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The potential of highly nutritious frozen stages of *Tyrophagus putrescentiae* as a supplemental food source for the predatory mite *Amblyseius swirskii*

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ABSTRACT

Astigmatid mites have potential as supplementary prey items to support generalist predator populations in crops. However, applying living prey mites has some disadvantages; if not predated they have the potential to cause crop damage and allergies. In this study, we evaluated various diets based on the astigmatid mite *Tyrophagous putrescentiae* (Schrank) as a supplemental food source for the predatory mite *Amblyseius swirskii* Ahias-Henriot. Eggs and larvae of *T. putrescentiae* were reared on a diet of dog food (rich in proteins and fat) or bran (rich in carbohydrate); they were offered either frozen or alive, and either with or without cattail pollen (*Typha angustifolia* L.). Oviposition rate of *A. swirskii* fed with frozen mite larvae reared on dog food was similar to the rate observed when they were fed with cattail pollen or living prey mites, but developmental time of *A. swirskii* was longer on this frozen diet than on a diet of living prey mites or pollen. Both living and frozen prey mites were, in contrast with cattail pollen, not suitable for oviposition by western flower thrips, *Frankliniella occidentalis* Pergande. In a greenhouse study, the use of frozen prey mite stages as supplemental food on chrysanthemum plants allowed populations of *A. swirskii* to establish, but not increase; in contrast, provision of living prey mites and pollen increased *A. swirskii* populations on plants. Hence, our study shows that living prey mites, but not frozen prey mites, had the greatest potential as a supplemental food source for *A. swirskii*.

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astigmatid mites; biological control; phytoseiidae; frozen hosts; western flower thrips

1. Introduction

Phytoseiid predatory mites are one of the most important groups of natural enemies used for biological control in greenhouse crops (Gerson & Weintraub, 2007; McMurtry & Croft, 1997; van Lenteren, Bolckmans, Köhl, Ravensberg, & Urbaneja, 2018). Within this family, *Amblyseius swirskii* Ahias-Henriot is currently the most economically

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important species which is commercially produced and applied in several countries as an effective predator against key greenhouse pests, including whiteflies, thrips, spider mites and tarsonemid mites (Calvo, Bolckmans, & Belda, 2011; Messelink, Van Maanen, van Holstein-Saj, Sabelis, & Janssen, 2010; Messelink, van Maanen, van Steenpaal, & Janssen, 2008; Nomikou, Janssen, Schraag, & Sabelis, 2002; van Maanen, Vila, Sabelis, & Janssen, 2010). *Amblyseius swirskii* originates from the Mediterranean area and is considered a type III generalist predatory mite (McMurtry, De Moraes, & Sourassou, 2013), meaning it not only feeds on different natural prey, but also on other non-prey food sources like pollen, nectar, plant exudates, honeydew and pycnial fluid from fungi (Goleva & Zebitz, 2013; Nomikou, Janssen, & Sabelis, 2003; Swirski, 1967). The ability of *A. swirskii* to develop and reproduce on non-pest prey species and/or alternative food sources is a huge benefit in establishing mass-rearing systems (Barbosa & de Moraes, 2015; Massaro, Martin, & de Moraes, 2016; Nguyen, Vangansbeke, & de Clercq, 2014). Furthermore, supplemental feeding also ensures that augmentative releases of *A. swirskii* are more likely to retain and increase populations in cropping systems (Hoogerbrugge, van Houten, van Baal, & Bolckmans, 2008; Huang et al., 2011; Messelink et al., 2014). One of the most commonly applied supplemental diets is pollen (Broufas & Koveos, 2000; Goleva & Zebitz, 2013; Ragusa & Swirski, 1975; van Rijn & Tanigoshi, 1999). A commercial product based on pollen from narrow-leaved cattail (*Typha angustifolia* L.) is currently used for maintenance and establishment of phytoseiid predatory mite populations following augmentation in greenhouses (Adar, Inbar, Gal, Gan-Mor, & Palevsky, 2014; Pijnakker, Arijs, de Souza, Cellier, & Wäckers, 2016; Vangansbeke et al., 2016).

Astigmatid mites are novel supplemental prey candidates to aid establishment of generalist predator populations in crops; they are easily mass-produced on inexpensive substrates (bran, yeast, flour), and their use as factitious prey in the mass production of predatory mites, is well studied (Barbosa & de Moraes, 2015; Castagnoli, 1989; Massaro et al., 2016; Ramakers & van Lieburg, 1988; Simoni, Nannelli, Goggioli, Guidi, & Castagnoli, 2006; Vangansbeke et al., 2014). To date a number of astigmatid mite species are used in the commercial mass production of several species of phytoseiid predators; these include *Carpoglyphus lactis* (L.), *Thyreophagus entomophagus* (Laboulbene) and *Tyrophagus putrescentiae* (Schrank) (Bolckmans & van Houten, 2006; Fidgett & Stinson, 2008). Several astigmatid mite species are used to rear *A. swirskii*, including *C. lactis* (Nguyen, Vangansbeke, Lü, & de Clercq, 2013), *Suidasia medanensis* Oudemans (Midthassel, Leather, & Baxter, 2013) and *T. putrescentiae* (Riahi, Fathipour, Talebi, & Mehrabadi, 2017).

