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**Comparative study on ecological
peculiarities of native and exotic phytoseiid
predators as agents for biological control**

生物的防除利用を目指した土着および輸入天敵カ
ブリダニ類の生態的特性に関する比較研究

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Abstract

In this thesis, I addressed the biology and bionomics of *Neoseiulus cucumeris* (Oudemans) and its most probable competitor *Amblyseius eharai* Amitai and Swirski to explain why *N. cucumeris* could not colonize citrus orchards. Moreover, I attempted to estimate the risk of *Amblyseius* (*Typhlodromips*) *swirskii* (Athias-Henriot) by a comparison of biology and bionomics between *A. swirskii* and *A. eharai*. Of course, to develop a high efficient method of mass-produce for *A. eharai* was a primary aim in this thesis. Furthermore, I studied on a native phytoseiid mite, *Typhlodromus bambusae* Ehara that is a very important and specialized natural enemy in bamboo plantation in China for comparing ecological peculiarities with above-mentioned phytoseiid mites.

The main results of this thesis can be divided 10 parts:

1. In order to know the optimal initial conditions and the rate of *A. eharai* and its prey, *C. lactis*, the initial population level (1000, 2000, 3000 individuals) and rate (predator/prey: 1:10, 1:20, 1:30 and 1:40) were assembled in the experiment of mass rearing. The results showed that 3000 individuals as the initial population was better than 1000 or 2000 individuals within 15 days (when the shortest producing period was expected). If the longer storage period (more than 15 days) was demanded, 2000 individuals as the initial population was the best choice. Similarly, the mass-producing efficiency of the rate (predator:prey) 1:40 was best if we need many *A. eharai* by 15 days after mass-production started. However, by 20-30 days, the rate

1:20 (predator : prey) showed a better efficiency than the other rates. However, a longer storage period is more important based on the industry standard, I suggested the combination of 2000 (initial population) and 1:20 (the rate of predator and prey) is optimal.

2. I had developed a high efficiency and cheap way to mass-produce *A. eharai*. In order to evaluate the potential of *Aleuroglyphus ovatus* Troupeau and *Carpoglyphus lactis* (Linnaeus), which have been used for mass-production of some other phytoseiids, as a prey for rearing *A. eharai*, the life history of *A. eharai* when it fed upon *A. ovatus* or *C. lactis* under laboratory conditions (25°C) was observed. The females and males of *A. eharai* could complete their development with *A. ovatus* as prey. However, *A. eharai* males could only survive 3-5 days and seldom mated with females. Therefore, *A. ovatus* was thought to be not a sufficient prey for mass-producing of *A. eharai*. On the other hand, the females or males *A. eharai* could develop to adulthood by feeding upon *C. lactis*, and the female developmental period (6.7 days from egg to adult) was shorter than that of *A. swirskii* and *N. cucumeris*. When supplying *C. lactis* as prey, the total fecundity of *A. eharai* was 51.1 eggs/female with the daily fecundity 2.5 eggs/female/day. Its net reproductive rate ($R_0 = 33.849$) was higher than *N. cucumeris*, but less than *A. swirskii*. The sex ratio was biased towards females (66.24%), while the intrinsic rate of increase ($r_m=0.253$) was highest. Thus it was suggested that *C. lactis* is a profitable prey mite for mass-producing *A. eharai*.

3. In order to evaluate the efficiencies of two predators on the biological control of

Panonychus citri McGregor, the life histories of *A. swirskii* and *A. eharai* with the prey *P. citri* were studied at $25 \pm 1^{\circ}\text{C}$. The results showed that the developmental period of the larval stage and a whole generation of *A. swirskii* were significantly shorter than those of *A. eharai*, but no significant differences in developmental period between these two species were observed in the other stages. In addition, the larva of *A. swirskii* could develop into a protonymph without prey, but prey was necessary for larval development of *A. eharai*. The fecundity of the adult female of *A. eharai* was significantly higher than that of *A. swirskii*. The net reproductive rate (R_0) of *A. eharai* was higher than those of *A. swirskii*, nevertheless there was not difference in the intrinsic rate of increase (r_m) between *A. eharai* and *A. swirskii*.

4. The ability of predatory mites to endure starvation and low humidity must be important to maintain their populations in unfavorable environments. The effects of starvation and humidity on the development and survival of *A. swirskii* and *A. eharai* were studied in the laboratory. The results showed that most eggs of *A. eharai* could not hatch at humidities lower than 60% R.H. When the prey was absent, protonymphs or gravid females of *A. swirskii* survived significantly longer than *A. eharai* at 60–100% R.H., respectively. Furthermore, at lower humidities (60–70% R.H.) the trend was very similar in the virgin females. It indicated that *A. swirskii* might be a stronger competitor relative to *A. eharai* under starved and low humidity conditions.

