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MORPHO-ECOLOGICAL STUDY OF REPRODUCTION AND EARLY ONTOGENESIS OF PHYTOSEIID MITES (ACARI: PHYTOSEIIDAE)

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ABSTRACT: This study has experimentally examined the relative offspring size, the larval feeding behavior and the protonymph resistance to food stress in phytoseiid mites with different food specializations. No correlation was found between egg size and female body size; however, relative egg size varied significantly among species. Among the six examined species, *Phytoseiulus persimilis* has produced the largest offspring. At the same time, its protonymphs survived for a shorter period in the absence of food, compared with the species producing smaller eggs. For instance, *Neoseiulus neoagrestis* protonymphs survived up to 6.5 days without food, whereas those of *P. persimilis* survived only for about 3.8 days under similar conditions. In *N. neoagrestis*, no differences were observed in the development rates between the non-feeding and feeding larvae, indicating that hunting and feeding are facultative during this stage. Moreover, larvae kept in groups developed faster than those kept individually. This acceleration of development may serve as a strategy to avoid cannibalism, which occurred at the rates of 15–25% in this study and was unaffected by the presence or absence of food. These findings suggest that the tolerance to food stress may represent a valuable screening criterion for selecting new phytoseiid species for biocontrol applications.

KEY WORDS: Phytoseiidae**,** egg volume, body size, food deprivation, larvae cannibalism

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INTRODUCTION

Predatory mites of the family Phytoseiidae are considered a key group of biological control agents (van Lenteren and Nicot, 2020). About 40 species are released weekly into greenhouses to protect crops grown on millions of hectares worldwide. The most widely used species are *Phytoseiulus persimilis*, *Neoseiulus cucumeris, N. californicus*, *Amblyseius andersoni* and *A. swirskii* (Knapp *et al.* 2018).

There are significant amounts of data collected on various aspects of phytoseiid biology, including the impact that host plants have on their hunting and reproductive behavior (Beard and Walter 2001; van Houten *et al*. 2013; Buitenhuis *et al.* 2014); the intraguild predation and cannibalism (Buitenhuis *et al*. 2010; Ghasemloo *et al*. 2016); as well as food specialization and food chains, involving the most dangerous greenhouse pests (Kolodochka 2006). The biotic potential of 76 phytoseiid species has been evaluated using life tables (Khanamani *et al*., 2017; Lee and Gillespie 2011; Al-Azzazy *et al.* 2018). The study of phytoseiid biology drives the screening of new biocontrol agents in the Phytoseiidae family.

Relative offspring size is a key trade-off that influences species fitness across all animals, including arthropods (Stearns 1992; Charnov 2002; Church *et al.* 2019). However, this parameter has remained largely unexplored in phytoseiids. Although several studies provide data on the dorsal shield length and egg size, no comparative analysis of these traits has been performed (Toyoshima and Amano 1998; Croft *et al.* 1999; Walzer and Schausberger 2015; Lv *et al.* 2016). Thus, the first objective of our study was to assess the interspecific variability in both absolute and relative egg size among phytoseiids.

Regarding the relative size of eggs, phytoseiids surpass most terrestrial arthropods (Walter and Proctor 2013). Large eggs contain substantial yolk reserves, which fuel the embryo development and support the early ontogenesis of the larva and possibly the protonymph. Therefore, the second objective of our research was to evaluate the developmental features of larvae and protonymphs under conditions of food stress (starvation), when maternal investments are the only energy source.

Previously, the feeding behavior of larvae has been studied in seven species of phytoseiids. In most cases, larvae can molt into protonymphs without feeding, indicating that larval feeding is facultative (Schausberger and Croft 1999). Obligate larval feeding, which may represent a more primitive trait, has been observed in only two species studied so far (McMurtry and Croft 1997; McMurtry *et al.* 2013).

The first two developmental stages (larva and protonymph) are significantly limited in prey selection due to their small size. Therefore, a key factor for their survival is resistance to food stress, specifically the ability to keep moving as long as possible while searching for prey. Under starvation conditions, larval and protonymph survival is determined by maternal investment in the offspring, in the form of the embryo yolk. We have hypothesized that species producing relatively large offspring will have an adaptive advantage. To test this hypothesis, it was first necessary to estimate the interspecific variability in the relative offspring size among phytoseiids with different larval feeding modes.