The use of astigmatid mites in greenhouses, as a supplemental food source for predators, has been explored in a few studies (Hoogerbrugge et al., 2008; Messelink et al., 2014). However, there are some risks associated with this approach and it should be done with caution. It is known that some species of astigmatid mites, including *T. putrescentiae*, can feed on soft plant tissues and damage them (Czaikowska, van de Vrie, & Kropczynska, 1988; Oliveira, Návia, & Frizzas, 2007). Also, some astigmatid mites are a source of allergens that can persist and accumulate in the environment, and may cause respiratory problems in workers (Arlian, Vyszenski-Moher, Johansson, & van Hage-Hamsten, 1997; Green & Woolcock, 1978; Johansson, Johansson, & van Hage-Hamsten, 1994). Moreover, living astigmatid mites secrete defensive oils and are mobile, which can limit successful prey capture by predatory mites, particularly young predators (Midthassel et al., 2013; Midthassel et al., 2016; Rifà & Griffiths, 2018). Supplementing the diet of predatory

mites with frozen stages of astigmatid mites in crops might, therefore, be an interesting approach to increase the likelihood of retaining released predatory mites. This has been suggested in two recent patents (Guichou, Kreiter, Ferrero, & Maignet, 2015; Rifà & Griffiths, 2018). In this study, we evaluated the potential of living and frozen stages of *T. putrescentiae* as supplementary foods for the predatory mite *A. swirskii* in laboratory and greenhouse trials. The patent of Guichou et al. (2015) suggests that, once frozen, the egg stages of astigmatid mites have longer shelf life (ca. 4–6 weeks) than the other stages (ca. 3 weeks). Based on this, we evaluated the performance of predatory mites on different stages of frozen astigmatid mites.

Not only can the life stage of the prey mite affect predator performance, but also the nutritional quality of the prey, as influenced by the prey's diet (Erban, Rybanska, & Hubert, 2015; Mayntz & Toft, 2001; Sarwar, Xu, & Wu, 2010). For this reason, we included two different prey mite diets: one with a high fat, high protein and low carbohydrate content (dog food); and one with a low fat, low protein and high carbohydrate content (bran). Furthermore, several studies have shown that generalist predatory mites have a significantly faster developmental time and higher reproductive output on mixed diets compared with single prey diets (Evans, Stevenson, & Richards, 1999; Messelink et al., 2008; Muñoz-Cárdenas et al., 2014). Whether positive effects of a mixed diet also occurs when using frozen prey mites as a food source was evaluated in this study by including mixtures of prey mites and cattail pollen as a treatment.

Previous studies evaluating alternative food sources for predatory mites have shown that some food sources, such as pollen, also benefit pests such as the western flower thrips, *Frankliniella occidentalis* Pergande (Hulshof, Ketoja, & Vänninen, 2003; Leman & Messelink, 2015; Vangansbeke et al., 2016). Therefore, it could be important when choosing alternative foods to select those that support the generalist predators more than omnivorous pests. For this reason, we also assessed the effects of the factitious diets on oviposition rates of *F. occidentalis*.

2. Materials and methods

2.1. Cultures of mites and thrips

The predatory mite *A. swirskii* was obtained from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands) and subsequently reared on the leaves of sweet pepper, *Capsicum annuum* L. cv. Spider (Enza Zaden, Enkhuizen, The Netherlands), which were placed abaxial side uppermost on water-saturated cotton wool in plastic containers (18×12×5 cm). The edges of the leaves were covered with wet tissue paper to provide sufficient moisture and also prevent the *A. swirskii* from escaping (van Rijn & Tanigoshi, 1999). A small piece of cotton thread was placed at the centre of the arena to serve as an oviposition substrate. Colonies were maintained under long day illumination (16L: 8D) in a climate chamber at 25°C and 70% RH. Every two days, the predators were fed with cattail pollen (*Typha angustifolia*) as a standard rearing diet (Nguyen et al., 2013). Cattail pollen was supplied by Biobest N.V., (Nutrimite ^{TM}) (Westerlo, Belgium) and stored at −20 °C. All laboratory trials were done with 4–5 d-old female *A. swirskii* collected from this laboratory culture, but for the greenhouse trial, the predatory mites were collected directly from the commercial product obtained from Koppert (reared on the storage mite, *C. lactis* with bran as a food substrate).

