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Long-term effects of cattail *Typha latifolia* pollen on development, reproduction, and predation capacity of *Neoseiulus cucumeris*, a predator of *Tetranychus urticae*

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Abstract The effects of cattail *Typha latifolia* L. pollen on development and reproduction of *Neoseiulus cucumeris* (Oudemans) was determined over 25 consecutive generations (G). The ability of *N. cucumeris* to locate, capture, and consume natural prey *Tetranychus urticae* (Koch) was assessed after the 10th generation (G10-switch) and the 20th generation (G20-switch). Results indicated that *T. latifolia* pollen had no effect on *N. cucumeris* development time between G1 and G25. *N. cucumeris* fecundity was significantly greater in the older than younger generations. Life table analysis revealed that net reproductive rate (R_0) was significantly higher for *N. cucumeris* fed *T. latifolia* at G10. Feeding on *T. latifolia* from G1-G5 resulted in lower intrinsic (r) and finite (λ) rates of increase. Feeding at G10 resulted in higher population growth rates. When switched to a diet of *T. urticae*, *N. cucumeris* immature development and fecundity were not significantly affected by generation. However, the values of r, gross reproductive rate (*GRR*), and λ were higher at the G20-switch than the G10-switch. Our results demonstrate that a diet of *T. latifolia* pollen supports *N. cucumeris* development and reproduction for 25 consecutive generations without reducing predation capacity. *T. latifolia* pollen is a suitable diet for long-term rearing of *N. cucumeris* for augmentative biological control of tetranychid mites.

Keywords Augmentative biological control · Mass rearing · Phytoseiidae · Population growth · Tetranychidae · *Tetranychus urticae*

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Introduction

Mass rearing of natural enemies is the foundation of augmentative biological control to reduce pest populations in agroecosystems around the world (van Lenteren 2012; Leppla et al. 2014). Augmentative biological control is considered as an environmentally safe alternative to chemical pest control (van Lenteren 2006; Leppla et al. 2014). Augmentative biological control often deploys natural enemies belonging to the family Phytoseiidae to control tetranychid mites and related arthropods, such as thrips and whiteflies (Fathipour and Maleknia 2016). One of the obstacles to efficient mass rearing of phytoseiids is the need to rear their prey, which requires culturing host plants.

This procedure can be costly because it involves rearing two species while only one of these is profitable (Driesche and Bellows 1996; Riddick and Chen, 2014). Similarly, the expense of providing factitious prey, e.g., storage mites (*Carpoglyphus lactis* L. and *Thyreophagus entomophagus* (Laboulbéne)), is high because of the need for both rearing space and labor costs. For the commercial viability of phytoseiid rearing operations, a cost-effective method of long-term rearing is a prerequisite (Grenier and De Clercq 2003). The availability of a suitable non-prey diet that is convenient and cheaper than natural prey could lead to cost effective mass rearing of phytoseiids.

Plant pollen is one of the non-prey food sources that might be used to increase predation of herbivores, thereby reducing herbivory on crop plants (Rijn et al. 2002; Lundgren 2009). The developmental and reproductive responses of phytoseiids to pollen vary significantly among plant and mite species (Goleva and Zebitz 2013; Ranabhat et al. 2014; Riahi et al. 2016). A list of phytoseiids that produce more progeny on pollen than prey has been compiled (McMurtry and Rodriguez 1987). Moreover, some phytoseiids survive longer and produce more progeny on pollen than natural or factitious prey (Riahi et al. 2016; Khanamani et al. 2017a). Therefore, mass production of phytoseiids can be cost effective when utilizing pollen resources.

Among the several high quality plant pollen species, only one product NutrimiteTM (Biobest N.V., Westerlo, Belgium), which is based on the narrow-leaved cattail (*Typha angustifolia* L.), is commercially available. This product has been recommended as an alternate food to support generalist phytoseiid populations in crop fields and greenhouses (Samaras et al. 2015). Both *T. angustifolia* and *Typha latifolia* L. can improve phytoseiid performance (Broufas and Koveos 2000; Goleva and Zebitz 2013; Vangansbeke et al. 2014). *Typha* species are anemophilous and produce high quantities of light-weight pollen grains (Samaras et al. 2015). Compared to other plant pollen species, i.e., mostly entomophilous species, *Typha* species are less expensive and less labor-intensive to collect (Goleva and Zebitz 2013). Although *Typha* species seem to be a promising candidate for mass rearing of generalist phytoseiids, there is little published information on the long-term mass rearing of different phytoseiids on this pollen.

