

Development, long-term survival, and the maintenance of fertility in *Neoseiulus californicus* (Acari: Phytoseiidae) reared on an artificial diet

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Abstract The effectiveness of non-prey food items, such as pollen, honeydew, and microbes, in maintaining phytoseiid mite populations is widely accepted. However, the availability of such naturally occurring non-prey foods varies with the season and surrounding environment; thus, it is difficult to manipulate and maintain supplies of these food sources. A great deal of research has examined the development and reproduction of phytoseiid mites on artificial diets. Although phytoseiid mites frequently develop, several studies have detected low fecundities of adult females reared on artificial diets. Therefore, the use of artificial diets for commercial propagation is often difficult. However, the potential of artificial diets to maintain phytoseiid mite populations has not yet been evaluated. In this study, we investigated the developmental success and survival of *Neoseiulus californicus* (McGregor) on an artificial diet. This mite may be one of the most effective phytoseiid species used in agricultural systems for the control of spider mites. *N. californicus* successfully developed on the artificial diets: 93.5–100% of individuals reached adulthood 4–7 days after hatching. The survival rates of gravid adult females maintained on the AD-1 artificial diet composed of yeast components, saccharides, and egg yolk at 25°C were 100, 80, and 48.9% over 36, 60, and 90 days, respectively. Moreover, >80% of the surviving females maintained on AD-1 for 36 or 60 days laid eggs after being switched to a diet of the spider mite *Tetranychus urticae* Koch, although they had laid few eggs during the maintenance periods on the artificial diet. Our results indicate that artificial diets can serve as a potentially useful food source for the long-term maintenance of *N. californicus* populations.

Keywords Alternative food · Biological control · Phytoseiid mite · Spider mite

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Introduction

Spider mites have been rapidly developing resistance to a series of acaricides (Croft and van de Baan 1988) and have recently assumed a new aspect of multiple resistance (Pree et al. 2002; Van Leeuwen et al. 2004; Kim et al. 2006). Thus, studies of the biological control agents and integrated pest management of spider mites have become increasingly important to spider mite management as well as to the control of other insect pests in agricultural fields, such as whiteflies and thrips (Gerson and Weintraub 2007; Weintraub 2007; Warner and Getz 2008).

Based on their feeding habits, phytoseiid mites have been classified into four groups ranging from specialized predators of *Tetranychus* species (Type I) to specialized pollen feeders (Type IV; McMurtry and Croft 1997; Croft et al. 1998, 2004). When prey herbivores are scarce or absent on crops, phytoseiid mite populations often survive on supplemental non-prey food items. If such non-prey items are available, Type II to IV phytoseiid mites tend to colonize plants regardless of the density of prey herbivores, suggesting that they can be used to manage colonies of incipient prey herbivores (Osakabe et al. 1987; van Rijn et al. 2002; Ozawa and Yano 2008). A population of *Euseius hibisci* (Chant) in California increased with increases in the amount of wind-borne pollen, allowing them to efficiently control *Panonychus citri* (McGregor) and maintain a low density in citrus groves (Kennett et al. 1979). In Italy, phytoseiid mites occur on grapevines even when spider mites are scarce, likely feeding on wind-borne pollen and/or preying on eriophyid and tydeid mites that exhibit seasonal increases (Duso et al. 2004). On deciduous fruit trees, such as grapevines and apples, powdery mildew can also cause increases in phytoseiid mite populations when densities of spider mites are low (Chant 1959; Zemek and Prenerová 1997; Duso et al. 2003). Moreover, several studies have shown that phytoseiid mites survive on honeydews produced by homopteran insects for some periods (Ferragut et al. 1987; Zhimo and McMurtry 1990; Nomikou et al. 2003).

However, the availability of naturally provided non-prey food items varies with the season and agricultural environment; thus, it is generally difficult to maintain ample supplies of these foods for phytoseiid mites in the field. Nevertheless, the above observations may be evidence enough that if alternative foods can be provided artificially, phytoseiid mites will be able to colonize plants and prevent increases in populations of spider mites.

A great deal of research has examined the development and reproduction of phytoseiid mites on artificial diets. Although phytoseiid mites (particularly the Type III and IV generalist species) frequently develop, many studies have detected low fecundities of adult females fed artificial diets (McMurtry and Scriven 1966; Kennett and Hamai 1980; Itagaki and Koyama 1986; Ochieng' et al. 1987; Shih et al. 1993). Because the primary goal of these previous studies was to exploit artificial diets for commercial propagation, experiments in this area have reached a standstill, and the potential for artificial diets to maintain phytoseiid mite populations has not yet been evaluated.

