Eur. J. Entomol. **112**(3): 446–452, 2015
doi: 10.14411/eje.2015.051
ISSN 1210-5759 (print), 1802-8829 (online)

Effects of diet on development and reproductive fitness of two predatory coccinellids (Coleoptera: Coccinellidae)

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Key words. Coleoptera, Coccinellidae, *Oenopia conglobata*, *Cheilomenes sexmaculata*, Aphididae, *Aphis gossypii*, Psyllidae, *Agonoscena pistaciae*, *Ephestia kuehniella* eggs, food suitability, life table

Abstract. Studies of prey suitability are needed to develop efficient mass rearing programs for generalist predators and to understand their potential contribution to integrated pest management. A laboratory study was conducted to evaluate the development and reproductive success of two predatory coccinellids, *Oenopia conglobata* (L.) and *Cheilomenes sexmaculata* (Fabricius), reared on diets of the common pistachio psyllid, *Agonoscena pistaciae* Burckhardt & Lauterer, the cotton aphid, *Aphis gossypii* (Glover) or a reference diet of *Ephestia kuehniella* Zeller eggs. Development and reproductive performance of the two coccinellids varied with diet, but egg fertility and immature survival did not. The developmental period (egg-adult) was shortest for both species on *A. gossypii*. This prey also yielded the shortest preoviposition period and greatest fecundity for *C. sexmaculata*. The psyllid diet was superior for reproduction in *O. conglobata*. For both predators, eggs of *E. kuehniella* were a better diet for development than for reproduction. Life table data indicated that the arboreal *O. conglobata* was better adapted to *A. pistaciae* on pistachio trees and might be a more effective biocontrol agent for this pest, despite the fact that *C. sexmaculata* had a higher intrinsic rate of increase on all diets.

INTRODUCTION

Most coccinellid species (about 90%) are predaceous, representing an important component of the natural enemies of Sternorrhyncha (aphids, coccids, aleyrodids and psyllids), among the most dangerous group of crop pests (Hodek et al., 2012). Coccinellids range widely from stenotopic to eurytopic species. Some species such as *Oenopia* (*Synharmonia*) *conglobata* (L.) are known to be restricted to deciduous trees (Hodek & Honěk, 1996). *Oenopia conglobata* is one of the most important predators of *Agonoscena pistaciae* Burckhardt & Lauterer (Hemiptera: Psyllidae), a key pistachio pest in Iran (Mehrnejad & Jalali, 2004). Field observations in Southeastern Iran show that this species is a common coccinellid in pistachio trees from April to October (Mehrnejad et al., 2011; Salehi et al., 2013) and mainly prefer to remain on psyllid-infested pistachio leaves even when aphids, especially the cotton aphid, *Aphis gossypii* (Glover), are abundant on herbaceous plants such as *Alhagi* sp. and *Glycyrrhiza* sp. in and around pistachio plantation areas. Earlier in March, however, when *O. conglobata* adults emerge from hibernation, the overwintered adults of *A. pistaciae* begin to deposit eggs on pistachio leaves and so the ladybirds may have to spend one generation on aphid-infested herbaceous plants (Jalali, 2001). *Cheilomenes sexmaculata* (Fabricius) is another psyllid predator in pistachio orchards; however, it does not appear in pistachio orchards until early July (Mehrnejad et al., 2011) when the weather is warmer. Both of these ladybeetles have been frequently reported as potential biological control agents of aphids and psyllids from different agro-ecosystems around the world, especially Asia and Europe (e.g. Fye, 1981; Khan & Khan, 2002; Erler, 2004; Singh & Omkar, 2009; Kenis et al., 2010; Rondoni et al., 2012).