A stock colony of the storage mite, *T. putrescentiae*, was provided by Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). Two colonies of these mites were established and maintained on two different food sources to obtain prey mites of different nutritional values. The prey mites were reared either on crushed dry dog food (Royal Canin, Veghel, The Netherlands), which represented a high fat, high protein and low carbohydrate diet (Erban et al., 2015), or on wheat bran (Havens, Maashees, The Netherlands), which represented a low fat, low protein and high carbohydrate diet (Erban et al., 2015). Both diets were supplemented with instant dry bakers' yeast (Mauripan, Hampton, United Kingdom) (50/50 by weight), known to improve the reproduction of predatory mites (Huang et al., 2013). *Tyrophagus putrescentiae* was reared for several generations in a plastic box (10 cm in diameter, 6 cm in high) that was embedded in a larger glass container (14 cm diameter, 8 cm high) filled with a 1 cm layer of a saturated KNO_3 solution (preventing the escape and also providing the necessary humidity) and covered with a lid (Kuwahara, Ishii, & Fukami, 1975). Both the colonies of *A. swirskii* and *T. putrescentiae* were maintained in a growth chamber at 25°C and 70% RH and 16 L: 8 D. Western flower thrips, *F. occidentalis* were maintained for many generations on flowering chrysanthemum plants (*Dendranthema grandiflora* Tzvelev cv. Tapas Time), in a separate greenhouse compartment, provided with artificial light and heating during winter. The plants were kept in cages to avoid contamination by other herbivores and replaced frequently.

2.2. Factitious foods

Ten factitious diets based on the storage mite *T. putrescentiae* and cattail pollen (*T. angustifolia*) were prepared (Table 1). The ratio of pollen to frozen diet was 1:1 (by weight). Eggs of *T. putrescentiae* were isolated from other life stages by sieving colonies through a 100 µm mesh screen. Eggs were stored at −20 °C for at least 4 h before use in the trials. A proportion of sieved eggs were not frozen but instead incubated for 48 h under the conditions described previously, until they hatched (more than 80%) and developed into larvae; these larvae were stored at −20 °C for at least 24 h before using in the trials. The frozen diets (eggs and larvae) were thawed at ambient laboratory temperatures (20 ± 2°C) for ca. 30 min before using in the trials. For all laboratory and greenhouse assays, cattail (*T. angustifolia*) pollen was used as a reference (Table 1).

Table 1. Different diets based on the prey mite, *Tyrophagus putrescentiae* and cattail pollen (*Typha angustifolia*).

No.	Foods treatments	Food substrates
1	cattail pollen	-
2	Mixed life stages of *T. putrescentiae*	wheat bran + dry yeast
3	Mixed life stages of *T. putrescentiae*	dog food + dry yeast
4	frozen eggs of *T. putrescentiae*	wheat bran + dry yeast
5	frozen larvae of *T. putrescentiae*	wheat bran + dry yeast
6	frozen eggs of *T. putrescentiae*	dog food + dry yeast
7	frozen larvae of *T. putrescentiae*	dog food + dry yeast
8	frozen eggs of *T. putrescentiae* + cattail pollen	wheat bran + dry yeast
9	frozen larvae of *T. putrescentiae* + cattail pollen	wheat bran + dry yeast
10	frozen eggs of *T. putrescentiae* + cattail pollen	dog food + dry yeast
11	frozen larvae of *T. putrescentiae* + cattail pollen	dog food + dry yeast

2.3. Oviposition of the predatory mite and thrips

Oviposition rates of the predatory mite, *A. swirskii*, on the 11 selected diets (Table 1) were measured over three consecutive days. Peak oviposition rates of phytoseiid mites (the first days after the pre-oviposition period) are known to be a good stand-in parameter for population growth rates (Janssen & Sabelis, 1992) and we therefore decided to limit the time for measuring oviposition to only 3 days. We developed a 'floating leaf disk method' for measuring oviposition rate of the predator. Same age gravid female *A. swirskii* (4-5 days since adult emergence) were placed individually on 2.5 cm sweet pepper (*C. annuum*) leaf discs in 5 cm diameter Petri dishes (the experimental unit). Each leaf disc was floating abaxial side uppermost on water (1 cm depth in the Petri dish) supported by a stand made from a modified paper clip. The stand had been glued to the base of the Petri dish before filling with water. Dishes were closed with a fine-mesh lid to allow ventilation. In this way, the leaf disc was completely surrounded by water, which prevented escape of the predatory mites. Each disc had a leaf axil as a domatium for *A. swirskii* oviposition (Faraji, Janssen, & Sabelis, 2002). Food was introduced into each experimental unit in the following quantities according to treatment: 0.01 g of pollen; 0.01 g frozen diets or 40–50 living prey life stages (predominantly eggs and larvae). Offered diets were replaced every other day and the old food was removed. For each food treatment there were 20 replicate experimental units. As eggs were laid by the predatory mites they were counted and removed daily to prevent cannibalism. Based on these oviposition trials, we determined the optimal numbers of living and frozen prey for subsequent trials.