Also, it is reasonable to compare the relative egg size with the developmental features of larvae and the protonymphs under food deprivation—to assess resilience to food stress during the early ontogenesis for species that differ substantially in their egg volume.

In the present study, we have assessed the relative size of the offspring in six phytoseiid species that differed markedly in their dorsal shield size. Two of these were closely related but differed in their reproductive mode: *Neoseiulus neoagrestis* (bisexual) and *N. agrestis* (thelytokous). Because females of these species are morphologically similar, they provided an excellent model for evaluating the influence of thelytoky on the relative offspring size and the maternal investment in the egg production.

MATERIALS AND METHODS

The origin and rearing of the mite populations

Neoseiulus neoagrestis V. Khaustov and Döker. The laboratory population was started by mass mating mites collected from the eastern coast of the Black Sea in Russia. The species is morphologically close to the thelytokous species *N. agrestis* but has a bisexual reproduction (Khaustov *et al.* 2022). The collected specimens have been adapted for breeding on *Thyreophagus entomophagus* (Laboulbène and Robin) (Acari: Acaridae).

Neoseiulus agrestis (Karg). The laboratory population is based on mites collected from the Altai Republic, Russia (Khaustov *et al.* 2022). The lab population was maintained using *Th. entomophagus* as a food source.

Laboratory populations of *Neoseiulus californicus* (McGregor), *N. cucumeris* (Oudemans), *Phytoseiulus persimilis* Athias-Henriot and *Transeius montdorensis* (Schicha) were obtained from the All-Russian Institute of Plant Protection, St. Petersburg. Their mass rearing was maintained on *Th. entomophagus* and *Tetranychus urticae* using standard methods (Bakasova 1976).

The mites were mass-reared in plastic containers (4.7 L in volume), with a mesh ventilated cover. The containers were kept in climate chambers Panasonic MLR-352H-PE at the temperature of 25±0,2 °C and 75±0,5% relative humidity. The temperature and humidity conditions were monitored during the experiments with the help of a data logger.

Morphometric analyses

The body size of phytoseiids was assessed using the length and width of the dorsal shield. The egg size of phytoseiids was assessed using the length (L) and width (W) dimensions. The egg volume was calculated using the ellipsoid equation: $LW^2\pi/6$. The sample size for each species comprised 30 females and 30–35 eggs. The measurements are presented in micrometers (µm).

The measurements of body and eggs size were performed using a compound biological microscope Mikromed 3 U3, equipped with a digital lamp ToupCam 9.0 with a sensor MT9J003 and the ToupTek ToupView program (x64), at 20× magnification.

To obtain microscopic preparations, we used the MiniMed (RF) glass slides (26×76×1 mm) and cover glasses (18×18×0.17 mm). A Hoyer medium was placed between the glasses. Mites' eggs were placed in a drop of medium; female mites were clarified in lactic acid for 2 days at a temperature of 60 °C in a dry-air thermostat. The obtained preparations were heated during the day at a temperature of 52 °C using an automatic heating table.

Early post-embryonic development of *Neoseiulus neoagrestis* and *Phytoseiulus persimilis*

The survival of phytoseids at the larval and the protonymph stages was assessed on two species, *N. neoagrestis* and *P. persimilis*. The mites were kept in 0.5 ml Eppendorf tubes with a snap-on lid with a 4 mm diameter hole and a conical bottom.

A sieve cloth with a cell size of 34/36 µm was placed between the tube and the Snap-On lid. As a source of moisture, a drop of water was applied daily to the sieve cloth using an insulin syringe fitted with a needle.

The eggs were transferred to a test tube using an Olympus SZX7 stereoscopic microscope, a histological needle and a fine-tipped artist's brush. Test tubes with selected eggs were placed on an individual tripod (100 sockets).

To create an isolated environment during the research, a tripod with test tubes was placed on a porcelain tray in a 12.9 L laboratory desiccator made of neutral glass. Humidity of 80–85% was maintained in the desiccator with the help of a saturated saline solution—300 ml of distilled water per 80 g of sodium chloride (NaCl). The temperature was maintained at 25–27°C. To control the climatic parameters, a trusted EClerk-M-RHT humidity and temperature meter was placed in the desiccator.

