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# Does feeding on pollen grains affect the performance of *Amblyseius swirskii* (Acari: Phytoseiidae) during subsequent generations?

Alireza Nemati[1,2] and Elham Riahi[1]

[1]Department of Plant Protection, Faculty of Agriculture, Shahrekord University, Shahrekord, Iran and
[2]Biotechnology Research Institute, Shahrekord University, Shahrekord, Iran

**Research Paper**

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**Author for correspondence:**
Alireza Nemati,
Email: Alireza.nemat@ymail.com

## Abstract

Diet is a critical component of the mass-rearing of biological control agents, but the impacts of diet are not always immediately obvious and can take several generations to manifest, resulting in poor survival, reproduction, and ability to kill prey under natural conditions. Our present study aimed to investigate the performance of a commercially-reared phytoseiid mite, *Amblyseius swirskii*, after four (G4) and six (G6) consecutive generations on pollen grains of two plant species, as well as its ability to find and kill its natural prey, *Tetranychus urticae*, after long-term rearing on each diet. We found no significant difference between the two diets in intrinsic and finite rates in G4. However, both diet and generation exerted a significant influence on the fecundity of *A. swirskii*. By G6, females reared on almond pollen had greater net reproductive and intrinsic rate compared to those reared on maize pollen. Conversely, *A. swirskii* fed on maize pollen consumed fewer prey than those reared on other diets, especially at higher prey densities. The findings have important implications for developing the mass-rearing program of *A. swirskii* on non-prey diets. Further research must explore the suitability of almond pollen in the large-scale culture of *A. swirskii*.

## Introduction

The mass-rearing of predatory biological control agents on their natural prey presents several logistical problems related to the maintenance of three trophic levels: the predator, their prey, and the prey's host plant. Each of these components requires considerable resources, hence significant savings can be found if the prey and plants are not required. One such system is that of phytoseiid mites, which are effective, commercially-reared predators of various insects and mites.

Phytoseiid mites are almost all predatory, yet not all species require prey to complete their life cycle. One such species is *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae). As a type III predator (McMurtry *et al.*, 2013), it is a generalist feeding on whiteflies, thrips, mites, and pollen. The species completes development and reproduction on natural prey (El-Laithy and Fowly, 1992), but also other foods such as pollen (Riahi *et al.*, 2016, 2017*a*; Khanamani *et al.*, 2017), factitious prey (Riahi *et al.*, 2017*b*), and artificial diets (Riahi *et al.*, 2017*c*, 2018). Non-natural prey (pollen and artificial diets) are also advantageous over natural prey because they are not prone to respiratory problems created when the stored-product mites *Carpoglyphus lactis* L. and *Thyreophagus entomophagus* (Laboulbene) are used for mass production of *A. swirskii* (Bolckmans and van Houten, 2006; Fidgett and Stinson, 2008). Thus, *A. swirskii* has become an important commercially-reared predator due to its ability to be reared on cost-effective diets.

Life table parameters, such as developmental rates, survival, and fecundity, are widely used to evaluate the impact of various factors on the success of predatory mites, including diet. The impact of diet on life table parameters is not necessarily obvious within one generation and may manifest over several generations, thus affecting the long-term quality of mass-reared biocontrol agents (Nguyen *et al.*, 2014). In addition to life table parameters, it is also important to assess the foraging behavior of a commercially-reared biocontrol agent, prior to their release (Fathipour and Maleknia, 2016). In this regard, functional and numerical responses are commonly measured traits. Although different kinds of functional response curves are recorded for phytoseiid mites, most are classified as type II (e.g., Shipp and Whitfield, 1991; Fan and Petit, 1994; Fathipour *et al.*, 2017).

Riahi *et al.* (2017*b*) found that *A. swirskii* individuals survived and reproduced on almond and maize pollen better than on factitious prey or even natural prey (*Tetranychus urticae* Koch). Therefore, they concluded that almond or maize pollen were the best diets for the mass-rearing *A. swirskii*. However, prior to applying this commercially, three aspects must be explored. Firstly, the pollen-only diet must produce continuous generations of high quality

(Cohen, 2004). Secondly, the predator should be able to effectively detect, capture, and kill its prey after long-term rearing (Grenier and De Clercq, 2003). Finally, any potential nutrient imbalances must be explored, which potentially express themselves as a decline in life table parameters over multiple generations (De Clercq *et al.*, 2005). Therefore, we investigate the multigenerational impact of both almond and maize pollen diets on *A. swirskii* reared for four and six consecutive generations, testing for possible declines in developmental, reproductive, and prey-capture performance.

## Material and methods

### Mite cultures

To raise the spider mite *T. urticae*, the natural prey of *A. swirskii*, bean seeds (*Phaseolus vulgaris* L. var. Khomein) were planted in pots and were kept at 25 ± 5°C, 65 ± 10% RH, under natural light in a greenhouse. The initial population of spider mites was collected from an infested cucumber greenhouse in the Esfahan region (Esfahan, Iran), which had never been exposed to pesticides and/or acaricides.