Prey quality has a direct impact on the growth, development and reproduction of predatory insects (Thompson, 1999). The suitability of a prey species can be evaluated by measuring its effect on biological attributes of the predator (Kalushkov & Hodek, 2001). Reproduction requires high energy resources that are supplied by food, which is a major regulatory factor in reproductive success (Houck, 1991). In order to understand the behaviour, biology and ecology of insects and develop pest management strategies, it is important to have a good knowledge of how insects interact with their food sources. Most coccinellid predators survive on a "mixed diet" composed of "essential" and "alternative" prey (Hauge et al., 1998; Evans et al., 1999; Nielsen et al., 2002). Essential prey supports development and reproduction, whereas alternative prey enables adults to survive when essential prey is scarce (Hodek, 1962; Mills, 1981; Evans et al., 1999). Kalushkov & Hodek (2001) suggest that quantitative data on a predator's rate of development, survival and reproduction indicate the adequacy of the prey. Although there have been several earlier studies evaluating the effects of diet quality and quantity on development and reproduction of *O. conglobata* and *C. sexmaculata* (e.g. Patnaik & Sahu, 1980; Agarwala & Choudhuri, 1995; Sugiura & Takada, 1998), only a few studies have constructed life tables for *O. conglobata* (Mehrnejad &

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Jalali, 2004; Hassani et al., 2009) and there are no detailed reports of food effects on life table parameters of *C. sexmaculata*. For a successful biological control program using a specific natural enemy, it is necessary to determine its population characteristics; life table studies are a powerful tool for such evaluations (Carey, 1993; Wittmeyer & Coudron, 2001). The objective of this study was to compare the development, reproduction and life table parameters of *O. conglobata* and *C. sexmaculata* on two natural prey species, *A. pistaciae*, a key pest of pistachio trees in Iran, and *A. gossypii*, a dominant aphid species on herbaceous plants in pistachio orchards (Jalali, 2001). The results may help for better understanding of the potential of these predators for augmentative biological control of key pests in pistacchio. Life table analysis can indicate which are the more promising candidates, both for mass rearing and for their performance in the field. Moreover, since the use of factitious food may make mass-rearing more economic (De Clercq, 2004), we also evaluated the quality of *E. kuehniella* eggs for development and reproduction of these two coccinellids.

MATERIAL AND METHODS

Stock cultures

Adults of *O. conglobata* and *C. sexmaculata* were originally collected from pistachio trees (*Pistacia vera*), infested by the common pistachio psyllid, *Agonoscena pistaciae* Burckhardt & Lauterer, in a pistachio garden at Vali-e-Asr University of Rafsanjan, Rafsanjan, Iran (Geocoding: 30°23′39.24″N and 55°55′39.25″E). Fresh pistachio leaves infested by *A. pistaciae* were obtained daily from a pistachio garden and were transferred to the laboratory for the experiments on psyllids. The colony of melon aphid (*Aphis gossypii*) was reared on cucumber (*Cucumis sativus*) at 25 ± 2°C and 60 ± 10% RH, and a photoperiod of 16L : 8D in greenhouse. A colony of the Mediterranean flour moth (*Ephestia kuehniella*) was maintained in an insectary on wheat flour at 27 ± 1°C and 50 ± 10% RH, and a photoperiod of 16L : 8D. Fresh eggs deposited by female moths were kept for at least one day in a refrigerator (–18°C) before being used in the experiments. The stock population of *O. conglobata* and *C. sexmaculata* were reared separately on each of three diets (nymphs of *A. pistaciae*, *A. gossypii* and eggs of *E. kuehniella*) under controlled conditions of 27.5 ± 1°C, 50 ± 10% RH and 16L : 8D photoperiod to obtain a new generation of each predator for the experiments. Based on earlier studies, these environmental conditions are almost optimum for laboratory rearing (shorter development time, lower mortality and higher reproduction output) of both coccinellids (Mirhosseini, 2013; Jalali et al., 2014).