In order to assess the resistance of *N. neoagrestis* to food stress, we have examined 4 variants of larval nutrition: individual rearing without feed, individual rearing with feed, group maintenance (3 individuals) without feed, group maintenance (3 individuals) with feed. *Th. entomophagus* eggs were used as a feed source.

At the first stage of the experiment, the larvae emerged from the eggs, which were previously transferred into Eppendorf tubes. The proportion of larvae that hatched from the eggs was 90–92%. Such high survival rate indicates that the transfer of the eggs did not cause them damage.

The molting of larvae on the protonymph was confirmed by the presence of exuviae in the test tube. The protonymph was distinguished from the larva by the presence of the fourth pair of legs. Subsequently, records were kept until the death of the examined individuals. The cannibalism rate among the larvae and the protonymphs of *N. neoagrestis* was measured in groups (20 groups of 3 individuals each were tested in each experimental run).

RESULTS

Interspecies variability in the relative egg size of phytoseiids

Based on the data on the relative size of eggs in six phytoseiids species, no correlation was found between egg size and female body size (Fig. 1). However, the relative egg size varied significantly among the species (Fig. 2). For instance, *P. persimilis* has eggs that are nearly twice as large, on average, as those of the other examined species.

N. neoagrestis has a larger body and egg size than *N. agrestis* (Fig. 1, $p < 0.05$). Although the difference in the relative egg size between these species is less than 6%, it remains statistically significant (Fig. 2, $p < 0.05$). It is worth noting that, based on the taxonomic features, *N. neoagrestis* differ from *N. agrestis* only with the GD2 pore on the dorsal shield.

Early post-embryonic development of *Neoseiulus neoagrestis* and *Phytoseiulus persimilis* in the absence of food

Juvenile individuals of *N. neoagrestis* and *P. persimilis* were maintained individually in the absence of food. The following parameters were assessed: 1) the mortality rate and the development time of larvae; 2) the duration of the protonymph survival without food. The mortality rate of larvae for both *P. persimilis* and *N. neoagrestis* was close to zero, indicating that most tested individuals of both species successfully developed and molted into protonymphs without feeding (Table 1). Juvenile *N. neoagrestis* remained viable and motile without food for an average period of 6.5 days, whereas *P. persimilis* had a significantly shorter corresponding period—3.8 days.

Development time and cannibalism rate of *Neoseiulus neoagrestis* on larval stage

Development time and cannibalism rate were examined using a two-factor experiment: 1) mites kept in groups or individually; 2) with or without food. A total of four experimental treatments were evaluated.

The survival rate of larvae in all experimental treatments was 7275%, regardless of food (present or absent) ($p=0.079$; $F=3.26$). These findings support the facultative nature of larval feeding in *N. neoagrestis*.

Both the rearing method and food availability are significant factors influencing the development rate of *N. neoagrestis* (Fig. 3, Table 2). Group rearing accelerates larval development.

In the presence of food, the larvae of *N. neoagrestis* consumed standard laboratory prey, *Th. entomophagus* eggs. This occurred in 39% of the tested groups and 65% of the individually kept