To serve as a viable alternative food source, an artificial diet must be able to maintain phytoseiid mites over the long term rather than increase the capacity for egg production, because an over-abundance of phytoseiid mites can lead to an over-consumption of the food resource and may cause an increase in the frequency of cannibalism (Schausberger 2003). On the other hand, the artificial diet must also allow gravid adult females to maintain fertility to elicit an adequate numerical response to spider mites at a later point in time.

In this study, we attempted to develop an artificial diet for use as an alternative food source for phytoseiid mites when prey spider mites are scarce. Previous studies have examined the development and oviposition of generalist phytoseiid mites (Types III and IV) on various artificial diets composed of yeast components, saccharides, and egg yolk (McMurtry and Scriven 1966; Kennett and Hamai 1980; Shih et al. 1993). We investigated the development, survival and egg production of *Neoseiulus californicus* (McGregor) on the artificial diet formulated by Kennett and Hamai (1980), with several modifications. We then investigated whether adult *N. californicus* females could survive on the artificial diet while maintaining their fertility in the long term.

Materials and methods

Mite cultures

N. californicus is a widespread Type II phytoseiid mite (McMurtry and Croft 1997; Luh and Croft 2001) that is native to Japan (Ehara and Amano 1998). This species is one of the most effective phytoseiid mites used for spider mite management in many agricultural crops and fruit orchards (Castagnoli et al. 1995). *N. californicus* can also develop and establish using pollen as a food source (Castagnoli and Simoni 1999).

The strain of *N. californicus* used in this study was obtained from the National Institute of Agrobiological Sciences and was originally collected in Matsukawa, Nagano Prefecture, Japan (35°36' N, 137°55' E; see Toyoshima and Hinomoto 2004) in September 2000. The strain was reared on *Tetranychus urticae* Koch in the laboratory at 25°C with photoperiod of 16L:8D, and the following experiments were conducted under the same conditions.

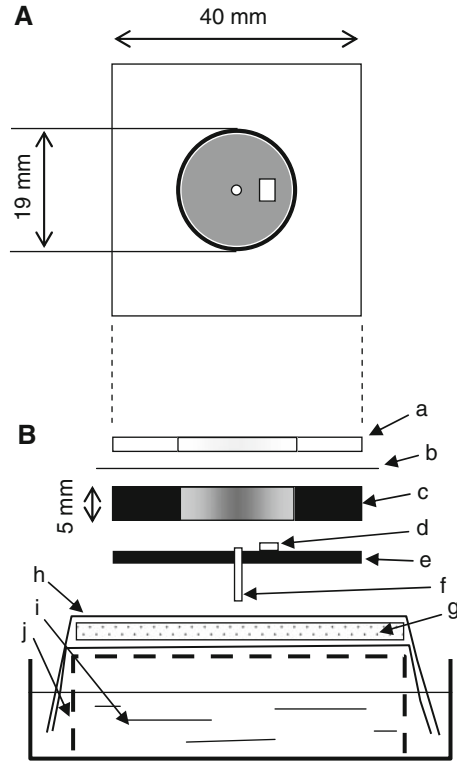
Preparation of artificial diet

The artificial diet consisted of honey, sucrose, tryptone (Bacto Tryptone, Difco), yeast extract (Bacto Yeast Extract, Difco), fresh egg yolk, and distilled water, and was prepared following Kennett and Hamai (1980), with several modifications. We prepared artificial diets (AD) of five different compositions: AD-1: 5% honey, 5% sucrose, 5% tryptone, 5% yeast extract, and 10% egg yolk; AD-2: 10% honey, 10% sucrose, 5% tryptone, 5% yeast extract, and 10% egg yolk; AD-3: 5% honey, 5% sucrose, 10% tryptone, 10% yeast extract, and 10% egg yolk; AD-4: 5% tryptone, 5% yeast extract, and 10% egg yolk; AD-5: 5% honey, 5% sucrose, and 10% egg yolk. During preparation, honey, sucrose and tryptone were dissolved into appropriate amounts of distilled water and sterilized using filtration (0.22- μ m pore size filters; SCGPU01RE, Millipore). The yeast extract and egg yolk were then mixed into the filtrate, and distilled water was added to adjust the weight appropriately.