Development and mortality

Only eggs laid within the previous 12 h were used for the start of each experiment. The egg clusters (approximately 150 eggs) from the first laboratory generations of *O. conglobata* and *C. sexmaculata* were reared on each of the three diets, placed separately in Petri dishes (6 × 1.5 cm) under growth chamber conditions (27.5 ± 1°C, 50 ± 10% RH, 16L : 8D photoperiod). To exclude cannibalism, the number of eggs was carefully noted for each Petri dish. Every 12 h, we counted the number of hatched eggs and checked for unhatched or lost eggs. We never noted missing eggs or dead larvae. Moreover, eggs which did not hatch were observed under a stereomicroscope to rule out any egg cannibalism. After egg hatch, 50 first instar larvae (< 12 h old) were carefully transferred into Petri dishes (6 × 1.5 cm) individually. Each larva was supplied with one of the three diets each day until pupation. The diets (eggs of *E. kuehniella* or different instars of psyllid or aphid nymphs) were provided ad libitum per Petri dish. The egg, larval and pupal development times and the mortality of pre-adult stages were recorded every 12 h. After adult emergence, they were weighed and sexed. These adults were used to assess life table parameters.

Life table study

15 freshly matured pairs of *O. conglobata* and *C. sexmaculata* adults were randomly selected from each diet treatment for life table studies. Females were placed separately in 100 mm diameter Petri dishes under the experimental conditions described above. To ensure egg fertilization, each female was paired with a male from its stock culture for 2 h every other day. Different nymphal instars of the melon aphid and common pistachio psyllid were maintained ad libitum on leaf discs. Eggs of *E. kuehniella* on paper discs were provided ad libitum to each test female every 12 h. Survival and fecundity of females and fertility of eggs laid were recorded twice daily for the first 21 days of adult life.

Data analysis

Before analysis, data were checked for normality using the Kolmogorov-Smirnov test (K-S test) and all were found to be normally distributed. Data were then analyzed by 2-way ANOVA (SPSS, 2006) with diet and predator species as fixed factors and, in the case of adult mass, by 3-way ANOVA with gender as an additional factor. When interaction terms were significant, independent variables were analyzed separately by one-way ANOVA. The means were compared with the Bonferoni test at 5% probability. Life table parameters were calculated using total development time, total mortality, sex ratio and reproductive data. A VBA-macro for the Jackknife method was used to calculate life table parameters for the first 21 days of adult life as described by Vantornhout et al. (2005). The parameters calculated were net reproductive rate (R_0), intrinsic rate of population increase (r_m), finite rate of increase (λ) and doubling time (DT). Mean Jackknife pseudo-values for each treatment were subjected to ANOVA followed by the Bonferoni test to compare life table parameters among prey-predator combinations ($\alpha = 0.05$). Percent survival, percent fertility and sex ratio were analyzed by Chi-square test.

RESULTS

Development and survival of immatures

Mean developmental times and adult fresh weights of *C. sexmaculata* fed with the three different diets are listed in Table 1. The developmental duration of egg ($F = 25.76$; $df = 2{,}459$; $p < 0.001$), L_1–L_4 ($F = 67.06$; $df = 2{,}127$; $p < 0.001$), and pupal stages ($F = 4.11$; $df = 2, 124$; $p = 0.02$) varied significantly between the diets. The complete developmental period was shortest (9.14 ± 0.07 days) when fed *A. gossypii* and longest (10.01 ± 0.08 days) on *A. pistaciae* ($F = 36.37$; $df = 2, 124$; $p < 0.001$). Both males ($F = 31.25$; $df = 2, 58$; $p < 0.001$) and females ($F = 9.09$; $df = 2, 63$; $p < 0.001$) showed significant variation in weight when fed different diets; however, total survival (egg-adult) did not vary significantly between diets ($x^2 = 1.29$; $df = 2$; $p = 0.525$).

Although the time to egg hatch for *O. conglobata* did not vary significantly with diet ($F = 2.42$; $df = 2, 237$; $p = 0.09$), the 1-way ANOVA for larval development times ($F = 125.58$; $df = 2, 167$; $p < 0.001$), to pupae ($F = 58.16$; $df =$

TABLE 1. Development time (days) for egg, larval (L_1–L_4), pupal and total immature stage, total survival (egg–adult) and adult weight of *Cheilomenes sexmaculata* and *Oenopia conglobata* at 27.5°C, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii.*