Neoseiulus cucumeris (Oudemans), a generalist phytoseiid, is classified as a type III predator (McMurtry et al. 2013). It has a high potential for use in greenhouse crop pest management programs (van Driesche et al. 1998; Sarwar 2019). There is considerable interest in using *N. cucumeris* because it is widely distributed, easy to rear, highly mobile, and adaptable to integrated pest management programs (Ranabhat et al. 2014). Although it has been reported that pollen diets can affect development and reproductive success of *N. cucumeris* (Rijn and Tanigoshi 1999; Ranabhat et al. 2014; Yazdanpanah et al. 2021a, b), the effects of pollen diets on *N. cucumeris* reproduction over several generations and subsequent predation capacity after being switched to natural prey are scarcely known. Therefore, this study investigates the effects of a pure diet of *T. latifolia* pollen on *N. cucumeris* development and reproduction over 25 consecutive generations. Furthermore, the capacity of *T. latifolia*-fed *N. cucumeris* to locate, capture, and consume natural prey *Tetranychus urticae* Koch (Acari: Tetranychidae) was determined in the laboratory.

Materials and methods

Typha latifolia pollen collection

Typha latifolia pollen was collected in early August 2018 from Dorud, Lorestan province, Western Iran. After separating the pollen grains and sieving them, they were dried in an oven at 40 °C for 36 h and frozen at − 20 °C for long-term storage.

Stock colonies of *T. urticae* and *N. cucumeris*

The *T. urticae* stock colony was reared on planted beans (*Phaseolus vulgaris* L. variety Khomein) in a greenhouse at Tarbiat Modares University, Tehran, Iran. *T. urticae* immatures and adults were collected from the fields of Agricultural Faculty of Tarbiat Modares University, Iran. Bean planting was continued during the experiments and the plants were used for maintaining the herbivorous mite colony. The original population of the predatory mite *N. cucumeris* was purchased from Bioplanet SRL, Cesena, Italy. Rearing arenas consisted of a green plastic sheet (18 × 13 × 0.1 cm), a sponge, and a Plexiglas box

(25 × 18 × 10 cm). The green plastic sheets were individually placed on the water-soaked sponges located in the Plexiglas boxes filled with water. Tissue papers were used for covering the edges of the sheets, and they were immersed in the water surrounding the boxes. This technique not only provides necessary water for mites but also prevents them from escaping. We added a few cotton fibers on the center of the sheets to provide shelter and oviposition sites and prevent mites from drowning. Different life stages of *T. urticae* were added randomly to the arenas, using a brush, twice a week to provide a food source.

Life table of *N. cucumeris*

Before starting the experiments, a random sample of *N. cucumeris* adults from the stock colony were transferred to the new green plastic substrate, described above, and fed *T. latifolia* pollen (the first generation, G1). The offspring produced by the first generation females was maintained on the same diet for up to 25 generations. The effects of *T. latifolia* pollen on *N. cucumeris* life table parameters were determined after 3, 5, 10, 15, 20, and 25 generations (G3, G5, G10, G15, G20, and G25, respectively). For this purpose, 70 same-aged eggs (age < 24 h) taken from the corresponding generation colonies were collected and transferred separately to the experimental arenas. These units were similar to the ones used in the *N. cucumeris* stock culture but on a smaller scale (approximately one third). The green plastic sheet (3 × 3 × 0.1 cm) was placed on a wet sponge placed in a plastic box (9 × 7 × 4 cm) containing water. The experimental arenas were monitored daily, and the incubation period was recorded. The duration and mortality of different immature stages were recorded daily using a stereomicroscope. After adult emergence, females and males from the same generation were coupled. The longevity and fecundity were recorded daily. These observations were followed until the death of the last individual. During the experiments, fresh *T. latifolia* pollen was offered in four days intervals, removing the older pollen to avoid contamination with fungi. All experiments were conducted under laboratory conditions at 25 ± 1 °C, 65 ± 5 RH, and a L:D 16:8 photoperiod.

Life table and predation capacity of *N. cucumeris*

The life table parameters and predation capacity of long-term reared *N. cucumeris* were assessed after ten (G10-switch) and 20 (G20-switch) generations to investigate their efficacy to encounter natural prey, *T. urticae*. One hundred females were randomly selected from each of the G10 and G20 colonies and transferred to new arenas. After 24 h, approximately 70 eggs were collected from the arenas and individually assigned to the experimental units as described in the previous experiment. All conditions and life table data recordings were similar to those explained in the previous experiment, except the food source. Twenty-five immatures (protonymphs and deutonymphs) of *T. urticae* were offered onto each unit to provide food for immature stages of the predator. However, after adults coupling, the number of *T. urticae* immatures (protonymphs and deutonymphs) was increased to 50 individuals. *N. cucumeris* predation rate was estimated by counting the number of *T. urticae* eaten daily. The consumed prey was replaced daily with new ones. To calculate the predation rate of *N. cucumeris*, the number of killed tetranychid mites was recorded daily during the life table experiments until the death of all individuals. Given that in the adult stage, each experimental unit contained an adult mite of each sex, a parallel experiment was done to calculate the proportion of prey in each unit consumed by the adult female as described by Riahi et al. (2017). For each treatment, about 60 eggs of the related colony were transferred to a unit similar to that explained above. Soon after the emergence of adults, 20 females and 20 males were separated and allowed to mate for 24 h, after which each adult was isolated in a unit similar to that used as experimental units. To provide food, 50 immatures of *T. urticae* were released onto each unit, and the number of mites killed was recorded daily until the death of the mite. Consumed prey were replaced daily. Then, the mean number of mites consumed per day was calculated for both sexes separately. Finally, the ratio of feeding rate of female to male was obtained per day and was used for estimating the exact predation rate of females and males.