5. Three predatory mites, either female or male, could develop adulthood when they performed intraguild predation. Moreover, they all could oviposit. The results indicated anyone among them was the intraguild predator to others. The r_m of 0.134

/day obtained from the present study when *A. swirskii* feeded solely upon *A. eharai* eggs at 25°C. Moreover, the r_m of *A. eharai* was 0.124 females/female/day when it preyed upon *A. swirskii* eggs. In addition, when *A. swirskii* preyed on *N. cucumeris* eggs, the r_m of 0.196 /day was obtained. The data was similar to the r_m of *N. cucumeris* 0.191 females/female/day, when *N. cucumeris* preying upon *A. swirskii* eggs. Therefore, either *A. swirskii* and *N. cucumeris* or *A. swirskii* and *A. eharai* had the similar r_m when they performed intraguild predation. When *N. cucumeris* eggs were supplied as prey, the r_m of *A. eharai* was 0.186 /day. This data was significantly higher than that of *N. cucumeris* when the latter performed intraguild predation with the eggs of former as prey. It suggested that the competitive ability of *A. eharai* was higher than *N. cucumeris* when they cohabited.

6. Three predatory mites species (female or male) all could develop to adulthood by cannibalism. However, the developmental period of egg-to-egg of cannibalistic *A. swirskii* was longest in three predatory mites, due to the longest preoviposition period (8.50 days). It indicated the conspecific eggs were not high quality food for reproduction of *A. swirskii*, because the preoviposition period of female *A. swirskii* was only within 2.58-3.35 days with *A. eharai* or *N. cucumeris* eggs as prey. It is noticeable that the reproduction of *A. eharai* was significantly higher when preyed upon conspecific eggs than heterospecific eggs. It suggested that the quality of heterospecific prey is not always higher than that of conspecific prey. Furthermore, we showed that *A. swirskii* could still reproduce, albeit at a much lower rate, when feeding solely upon conspecific eggs.

7. How competition between species having similar ecological niche affects their coexistence has been an important ecological theme. On the other hand, species displacement by introduced or invaded species is also very important problem in biological control and conservation ecology. I attempted to observe whether two phytoseiid species, among *A. eharai*, *A. swirskii* and *N. cucumeris*, coexist with their extraguild prey *C. lactis* in closed cages for three species of phytoseiid mites under 25 °C, long-day length and 60-80 % R.H. conditions. At first we determined that a single population (initial density was 10 females/cage) of each phytoseiid species attained plateau for 18 to 25 days with extraguild prey after their introduction into the experimental apparatus, suggesting there were density dependent factors. By regression analyses hypothesized Lotka-Volterra equation, the population increase rate (r) and carrying capacity (K) of each species were estimated from the observed population dynamics data. Next, we observed the interaction of two phytoseiid species (5 females + 5 females) under abundant extraguild prey conditions. In all combinations of species, one species became extinction and the other increased its population, even though there were sufficient extraguild preys. *A. swirskii* was always the winner when it accommodated into a closed cage either with *A. eharai* or with *N. cucumeris*. Furthermore, *A. eharai* was winner in the competition with *N. cucumeris*. The extinction was caused by a kind of competition. We made numerical calculation using modified Lotka-Volterra equations by assuming two factors, intraguild predation and competition other than predation. By comparing the sensitivity of two kinds of factors by the numerical calculation, i.e. intraguild predation and competition other than predation, to actual population dynamics of paired species, we suggested

that the intraguild predation is more plausible factor to explain the present results in all the combination of interactions.