Rearing microcosms

To examine the development and egg production of phytoseiid mites, we used modified Munger cells (Munger 1942; Morse et al. 1986; Fig. 1) as rearing microcosms (hereafter, RM) to individually rear *N. californicus* on artificial diets. Each microcosm consisted of a transparent acrylic board (top board; 40 × 40 mm, 2 mm thick) with a 19-mm diameter hole in the center, a black acrylic board (middle board; 40 × 40 mm, 5 mm thick) with an

Fig. 1 Rearing microcosms used for *Neoseiulus californicus* reared on artificial diets. **(a)** a top view, **(b)** the assembly (a side view), a: top board (40 × 40 mm, 2 mm thick) with a 19-mm diameter hole, b: clear polymethylpentene food-wrap film, c: middle board (40 × 40 mm, 5 mm thick) with a 18-mm diameter hole, d: filter paper (2 × 3 mm) that absorbed 2 μl of the liquid artificial diet, e: bottom board (40 × 40 mm, 2 mm thick) with a 1-mm diameter hole, f: piece of Kimwipe used to stop up the hole in the bottom board, g: water-saturated cotton, h: strips of Kimtowel, i: water, j: a basket placed upside down



18-mm diameter hole in the center, and a black acrylic board (bottom board; 40 × 40 mm, 2 mm thick) with a 1-mm diameter hole in the center. Clear polymethylpentene food-wrap film (Japanese Consumer's Cooperative Union) was stretched between the top and middle boards and was pierced 45 times with a fine needle for ventilation. The vents on the film were small enough to prevent *N. californicus* larvae from escaping. The hole of the bottom board was plugged with a piece of Kimwipe (Crecia, Tokyo, Japan), and a small piece of filter paper (2 × 3 mm; No. 2, Advantec) that had absorbed 2 μl of liquid artificial diet, which was enough for a larva to attain adulthood, was placed on the bottom board. Two paper clips were attached to each RM and then used to affix the RMs to a strip of Kimtowel (Crecia) placed on top of water-saturated cotton. Water was supplied to each mite inside the RMs through the Kimwipe in the hole on the bottom board. Each phytoseiid mite could freely access both the artificial diet and water. Before setting up the RMs, all sections were sterilized for 40 min by ultraviolet irradiation with a disinfectant lamp.

Development of *Neoseiulus californicus* on artificial diets

Eggs of *N. californicus* were individually transferred from mite cultures into the RM cells (31, 32, 30, 20, and 22 eggs were used for the experiments testing AD-1, AD-2, AD-3, AD-4, and AD-5, respectively). The developmental stage of each individual was determined based on the number of exuviae present in the RM by the observation through the clear polymethylpentene film using a binocular microscope every day until adult emergence or the 15th day after hatching. Slide specimens of all developed adults were prepared using

Hoyer's medium (Gutierrez 1985), and their sex was determined under a microscope by observing the spermatheca in females or the spermatodactyl in males. Individuals that were still juveniles on the last day or that died during the 15-day experiments were classified as undeveloped individuals in data analyses. We tested the duration of development among the artificial diets in each sex individually using a one-way ANOVA for each sex followed by the Tukey–Kramer method using StatView Ver. 5.0 (SAS Institute).

Effects of food type consumed during juvenile stages and after adult emergence on egg production

From 30 to 50 *N. californicus* eggs were transferred from mite cultures to detached kidney bean leaves (ca. 6 cm in diameter) heavily infested with *T. urticae* and placed on water-saturated cotton in three Petri dishes. We prepared six Petri dishes to rear *N. californicus* on the AD-1. Approximately 40 *N. californicus* eggs were introduced onto detached kidney bean leaves in the Petri dishes, which were also ca. 6 cm in diameter but divided in half (20 eggs per a half leaf). To supply AD-1 to the leaves, small pieces of filter paper (5 × 10 mm) were laminated with laminating films (approximately 10 × 15 mm and 0.1 mm thick; KLM-15F220307-20, Kokuyo) using a laminator (Pouch Laminator L210, GBC). Four small square holes were pierced in one side of the laminating film to expose a portion of the inner filter paper. Using a micropipette, AD-1 was injected onto the filter paper until it was saturated. The laminated and AD-1-saturated filter papers were then placed on the leaves with the exposed-filter paper-side down (two pieces per half leaf). To avoid contact between the filter paper and the leaf surface, the four corners of the laminating film were bent downward appropriately. The reason why we divided the leaves to provide AD-1 was because narrower available spaces were likely to make access to AD-1 easier for the phytoseiid mites. We did not find visible cannibalisms during the rearing periods in both the cases that *T. urticae* and AD-1 were provided.