Statistical analysis

Raw data from the experiments were analyzed using the TWOSEX-MSChart software based on the age-stage, two-sex life table theory (Chi and Liu 1985; Chi 1988, 2019a). All parameters including duration of different life stages, fecundity, adult and total pre-oviposition periods (APOP and TPOP), oviposition period, and population growth parameters were calculated by the mentioned program (Chi 2019a). Variances and SE estimations of the parameters were performed by the bootstrap procedure (100,000 samples) (Huang and Chi 2012). Multiple comparison among different generations was carried out using the paired bootstrap test. When multiple comparisons are being made, the Type I error rate will rise (Noble 2009). Therefore, when paired comparisons were performed in this study, the Bonferroni correction was used.

Predation rate data were analyzed using the CONSUME-MSChart software (Chi 2019b). Using this program and the procedures outlined in Chi and Yang (2003), the following parameters were estimated: the finite predation rate (ω), stable predation rate (ψ), net predation rate (C_0), and transformation rate (Q_p). Similarly, the variances and SE of the predation parameters were obtained using the bootstrap resampling method (100,000 samples), and comparisons were made using the paired bootstrap test (Bahari et al. 2018).

Results

Life table of *N. cucumeris*

The effect of long-term feeding (1, 3, 5, 10, 15, 20, and 25 generations) on cattail pollen on the development of the predatory mite *N. cucumeris* is presented in Table 1. The embryonic period decreased with increasing the number of generations. The nymphal and total pre-adult periods in some of the mentioned generations were substantially different. There was no significant difference between the first (G1) and 25th (G25) generations in terms of developmental time. The developmental time varied from 7.66 to 8.41 days in G10 and G5, respectively. There was no significant difference in male and female longevity of *N. cucumeris* among different generations (Table 1). The longevity ranged from 56.27 to 71.48 days for females and from 43.24 to 28.10 days for males. In addition, the total life span varied from 55.98 days (in the 5th generation) to 71.33 days (in the 15th generation) and was not affected by the long-term rearing on *T. latifolia* pollen. Moreover, the adult pre-oviposition period (APOP) and the total pre-oviposition period (TPOP) in G20 were significantly shorter than in other generations. Furthermore, they did not differ between G1 and G25. The females of G15-G25 had longer oviposition days than the females of G1-G5 (Table 1). The female fecundity in the older generations was significantly higher than the younger generations.

The survival rate (s_{xj}) of different stages of *N. cucumeris* during 25 generations of rearing on *T. latifolia* pollen is illustrated in Fig. 1. These curves display the probability that a newly hatched *N. cucumeris* will survive to age x and stage j. Obvious overlapping in the survival curves of different stages is a factor behind the variable developmental rate among individuals. The female and male survival rates were lower when *N. cucumeris* were reared on *T. latifolia* pollen for a shorter period (G1, G3, and G5) than an extended period (G10-G25). The age-specific survivorship (l_x) of consecutive generations of *N. cucumeris* reared on *T. latifolia* pollen is plotted in Fig. 2. This parameter, calculated by pooling the survival of all individuals of the cohort, describes the probability that a newly laid egg would survive to age x. The age-stage fecundity (f_{xj}) gives the daily mean number of eggs laid by an adult *N. cucumeris* female at age x (Fig. 2). The peak values of f_{xj} were recorded on 13th day (1.61 eggs), 12th day (1.52 eggs), 17th day (1.87 eggs), 14th day (1.62 eggs), 15th day (1.90 eggs), 12th day (2.02), and 22nd day (1.90 eggs) which appeared when *N. cucumeris* were reared for 1, 3, 5, 10, 15, 20 and 25 generations on *T. latifolia* pollen, respectively. The curve of m_x, the mean number of eggs laid per individual at age x, showed that the reproduction began and finished at different ages in different generations (Fig. 2).