8. As another factor of competition between species, I conducted an experiment about reproductive interference. No females of three phytoseiid mites could lay eggs, when they were accommodated into a closed cage with two heterospecific males. Moreover, no reproductive interference was observed between *A. eharai* and *N. cucumeris*, and between *A. swirskii* and *N. cucumeris*. However, a noticeable interference between *A. eharai* and *A. swirskii* was observed: There was no significant difference in the fecundity of *A. swirskii* between "two conspecific males" and "one conspecific and one *A. eharai* males". *A. swirskii* female with one conspecific male and one heterospecific male did not decrease its fecundity. However, *A. eharai* females cohabited with "one conspecific male" and "*A. swirskii* male" significantly decreases its fecundity. It suggested that there is some kind of reproductive interference between them. Nevertheless, *A. eharai* females could not lay eggs when they cohabited with only *A. swirskii* males. Because the mating behavior was observed between *A. eharai* females and *A. swirskii* males, a hypothesis that *A. eharai* females could successfully mate *A. swirskii* males, and the reproductive incompatibility caused the decrease of *A. eharai* fecundity is plausible. Since the fecundity of *A. eharai* females was descending when it cohabited with one conspecific male and one *A. swirskii* male, I suggested that the heterospecific mating sometimes occurred, and then the sperms from *A. swirskii* occupied the partial space of spermatheca of *A. eharai* females, which disturbed the fertilization of *A. eharai* eggs.

9. The predators firstly prey upon the phytophagous pests in general, due to their natural feeding habits. However, if two species of predator coexist in a habitat, any predator should make a choice between another predator (intraguild predation) and pests (extraguild prey). In the present study, the predation rate of *A. swirskii* females to *N. cucumeris* eggs was ten times compared with the predation rate to conspecific eggs, even though there were sufficient extraguild preys, *C. lactis*. On the contrary, *N. cucumeris* equally preyed upon both conspecific and *A. swirskii* eggs. In addition, *A. swirskii* showed obvious preference for *A. eharai* eggs. On the other hand, *A. eharai* females equally preyed upon both conspecific and *A. swirskii* or *N. cucumeris* eggs, but they preferably ate *N. cucumeris* larvae. In the combination of *A. eharai* and *N. cucumeris*, both predators equally preyed upon the conspecific and heterospecific eggs. The results showed that *A. swirskii* would win in the competition either with *A. eharai* or with *N. cucumeris* as shown in the competition experiments. In addition, *A. eharai* would be a winner when it competed with *N. cucumeris*, due to the higher predation rate of *A. eharai* to *N. cucumeris* larvae.

10. There was an important difference between cannibalism between unrelated individuals and between a mother and its offspring, because the former can be defined as a form of intraspecific competition, but the latter affects the inclusive fitness of individuals. Many examples of cannibalism have been reported in predacious phytoseiid mites. Furthermore, sib cannibalism avoidance is known in several species. However, whether females' actually prey upon their offspring under starved conditions has yet to be established. Here, female performance towards their

offspring under no-prey-other-than-offspring conditions was observed in four phytoseiid species, *A. eharai*, *A. swirskii*, *N. cucumeris* and *T. bambusae*. *T. bambusae* females only survived for 4.14 ± 0.42 days and there was a significant difference in survival period between *T. bambusae* and the other three species (all survived more than 8 days). *N. cucumeris* females survived longer than *A. eharai* and *A. swirskii* females, whereas there was no difference between *A. eharai* and *A. swirskii* females. On the other hand, the offspring of *A. eharai*, *A. swirskii* and *N. cucumeris* died earlier in mother-presence than in mother-absence (egg alone) experiments, suggesting that cannibalistic interactions occur between mother and offspring. The survivorship of *T. bambusae* offspring in the mother-presence condition did not differ from the mother-absence condition, indicating that kin cannibalism is rare in this species.

Base on the present study, I concluded that the exotic predatory mite, *A. swirskii*, should be restricted for use in open fields in China. Because *A. swirskii* have high abilities of competition, there is a high risk of native species displacement. The fact that *A. swirskii* excluded population of *A. eharai* under laboratory conditions must indicate such fear. In addition, why *N. cucumeris* did not colonize citrus orchard in China could be partly explained by the inequality in intraguild predation between *N. cucumeris* and a native species, *A. eharai*.

Chapter 1. Introduction

The main objective of this research is to establish biological control in agricultural fields, such as citrus orchards and bamboo plantations in China. There are several useful predatory mites to control pest spider mites and small insects. Thus I addressed the ecological peculiarities of two indigenous predator species, *Amblyseius eharai* Amitai & Swirski and *Typhlodromus bambusae* Ehara and two introduced species, *Amblyseius swirskii* (Athias-Henriot) and *Neoseiulus cucumeris* (Oudemans) in the details.