The predatory mite *A. swirskii* was first acquired from Koppert Biological System (Swirski-Mite Plus®) in 2015 and then was cultured in a growth chamber set at 25 ± 1°C and 65 ± 10% RH, as well as a photoperiod of 16L:8D. To culture the mites, a foam pad was placed in a plastic rectangular dish filled with water. A green plastic sheet was put on the pad and its edges were covered with tissue paper strips. Some sewing threads were located on the plastic sheet serving as both oviposition substrate and shelter. Every 2 days, bean leaves severely infested with spider mites were added on the sheet. The study was conducted in 2018–2019 in the laboratory of the Entomology, Faculty of Agriculture, Shahrekord University, Iran.

### Pollen collection

Corn (*Zea mays* L. var. Single-cross 301) seeds were acquired from the Agricultural and Natural Resources Research Center, Chaharmahal & Bakhtiari, Iran, and were cultivated in an experimental field located in the campus of Shahrekord University. A uniform area was selected, with well-drained soils (clay loam), and fertilized with 50-60-30 N-P2O5-K2O kg $ha^{-1}$ before cultivation. Two to three weeks after sowing, urea (200 kg $ha^{-1}$) was applied as a top-dressing fertilizer, and the soil was hilled up. After collecting their anthers, the pollen was gathered by drying and shaking them at room temperature. Almond (*Prunus dulcis* (Mill.) D.A. Webb) pollen was separated by brushing the blooms collected from a garden at Saman city. Pollen was kept in a refrigerator during the experimental periods.

### Multi-generation rearing

Twelve hours before initiating the long-term mass-rearing of *A. swirskii* on two species of pollen grains, several new threads were put in the original culture of the predator. Then, the threads were transmitted to the new experimental units which were similar to the stock colonies while with a smaller size. Next, the relevant pollen grains were added to each unit *ad libitum* after the eggs hatched, which continued in each of the 10 replicates for each pollen type for up to six generations. Additionally, the eggs from females of the third and fifth generations were collected for the experiments to evaluate the performance of *A. swirskii* in the fourth (G4) and sixth (G6) generations. Furthermore, the units were refreshed every 4 days to provide fresh pollen while avoiding contamination with fungi.

### Life table experiments

The population growth parameters of *A. swirskii* were determined after three and five generations of rearing on almond and maize pollen. The experiments were performed at 25 ± 1°C and 65 ± 10% RH and a photoperiod of 16L:8D h. Eggs deposited from the females of the third and fifth generations were transferred individually to the experimental units. The predators were offered the respective pollen after the emergence of larvae. The experimental units were monitored twice per day and the development time of life stages and their survival were noted. After the emergence of adults, each female was coupled with a male and transferred to a new experimental unit and supplied with the same diet on which they were reared formerly. To obtain data on adult longevity, fecundity, and survival, observations were performed daily until the end of experiments.

The data were analyzed using the age-stage two-sex life table method (Chi and Liu, 1985; Chi, 1988). All parameters including age-stage-specific survival rate ($s_{xj}$), age-stage-specific fecundity ($f_{xj}$) of females, age-specific survival rate ($l_x$), age-specific fecundity ($m_x$), as well as population growth parameters [intrinsic rate of increase ($r$), finite rate of increase (λ), net reproductive rate ($R_0$), gross reproductive rate (GRR), and mean generation time ($T$)] were estimated using TWOSEX-MS Chart (Chi, 2016). The standard errors of all parameters were calculated using the bootstrap technique with 40,000 bootstraps (Riahi *et al.*, 2016, 2017*a*; Khanamani *et al.*, 2017). Further, a two-way analysis of variance was performed to evaluate the effects of the diet and generation on all parameters. All the mean comparisons were implemented by the paired bootstrap test based on the confidence interval.

### Functional response experiments

The functional response was designed to investigate the invasion ability of the mass-reared predators on pollen diets (maize pollen: strain M and almond pollen: strain A) against the natural prey (*T. urticae*). The results were compared with the data of those who were reared on *T. urticae* (strain T). The experimental units for functional response studies were a plastic petri dish (with a diameter of 8 cm and a height of 1.5 cm) containing a circular bean leaf (with a diameter of 3 cm). Then, each bean leaf was placed on a cotton layer soaked with water. Additionally, seven different densities (i.e., 2, 4, 8, 16, 32, 64, and 128) of *T. urticae* nymphs and eight replicates for each density were conducted to record their functional response. One predator (48–72 h old) was introduced per leaf disc immediately after spreading the prey on a bean leaf and the number of the consumed prey was counted after 24 h. These experiments were conducted in the same conditions as the life table experiments (i.e., at 25 ± 1°C and 65 ± 10% RH and a photoperiod of 16L:8D h).