Five days after the transfer of eggs, 64 adult females of *N. californicus* were randomly collected from the leaves to which *T. urticae* had been supplied as prey, whereas 96 adult females were also randomly collected 7 days after egg transfer from the leaves to which AD-1 had been supplied. All adult females were likely to have been gravid, because they had emerged under mass rearing conditions with both females and males and all females laid eggs within the experimental periods. To minimize the effect of food consumed prior to experiments, we placed individual adult females into 1.5-ml test tubes containing a small amount of distilled water and were starved for 2 days (but could freely access the water). These adult females (approximately 3–4 days old after adult emergence) were then used to determine their fertility on diets of *T. urticae* and AD-1. Half of the adult females that developed as juveniles on either *T. urticae* or AD-1 were individually introduced to kidney bean leaves (2 × 2 cm) on which >20 *T. urticae* eggs (with 3–5 adult females) were maintained throughout the experimental period. The remaining half of adult females were individually introduced into RMs to which AD-1 was supplied as described above. The number of eggs laid by each female was monitored every day for 5 days. Adult females reared on AD-1 were then individually transferred to kidney bean leaves containing *T. urticae* eggs (as described above), and the number of eggs laid by each female was checked for the next 5 days. If females accidentally died (e.g., trapped by water or artificial diet) or escaped, the data were excluded from the following data analyses. Using two-way ANOVA, we tested for the effects of two factors: (1) diet during juvenile stages (*T. urticae* or AD-1) and (2) diet for 5 days after adult emergence (*T. urticae* or AD-1), on the total

number of eggs produced by females during the first 5 days after beginning a diet of *T. urticae*. Additionally, we also tested for the effects of (3) diet during juvenile stages on the total number of eggs produced by females feeding AD-1 during the 5 days using Mann–Whitney *U*-test.

Long-term preservation of adult females on an artificial diet

A large number of *N. californicus* eggs were transferred from mite cultures to detached kidney bean leaves placed on water-saturated cotton in Petri dishes, and hatched individuals were reared on *T. urticae*. After 5 days, mature (and likely gravid) individual adult females were placed into 1.5-ml test tubes containing a small amount of distilled water and were exposed to a 2-day fast. 15, 30, and 60 adult females were then individually introduced into RMs to which AD-1 was supplied as described above and were maintained for 36, 60, or 90 days, respectively. Control adult *N. californicus* females were maintained in RMs to which only distilled water was supplied ($n = 30$). During these experiments, adult females were individually moved to newly prepared RMs every 2 weeks or if signs of molding developed on the AD-1-saturated filter paper. After the 36-, 60-, and 90-day treatments, survived females were individually transferred to kidney bean leaves containing >20 *T. urticae* eggs (with 3–5 adult females), and the number of eggs laid by each female was monitored daily for 8 days.

If females accidentally died (e.g., trapped by water or artificial diet) or escaped on a way of above treatments, the data were excluded from the following data analyses. Consequently, the data of 13, 25, and 47 adult females were used for the data analyses for 36-, 60-, and 90-day treatments, respectively. We used a one-way ANOVA followed by Tukey–Kramer method to compare the number of eggs produced by adult females for the first 5 days after switching the diet to *T. urticae*. In this statistical analysis, we included data for *N. californicus* females reared on *T. urticae* during juvenile stages and then fed AD-1 (or not) for 5 days during the above experiments (see Section “Effects of food type consumed during juvenile stages and after adult emergence on egg production”).

Results

Development on artificial diets

Regardless of concentration, *N. californicus* developed well on diets of AD-1, AD-2, and AD-3, whereas it did not develop on the diets that lacked saccharides (AD-4) or yeast components (AD-5; Table 1). The developmental rates of females did not significantly differ between AD-1, AD-2, and AD-3. However, the development of males on AD-3 was slower than that on AD-1. Therefore, we chose AD-1 for use in subsequent experiments (Table 1).