1.1. The research background

The citrus fruit is one of the foremost agricultural products in China, also in the world. There were 2430 thousand hectare of citrus in China until 2013, the main producing areas were located at Jianxi, Shichuan, Guangxi, Guangdong, Hubei, Chongqing, Fujian, Zhejiang and Guizhou provinces. The cultivated breeds were *Citrus sinensis*, orange, *Citrus reticulata*, pomelo and lemon, respectively, and *C. sinensis* is the main varieties. According to the government report, the total output was over 3.276 million tons in 2013, and it was 24.56% of the world's total citrus production. So, citrus is very important for Chinese agriculture. In addition, Moso bamboo, *Phyllostachys pubescens* (Mazel) plantation is another important crop in Fujian province.

However, China is not a powerful country among citrus producing countries, even though the total citrus fruit production of China has exceeded that of Brazil, American, Mexico and Spain base on FAOSTAT data (2007). The low quality of fruit

with many pests is the main reason. Large amounts of various chemical pesticides were sprayed into citrus orchards every year, which is an important reason resulted in the low quality of citrus fruits. Nevertheless, the pesticides are necessary for obtaining the high yield, because there are many pests in Chinese citrus orchards.

According to the previous reports, 853 pest species can damage citrus (Zhang *et al.* 1997), which belong to Noctuidae, Coccidae, Cicadellidae, Acrididae, Aleyrodidae, Coreidae, Papilionidae, Rutelidae, Chrysomelidae, Thripidae, Cetonidae, Pseudococcidae, Curculionidae, Lymantriidae, Limacodidae and Tetranychidae, respectively. Among them, pest mites are the primary in anywhere of China (Zhang *et al.* 1997), including *Panonychus citri* McGregor, *Eotetranychus kankitus* Ehara and *Phyllocoptruta oleivora* Ashmead (Zhang *et al.* 1997; Ji *et al.* 2012). To control these pest mites, citrus farmers generally spray acaricide 6 to 12 times per year (Wang 2004). However, in the 1970s and 80s, these pest mites had never been so important. Many reports suggested that bactericide and pesticide are responsible for increasing damage of pest mites (Zhang *et al.* 2003; Ji *et al.* 2012). For example, copper compounds and pyrethroids, they have been frequently used. However, the former killed the *Hirsutella thompsonii* Fisher which is an efficient parasitic fungal of citrus rust mite (Aghajanzadeh *et al.* 2006). Furthermore, the later significantly reduced the populations of natural enemies, because it is a high toxicity and nonselective pesticide to all phytoseiid mites in comparison with their prey (Croft and Whalon 1982).

Whether natural enemies certainly can control pest mite populations when the spraying of chemical pesticides is stopped? Obviously, the answer is negative. Firstly, sometimes the pesticides are necessary to control other pest insects and/or diseases

other than pest mites. Secondly, natural enemies cannot always perform well, because their populations are very scarce relative to its prey in early spring of every year (Ji *et al.* 2012). Because of them, the artificial introduction of natural enemies in agricultural ecosystems becomes necessary to control the pest mite populations.

In fact, there are 536 species of natural enemy had been reported in Chinese citrus orchard, including 21 species of predatory mites (Zhao 2000), for example, *Agistemus exsertus* Gouzalez, *Amblyseius makuwa* Ehara, *Amblyseius newsami* (Evans), *Amblyseius eharai* Amitaiet and Swirski, *Amblyseius herbicolus* (Chant), *Amblyseius orientalis* Ehara, *Anystis baccarum* (Linnaeus), *Euseius nicholsi* Ehara & Lee, *Euseius ovalis* (Evans), *Neoseiulus pseudolongispinosus* Xin, Liang & Ke, *Neoseiulus longispinosus* (Evans) and so on (Pu *et al.* 1990; Xu *et al.* 2013). Among them, *A. exsertus* widely distributed over most of citrus and other fruit trees in China. *A. eharai*, *E. nicholsi* and *E. ovalis* were also dominant in many districts (Ji *et al.* 2012). However, these predatory mites cannot control the population of pest mites in natural condition due to their lower density early in the spring (Ji *et al.* 2012). Although the predacious mites usually increase their populations and control the populations of pest mites in autumn when farmer has ceased chemical pesticide spraying, citrus farmers hardly accepted such conditions.

An approach to overcome this problem is to release mass-produced natural enemies in response to the increases of pests. In the past 30 years, many species of predatory mite had been released into citrus orchards to control the citrus pest mites, for example, *A. newsami*, *E. nicholsi*, *A. orientalis*, *A. deleoni* (synonym of *A. eharai*) and *Amblyseius aiawai* Ehara & Bhandhufalck and so on (Ye *et al.* 1985; Li *et al.*

1992; Xiong *et al.* 1988; Gan *et al.* 2001). Unfortunately, these attempts failed, because those predatory mites are relatively difficult to produce on a large scale with low cost (Peng *et al.* 2009; Xu *et al.* 2013).