The type of functional response was determined using a polynomial function presented in Juliano (2001). Further, to estimate the functional response parameters including the handling time ($T_h$) and attack rate ($a$), Rogers' (1972) random predator equation was employed for type II functional responses using the SAS software (SAS Institute, Cary, NC, USA). Furthermore, the general linear model was conducted utilizing the SPSS software, version

**Table 1.** Different life stage duration, development time, and adult longevity (mean ± SE, in days) of *Amblyseius swirskii* fed in the fourth (G4) and sixth (G6) generations on two pollen diets

| | Diet/generation | | | |
|---|---|---|---|---|
| Parameter | Almond pollen/G4 | Almond pollen/G6 | Maize pollen/G4 | Maize pollen/G6 |
| Egg (d) | 2.03 ± 0.05 b | 2.02 ± 0.04 b | 2.21 ± 0.07 a | 2.24 ± 0.08 a |
| Larva (d) | 1.09 ± 0.05 a | 1.07 ± 0.04 a | 1.00 ± 0.00 a | 1.00 ± 0.00 a |
| Protonymph (d) | 2.03 ± 0.08 a | 2.02 ± 0.07 a | 1.97 ± 0.08 b | 2.13 ± 0.09 a |
| Deutonymph (d) | 1.62 ± 0.09 b | 1.35 ± 0.08 c | 1.59 ± 0.08 b | 1.81 ± 0.07 a |
| Pre-adult (d) | 6.75 ± 0.11 b | 6.46 ± 0.11 c | 6.76 ± 0.12 b | 7.16 ± 0.15 a |
| Female adult longevity (d) | 59.45 ± 4.10 b | 61.85 ± 3.79 b | 65.67 ± 4.73 a | 65.40 ± 5.60 a |
| Male adult longevity (d) | 32.90 ± 3.66 d | 40.92 ± 3.53 c | 53.54 ± 3.34 a | 48.68 ± 2.47 b |

The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same row are significantly different ($P < 0.05$, paired-bootstrap test).

**Table 2.** Reproduction and reproductive periods (mean ± SE) of *Amblyseius swirskii* in the fourth (G4) and sixth (G6) generations on two pollen diets

| | Diet/generation | | | |
|---|---|---|---|---|
| Parameter | Almond pollen/G4 | Almond pollen/G6 | Maize pollen/G4 | Maize pollen/G6 |
| APOP (d) | 1.68 ± 0.14 b | 1.50 ± 0.11 b | 2.25 ± 0.14 a | 2.40 ± 0.10 a |
| Oviposition period (d) | 23.00 ± 1.16 b | 25.96 ± 1.27 a | 22.04 ± 1.46 b | 18.32 ± 0.85 c |
| TPOP (d) | 8.50 ± 0.19 c | 8.19 ± 0.18 d | 9.21 ± 0.26 b | 9.84 ± 0.17 a |
| Fecundity (eggs/female) | 41.91 ± 2.17 b | 46.85 ± 2.18 a | 36.35 ± 2.03 c | 31.40 ± 1.30 d |

APOP, adult preovipositional period; TPOP, total preovipositional period (from egg to first oviposition).
The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same row are significantly different ($P < 0.05$, paired-bootstrap test).

22, to analyze prey consumption. Eventually, the pairwise multiple comparison procedures were performed using the Tukey test since the interaction between the main factors (i.e., the predator strain and prey density) was significant ($P < 0.05$).

## Results

### Life history traits

The developmental time of *A. swirskii* did not differ between the diets in G4, but was significantly faster on almond pollen compared to maize pollen by G6 (table 1). Additionally, on both types of pollen, the pre-adult duration of the sixth generation was significantly faster than the fourth generation. There was no interaction among the main factors affecting developmental time ($F = 3.359$, df = 1, $P = 0.069$). Females and males reared on maize pollen lived significantly longer compared to those reared on almond pollen in both the fourth and sixth generations (table 1). Regarding female and male adult longevity, there was no interaction between diet and generation (female: $F = 0.140$, df = 1, $P = 0.710$; male: $F = 3.878$, df = 1, $P = 0.057$).

Generation had no effect on life span for females (table 1). The impact of generation was less clear on males, differing depending on diet. Males raised on almond pollen had significantly longer lives in the G6 generation, but those raised on maize pollen had significantly shorter lives in the G6 generation.

Despite similar longevity, females reared on almond pollen laid significantly more eggs than those reared on maize pollen, and also had a shorter pre-ovipositional period (table 2). A similar trend was found in pre-oviposition periods (APOP, TPOP; table 2), as indicated by the significant interaction between the main factors (APOP: $F = 72.823$, df = 1, $P < 0.0001$; TPOP: $F = 5.495$, df = 1, $P = 0.021$; Fecundity: $F = 99.832$, df = 1, $P < 0.0001$).

Generation also exerted a significant influence on the fecundity of *A. swirskii*. By G6, females reared on almond pollen had significantly longer ovipositional periods, and also greater fecundity, while those reared on maize pollen had significantly shorter ovipositional periods and significantly lower fecundity (table 2).