Coccinellid species	Food	Developmental time[a]				Total survival (%)	Adult weight[a] (mg)	
		Egg	L_1–L_4	Pupa	Total		Female	Male
C. sexmaculata	*A. pistaciae*	1.88 ± 0.02c	5.38 ± 0.05d	2.78 ± 0.04e	10.01 ± 0.08d	73.49	8.65 ± 0.37bc	6.45 ± 0.25de
	A. gossypii	1.85 ± 0.02c	4.38 ± 0.06f	2.92 ± 0.03d	9.14 ± 0.07f	75.12	10.75 ± 0.33a	9.09 ± 0.24a
	E. kuehniella eggs	1.99 ± 0.01b	4.97 ± 0.07e	2.79 ± 0.04de	9.76 ± 0.08e	67.63	9.84 ± 0.35ab	7.96 ± 0.21b
O. conglobata	*A. pistaciae*	2.44 ± 0.02a	8.09 ± 0.02b	4.92 ± 0.04a	15.44 ± 0.04b	81.46	8.83 ± 0.19b	7.23 ± 0.13c
	A. gossypii	2.49 ± 0.03a	7.61 ± 0.09c	4.26 ± 0.05c	14.34 ± 0.09c	82.86	8.21 ± 0.18c	7.01 ± 0.10cd
	E. kuehniella eggs	2.50 ± 0.02a	9.14 ± 0.08a	4.69 ± 0.04b	16.30 ± 0.10a	77.12	7.56 ± 0.12d	6.28 ± 0.11e
		$F = 296.88$ $df = 5{,}699$ $p < 0.001$	$F = 831.91$ $df = 5{,}299$ $p < 0.001$	$F = 566.30$ $df = 5{,}284$ $p < 0.001$	$F = 1639.07$ $df = 5{,}284$ $p < 0.001$	$X^2 = 8.20$ $df = 5$ $p = 0.146$	$F = 19.66$ $df = 5{,}149$ $p < 0.001$	$F = 34.80$ $df = 5{,}137$ $p < 0.001$

[a] Means ± SEM within the same column followed by the same letter are statistically equivalent (Bonferoni test, $\alpha = 0.05$).

2, 155; $p < 0.001$) and total development time ($F = 151.15$; $df = 2, 155$; $p < 0.001$) were significant and indicated a predator-diet interaction (Tables 1 and 2). The complete developmental period of *O. conglobata* was the shortest (14.34 ± 0.09 days) when fed *A. gossypii*, followed by *A. pistaciae* (15.44 ± 0.04 days) and was longest (16.30 ± 0.10 days) when fed *E. kuehniella* eggs. Adult weight was affected by diet (males: $F = 18.28$; $df = 2, 74$; $p < 0.001$ and females: $F = 14.15$; $df = 2, 81$; $p < 0.001$); however, total survival of *O. conglobata* did not differ significantly between the three diets ($x^2 = 1.18$, $df = 2$, $p = 0.554$).

Two-way ANOVA indicated significant variations in developmental (egg, larva, pupa and egg-adult) times with significant predator × diet interactions (Table 2).

TABLE 2. ANOVA of developmental times and body mass at emergence of *Cheilomenes sexmaculata* and *Oenopia conglobata*, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii*.

Source of variation	*df*	*F*	*p*
Egg	5	296.88	< 0.001
Predator	1	1429.11	< 0.001
diet	2	13.91	< 0.001
Predator × diet	2	6.83	0.001
Error term	699		
L_1–L_4	5	831.91	< 0.001
Predator	1	3751.81	< 0.001
diet	2	131.17	< 0.001
Predator × diet	2	60.11	< 0.001
Error term	294		
Pupa	5	566.30	< 0.001
Predator	1	2715.00	< 0.001
diet	2	19.03	< 0.001
Predator × diet	2	46.88	< 0.001
Error term	279		
Total	5	1639.07	< 0.001
Predator	1	7800.75	< 0.001
diet	2	146.75	< 0.001
Predator × diet	2	41.54	< 0.001
Error term	279		
Fresh mass of females	5	19.66	< 0.001
Predator	1	54.33	< 0.001
diet	2	5.81	0.004
Predator × diet	2	17.15	< 0.001
Error term	144		
Fresh mass of males	5	34.80	< 0.001
Predator	1	48.94	< 0.001
diet	2	27.12	< 0.001
Predator × diet	2	39.10	< 0.001
Error term	132		