No differences were observed among gross reproductive rate (*GRR*) of *N. cucumeris* when fed on the cattail pollen across different generations (Table 1). The net reproductive rate (R_0) was significantly higher when *N. cucumeris* fed on cattail pollen more than ten generations compared with the lower ones (Table 1). In other words, this parameter had an increasing trend until the 10th generation and then statistically

Table 1 Mean (± SE) duration of different life stages (day), fecundity (eggs per female), APOP (adult pre-oviposition period, duration from adult emergence to first oviposition), TPOP (total period from egg to first oviposition), and population parameters of *N. cucumeris* reared on *T. latifolia* pollen over 25 generations (G1–G25)

Parameter	G1	G3	G5	G10	G15	G20	G25
Egg (days)	3.06 ± 0.15a	2.57 ± 0.08ab	2.55 ± 0.08ab	2.43 ± 0.09bc	2.46 ± 0.09b	2.39 ± 0.08bc	2.25 ± 0.06c
Larva (days)	1.06 ± 0.04a	1.03 ± 0.03a	1.00 ± 0.00a	1.03 ± 0.03a	1.03 ± 0.03a	1.00 ± 0.00a	1.02 ± 0.02a
Protonymph (days)	2.06 ± 0.10abcd	1.89 ± 0.06 cd	2.17 ± 0.06abc	2.03 ± 0.06bd	2.23 ± 0.10abc	2.24 ± 0.07ab	2.42 ± 0.07a
Deutonymph (days)	2.23 ± 0.11a	2.30 ± 0.10a	2.68 ± 0.18a	2.17 ± 0.06a	2.51 ± 0.10a	2.39 ± 0.08a	2.45 ± 0.07a
Pre-adult (days)	8.29 ± 0.13a	7.78 ± 0.12ab	8.41 ± 0.21a	7.66 ± 0.11b	8.23 ± 0.71a	8.02 ± 0.09ab	8.12 ± 0.08a
APOP (days)	3.24 ± 0.10a	3.00 ± 0.44a	2.62 ± 0.20a	3.00 ± 0.42a	2.87 ± 0.08a	2.41 ± 0.11b	3.27 ± 0.18a
TPOP (days)	11.57 ± 0.27a	10.76 ± 0.47a	10.94 ± 0.25a	10.69 ± 0.41a	11.23 ± 0.18a	10.46 ± 0.14b	11.55 ± 0.2a
Oviposition (days)	17.33 ± 2.44b	20.56 ± 1.82b	21.00 ± 2.85ab	25.52 ± 1.48ab	29.43 ± 1.79a	29.68 ± 1.83a	27.14 ± 1.11a
Female longevity (days)	71.48 ± 9.60a	64.36 ± 4.88a	61.73 ± 8.38a	63.52 ± 4.86a	70.83 ± 4.83a	60.16 ± 4.22a	56.27 ± 2.95a
Male longevity (days)	28.10 ± 4.56a	35.67 ± 2.99a	39.00 ± 4.60a	40.00 ± 9.88a	37.33 ± 3.72a	40.83 ± 5.74a	43.24 ± 3.49a
Total lifespan (days)	65.77 ± 7.56a	62.84 ± 4.09a	55.98 ± 4.53a	67.14 ± 4.57a	71.33 ± 4.44a	63.45 ± 3.64a	60.18 ± 2.42a
Fecundity (eggs per female)	22.81 ± 3.17c	28.04 ± 2.46bc	28.88 ± 3.71abc	36.93 ± 2.11ab	41.44 ± 2.31a	39.68 ± 2.25a	39.55 ± 1.52a
GRR (eggs per individual)	34.33 ± 5.98a	35.76 ± 6.45a	21.89 ± 4.60a	34.80 ± 3.15a	37.04 ± 3.93a	35.73 ± 3.03a	29.12 ± 2.58a
R_0 (eggs per individual)	14.54 ± 2.74c	17.05 ± 2.58bc	10.67 ± 2.52c	30.60 ± 2.91a	31.88 ± 3.29a	28.78 ± 2.95ab	26.77 ± 2.51ab
r (day^{-1})	0.1203 ± 0.009c	0.1477 ± 0.009c	0.1095 ± 0.01bc	0.1751 ± 0.006a	0.1692 ± 0.006a	0.1683 ± 0.006a	0.1582 ± 0.005ab
λ (day^{-1})	1.1278 ± 0.010c	1.1592 ± 0.01c	1.1116 ± 0.01bc	1.1914 ± 0.007a	1.1843 ± 0.007a	1.1833 ± 0.007a	1.1714 ± 0.006ab
T (day)	22.13 ± 1.20a	19.16 ± 0.71a	21.28 ± 1.17a	19.52 ± 0.53a	20.43 ± 0.37a	19.93 ± 0.39a	20.75 ± 0.3a

The SE were estimated by using the bootstrap technique with 100,000 samples. Mean values followed by different letters in the same row are significantly different ($P < 0.05$), based on paired bootstrap test with Bonferroni correction

GRR gross reproductive rate, R_0 net reproductive rate, r intrinsic rate of increase, λ finite rate of increase, and T mean generation time