### Survival and fecundity curves

On almond pollen, the highest survival rate of females (0.634) and males (0.292) in G6 was higher than that of G4 (i.e., 0.579 and 0.263, respectively) (fig. 1). However, when maize pollen was offered, the survival rate of females and males was highest in G6 and G4, respectively.

The maximal value of $m_x$ was 1.719 eggs individual$^{-1}$ day$^{-1}$ (on almond pollen/G4), 1.595 (on maize pollen/G4), 1.710 (on almond pollen/G6), and 1.968 (on maize pollen/G6) (fig. 2). Finally, the overlap among different stages of the survival rates cannot be perceived in the age-specific survivorship ($l_x$) curves (fig. 2) compared to $s_{xj}$ curves (fig. 1).

### Population growth parameters

The population growth parameters are influenced by both diet and generation (table 3). In both generations, the individuals reared on almond pollen demonstrated significantly higher

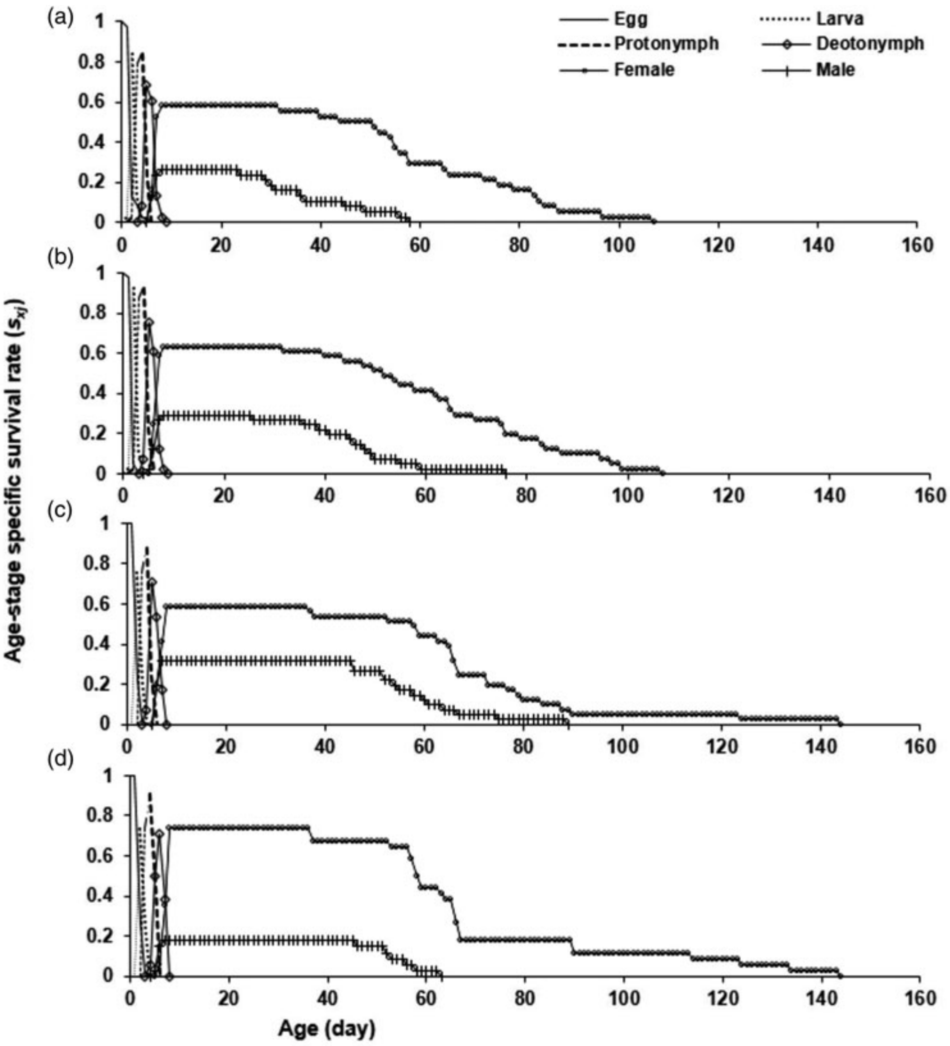

**Figure 1.** Age-stage-specific survival rate ($s_{xj}$) of *Amblyseius swirskii* in the fourth (G4) and sixth (G6) generations on two pollen diets. (a) Almond pollen/G4. (b) Almond pollen/G6. (c) Maize pollen/G4. (d) Maize pollen/G6.

gross and net reproductive rate. As regards net reproductive rate, females fed on almond pollen had significantly higher $R_0$ values in G4 compared with those raised on maize pollen. Furthermore, the intrinsic ($r$) and finite ($\lambda$) rates of increase in G6 were significantly higher compared to G4, but on a diet of maize pollen, similar growth rates were observed in both generations (table 3).