Reproductive potential and life table parameters on different diets

The female reproductive potential of *C. sexmaculata* on three diets is presented in Table 3. The 1-way ANOVA was marginally non-significant for variation in length of the preoviposition period on different diets ($F = 2.80$; $df = 2, 35$; $p = 0.07$). A non-significant difference was also recorded in the percent egg fertility on the three diets ($x^2 = 0.84$; $df = 2, 35$; $p = 0.655$). Mean daily and total fecundity of *C. sexmaculata* during the first 21 days of adult life were significantly different between diets (MDF: $F = 71.94$; $df = 2, 35$; $p < 0.001$ and MTF: $F = 70.85$; $df = 2, 35$; $p < 0.001$) with much lower egg production for ladybirds fed eggs of *E. kuehniella* compared to *A. gossypii* or *A. pistaciae* (Table 3).

The preoviposition period of *O. conglobata* females was statistically different across the three diets ($F = 7.22$; $df = 2, 42$; $p < 0.001$) (Table 3). Females of *O. conglobata* began laying eggs sooner when fed *A. pistaciae* (4.20 ± 0.11 days) compared to *A. gossypii* (5.53 ± 0.41 days) and *E. kuehniella* eggs (5.87 ± 0.38 days). Although two-way ANOVA revealed a non-significant predator×diet interaction for preoviposition period, the overall model indicated a significant interaction for fecundity (Table 4).

As with *C. sexmaculata*, egg fertility of *O. conglobata* was not affected by diet ($x^2 = 1.37$, $df = 2, 42$; $p = 0.505$); however, the suitability of *E. kuehniella* eggs for egg production was the lowest among the three diets (MDF: F = 5.18; $df = 2, 42$; $p < 0.001$; MTF: $F = 37.85$; $df = 2, 42$; $p < 0.001$, Table 3).

Based upon life table analysis, *E. kuehniella* eggs provided the lowest nutritional quality for *C. sexmaculata* (Table 5). The intrinsic rate of increase (r_m), and finite rate of increase (λ) were highest when fed *A. gossypii*; however, a similar net reproductive rate (R_0) value was obtained when

TABLE 3. Reproduction of *Cheilomenes sexmaculata* and *Oenopia conglobata* at 27.5°C, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii*[a].

Coccinellid species	Food	Pre-oviposition period (days)[b]	Total no. of eggs	Eggs/female/day	Egg fertility (%)
C. sexmaculata	*A. pistaciae*	2.67 ± 0.14c	642.17 ± 41.67a	35.08 ± 2.29a	82.18
	A. gossypii	3.00 ± 0.01bc	669.00 ± 21.91a	37.17 ± 1.22a	83.63
	E. kuehniella eggs	4.09 ± .84bc	164.27 ± 35.67c	9.32 ± 1.87d	78.64
O. conglobata	*A. pistaciae*	4.20 ± 0.11b	379.93 ± 7.47b	22.63 ± 0.46b	86.90
	A. gossypii	5.53 ± 0.41a	267.20 ± 17.14b	18.61 ± 1.18c	83.12
	E. kuehniella eggs	5.87 ± 0.38a	192.80 ± 18.82c	12.63 ± 1.18d	81.49
		$F = 12.29$ $df = 5,82$ $p < 0.001$	$F = 82.31$ $df = 5,82$ $p < 0.001$	$F = 66.55$ $df = 5,82$ $p < 0.001$	$X^2 = 2.60$ $df = 5$ $p = 0.76$

[a] Data are for the first 21 days of adult life. [b] Means ± SEM within the same column followed by the same letter are statistically equivalent (Bonferoni test, $\alpha = 0.05$).

reared on both *A. gossypii* and *A. pistaciae* ($p = 0.546$). The population doubling time (*DT*) was shortest on *A. gossypii* ($2.25 \pm 0.14 \times 10^{-2}$ days) and longest on *E. kuehniella* eggs ($3.32 \pm 2.04 \times 10^{-2}$ days).