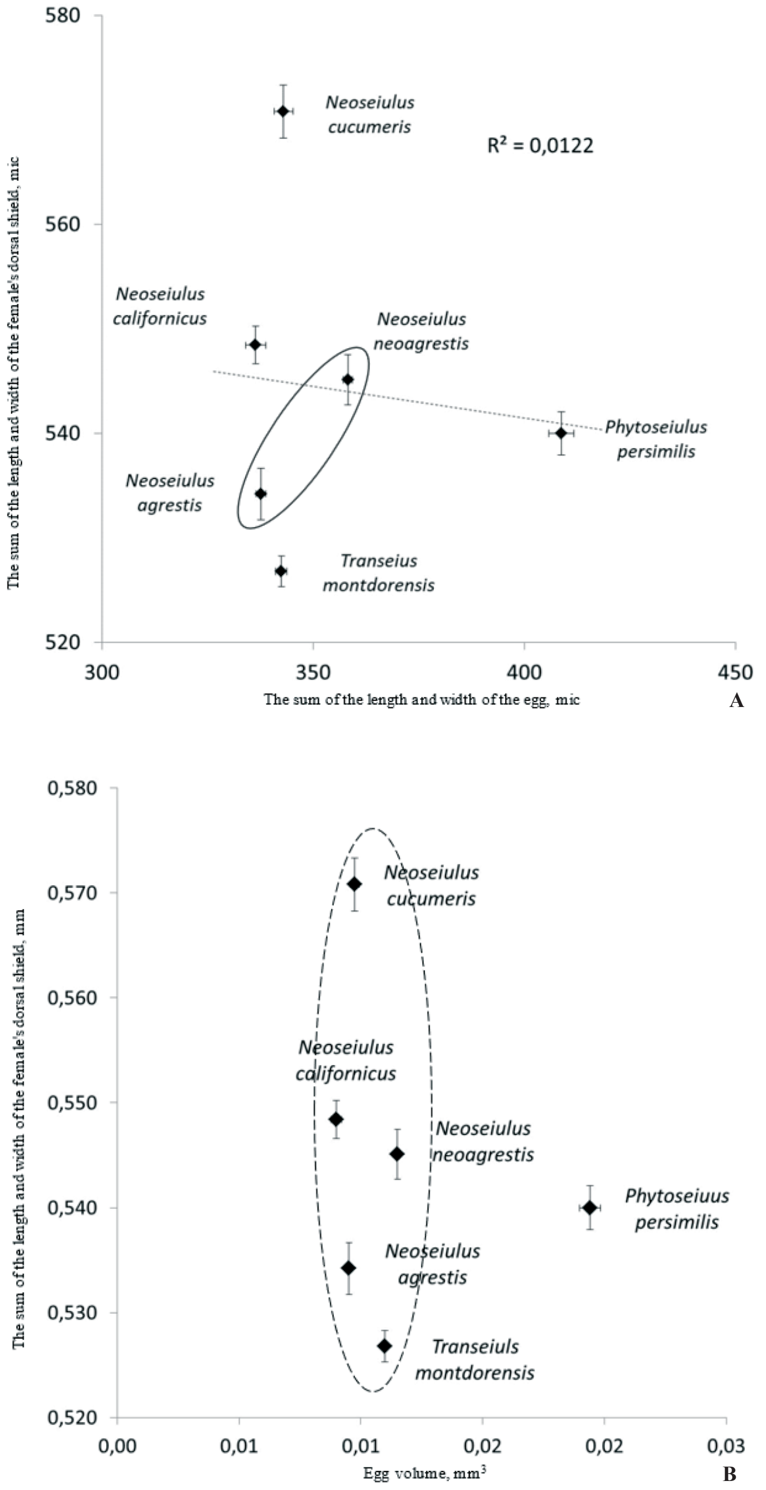

Fig. 1. Morphometric indicators for 6 phytoseiid species. A—size of the dorsal shield and egg (sum of the length and width measurements). B–size of the dorsal shield (sum of the length and width measurements) and egg volume.

larvae. The differences are statistically insignificant (p>0.05).

In experiments where larvae of *N. neoagrestis* were kept in groups, cannibalism has been noticed. The results indicate that larvae consume other larvae less frequently than they do *Th. entomophagus* eggs. Larval cannibalism occurs at the rates of 15–25% and remains consistent regardless of the