Oviposition rates of female western flower thrips, *F. occidentalis* were measured over 4 consecutive days using a modification of the double parafilm method described by Teulon and Penman (1991). An experimental unit consisted of a perspex cylinder (30 mm high and 25 mm diameter) that was closed at one end with a mesh (size 80 μm) to allow ventilation and at the other end by two layers of stretched parafilm. After adding a food treatment, three female *F. occidentalis* of unknown age were placed in each unit and the first layer of parafilm immediately put in place to retain the thrips inside the cylinder. Then small droplets of water (about 0.05 ml), were placed on the surface of the first layer of parafilm and then covered with the second layer of parafilm. The water layer between the two layers of parafilm was used for thrips oviposition. Three diets were tested: 1) cattail pollen (0.02 gr/unit), 2) Mixed living life stages of *T. putrescentiae* (about 100 mites, predominantly eggs and larvae) and 3) frozen larvae of *T. putrescentiae* (0.02 gr/unit) (i.e. diets 1, 3 and 7; respectively, Table 1). There were 50 replicate experimental units for each treatment. For both oviposition trials, we omitted from the analysis the data from the first day, because those eggs had been produced on pre-experimental diets (Sabelis, 1990).

2.4. Juvenile development and survival of A. swirskii

Based on the observed predatory mite oviposition rates for the different diets, we selected 3 diets to assess in addition juvenile developmental time and survival of *A. swirskii* (i.e. diets 1, 3 and 7; Table 1). To obtain synchronised predatory mite eggs, 100 gravid females were transferred from the rearing cultures to a new rearing unit (similar to the oviposition

experimental unit, but bigger) with cattail pollen and left for 24 h. Then their eggs were individually transferred to the experimental units (floating leaf disk method), as described for the oviposition trials. Diets were added to each unit (0.01 g) after the emergence of larvae; the old diet was removed every 48 h and replaced with a fresh diet. The duration of each life stage was determined by recording the presence of exuvia as evidence of moulting. Survival and development of individuals were recorded daily until mites reached adulthood. There were 20 replicate experimental units for each diet. All laboratory experiments were done in a climate chamber under the conditions described previously.

2.5. Greenhouse trial

Based on the laboratory trial results, four different supplementary food treatments were selected to assess the effects of on establishment and population growth of the predatory mite, *A. swirskii* in a greenhouse compartment 24 m^2 in area. Young chrysanthemum plants (*Dendranthema* X *grandiflorum* cv. Baltica) were supplied by Deliflor (Maasdijk, The Netherlands) and were planted in 12 cm diameter pots filled with peat. Each experimental unit (serving as a replicate) contained four pots, each with one plant bearing between four and six leaves at the beginning of the trial. All plants were placed on water-saturated irrigation mats to prevent predatory mite migration and minimise contamination amongst treatments. Each treatment had four replicates, thus a total of 16 pots per food diet were used. The plants were irrigated with a standard nutrient solution using an ebb-and-flow irrigation system for 10 min per day. The four food treatments were: 1) cattail pollen, 2) mixed living life stages of *T. putrescentiae*, 3) frozen larvae of *T. putrescentiae* and 4) frozen larvae of *T. putrescentiae* + cattail pollen. The prey mites in all treatments were reared on dog food. Before releasing the predatory mites, they were collected using a fine brush and placed in groups of ten per sweet pepper leaf disc (4 cm diameter) and then transferred to the chrysanthemum plants. We released five adults of *A. swirskii* per plant. Food treatments (0.05 g/plant) were added shortly after the predator releases by dusting with a fine brush to achieve an even distribution. For the treatment containing a mixture of living life stages of *T. putrescentiae*, approximately 500 different mobile stages were released per plant (counted based on weight). Population growth was monitored weekly for 5 consecutive weeks (before flowering began) by counting all stages of *A. swirskii* on eight randomly picked leaves per replicate (two leaves per plant). The experiment was set-up as a completely randomised design and all units were distributed over one big table (7 m^2) with similar conditions for all replicates. Temperature and relative humidity were monitored every 5 min with a climate recorder (Hoogendoorn Growth Management, Vlaardingen, the Netherlands) during the experiments. The average temperature was 23.1°C (range 17.1–27.5°C) and the average relative humidity 72% (range 46–87%).

2.6. Statistical analysis

Daily oviposition rates of *A. swirskii* and *F. occidentalis* and also duration of immature stages of the predatory mite were analysed using a generalised linear model (GLM) with a Poisson error distribution of the data. Differences amongst treatments were tested using Fisher's LSD (Least Significant Difference) method at the 5% level of

significance. For the greenhouse trial we used a generalised linear mixed model (GLMM) with time as a random factor in order to analyze overall treatment effects through time. A Poisson error distribution was applied for the predator densities (total numbers of all stages). Differences amongst treatments were also determined using an LSD test ($p < 0.05$). All statistical analyses were done using the statistical package GenStat (Release 19.1).