Net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) were highest and population doubling time (*DT*) was the lowest when fed *A. pistaciae*, followed by *A. gossypii*. Life table parameters were weakest for coccinellids reared on *E. kuehniella* eggs (Table 5). Further, the effect of studied factors and their interaction was significant for the parameters, R_0, r_m, λ and *DT* (Table 6).

DISCUSSION

Food quality strongly influenced the development and reproduction of the two coccinellids. Differences in the life history data of *C. sexmaculata* and *O. conglobata* on the three diets were significant, indicating major differences in prey suitability. Although *E. kuehniella* eggs were probably an adequate diet for the development of the two ladybird species, *C. sexmaculata* in particular, it was clearly an inferior diet for reproduction in both species. Females of the two predators that were offered *E. kuehniella* eggs expressed a much lower daily and total fecundity compared with females fed natural prey. The lower fresh body weight on the moth egg diet and the higher reproductive output on aphid and psyllid diets might be due to increased prey consumption on the natural prey, leading to better conversion of food into eggs (Dixon & Agarwala, 2002; Honěk et al., 2008; Vargas et al., 2012) and vice versa with less suitable diet (i.e. eggs of *E. kuehniella*). Earlier studies have shown that in certain coccinellids (Michels & Flanders, 1992; Pervez & Omkar, 2004) including *C. sexmaculata* (Omkar & Bind, 2004), there is a positive correlation between the amount of food consumed by the larvae and the number of eggs they subsequently produced; however, we did not record the rate of food consumption in our study. The differences in reproductive rates observed here might be related to the fact that ingested natural prey may be converted to body mass more efficiently than unnatural foods (Jalali et al., 2009). The finding that *E. kuehniella* eggs are a much better diet for development than for reproduction in both ladybird species supports the argument by Michaud (2005) that larvae and adults of ladybird beetles may have different nutritional requirements. This was also observed in *Coleomegilla maculata* De Geer (Michaud & Jyoti, 2008; Riddick et al., 2014) and *Hippodamia convergens* Guerin (Michaud, 2000). Despite the wide variation in development times and oviposition output, diet had no significant effect on egg fertility. In the present study, fecundity proved a much better predictor of reproductive success; in both coccinellids, females consuming natural (aphid or psyllid) prey deposited significantly more eggs than those feeding on moth eggs, despite producing similar progenies. Aphid and psyllid diets appear to be much better protein sources for ovigenesis but are probably similar to *E. kuehniella* eggs in some nutrients required for egg fertility. As with the natural diets, *E. kuehniella* eggs are sufficiently palatable and nutritious enough to support the yolk content needed for nourishing the embryo as well as providing healthy and motile sperm in males; however, this monotypic diet should be supplemented with some plant material such as pollen to enhance reproductive output, as observed in some other predatory ladybirds such as *Adalia bipunctata* L. (De Clercq et al., 2005; Jalali et al., 2009) and *Harmonia axyridis* (Pallas) (Berkvens et al., 2008) and

TABLE 4. ANOVA of reproductive parameters of *Cheilomenes sexmaculata* and *Oenopia conglobata*, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii.*

Source of variation	*df*	*F*	*p*
Preoviposition period	5	12.15	< 0.001
Predator	1	40.24	< 0.001
diet	2	7.40	0.001
Predator × diet	1	1.78	0.175
Error term	77		
Daily fecundity	5	66.04	< 0.001
Predator	1	62.02	< 0.001
diet	2	101.38	< 0.001
Predator × diet	2	33.27	< 0.001
Error term	77		
Total fecundity	5	81.02	< 0.001
Predator	1	108.92	< 0.001
diet	2	105.27	< 0.001
Predator × diet	2	41.71	< 0.001
Error term	77		

Table 5. Life table parameters of female *Cheilomenes sexmaculata* and *Oenopia conglobata* at 27.5°C, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii*[a].