Effects of food types during juvenile developmental stages and after adult emergence on egg production

During the first 5 days of the experimental period, the egg production of adult *N. californicus* females fed *T. urticae* ($n = 31$ and 48 for females reared on *T. urticae* and AD-1 during juvenile stages, respectively) reached approximately 3 eggs day⁻¹ within 2 or

Table 1 Percentages of individuals completing preimaginal development and preimaginal developmental time of *Neoseiulus californicus* on artificial diets

Artificial diet	<i>n</i>	Development (%)		<i>n</i>	Developmental duration (mean days \pm SE) ^a
AD-1	31	93.5	♀	15	5.4 \pm 0.2 ns
			♂	7	4.6 \pm 0.3 a
AD-2	32	100	♀	22	5.7 \pm 0.2
			♂	5	4.8 \pm 0.4 ab
AD-3	30	100	♀	20	6.2 \pm 0.3
			♂	6	6.3 \pm 0.7 b
AD-4	20	0			
AD-5	22	0			

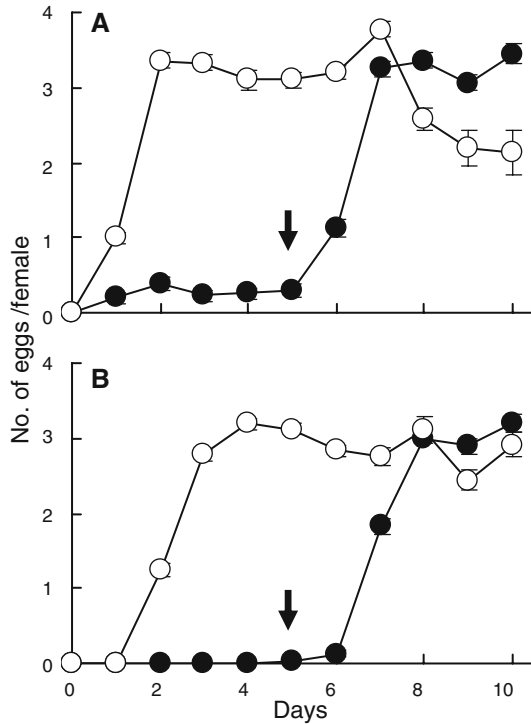
^a Different letters to the right of the column indicate significant differences among the artificial diets in males (Tukey–Kramer methods, $P < 0.05$). No significant difference among the artificial diets were detected for females (one-way ANOVA, $P = 0.0722$)

3 days, regardless of their diet during their juvenile stages (Fig. 2). In contrast, females fed AD-1 laid few eggs during 5 days. The females reared on *T. urticae* during juvenile stages ($n = 31$) produced somewhat more eggs than those reared on AD-1 during their juvenile stages ($n = 47$) (Mann–Whitney U -test; $U_{[31,47]} = 220.5$, $P < 0.0001$; Fig. 2). The egg production of adult females fed AD-1 became active and reached approximately 3 eggs day⁻¹ after being switched to a diet of *T. urticae* (Fig. 2). The number of eggs produced during the first 5 days after beginning a diet of *T. urticae* was larger in females reared on *T. urticae* during juvenile stages than females reared on AD-1 during juvenile stages, regardless of whether they were fed AD-1 after adult emergence (two-way ANOVA; $df = 1$, $F_{[1,153]} = 345.57$, $P < 0.0001$). In contrast, for the first 5 days after beginning a diet of *T. urticae*, females that had fed on AD-1 after adult emergence laid more eggs than females that had never fed on AD-1 (two-way ANOVA; $df = 1$, $F_{[1,153]} = 8.70$, $P = 0.0037$). However, this effect may have been caused by the fact that females that did not feed on AD-1 experienced a 2-day fast just before beginning a diet of *T. urticae*, whereas females that were switched from AD-1 to *T. urticae* did not fast prior to the switch. There was no significant effect of the interaction between diet fed during the juvenile stages and the diet fed after adult emergence on egg production during the first 5 days after beginning a diet of *T. urticae* (two-way ANOVA; $df = 1$, $F_{[1,153]} = 0.68$, $P = 0.4104$).