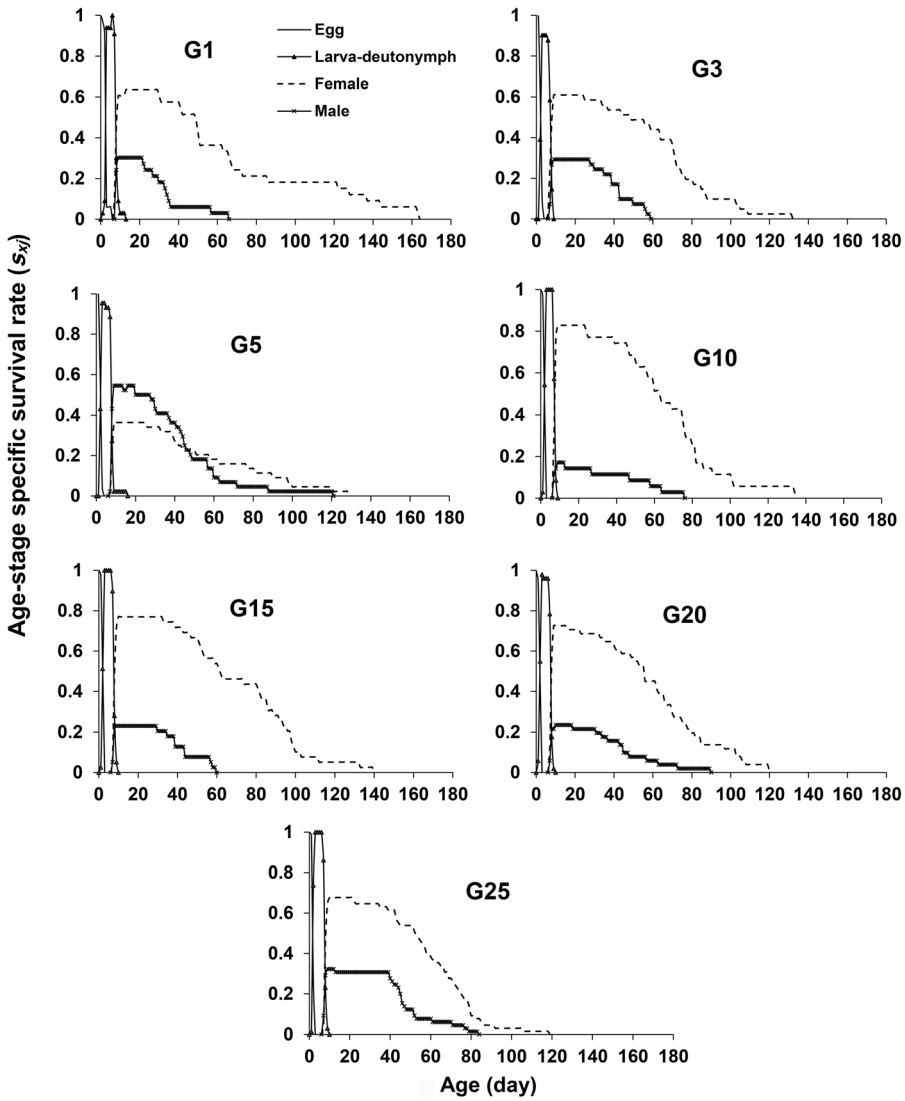

Fig. 1 The age-stage survival rate (s_{xj}) of *N. cucumeris* reared on *T. latifolia* pollen over 25 generations

remained constant. Feeding on cattail pollen for a short period (G1-G5) caused lower intrinsic (r) and finite (λ) rates of increase of *N. cucumeris*, while rearing for more than ten generations resulted in higher rates. The mean generation time (T) was not influenced by the time of rising on cattail pollen. Data showed that feeding for one and five generations on this pollen prolonged the T period of *N. cucumeris*, while other generations led to shorter T (Table 1).

Life table and predation capacity of *N. cucumeris*

Table 2 shows the developmental and oviposition parameters of 10- and 20-generation reared *N. cucumeris* on cattail pollen (G10-switch and G20-switch, respectively) when offered *T. urticae*. The egg, larva, and protonymph durations did not differ significantly between the two treatments (Table 2). The deutonymphal period of G20-switch was longer than G10-switch. Conversely, no significant differences were found in the pre-oviposition period and the number of eggs laid per female between the two treatments. Females and males of G10-switch lived significantly