3. Results

3.1. Oviposition of predatory mite and thrips

Oviposition rates of *A. swirskii* were significantly different amongst diet treatments ($F_{10,209} = 29.94$, $p < 0.001$, Figure 1). Amongst the four frozen factitious diets (without pollen) the provision of frozen larvae of *T. putrescentiae* reared on dog food achieved a significantly higher oviposition rate in *A. swirskii* than the other frozen diets, all of which resulted in very low oviposition rates (Figure 1). Provision of frozen larvae of *T. putrescentiae* achieved significantly higher oviposition rates in *A. swirskii* than frozen eggs, especially when dog food was the food source for the prey mite rearing (Figure 1). Adding cattail pollen to the frozen mites did not increase oviposition rates compared with the treatment with only cattail pollen (Figure 1). Two treatments including frozen

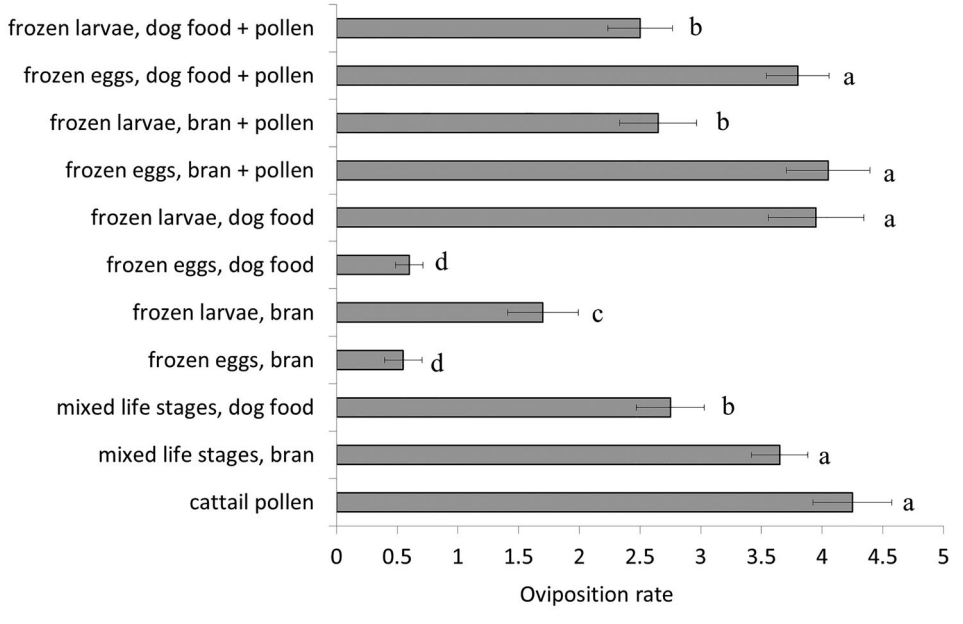

Figure 1. Oviposition rates of the predatory mite *Amblyseius swirskii* on different diets based on the prey mite *Tyrophagus putrescentiae* in comparison with cattail pollen (*Typha angustifolia*). Dog food and bran indicate the food substrates on which the prey mite had been reared. Yeast was also part of these diets in all the prey mite treatments (see Table 1 for details). Shown are the mean numbers of eggs (± SE) per female per 2 consecutive days (combined data of day 2 and day 3), since the predators were allowed to feed on the different diets. Different letters beside the bars indicate significant differences amongst treatments (LSD test: $p < 0.005$).

larvae of *T. putrescentiae* (reared on both bran and dog food) + cattail pollen even resulted in a significant decrease in oviposition rates compared with cattail pollen alone (Figure 1). In contrast, significantly higher oviposition rates were achieved by *A. swirskii* when supplemental living prey mites were reared on bran compared with when they were reared on dog food (Figure 1).

Food treatments also had a significant effect on the oviposition rates of *F. occidentalis* over four consecutive days ($F_{3,196} = 561{,}0$ $p < 0.001$, Figure 2). The highest oviposition rate was achieved when cattail pollen was the supplementary diet (Figure 2); mixed living life stages and frozen larvae of *T. putrescentiae* (both reared on dog food) were unsuitable for *F. occidentalis* resulting in oviposition rates that were similar to those in the treatment without food (Figure 2).

3.2. Juvenile development and survival of A. swirskii

The predatory mite, *A. swirskii*, was able to develop and survive of on all three diets evaluated. Significant differences amongst treatments were observed for the duration of the egg stage ($F_{2,57} = 12.57$, $p < 0.001$), the deutonymph stage ($F_{2,57} = 5.39$, $p = 0.007$) and the total juvenile development time ($F_{2,57} = 15.07$, $p < 0.001$) (Table 2). The shortest and longest juvenile development times for *A. swirskii* were observed on diets of cattail pollen and frozen prey larvae, respectively. The percent survival of juvenile stages was >95% on all diets evaluated (Table 2).