Survival of adult females fed AD-1 and egg production after long-term maintenance

All adult females of *N. californicus* that were supplied only distilled water died after 17 days (Fig. 3). In contrast, the survival rates of females provided AD-1 were 100, 80, and 48.9% after the 36-, 60-, and 90-day maintenance periods, respectively, and 92, 68, and 27.7% of the females ultimately survived the following 8-day observation of egg production while on a diet of *T. urticae* (Fig. 4). During the maintenance periods, survived females laid few eggs: 1.9 \pm 0.5 (mean \pm SE; $n = 13$), 2.2 \pm 0.3 ($n = 20$), and 4.3 \pm 0.6 ($n = 23$) eggs were laid in total during the maintenance periods of 36, 60, and 90 days, respectively. The females experiencing a 36-day maintenance period recovered

Fig. 2 Changes in the egg production of *Neoseiulus californicus* adult females that were reared on *Tetranychus urticae* (a) or the artificial diet (AD-1; b) as juveniles, fed *T. urticae* (open circles) or the artificial diet for the first 5 days (and then fed *T. urticae* for an additional 5 days; solid circles). Arrows indicate the day when diets for *N. californicus* were shifted from the artificial diet to *T. urticae*. Vertical bars indicate standard errors



their fertility after a diet switch to *T. urticae*, and egg production reached 3 eggs female⁻¹ day⁻¹ after 4 days (Fig. 4a). Although recovered egg production decreased as the length of the maintenance period increased, substantial proportion of surviving females produced eggs after the switch to *T. urticae* in every maintenance treatment (Fig. 4b, c).

The percentages of adult females that laid eggs during the 5 days after the diet switch to *T. urticae* was as high as 80% for females reared on AD-1 for 36 or 60 days but was substantially lower for females reared on AD-1 for 90 days (21.7% laid eggs; Fig. 5). The number of eggs produced during the 5 days after the switch to *T. urticae* decreased as the length of the maintenance period increased (Tukey–Kramer method, $P < 0.05$), although

Fig. 3 Survival curve of starved *Neoseiulus californicus* adult females that were only supplied distilled water. The females had been reared on *Tetranychus urticae* during their juvenile stages

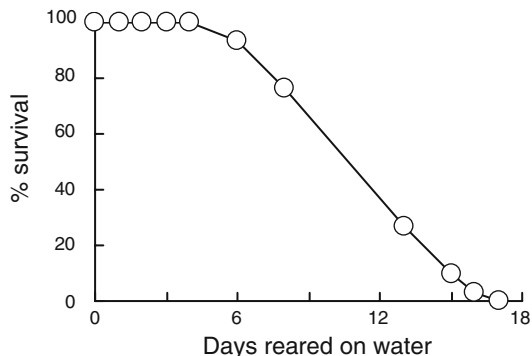
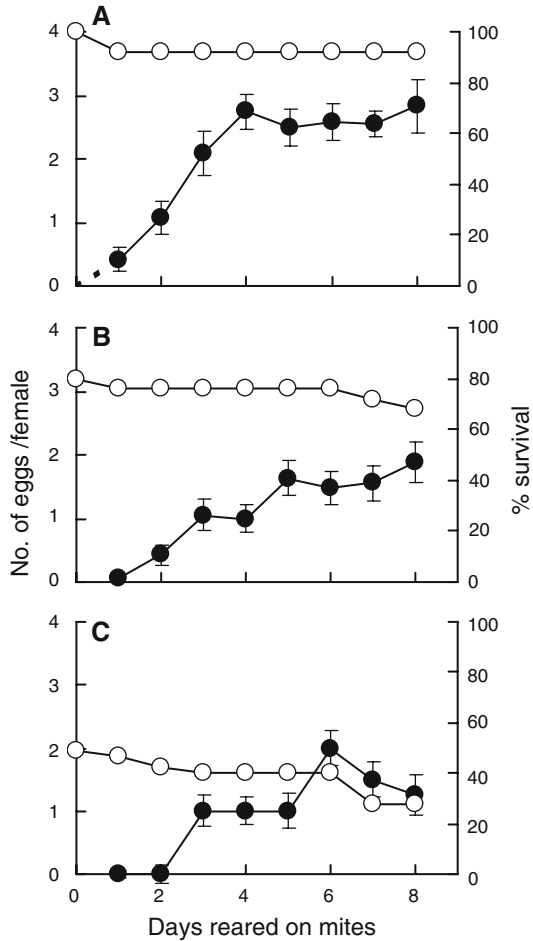


Fig. 4 Changes in the survival rate (open circles) and egg production (solid circles) of *Neoseiulus californicus* adult females fed *Tetranychus urticae* after rearing on the artificial diet for 36 (a), 60 (b), and 90 (c) days. The females had been reared on *T. urticae* during their juvenile stages. Vertical bars indicate standard errors