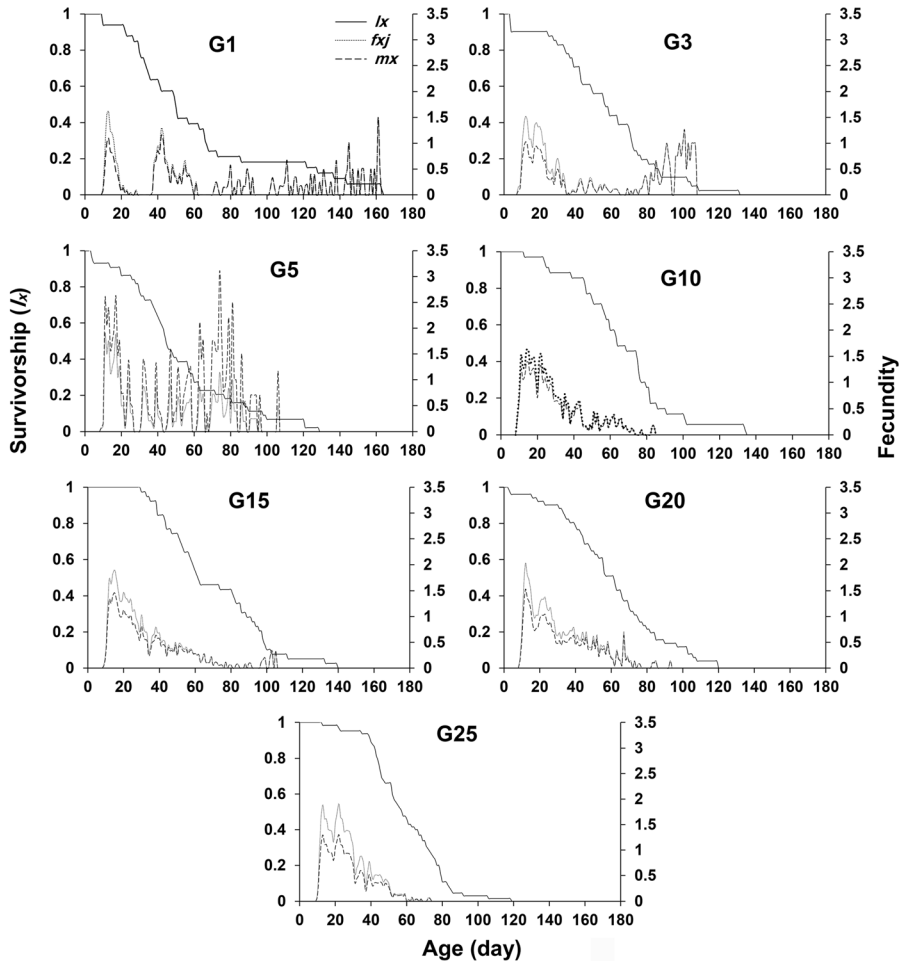

Fig. 2 The age-specific survivorship (l_x), age-stage specific fecundity of females (f_{xj}) (eggs) and age-specific fecundity (m_x) of *N. cucumeris* fed *T. latifolia* pollen over 25 generations (m_x and f_{xj} refer to the right y-axis)

more days than the females and males of G20-switch (Table 2). Likewise, the oviposition period differed significantly between the two treatments. The s_{xj} curves of 10- and 20-generation reared *N. cucumeris* on cattail pollen when offered *T. urticae* are shown in Fig. 3. The individuals of the cohort survived longer in G10-switch than in G20-switch.

Different rearing periods on the previous food source resulted in significantly different population growth parameters of the predator when it was offered the natural prey (Table 3). The results showed that the intrinsic rate of natural increase (r), gross reproductive rate (GRR), and finite rate of increase (λ) in G20-switch was higher than in G10-switch. By contrast, the latter had a longer mean generation time compared to the former. No significant influence of the generation was observed in terms of the net reproductive rate of *N. cucumeris*.

The mean predation rate of different stages of *N. cucumeris* and other predation parameters including the net, stable, and finite predation rates are presented in Table 3. A significantly different predation rate of different stages was observed between the two treatments. Protonymphs and deutonymphs of the G20-switch consumed significantly more prey than the G10-switch. The *N. cucumeris* pre-adult predation rate after 20 generations of rearing on *T. latifolia* was higher than those reared after just ten generations. Conversely, the females and males of the latter consumed more *T. urticae* than the females and males

Table 2 Mean (± SE) duration of different life stages (day), fecundity (eggs per female) and population growth parameters of two long-term *N. cucumeris* populations fed *T. latifolia* for ten and 20 generations, then switched to natural prey *T. urticae*

