, Specty et al. (2003) found that *E. kuehniella* eggs have two times the amino acid content and three times greater lipid content than the pea aphid *Acyrtosiphon pisum* (Harris), and that these differences were related to variation in the size and fecundity of the coccinellid predator *Harmonia axyridis* Pallas reared on those prey. Lepidopteran eggs may also contain additional factors that enhance reproduction in *Orius* species (Ferkovich and Shapiro 2004).

Compared with other species of *Orius*, few studies have examined the potential of *O. albidipennis* as a biological control agent. However, it is among the most common species of *Orius* in much of its native range (Tawfik and Ata 1973; Hernandez and Stone-dahl 1999) where it would be suitable for augmentative biological control (van Lenteren et al. 2003;

Louda et al. 2003). The results of our studies provide certain basic biological data on *O. albidipennis* and its potential impact on various prey species in the field. Data on predation rates and population growth are important for forecasting the role of *O. albidipennis* as a biological control agent. Although laboratory based data need to be corroborated with field studies, our results show that *O. albidipennis* can survive and reproduce successfully on alternative types of prey in the absence of more favourable types of prey. Furthermore, based on findings for *O. insidiosus* (Harwood et al. 2007), it is likely that *O. albidipennis* would switch among available prey types in the field. This exemplifies one highly favourable trait of *Orius* species as biological control agents, that they are able to persist when target prey are scarce (Hassell and Rogers 1972). While this trait is often cited as making *Orius* spp. a good biocontrol agent, differences in prey quality need to be considered to better understand predator–prey dynamics in the field (Sabelis and van Rijn 1997; Vacante et al. 1997). For example, predation on poor quality prey would slow down predator population growth and reduce the ability of predator populations to control alternative herbivore pests.

In addition to the ecological relevance of our findings, they also can serve to assist with the development of mass rearing of predators in developing countries such as Egypt where the dynamics of biological control production practices may differ from those in developed countries (Altieri et al. 1997; Silveira et al. 2004). While our results indicate that *E. kuehniella* is the most suitable diet for *O. albidipennis*, *G. ficorum* larvae can be a suitable prey. Further, *T. urticae* eggs and *T. vaporariorum* eggs could be used as alternative diets in maintaining *O. albidipennis* if more suitable prey are not readily available.

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Islam Sobhy This research is part of his MSc project, investigating factors affecting the mass production of the anthocorid predatory *Orius albidipennis*. This work was carried

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