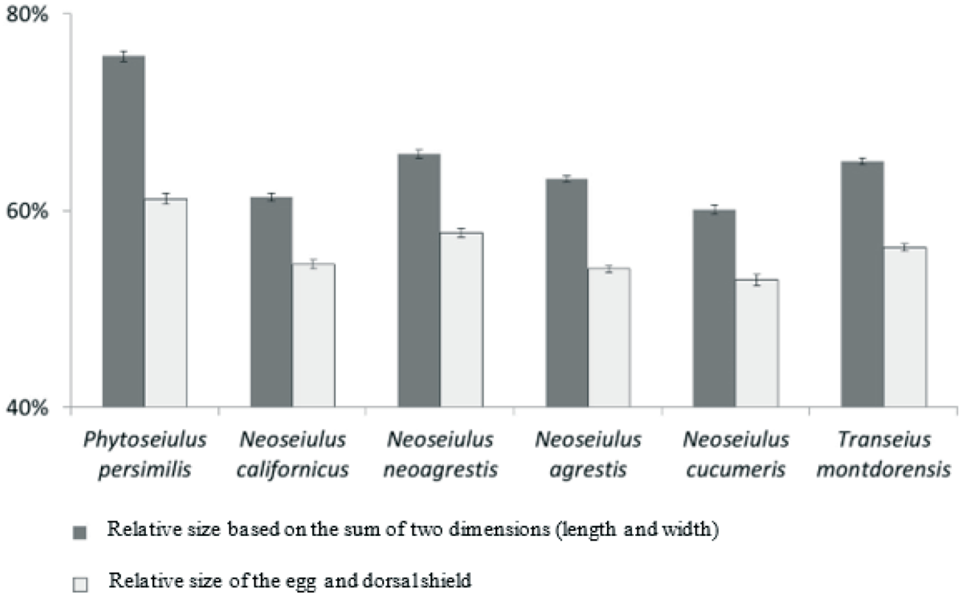

Fig. 2. Interspecific differences in the relative size of the eggs in phytoseiid mites.

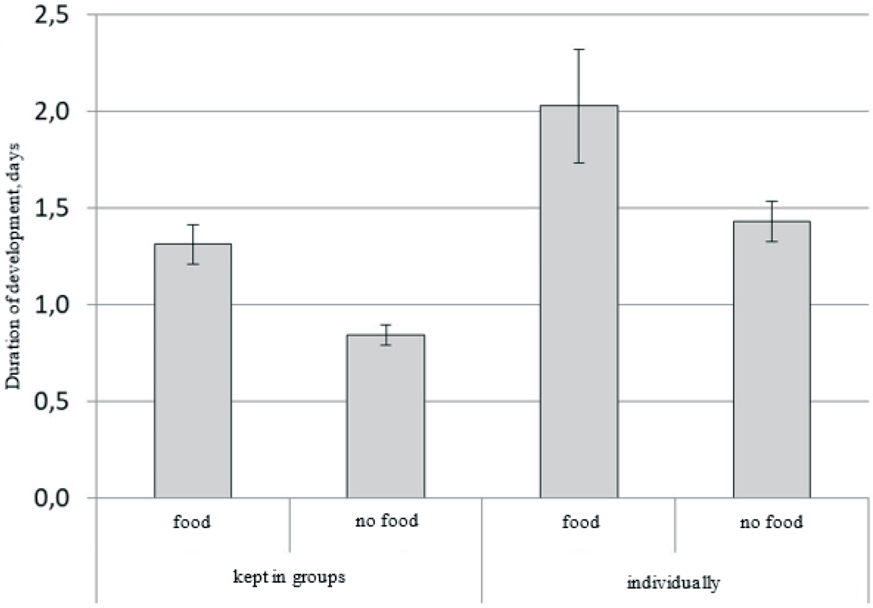

Fig. 3. Larval development time of *N. neoagrestis*.

presence or absence of food. Meanwhile, the frequency of the laboratory prey consummation was 39%. Also, in this experimental variant (group keeping in the presence of food), we observed no difference in the larval development rate between the non-feeding and the feeding larvae. For the feeding larvae, it did not matter whether they consumed *Th. entomophagus* eggs or the conspecific larvae; in either case, they molted at the same time (Tables 3, 4). This indicates that feeding is facultative for the *N. neoagrestis'* larval stage.

The spontaneous level of cannibalism (in the presence of food) varies insignificantly among both the larvae and the protonymphs. In the absence of food, nymphal cannibalism has increased 2.4-fold (Fig. 4, Table 5). In case of the larvae, the absence