Parameter	G10-switch	G20-switch
Egg (days)	2.31 ± 0.09a	2.38 ± 0.08a
Larva (days)	1.02 ± 0.02a	1.00 ± 0.00a
Protonymph (days)	2.57 ± 0.11a	2.64 ± 0.09a
Deutonymph (days)	1.93 ± 0.06b	2.13 ± 0.05a
Pre-adult (days)	7.83 ± 0.16a	8.15 ± 0.10a
APOP (days)	2.70 ± 0.08a	2.55 ± 0.17a
TPOP (days)	10.54 ± 0.18a	10.66 ± 0.21a
Oviposition days (days)	27.57 ± 1.53a	21.89 ± 1.14b
Female longevity (days)	57.49 ± 3.14a	32.60 ± 1.98b
Male longevity (days)	61.20 ± 15.68a	32.50 ± 8.94a
Total life span (days)	65.76 ± 3.20a	40.74 ± 1.99b
Fecundity (eggs per female)	44.57 ± 2.53a	48.76 ± 2.47a
GRR (eggs per individual)	41.48 ± 3.23b	51.31 ± 2.82a
R_0 (eggs per individual)	38.99 ± 3.10a	42.53 ± 3.06a
r (day^{-1})	0.1826 ± 0.004b	0.2046 ± 0.004a
λ (day^{-1})	1.2003 ± 0.005b	1.2271 ± 0.005a
T (day)	20.05 ± 0.32a	18.32 ± 0.26b

Mean values followed by different letters within the same row are significantly different ($P < 0.05$), based on paired bootstrap test with 100,000 samples

GRR gross reproductive rate, R_0 net reproductive rate, r intrinsic rate of increase, λ finite rate of increase, and T mean generation time

of the former (Table 3). Moreover, the net predation rate (C_0) in the G10-switch (723.47 prey) was significantly greater than that in the G20-switch (496.08 prey). Furthermore, the stable predation rate (ψ) and finite predation rate (ω) in the G20-switch were significantly higher than in the G10-switch. A *N. cucumeris* female of the G10-switch needed approximately 18.63 *T. urticae* individuals to produce an egg, whereas a female of the G20-switch required approximately 11.69 *T. urticae* individuals (Table 3).

Discussion

According to this study, *N. cucumeris* completed its development and reproduced for 25 consecutive generations on a diet of *T. latifolia* pollen. Similarly, successful development and reproduction of other phytoseiid mites on alternative diets for more than a single generation have been reported, e.g., *N. californicus* (on almond pollen for up to 20 generations) (Khanamani et al. 2017b) and *Amblyseius swirskii* Athias-Henriot (on pollen diet, factitious prey, and artificial diet for up six generations) (Nguyen et al. 2014; Nemati and Riahi 2020).

The life table parameters best describe the survivorship, fecundity, and population growth potential of insects and mites. Among the parameters, r is more important. It considers fecundity, development, and survival rate combined (Chen et al. 2017). According to demographic theory, when r is greater than zero, the food is suitable for population growth (Chen et al. 2017). The results of this study support this theory (Table 1). The r value increased until the 10th generation and remained constant until the 25th generation, suggesting that *T. latifolia* is a suitable diet for continuous rearing of *N. cucumeris* for 25 generations. The net and gross reproductive rates are critical indicators of population growth. These parameters are usually affected by food sources and rearing time (Nguyen et al. 2014; Nemati and Riahi 2020). The former is dependent on the number of eggs, while the latter depends on fecundity and adult eclosion (Huang and Chi 2012). In this study, *N. cucumeris* had a

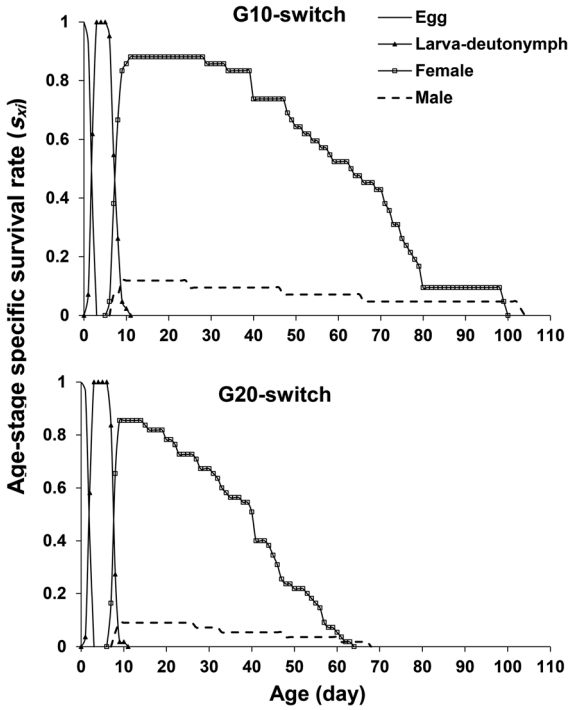

Fig. 3 The age-stage survival rate (s_{xj}) of two long-term reared populations of *N. cucumeris* fed *T. latifolia* pollen, then switched to natural prey *T. urticae*

higher net reproductive rate in the latter generations than the former ones. Furthermore, *GRR* was not significantly different amongst the different generations. Overall, this study suggests that *N. cucumeris* populations experienced increased fitness at the older generations.