### *Functional response*

Based on the results, a type II functional response (i.e., a curvilinear rise) to *T. urticae* nymphs was revealed for all the tested strains (table 4 and fig. 3). Additionally, the linear coefficient was negative on three strains approaching a plateau at higher prey densities (fig. 3). The maximum attack rate ($T/T_h$, 59.524 prey day$^{-1}$) and the minimum handling time (0.4032 h) were observed for the mites reared on almond pollen (strain A) (table 5). In addition, the attack rate ($a$) of the individuals reared on *T. urticae* (strain T) was higher than on almond pollen and the latter was itself higher than on maize pollen (strain M).

The interaction between the main factors, namely, *T. urticae* density and *A. swirskii* strain, is significant for mean prey consumption (table 6). As shown, no difference was observed between the mean number of the prey consumed for the mites reared on almond pollen (strain A) and *T. urticae* (strain T) at all prey densities (table 7). Eventually, *A. swirskii* fed on maize pollen (strain M) consumed fewer numbers of *T. urticae* nymphs per day compared to A and T strains, particularly at higher prey densities.

## Discussion

In the present study, the potential of two alternative pollen-only diets was in respect to the development and the reproduction of *A. swirskii* during six generations of rearing. Additionally, the effects of long-term rearing on these diets on the prey-capture ability of the predator were evaluated, finding that mites reared on almond pollen were just as effective as mites reared on a diet of natural prey. These results are relevant because the quality of the laboratory-reared organisms over time is highly significant for the mass production of biocontrol agents. Furthermore, pollen is a significantly cheaper food, thus reducing the costs of rearing these biocontrol agents.