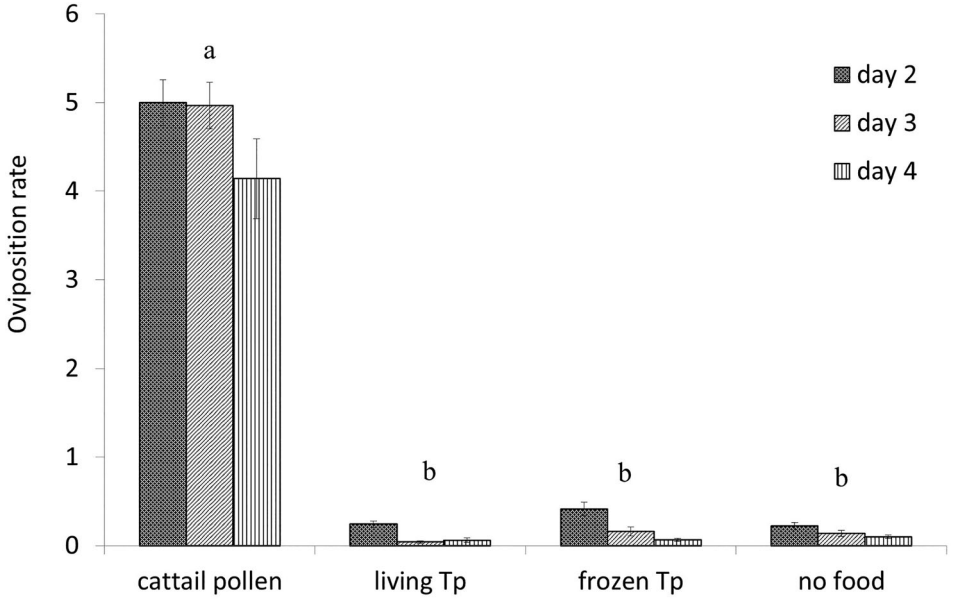

Figure 2. Mean (±SE) number of eggs per female western flower thrips, *Frankliniella occidentalis*, when feeding on three different food sources over 4 consecutive days. The food diets were cattail pollen (*Typha angustifolia*), living Tp (mixed life stages of *Tyrophagus putrescentiae* reared on dog food + yeast), frozen Tp (frozen larvae of *T. putrescentiae* reared on dog food + yeast). Different letters represent significant differences amongst treatments (LSD test: $p < 0.05$), based on the total number of eggs produced in 3 days (data first day omitted).

Table 2. Mean developmental time (days ± SE) of immature stages of the predatory mite *Amblyseius swirskii* when fed on different food sources; cattail pollen (*Typha angustifolia*), living Tp (mixed life stages of *T. putrescentiae* reared on dog food + yeast) and frozen Tp (frozen larvae of *T. putrescentiae* reared on dog food + yeast).

	Immature stages					
Food source	Egg	Larva	Protonymph	Deutonymph	Total juvenile developmental time	Survival percent
cattail pollen	2.2 ± 0.09 a	1 ± 0 a	1.95 ± 0.13 a	1.4 ± 0.15 a	6.6 ± 0.22 a	> 95%
living Tp	2 ± 0.10 a	1 ± 0 a	2.4 ± 0.18 a	1.5 ± 0.15 a	6.9 ± 0.16 a	> 95%
frozen Tp	2.7 ± 0.10 b	1.05 ± 0.5 a	2.3 ± 0.16 a	2 ± 0.10 b	8.05 ± 0.19 b	> 95%

Different letters within the same column indicate significant differences among treatments (LSD test: $p < 0.05$).

3.3. Greenhouse trial

Population dynamics of the predatory mite, *A. swirskii*, on chrysanthemum plants were affected significantly by the type of diet provided ($F_{3,72} = 8.87$, $p < 0.001$; Figure 3). Overall predatory mite densities were not significantly different between the two treatments containing pollen and living stages of *T. putrescentiae* (Figure 3). Predator densities in all treatments increased over time, except in the frozen prey mite treatment where they