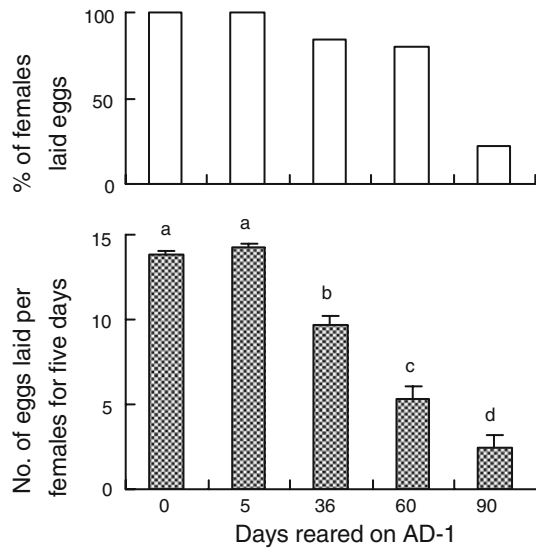


the egg production of females experiencing a 5-day maintenance period did not differ from that of females that had not been fed AD-1 (Fig. 5).

Discussion

The majority of phytoseiid mite species that were shown to successfully develop on ADs in previous studies comprised Type III or IV generalists (McMurtry and Scriven 1966; Kennett and Hamai 1980; Itagaki and Koyama 1986; Ochieng’ et al. 1987; Shih et al. 1993). Kennett and Hamai (1980) reported that no individuals of *Galendromus occidentalis* (Nesbitt) (a Type II phytoseiid mite) developed on an AD composed of yeast components, saccharides, and yolk. In contrast, *N. californicus* (Type II) developed well on the ADs in this study, although we cannot determine the cause for this drastically different response. However, no adults emerged if either saccharides (AD-4) or yeast components (AD-5) were absent from the diet, suggesting that these components

Fig. 5 Relationships between the duration of maintenance on a diet of AD-1 and egg production of adult *Neoseiulus californicus* females during the first 5 days after a diet switch to *Tetranychus urticae*. Vertical bars indicate standard errors. Different lowercase letters in the lower panel indicate significant differences among treatments (Tukey–Kramer method, $P < 0.05$)



compensate for the lack of ingredients essential to the development and/or feeding behavior of *N. californicus*. For *N. californicus* juveniles, the 5% concentrations each of honey, sucrose, tryptone, and yeast extract might be adequate for development to adulthood, because increased concentrations (10%) of these ingredients had no effect on the success or rate of development. In fact, a more concentrated (i.e., thicker) diet may hinder phytoseiid mites from feeding and prolong the duration of development.

Regardless of the diet consumed during juvenile developmental stages, adult females reared on AD-1 laid only a few eggs, similar to previous studies (McMurtry and Scriven 1966; Kennett and Hamai 1980; Shih et al. 1993; but see Ochieng' et al. 1987). However, if these adult females were switched from AD-1 to *T. urticae*, they began to produce eggs. Although the short-term (5 days) fertility subsequent to the switch decreased as the length of the maintenance period increased, the recovery of egg production occurred without a second mating, even after long-term survival (90 days) on the artificial diet. These results strongly suggest that in terms of long-term survival, an artificial diet may be useful as an alternative food source for *N. californicus*. In addition, our findings demonstrate that a substantial portion of the spermatozoa injected into females immediately following adult emergence (but prior to the maintenance period) was viably maintained during the maintenance periods.

Mating status and fertility affect the longevity of adult female phytoseiid mites. Repeatedly mated females often lay more eggs but have shorter longevities (Ji et al. 2007; Pappas et al. 2007; Gotoh and Tsuchiya 2008; but see Momen 1993). Moreover, virgin females have higher survival rates than single-mated females in *Phytoseiulus persimilis* Athias-Henriot, *Amblyseius andersoni* (Chant), and *Kampimodromus aberrans* (Oudemans) (Amano and Chant 1977, 1978; Pappas et al. 2007). In *N. californicus*, the fecundity of females decreases with the age at first copulation: females that experienced unmated periods of 56 and 70 days laid 55 and 32% of the number of eggs, respectively, laid by females that copulated immediately after emergence (Gotoh and Tsuchiya 2008).