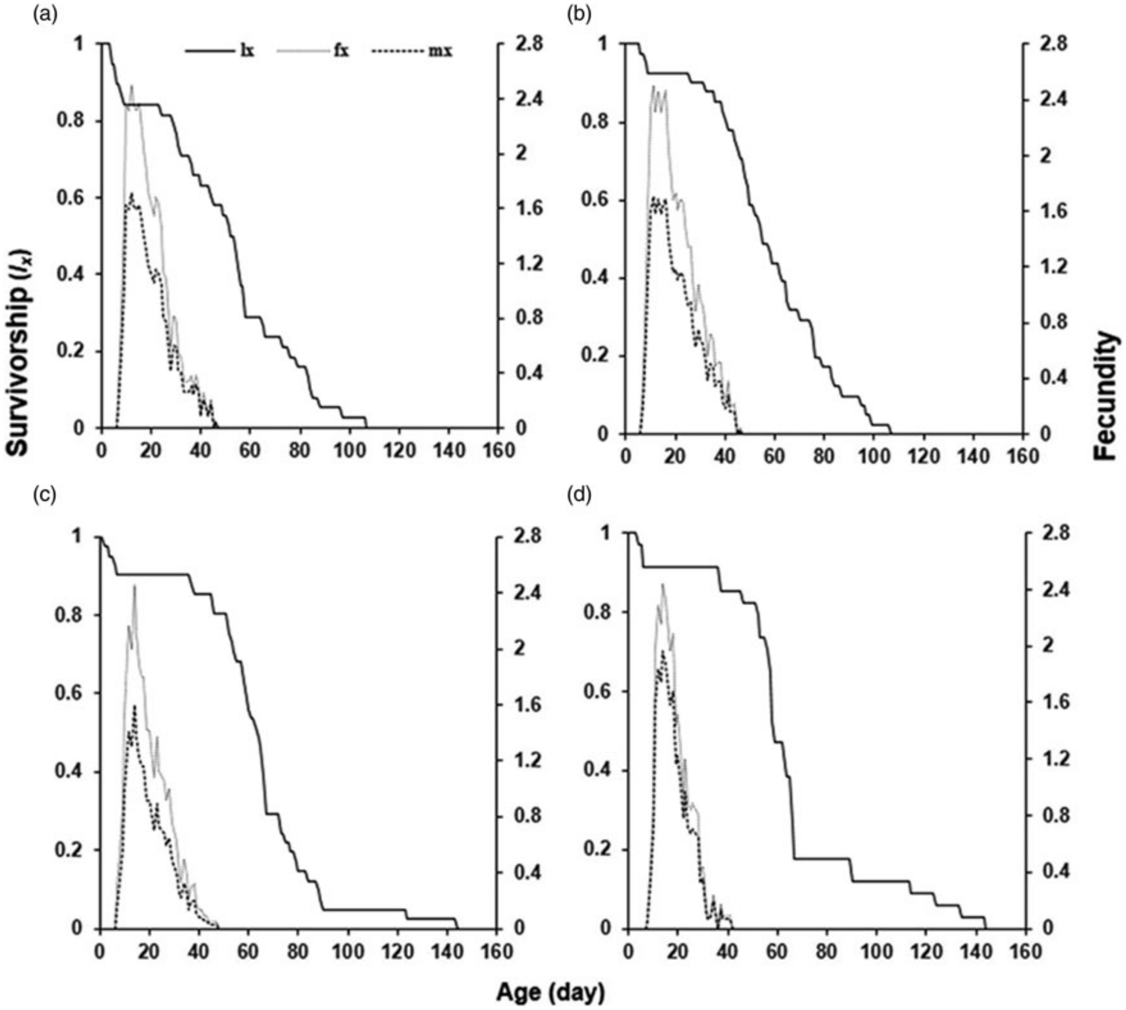

**Figure 2.** Age-specific survivorship ($l_x$), age-stage fecundity of female ($f_{x5}$), and age-specific fecundity ($m_x$) of *Amblyseius swirskii* in the fourth (G4) and sixth (G6) generations on two pollen diets. (a) Almond pollen/G4. (b) Almond pollen/G6. (c) Maize pollen/G4. (d) Maize pollen/G6.

**Table 3.** Population growth parameters (mean ± SE) of *Amblyseius swirskii* in the fourth (G4) and sixth (G6) generations on two pollen diets

| Diet/generation | GRR (offspring/individual) | $R_0$ (offspring/individual) | $r$ ($d^{-1}$) | $\lambda$ ($d^{-1}$) | $T$ (d) |
|---|---|---|---|---|---|
| Almond pollen/G4 | 29.65 ± 2.28 a | 24.26 ± 2.21 a | 0.1995 ± 0.0069 b | 1.2207 ± 0.0084 b | 15.99 ± 0.20 b |
| Almond pollen/G6 | 32.50 ± 2.44 a | 22.71 ± 2.41 ab | 0.2107 ± 0.00622 a | 1.2345 ± 0.0077 a | 16.98 ± 0.19 b |
| Maize pollen/G4 | 23.56 ± 1.99 b | 21.22 ± 1.92 b | 0.1833 ± 0.00654 b | 1.2012 ± 0.0078 b | 16.66 ± 0.19 a |
| Maize pollen/G6 | 25.35 ± 1.44 b | 23.09 ± 1.49 b | 0.1884 ± 0.0045 b | 1.2073 ± 0.0054 b | 16.66 ± 0.14 a |

The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same column are significantly different between diets using the paired bootstrap test ($P < 0.05$). (GRR: gross reproductive rate; $R_0$: net reproductive rate; $r$: intrinsic rate of increase; λ: finite rate of increase; $T$: mean generation time).

Both the pre-adult development and total pre-oviposition period on almond pollen were significantly shorter and the fecundity was higher in G6 compared to the maize pollen in G4 (tables 1, 2). These reductions and increases exerted an influence on the intrinsic rate of increase in G6. Furthermore, the performance of the predator remained constant across the generations on maize pollen. More importantly, the population growth parameters on almond pollen in G4 and G6 in the current study were superior to those in G1 by Riahi *et al.* (2017*a*, 2017*b*), indicating a trend of improved performance over generations.

This trend was also found by Nguyen *et al.* (2014), who assessed the fitness of *A. swirskii* on different factitious prey and artificial diets in the subsequent generations. Among the tested diets, only cysts of *Artemia franciscana* Kellogg led to an increase in the performance of the predator over the six generations. In addition, the demographic parameters of *A. swirskii* fed on almond pollen in both G4 and G6 (table 3) was better than previous results, whether it be natural prey (El-Laithy and Fouly, 1992; Riahi *et al.*, 2017*b*), different insects (Nomikou *et al.*, 2001; Wimmer *et al.*, 2008), factitious prey (Nguyen

**Table 4.** Maximum-likelihood estimates from logistic regression of the proportion of *Tetranychus urticae* nymphs consumed by different strains of *Amblyseius swirskii* as a function of initial prey density

| Strain | Parameter | Estimate (±SE) | $\chi^2$ | *P* |
|---|---|---|---|---|
| T | $P_0$ | $1.4834 \pm 0.3158$ | 22.07 | <0.0001 |
| | $P_1$ | $-0.0245 \pm 0.0235$ | 1.09 | 0.2969 |
| | $P_2$ | $-0.00006 \pm 0.000441$ | 0.02 | 0.8962 |
| | $P_3$ | $8.808 \times 10^{-7} \pm 2.168 \times 10^{-6}$ | 0.17 | 0.6846 |
| A | $P_0$ | $1.0130 \pm 0.2898$ | 12.22 | 0.0005 |
| | $P_1$ | $-0.00649 \pm 0.0221$ | 0.09 | 0.7688 |
| | $P_2$ | $-0.00032 \pm 0.000419$ | 0.57 | 0.4512 |
| | $P_3$ | $2.067 \times 10^{-6} \pm 2.07 \times 10^{-6}$ | 1.00 | 0.3179 |
| M | $P_0$ | $-0.1509 \pm 0.2640$ | 0.33 | 0.5676 |
| | $P_1$ | $-0.00783 \pm 0.0207$ | 0.14 | 0.7059 |
| | $P_2$ | $6.429 \times 10^{-6} \pm 0.000399$ | 0.00 | 0.9872 |
| | $P_3$ | $-1.33 \times 10^{-7} \pm 1.988 \times 10^{-6}$ | 0.00 | 0.9468 |

Strain A: the mass-reared predator on the almond pollen; strain T: the mass-reared predator on *T. urticae*; strain M: the mass-reared predator on the maize pollen.