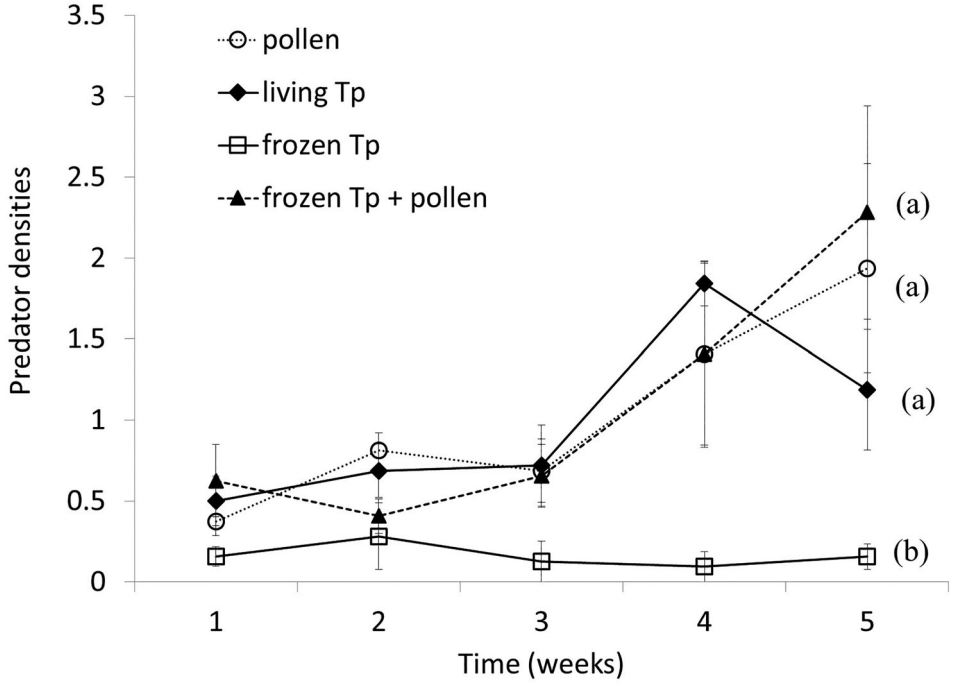

Figure 3. Population dynamics of the predatory mite *Amblyseius swirskii* on chrysanthemum plants in the presence of four types of food sources: pollen (cattail pollen, *Typha angustifolia*), living Tp: (mixed life stages of *Tyrophagus putrescentiae* reared on dog food + yeast), frozen Tp: (frozen larvae of *T. putrescentiae* reared on dog food + yeast) and frozen Tp + pollen: ([frozen larvae of *T. putrescentiae* reared on dog food + yeast] + cattail pollen). Different letters indicate significant differences amongst treatments through time (LSD test: $p < 0.05$).

remained very low throughout (Figure 3). Adding cattail pollen to the frozen mites did not increase overall predatory mite densities compared to the treatment with only cattail pollen (Figure 3).

4. Discussion

The laboratory trials in this study demonstrated that there was potential to use frozen stages of astigmatid mites (*T. putrescentiae*) as food sources for generalist predatory mites. Interestingly, both the stage and the diet of the prey mite strongly affected their suitability as factitious diets for the predatory mite. Only provision of larval stages of *T. putrescentiae* reared on a protein-rich and fat-rich diet (dog food) resulted in high oviposition rates of the predatory mite, *A. swirskii* (Figure 1). Erban et al. (2015) showed that population growth of *T. putrescentiae* was much higher on a diet with high-protein and high-fat content than on a diet with low-protein and low-fat content. The prey mite population growth rate may be an indication for the nutritional value of prey mites for predatory mites. Sarwar et al. (2010) compared the effects of different flour diets (wheat, soybean and maize) as food substrates firstly for *T. putrescentiae,* but also indirectly for the predatory mite, *Neoseiulus pseudolongispinosus* (Xin, Liang and Ke) when it fed on the prey mites that had been fed different flours. In their study, wheat flour resulted in the highest population growth of the prey mite, which also resulted in the fastest juvenile development of the predatory mite.

In our study, provision of the diet based on frozen larvae of *T. putrescentiae* reared on dog food and living stages of the prey mite reared on bran achieved the same oviposition rate in *A. swirskii* as provision of cattail pollen. This is in contrast with the study of Riahi et al. (2017) who reported that living immature stages of *T. putrescentiae* reared on fungi and *Gaeumannomyces graminis* var. *tritici* was an inferior diet for *A. swirskii* leading to a significant reduction in fecundity and intrinsic rate of increase compared with maize and almond pollens. Possible reasons for this discrepancy are the use of different diets for the prey mite rearing and the use of different stages of prey mites. Based on capture success rate, Midthassel et al. (2013) claimed that *A. swirskii* preferred eggs and immature stages of the prey mite, *Suidasia medanensis* Oudemans compared with adults. Stronger defense behaviour and higher mobility of the adult prey mites were suggested as the main reason for this preference. Also the nutritional value of the prey mite stage might play a role. The type and quantity of proteins is different between egg and larval stages of arthropods. During pre-imaginal development, yolk protein (vitellin) changes to larval protein (Sloggett & Lorenz, 2008). This change may explain the significantly higher oviposition rates of *A. swirskii* on frozen larvae of *T. putrescentiae* (reared on both bran and dog food) compared with frozen eggs (Figure 1).