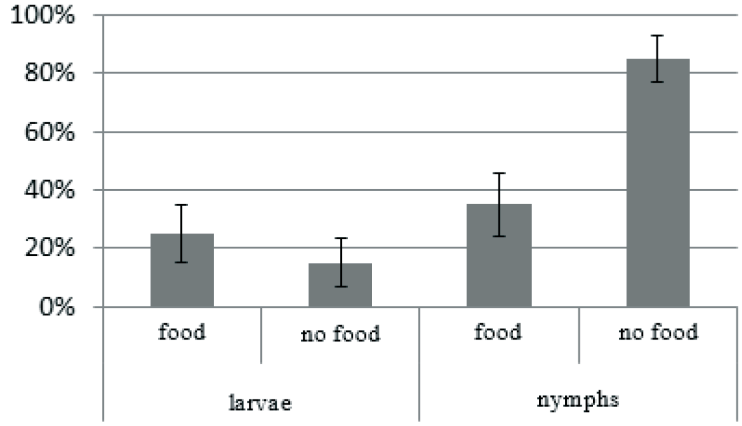

Fig. 4. Cannibalism rate among larvae and protonymphs of N. neoagrestis reared in groups.

of food did not lead to an increase in cannibalism, likely due to the facultative nature of their feeding.

DISCUSSION

Relative offspring size

Several studies have reported data on the egg size (long diameter or volume), which was measured independently of female body size (dorsal shield length) (Croft *et al.* 1999). Even so, it would be difficult to combine such data from different studies into one dataset, since the morphometric parameters depend on the temperature and the food conditions. Finally, only two datasets are suitable for estimating the interspecific variability in the phytoseiid offspring relative size with different types of larval feeding. There are 6 species from this study and 13 species from the results obtained by Croft *et al*. (1999). A separate analysis of these datasets found no correlation between egg size and female body size (Fig. 5). Similar results have previously been noted for the mite species from the suborder Dermanyssiae (Mesostigmata) (Walter and Proctor 2013).

Among the tested species, the smallest relative size of the offspring was found in *N. cucumeris* and

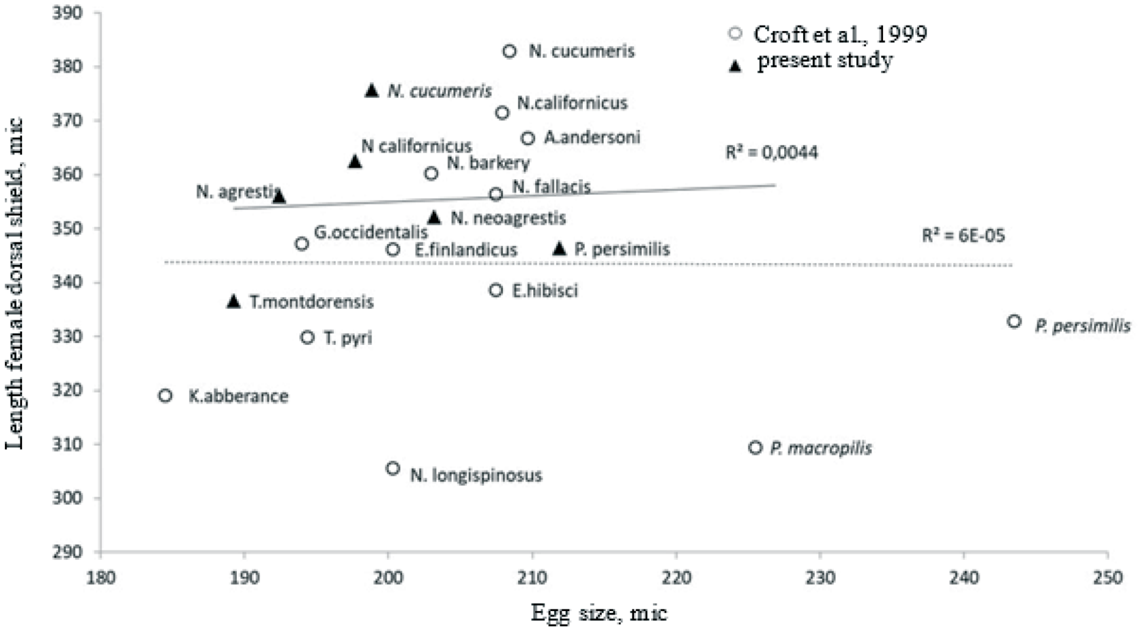

Fig. 5. Egg and body size of phytoseiids (original illustration based on the original and published data).