*et al.*, 2013), or various artificial diets (Nguyen *et al.*, 2015; Riahi *et al.*, 2017*c*). As a result, almond pollen is considered the most suitable diet for the rearing of *A. swirskii*.

The most important contributing factors influencing the functional response of predators are pesticides, the characteristics of the plant, the stage of the prey, the age of the predator, humidity, and diet (Castagnoli and Simoni, 1999; Poletti *et al.*, 2007; Ahn *et al.*, 2010; Farazmand *et al.*, 2012; Khanamani *et al.*, 2017). A type II functional response to *T. urticae* nymphs was recognized for all the three mass-produced predator strains (table 4), which corroborate with the findings of a great number of previous studies in this field (e.g., Xiao *et al.*, 2013; Fathipour *et al.*, 2017). Further, *A. swirskii* of strain M (i.e., mass-reared on maize pollen) and A (i.e., mass-reared on almond pollen) spent the longest and the shortest amount of the handling time to consume the prey, respectively (table 5). In other words, the individuals of strain A allocated a shorter time to non-searching activities (e.g., resting) compared to strains M and T, which resulted in an increased predation rate. Furthermore, the values of $a$ and $T_h$ reported by Fathipour *et al.* (2017) represented lower attack rates and handling times of *A. swirskii* on *T. urticae* compared to the data obtained by the present study. These differences may be due to the dissimilation in the applied prey stages, the nutritional history of the predator, and the host plant used for *T. urticae* rearing. Additionally, Khanamani *et al.* (2017) evaluated the attack rate and handling time values of *Neoseiulus californicus* McGregor females after 20 generations of mass-rearing on almond pollen and *T. urticae*. Their $a$ and $T_h$ values were higher and lower, respectively, compared to the results of the current study regarding the corresponding values on similar prey stages.

Although the mass-rearing of a biocontrol agent on foods other than the prey has various advantages, sustaining the ability to find and kill the target prey is vital (Grenier and De Clercq, 2003). Considering the results of the present study, *A. swirskii* maintains its ability to find, seize, and kill its natural prey (i.e., *T. urticae*) after the six generations of rearing on almond and maize pollen. These findings are consistent with the results of other studies that reported successful predation ability of phytoseiid mites after multiple generations of rearing on different

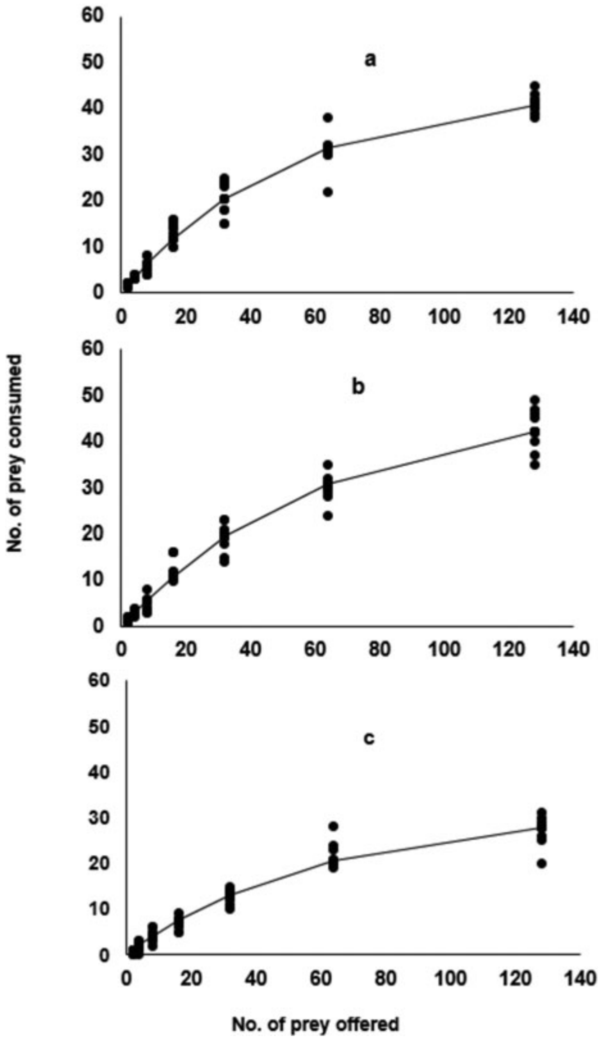

**Figure 3.** The functional response (type II) of *Amblyseius swirskii* from three strains (T, A, and M) on different densities of *Tetranychus urticae*. (a) Strain A: the mass-reared predator on the almond pollen. (b) Strain T: the mass-reared predator on *T. urticae*. (c) Strain M: the mass-reared predator on the maize pollen.