The highest value of r in our study was 0.175 day^{-1}, which is in most cases higher than the values reported by Ranabhat et al. (2014) when the predatory mites fed on pollen of apple, birch, Christmas cactus, horse chestnut, maize, or tulip (0.149, 0.127, 0.155, 0.180, 0.101 or 0.167 day^{-1}, respectively); or by van Rijn and Tanigoshi (1999) when the mites reared on castor pollen and *T. urticae* (0.179 and 0.147 day^{-1}, respectively), or by Al-Shemmary (2018) when three factitious prey including *Anagasta* (*Ephestia*) *kuehniella* (Keller) (Lepidoptera: Pyralidae), *Sitotroga cerealella* (Oliv.) (Lepidoptera: Gelechiidae), and *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) were offered as food to *N. cucumeris* (0.126, 0.110, and 0.085 day^{-1}, respectively). By contrast, the results in this study were slightly lower than those reported by van Rijn and Tanigoshi (1999) when *N. cucumeris* was offered broad bean (*Vicia faba* L.) pollen (0.208 day^{-1}), or by Nguyen et al. (2015) when *T. latifolia* (0.185 day^{-1}) was used as a diet. Furthermore, the intrinsic rate of increase of *N. cucumeris* after 25 generations of rearing on *T. latifolia* pollen (0.158 day^{-1}) was higher than the value reported for *N. cucumeris* reared for one generations on other pollen species (Ranabhat et al. 2014), natural prey (Rijn and Tanigoshi 1999), factitious prey (Al-Shemmary 2018), and artificial diet (Nguyen et al. 2015).

Table 3 Mean (± SE) predation rates for *N. cucumeris* reared on *T. latifolia* pollen for ten and 20 generations, then switched to natural prey *T. urticae*

Stage/statistic	Long-term reared *N. cucumeris* population	
	G10-switch	G20-switch
Protonymph (prey)	29.33 ± 1.17b	38.70 ± 1.68a
Deutonymph (prey)	19.67 ± 0.76b	39.87 ± 1.50a
Pre-adult (prey)	49.00 ± 7.56b	78.51 ± 10.59a
Female adult (prey)	700.58 ± 6.08a	443.05 ± 6.93b
Male adult (prey)	482.18 ± 2.24a	282.72 ± 2.45b
Net predation rate (C_0) (prey)	723.47 ± 42.25a	496.08 ± 25.55b
Stable predation rate (ψ) (prey)	5.69 ± 0.13b	8.14 ± 0.17a
Finite predation rate (ω) (prey per day)	6.83 ± 0.17b	10.00 ± 0.23a
Transformation rate (Q_p) (prey per viable predator egg)	18.63 ± 1.36a	11.69 ± 0.56b

Mean values followed by different letters within the same row are significantly different ($P < 0.05$), based on paired bootstrap test with 100,000 samples

Switching *N. cucumeris* individuals from *T. latifolia* pollen to natural prey *T. urticae* after ten and 20 generations revealed that the quality of *N. cucumeris* did not decrease over time. However, a considerable increase in life table parameters was observed. For instance, switching from *T. latifolia* pollen to *T. urticae* after ten generations caused 17.82, 78.93, and 4.26% increases in *GRR*, R_0, and *r* values, respectively. Switching from the *T. latifolia* pollen to *T. urticae* after 20 generations increased the mentioned values, even more, showing a 43.60, 47.78, and 22.64% increase, respectively.

Predators must maintain the potential to locate, seize, and kill target prey after long-term rearing on unnatural prey or artificial diet (Grenier and De Clercq 2003). According to the results in this study, *N. cucumeris* did not lose its ability to capture and kill natural prey (*T. urticae*) after 20 generations of rearing on *T. latifolia* pollen. Similarly, *A. swirskii* retained its predation potential after six generations of rearing on different artificial diets, factitious prey (Nguyen et al. 2014), and pollen diets (Nemati and Riahi 2020). Khanamani et al. (2017b) also indicated that *N. californicus* sustained its predation capacity on *T. urticae* after multiple generations of rearing on almond pollen. In the current study, *N. cucumeris* immatures, females, and males of the G20-switch consumed more *T. urticae* than the G10-switch. Immatures of the 10th generation- and 20th generation-reared *N. cucumeris* consumed approximately 49 and 78 *T. urticae* mobile immatures in 7.83 and 8.15 days to develop into adults, respectively.

In conclusion, *T. latifolia* pollen supported development, survival, and reproduction of *N. cucumeris* in the absence of natural prey for 25 generations without reducing predation capacity when switched to natural prey. This production could be more cost-effective than using natural prey as a single food source. However, further research is needed to assess the performance and quality of *N. cucumeris* after more than 25 generations of feeding on *T. latifolia* pollen. In addition, the predation capacity of *T. latifolia*-fed *N. cucumeris* should be assessed under greenhouse or open field conditions.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The manuscript is original and none of the material has been published or is under consideration elsewhere. The experiments used arthropods cultured in accordance with institutional guidelines.

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