The oviposition rates of *A. swirskii* fed with frozen prey mite larvae reared on dog food were similar to those fed on pollen of living prey mites fed on bran. However, the juvenile developmental time of *A. swirskii* was significantly longer on this diet compared with living stages of prey mites or pollen, showing the frozen diet was of inferior quality. The freezing process probably has adverse effects on nutritional quality of factitious foods. During freezing and even long-time cold storage, the activity of proteases and other metabolic enzymes is not entirely prevented, leading to cell and tissue breakdown and nutrient loss; this explains the decrease in quality of frozen diets (Léger, Bengtson,

Simpson, & Sorgeloos, 1986). Midthassel et al. (2013) also showed that freeze-killed *S. medanensis*, had thicker cuticle than living *S. medanensis*; this prevented *A. swirskii* from easy penetration of the idiosoma and restricted feeding to the coxae and gnathosoma.

Despite these limitations, the ability of *A. swirskii* to complete development on the frozen larval prey mites reared on protein-rich food and their high oviposition rates, suggests this diet has potential to support predatory mites in crops. However, providing this frozen supplemental diet did not successfully support *A. swirskii* on chrysanthemum plants in the greenhouse. Although populations established, they did not increase in densities. The possible reasons for this failure may be related to several factors. Firstly, fluctuations in greenhouse temperature and relative humidity may change the nutritional quality of the diets and affect the ability of predators to extract sufficient nutrients (Vangansbeke et al., 2016). For example, high variation in temperature and relative humidity had adverse effects on hydration of decapsulated brine shrimp cysts (*Artemia* spp.) (Artefeed) and decreased their suitability as food for *A. swirskii*; subsequently this reduced establishment of the predatory mite (El-Magsodi, Bossier, Sorgeloos, & van Stappen, 2014; Vangansbeke et al., 2016). Secondly, the delayed juvenile developmental time of *A. swirskii* feeding on the frozen diet would ultimately lead to slower population growth in the greenhouse.

The fact that *A. swirskii* was able to reproduce in the laboratory and greenhouse on living stages of *T. putrescentiae* is interesting, knowing that several attempts for mass production of the predator on this prey mite have failed (Riahi et al., 2017; personal experience of authors). Currently, *Carpoglyphus lactis* L. is used for commercial mass production of *A. swirskii* (Calvo, Knapp, van Houten, Hoogerbrugge, & Belda, 2015; Nguyen et al., 2014). *Tyrophagus putrescentiae* excretes alarm pheromones such as neryl formate as a defense mechanism that induces escape behaviours and reduces successful capture by predatory mites (Howard, Kuwahara, Suzuki, & Suzuki, 1988; Kuwahara et al., 1975; Midthassel et al., 2013; Rifà & Griffiths, 2018). A possible explanation for the differences we observed between our results and mass rearing systems is that these oil secretions have a greater impact at high densities of the astigmatid mite in rearing systems, but not in small arenas on in the laboratory experiments or on plants.

Adding cattail pollen to the frozen diets did not significantly enhance oviposition rates and population densities of *A. swirskii* in either the laboratory or the greenhouse trials. This is similar to the observations of others. Addition of castor pollen to two factitious prey diets (*Suidasia pontifica* Oudemans and *T. putrescentiae*), and also to two natural prey (*Tetranychus truncatus* Ehara and *T. kanzawai* [Kishida]), did not significantly improve survival, development or oviposition rates of the predatory mite *Amblyseius longispinosus* (Evans) (De Leon-Facundo & Corpuz-Raros, 2005). In contrast, Sarwar (2016) found that when maize and mung bean pollens were provided in combination with different life stages of *T. putrescentiae*, biological parameters such as development and reproduction of the predatory mite, *Neoseiulus cucumeris* (Oudemans), significantly improved compared with each diet alone. This inconsistency amongst studies may be due to differences in the type of pollen, species of prey, species of predatory mite, experimental conditions, and/ or methods.

Our study, for the first time, assessed the nutritional quality of living and frozen factitious prey mites for *F. occidentalis* in comparison with pollen. Our results confirm previous studies showing that cattail pollen is a very suitable food source for western

flower thrips, *F. occidentalis,* which may in some cases be a risk for using it as a supplemental food source for predatory mites (Hulshof et al., 2003; Leman & Messelink, 2015; Vangansbeke et al., 2016). In contrast, we observed very low oviposition rates of thrips on the prey mite diets, which may be an important advantage when using them as supplemental food in biological control systems compared to food sources that also support thrips.

Summarising, we showed that stage (mixed living, frozen eggs or frozen larvae) and food substrate (dog food or bran) of *T. putrescentiae* affected the reproduction of *A. swirskii*. The laboratory results indicated that frozen larvae reared on a protein-rich diet might be promising to use as a supplemental food source for *A. swirskii*, but when applied in the greenhouse, only living prey mites and not frozen stages could increase predatory mite densities. Yet, our study may stimulate further studies to develop alternative food sources based on frozen mites, for example to improve the shelf life and nutritional quality of the frozen diets or to assess the potential of frozen stages of other astigmatid mite species.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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