N. californicus (Fig. 5), whose larvae in natural conditions do not feed or feed facultatively (Chittenden and Saito 2001). The above cases illustrate that with a relative egg size of 53–54%, larvae have enough maternal resources for molting into the next developmental stage without additional nutrition.

The authors believe that the maternal investment in egg production is approximately equal in all tested species of phytoseiids. Even species with relatively small offspring have enough nutrients in their eggs for the larval development and the survival of the protonymphs in the absence of food for several days. For example, in *N. neoagrestis*, starving protonymphs remained viable for 6.5 days, exceeding the average duration reported for all previously studied phytoseiids.

The relative offspring size in phytoseiids is consistently large across all tested species. The eggs constitute approximately 50–70% of the female body size. This is significantly higher compared to the insects of the same size class (up to 400 μm), particularly parasitoids from the genus *Trichogramma*, which are similar in size to phytoseiids. On average, phytoseiid eggs are 1.5–2 times larger (180–250 μm) than those of *Trichogramma* (100–140 μm) (Saakian-Baranova 1990; Boivin 2010). This difference is primarily due to their distinct lifestyles: phytoseiids, as predators, must survive by actively hunting, whereas parasitic trichogrammatids passively obtain nutrients from their hosts. In terms of their substantial maternal investment in the offspring, phytoseiids represent a unique case among the studied microarthropods.

Comparative analysis of the early ontogenesis of *Neoseiulus neoagrestis* and *Phytoseiulus persimilis*

The first two stages of the post-embryonal development (larva and protonymph) account for less than 10% of the total life cycle duration in phytoseiids. However, this brief period is critical for the survival of the individuals. Mortality during these early stages is very high for two main reasons: 1) vulnerability to predators (including conspecifics); 2) larvae and protonymphs are the most common victims of cannibalism (Walzer 1999; Schausberger 2003).

The ability of phytoseiids to search and capture prey during early ontogeny is limited because of their microscopic size (e.g., in *N. neoagrestis*, the egg is 203.2 μm, larva—172.7 μm, protonymph—216.8 μm). The range of suitable prey for the larvae and the protonymphs is mostly restricted to the eggs of the phytophagous mites, which cannot resist.

While larval feeding is mostly facultative, for the protonymph, successful hunting is essential for survival. The longer the protonymphs remain active in search of suitable prey, the higher their chances of survival. Therefore, their resilience to food stress is one of their most important adaptations. Because of it, one of the aspects of our study was to compare the survival rate and the development duration of larvae and the protonymphs in the absence of food.

The obtained results show that the larvae of *P. persimilis* develop twice as fast as those of *N. neoagrestis*, despite the eggs of *P. persimilis* being 1.7 times larger than those of *N. neoagrestis*. Typically, smaller species develop faster. However, in this case, the larger larvae of *P. persimilis* molted sooner than the smaller larvae of *N. neoagrestis*, indicating the opposite trend. One possible explanation for this could be a significantly higher metabolic rate of the larger species, *P. persimilis*.

High metabolic and developmental rates of *P. persimilis* at the larvae stage can be seen as an advantage. But at the protonymph stage, it might have negative consequences for the species. Namely, in our experiments, the protonymphs of *N. neoagrestis* have maintained searching activity without food for 6.5 days, whereas for *P. persimilis* this period was shorter—3.8 days. The difference between the species is highly significant (Table 1).

From our perspective, this result is likely due to the higher metabolism rate of *P. persimilis*. The intensity of metabolism and starvation resistance (i.e., survival in the absence of food) are related through a trade-off relationship: the more intense the metabolic processes are, the faster the species' reserves are depleted during starvation (Stoks *et al*. 2006). Among arthropods, such relationship is noted for antlion larvae (Gotthard *et al.* 1994; Scharf *et al*. 2009).

In the presence of food, protonymphs of *P. persimilis* have an advantage due to their higher development rate, which is in turn based on their rapid metabolism. However, during the periods of temporary prey absence, *N. neoagrestis* gains an advantage by utilizing energy more economically, and, consequently, its protonymphs have more chances to find prey and survive.