Coccinellid species	Diet	Life table parameter[b]			
		Net reproductive rate, R_0 (females/female)	Intrinsic rate of increase, r_m (females/female/day)	Finite rate of increase, λ (females/female/day)	Doubling time, DT (days)
C. sexmaculata	*A. pistaciae*	254.9453 ± 1.3834a	0.2831 ± 0.0004b	1.3272 ± 0.0005b	2.4489 ± 0.0035e
	A. gossypii	256.8478 ± 0.5620a	0.3082 ± 0.0002a	1.3609 ± 0.0003a	2.2494 ± 0.0014f
	E. kuehniella eggs	55.3324 ± 1.0982e	0.2090 ± 0.0013c	1.2324 ± 0.0016c	3.3184 ± 0.0204d
O. conglobata	*A. pistaciae*	161.4717 ± 0.2121b	0.1824 ± 0.0001d	1.2001 ± 0.0001d	3.8003 ± 0.0011c
	A. gossypii	109.0710 ± 0.4674c	0.1796 ± 0.0003e	1.1967 ± 0.0003e	3.8595 ± 0.0057b
	E. kuehniella eggs	77.3174 ± 0.5043d	0.1587 ± 0.0003f	1.1720 ± 0.0003f	4.3680 ± 0.0079a
	F	13772.98	16637.61	17411.56	11152.13
	df	5,88	5,88	5,88	5,88
	p	< 0.001	< 0.001	< 0.001	< 0.001

[a] Data are for the first 21 days of adult life. [b] Means ± SEM within the same column followed by the same letter are statistically equivalent (Bonferoni test, α = 0.05).

other predatory insects (Cocuzza et al., 1997; Vandekerkhove & De Clercq, 2010); however, further studies are necessary to identify suitable plant material for *C. sexmaculata* and *O. conglobata*.

It is well known that the survival rate of many coccinellid species is closely associated with the quality of their diet (e.g. Michaud, 2000; Omkar & Srivastava, 2003; Zhang et al., 2012; Mehrparvar et al., 2013; Silva et al., 2013). The fact that the three food treatments in our study were from different insect taxonomic groups (and thus possibly with completely different nutritive quality), food quality did not affect immature survival of either coccinellid species. It appears that on the suboptimal diet, larvae of the two ladybird species decrease their development rate and possibly consume higher amounts of food to grow to a threshold size critical for pupation and subsequent emergence to adult (see Phoofolo et al., 2007). Thus, if the quality of food is just enough to allow growth and development to this threshold size, then all individual larvae should potentially survive to become adults despite differences in body weight (Table 1). This may be evidence of an adaptation for coping with suboptimal foods under field conditions when optimal prey is scarce.

Table 6. ANOVA of life table parameters of *Cheilomenes sexmaculata* and *Oenopia conglobata*, fed on a factitious food, *Ephestia kuehniella* eggs and two natural prey, *Agonoscena pistaciae* and *Aphis gossypii*.

Source of variation	df	F	p
r_m	5	16673.61	< 0.001
Predator	1	55346.35	< 0.001
diet	2	8511.94	< 0.001
Predator × diet	2	3336.98	0.001
Error term	83		
λ	5	17411.56	< 0.001
Predator	1	57136.46	< 0.001
diet	2	8964.40	< 0.001
Predator × diet	2	3819.22	< 0.001
Error term	83		
DT	5	11152.13	< 0.001
Predator	1	40580.15	< 0.001
diet	2	5619.10	< 0.001
Predator × diet	2	600.38	< 0.001
Error term	83		
R_0	5	13772.98	< 0.001
Predator	1	14786.52	< 0.001
diet	2	20309.28	< 0.001
Predator × diet	2	6889.68	< 0.001
Error term	83		