**Table 5.** Estimate (±SE) of instantaneous attack rate and handling time of three strains of *Amblyseius swirskii* on nymphs of *Tetranychus urticae* using the Rogers type II model

| Strain | Type | $a$ ($h^{-1}$) | $T_h$ (h) | $T/T_h$ (prey/day) | $R^2$ |
|---|---|---|---|---|---|
| T | II | 0.0330 ± 0.00291 | 0.4545 ± 0.0223 | 52.8052 | 0.95 |
| A | II | 0.0572 ± 0.0055 | 0.4032 ± 0.0247 | 59.5238 | 0.96 |
| M | II | 0.0700 ± 0.0068 | 0.5999 ± 0.0383 | 40.0067 | 0.90 |

($a$) Attack rate, $T_h$; handling time, $T/T_h$; maximum attack rate, $R^2$ = [1–(residual sum of squares/corrected total sum of squares)]. Strain A: the mass-reared predator on the almond pollen; strain T: the mass-reared predator on *T. urticae*; strain M: the mass-reared predator on the maize pollen.

**Table 6.** General linear model indicating the effect of strains (either the mass-reared predator on the almond pollen or *T. urticae* or the maize pollen) and prey densities (2, 4, 8, 16, 32, 64, 128) on prey consumption of *Amblyseius swirskii*

| Source | Sum of squares | Df | Mean square | $F$ | $P$- value |
|---|---|---|---|---|---|
| Strain | 1213.726 | 2 | 606.863 | 93.047 | <0.001 |
| Density | 26,517.226 | 6 | 4419.538 | 677.624 | <0.001 |
| Strain × density | 852.274 | 12 | 71.023 | 10.890 | <0.001 |
| Error | 958.70 | 147 | | | |
| Total | 64,922.00 | 168 | | | |

**Table 7.** Daily consumption (mean ± SE) of *Tetranychus urticae* nymphs by three strains of *Amblyseius swirskii* at different prey densities

| Prey density | Strain | | |
|---|---|---|---|
| | T | A | M |
| 2 | 1.50 ± 0.19 fg | 1.38 ± 0.18 fg | 0.50 ± 0.19 g |
| 4 | 3.36 ± 0.18 efg | 3.13 ± 0.23 efg | 1.88 ± 0.35 fg |
| 8 | 5.36 ± 0.59 ef | 4.63 ± 0.60 efg | 4.13 ± 0.52 efg |
| 16 | 13.50 ± 0.85 d | 13.00 ± 0.91 d | 6.88 ± 0.52 e |
| 32 | 20.25 ± 1.49 c | 19.25 ± 1.19 c | 12.63 ± 0.60 d |
| 64 | 30.75 ± 1.54 b | 29.88 ± 1.13 b | 21.88 ± 1.06 c |
| 128 | 41.13 ± 1.81 a | 42.63 ± 1.76 a | 27.13 ± 1.23 b |

The means followed by different letters in the table are significantly different ($P < 0.01$, Tukey test after 3 × 7 factorial design with the general linear model; factor 1: the strain of predator with three levels; factor 2: prey density with seven levels).
Strain A: the mass-reared predator on the almond pollen; strain T: the mass-reared predator on *T. urticae*; strain M: the mass-reared predator on the maize pollen.

food diets (e.g., Nguyen *et al*., 2014; Khanamani *et al*., 2017). Furthermore, the results of the current study showed that the daily predation rate of *A. swirskii* mass-reared on maize pollen was considerably lower compared to natural prey and almond pollen diets, which may be due to the longer handling time and the lower attack rate estimated by the model (tables 5, 7). Furthermore, the individuals of strains A and T consumed the same number of prey during the period of 24 h at different prey densities. In other studies, Khanamani *et al.* (2017) found that the predation rate of *N. californicus* was the same between individuals mass-reared on almond pollen and *T. urticae* at lower prey densities. Nguyen *et al.* (2014), who explored predation rates of *A. swirskii* on immature *Frankliniella occidentalis* (Pergande) reared on five different diets over six generations, found that most diets had no effect. The exception was *Ephestia kuehniella* Zeller eggs, where females of the first generation killed more prey compared to the sixth generation.

In conclusion, we showed that *A. swirskii* successfully develops and reproduces on almond pollen, with increased performance over generations in several parameters. In contrast, maize pollen is a poor diet for mass-rearing of *A. swirskii*, with decreased performance over generations. More surprisingly, mites reared on almond pollen were equivalent or even better than mites reared on natural prey. This finding has important implications for developing the mass-rearing program of *A. swirskii* on non-prey food items. However, more studies are needed regarding evaluating the suitability of the almond pollen in the large-scale cultures of *A. swirskii*. Finally, other studies concerning the effects of long-term rearing (beyond ten generations) of *A. swirskii* on almond pollen are subject to further investigation.

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