Initially, we hypothesized that phytoseiids with relatively large offspring gain an adaptive advantage at the early juvenile stages of development, protonymphs included. However, the analysis of the original and published data does not support this hypothesis. *P. persimilis* has the largest relative offspring size among all studied phytoseiids, but its protonymphs die sooner in the absence of food, compared to the species with smaller offspring: *N. neoagrestis* (present study) and *N. californicus* (Chittenden and Saito 2001). It appears that the interspecific differences in the egg size among phytoseiids do not have a decisive impact on the protonymphs' resilience to food stress. The key factor is most likely the rate of their metabolism.

The larvae of *N. neoagrestis* that had no access to food molted significantly sooner than those that had access to food (Fig. 3, Table 2). Feeding (or perhaps just the presence of prey) seems to slow down larval development. It can be hypothesized that after catching and handling prey, larvae require additional time for digestion. All these factors collectively could delay molting.

When the larvae of *N. neoagrestis* were kept in groups, they developed faster than those kept individually (Fig. 3). A possible explanation for this phenomenon is that the presence of conspecific larvae acts as a stress factor, triggering their molt. This is plausible because larvae already possess all the necessary nutrients to molt into the protonymph stage.

Larvae likely require some time to develop the fourth pair of legs, but, overall, they can accelerate their development to avoid larval cannibalism. The aforementioned process has occurred in the present study.

CONCLUSION

The interspecies variations in the phytoseiid egg size do not directly reflect differences in the maternal investment. *P. persimilis* has the largest offspring size among the tested species, but, in the absence of food, its protonymphs die sooner than the protonymphs of the species with smaller eggs—*N. neoagrestis* and *N. californicus* (present study; Chittenden and Saito 2001). Likely, *P. persimilis* is more sensitive to food stress due to its high metabolic rate.

Phytoseiid species with a high level of resistance to food stress— such as *N. neoagrestis*—are more suitable for preventive releases as part of the "standing army" biocontrol strategy. This approach involves periodic releases of natural enemies before pests occur (Pijnakker *et al.* 2020). Under these conditions, predators must survive without food until the next release, typically about a week. While this is feasible for adult phytoseiids, it is challenging for juveniles, especially in species that are highly sensitive to food stress. However, *N. neoagrestis* has a realistic chance of surviving under such conditions, making it a promising candidate for the preventive inoculation of natural enemies in modern industrial greenhouses.

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Table 1.
Biological characteristics of the early post-embryo development of *N. neoagrestis* and *P. persimilis* in the absence of food.

Trait	*N. neoagrestis*	*P. persimilis*
Mortality rate of larvae, %	4.0±3.4	0+3.7
Mortality rate of protonymphs, %	100–3.6	100–4.0
Development time of larvae, days	1.4±0.12	0.7±0.04
Viability time of protonymphs, days	5.8±0.44	3.6±0.23
Total viability time of larvae and protonymphs, days	6.5±0.7	3.8±0.34

Table 2.
Factors influencing the larval development time of *N. neoagrestis* (the results of two-way ANOVA, n=30).

Factors	**F**	**p**	**Factor impact (η^2)**
Rearing method (mites are kept individually or in groups)	28.254	0.0000009	0.254
Food (present or absent)	19.056	0.0000364	0.187
Interaction of factors	0.264	0.6085376	0.003

Table 3.
Development time of *N. neoagrestis* larvae in the presence of food (*Th. entomophagus* eggs) under group rearing condition (20 groups).

Larval behavior	**Prey**	**Frequency, %**	**Development time, days**
Non-feeding	—	45±5.8	1.2±0.17
Feeding	Conspecific larvae	20±3.8	1.4±0.23
	Lab prey	35±5.4	1.4±0.17

Table 4.
Feeding behavior impact on the development time of *N. neoagrestis* larvae (the results of two-way ANOVA, n=20).

Larval behavior	**F**	**p**	**Factor impact (η^2)**
Feeding or non-feeding larvae	0.668	0.426	0.040
Choose of pray (conspecific larvae or lab pray)	0.335	0.720	0.043

Table 5.
Cannibalism rate of larvae and the protonymphs of *N. neoagrestis* (the results of two-way ANOVA, n=20).

Factors (experimental conditions)	**F**	**p**	**Factor impact (η^2)**
Larvae are kept without food	0.603	0.442	0.016
Protonymphs are kept without food	13.380	0.01	0.260