Based on life table data, the values for intrinsic rate of natural increase of *C. sexmaculata* were higher than those of *O. conglobata* on each diet tested. Thus, *C. sexmaculata* might be a more efficient natural enemy than *O. conglobata* when it preys on psyllids or aphids. *C. sexmaculata* showed much greater potential for increase of its population than *O. conglobata* regardless of the food they consume; however, the three diets showed major differences in their suitability. Although *A. gossypii* was the most suitable diet for *C. sexmaculata*, resulting in greater values for net reproductive rate, intrinsic rate of natural increase and finite rate of increase and the shortest doubling time, the life table parameters of *O. conglobata* were the best when it developed on *A. pistaciae*. *O. conglobata* is known to thrive principally in arboreal habitats (Hodek & Honěk, 1996). Field observations by Mehrnejad et al. (2011) showed that *O. conglobata* is one of the most abundant ladybirds among 17 species recorded from wild and cultivated pistachio trees in Southeastern Iran. This species is common on pistachio trees from April to October (Mehrnejad et al., 2011; Salehi et al., 2013); however, its oviposition behaviour is highly affected by psyllid abundance and the proportion of females laying eggs. The size of egg clutches decreases during midsummer. Females mainly prefer to remain on psyllid-infested pistachio leaves even when aphids, especially *Aphis gossypii*, are abundant on herbaceous plants such as *Alhagi* sp. and *Glycyrrhiza* sp. in and around pistachio plantation areas (Jalali, 2001; Mehrnejad et al., 2011). Although we do not know much on the food habits of *C. sexmaculata* in pistachio plantations, a 2-year field survey by Mehrnejad et al. (2011) showed that this coccinellid is much less abundant than *O. conglobata* in pistachio trees in Southeastern Iran, appearing in pistachio orchards in early July when the weather is warmer. *C. sexmaculata* is a common predatory coccinellid in warm and humid climate zones such as Far Eastern and south Asian countries (Agarwala & Ghosh, 1988) and apparently is a stenotopic species, preferring herbaceous plants. This ladybird was introduced into North America to help control the green bug, *Schizaphis graminum* (Rondani), on cereals (Cartwright et al., 1977). Prey preference studies suggested that the cowpea aphid, *Aphis craccivora* Koch on bean plants is one of the most suitable hosts of this predaceous coccinellid (see Agarwala et al., 2001 for a review). Thus, the arboreal *O. conglobata* seems to be better adapted than *C. sexmaculata* to psyllid prey on pistachio, possibly because it evolved for a much longer period of time with this prey in pistachio habitats. The longer development time and lower fecundity of *C. sexmaculata* reared on psyllids is probably indicative of its poor palatability or poor quality over an aphid diet. It might also suggest the possible presence of some allelochemicals in the pistachio plant that make this prey unsuitable for *C. sexmaculata*. In other coccinellids, it is known that allelochemicals and secondary metabolites of host plants can make prey less suitable and decrease fecundity (Francis et al., 2001), and long-term coevolution between predators and prey can lead to the development of better adapted strategies for optimal use of a specific prey (Abrams, 1986; Albuquerque et al., 1997; Berthiaume et al., 2007).

In conclusion, *E. kuehniella* eggs were a much better diet for development than for reproduction in both predators, which suggests that suitability should be assessed independently for larval development and adult reproduction because of potentially divergent nutritional requirements between these life stages. We hypothesize that the arboreal *O. conglobata* should be better adapted to *A. pistaciae* on pistachio trees than *C. sexmaculata*, which evolved in close association with aphids on herbaceous plants. Although *C. sexmaculata* demonstrated a much higher intrinsic population growth potential than the other ladybird beetle, the stenotopic habit of arboreal specialists like *O. conglobata*, coupled with its tendency to remain in pistachio trees even with excess food on herbaceous plants, may make it a good biocontrol agent for some pistachio pests including *A. pistaciae*.

ACKNOWLEDGEMENTS. The authors thank W. Jones for a critical review of this manuscript, and M. Ziaaddini for statistical consultation. We are grateful to two anonymous reviewers whose comments improved the manuscript and to the Department of Plant Protection, Vali-e-Asr University of Rafsanjan the use of greenhouse facilities.

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Received August 14, 2014; revised and accepted February 18, 2015