Neoseiulus californicus may be longer-lived than most phytoseiid mite species (Toyoshima and Hinomoto 2004; Gotoh et al. 2004, 2006), particularly a specific

commercial strain (Spical, Koppert Biological Systems). However, in experiments at 20 and 25°C, adult females of native Japanese strains that feed on *T. urticae* tend to die no later than 70 days after hatching (Gotoh et al. 2004; Toyoshima and Hinomoto 2004). The commercial strain (Spical) of *N. californicus* also went extinct after approximately 100 days in experiments at both 20 and 25°C, although they survived longer when fed on *Tetranychus kanzawai* Kishida or *Amphitetranychus viennensis* (Zacher) (Toyoshima and Hinomoto 2004; Gotoh et al. 2006). We obtained the adult females used in the maintenance experiments by rearing them for approximately 6 days after hatching. Thus, the survival rates after long-term maintenance on a diet of AD-1 were equivalent to or higher than the survival rates observed in those previous studies. In addition, even though they survived longer, gravid *N. californicus* females fed spider mites tended to stop oviposition within 1 month. In contrast, gravid adult females fed on a diet of AD-1 maintained their ability to produce eggs, and the peak of oviposition activity occurred later. This particular consequence of AD-1 may be advantageous for a numerical response by *N. californicus* to spider mites that may occur later in the growing season.

Supplemental non-prey food items may promote the maintenance of phytoseiid mite populations during periods when prey herbivores are scarce or absent on crops (Nomikou et al. 2003). Pollen from several plant species serve as complete alternative food source on which some phytoseiid mites can develop and reproduce normally (Osakabe 1988; Tanigoshi et al. 1993; McMurtry and Croft 1997; Broufas and Koveos 2000; Nomikou et al. 2003). Powdery mildew (Chant 1959; Zemek and Prenerová 1997; Duso et al. 2003) and honeydew produced by homopteran insects (Ferragut et al. 1987; Zhimo and McMurtry 1990; Nomikou et al. 2003) can also serve as alternative foods for phytoseiid mites. Similarly, artificial supplements of honey can help phytoseiids to survive for certain periods of time (El-Banhawy 1975; Ashihara et al. 1978; Badii and McMurtry 1983). Moreover, *Typhlodromips swirskii* (Athias-Henriot) exhibits similar survival rates on clean leaves as on pollen supplements (Nomikou et al. 2003), and *Typhlodromalus limonicus* (Garman and McGregor) survives longer when fed exudate than when preying on the cassava green mite, *Mononychellus tanajoa* (Bondar) (Toko et al. 1994).

Pollen and powdery mildew are high quality foods, and for some phytoseiid mite species, these food sources are more suitable for development and/or reproduction than animal prey (Osakabe 1988; McMurtry and Croft 1997). However, in many cases, honeydew and plant-derived foods are inferior in terms of development and reproduction (Nomikou et al. 2003; Ozawa and Yano 2008). Moreover, the experience of feeding on non-prey food items may affect the recovery of reproduction during subsequent opportunities to eat preferred foods. For example, if *T. limonicus* feeds on exudate before preying on spider mites, its fecundity remains at a similarly low level as when it feeds on exudate alone (Toko et al. 1994). Therefore, it is very important to evaluate the effects of non-prey food on the maintenance of phytoseiid populations for biological control and the recovery of reproduction during subsequent bouts of preying on animal food items, such as spider mites or other insect pests (e.g., thrips and whiteflies) (Castagnoli and Simoni 1999; Castagnoli et al. 2001). However, very little research has addressed these issues.

Although fecundity decreased as the length of the maintenance period increased, *N. californicus* females reared on AD-1 for more than 1 month maintained their fertility. Consequently, their peak in oviposition, which often ceases within 1 month after hatching (Gotoh et al. 2004; Toyoshima and Hinomoto 2004), may be shifted to a time at which they can forage on spider mites. The observed decrease in the fecundity of adult females after the 90-day maintenance treatment suggests that the limit of *N. californicus* for maintaining fertility on AD-1 is approximately 3 months. However, females produced

some eggs (viability was preliminarily confirmed) during the maintenance experiments, and *N. californicus* developed to fertile adulthood on AD-1. These results suggest that AD-1 has the potential to maintain *N. californicus* for periods longer than those in our maintenance experiments, because the progeny developing on AD-1 would likely out-survive their parental females.

Our findings elucidate the possibility of exploiting artificial diets as an alternative means for maintaining phytoseiid mite populations on crops. Furthermore, our results highlight that artificial diets can be used as a food source supplied during the delivery of commercially manufactured phytoseiid mites. For either potential use of artificial diets, the development of a nontoxic preservative and a method for preventing desiccation will be indispensable for the practical use of artificial diets. Whereas, those would be worthwhile to more elaborate on the practicability of using artificial diets in the field.

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