Ramakers and Van-Lieburg (1982) discovered that storage mites, which are very easy to rear with some crops and yeast, could be used to mass-produce some phytoseiid mites as alternative prey. They developed a commercialized production method of *Amblyseius mckenziei* Schuster and *N. cucumeris*. This method makes it possible to mass-produce predatory mites with very low cost. In 1996, Fujian academy of agriculture sciences of China introduced *N. cucumeris* from BCP Company of England. Until 2000, we developed the mass-produce systems of *N. cucumeris* with *Aleuroglyphus ovatus* (Troupeau) as prey mite (Zhang *et al.* 2002). Then this predatory mite was widely used in citrus orchards to control the citrus spider mites. Many reports suggested it performed well to control the population of *P. citri* (Zhang *et al.* 2003). However, some problems had been left; for example, this predator has low efficiency to control *E. kankitus* and *P. oleivora* (Ji *et al.* 2012). In addition, *N. cucumeris* cannot establish its population for long time on the citrus in China. In this thesis, I would contrast the biology and bionomics between *N. cucumeris* and its most probable competitor *A. eharai*, which is the dominant predatory mite in Chinese citrus orchards (Ji *et al.* 2012), to explain why *N. cucumeris* could not colonize citrus orchards.

Another introduced predator species, *A. swirskii* with stronger ability to adapt to citrus ecosystem, would be a preferable alternative (Hale 2006). This species belong to Subtype III-b—Generalist predators living on glabrous leaves according McMurtry

et al. (2013). Therefore, it was expected to adapt the leaves of citrus more than *N. cucumeris*. Although *A. swirskii* had been introduced into China (Ji *et al.* 2010), it however have not been widely used because considering the possible invasion risk. A similar risk had been confirmed in *Typhlodromus pyri* Scheuten that had excluded *Amblyseius andersoni* Chant in German apple orchards (Lange and Trautmann 1994). Furthermore, it was known that *Neoseiulus californicus* (McGregor) displaced *Neoseiulus womersleyi* Schicha in the central and southwestern Japan (Gotoh *et al.* 2014). Several studies indicated that the risk was closely related to interspecific competition (Wan *et al.* 2009). Therefore, it is very important to estimate the possible invasion risk of introduced *A. swirskii* before releasing into the citrus ecosystem. In this study, I compared the biology and bionomics between *A. swirskii* and its most probable competitor *A. eharai*, which is a dominative predatory mite in Chinese citrus orchards (Ji *et al.* 2012).

On the other hand, other than these exotic predatory mite species, the utilization of native species may be a better choice for the biocontrol of pest mites, because there is no invasion risk. Furthermore, native predatory mites have obviously stronger adaptability to citrus ecosystem of China, because they might originate from China ecosystems. However, to use native predator species for the control of citrus pests, the development of efficient mass rearing method is necessary. Then I attempted to develop a method to mass-produce *A. eharai* with low cost.

Apart from the problems in citrus orchards in China, pest mites have been very serious in moso bamboo plantations (Zhang *et al.* 1997). In order to understand the ecological peculiarities of phytoseiid mites, I also studied on the biology of *T.*

bambusae that is considered the most important natural enemy of bamboo pest mites in China. Because there is no way to mass-produce this predator species by alternative food, such as *C. lactis*, the study on this species became a little bit fragmentary. However, it is worthwhile to observe this specialized predator (type I life style, Subtype I-b—Specialized predators of web-nest producing mites (Tetranychidae) in McMurtry *et al.* (2013)) in comparison with the other three phytoseiid species.

1.2. Brief introduction of four phytoseiid mites observed in this study

1.2.1. *Amblyseius eharai* Amitai & Swirski

According to McMurtry *et al.* (2013), *A. eharai* has the type III life style, i.e. subtype III-b: Generalist predators living on glabrous leaves.

This species was denominated by Amitai and Swirski in 1981 (Amitai and Swirski 1981). *Amblyseius deleoni* Muma & Denmark and *Amblyseius largoensis* (Muma) were its synonym. It is distributed China, Japan, Malaysia and Korea (Wu 2008). Many studies in China have shown that *A. eharai* is an effective natural enemy of *P. citri*. In addition, *A. eharai* was a dominant predatory mite in tea, loquat, lichi, longan, ornamental, bamboo and so on. Kakimoto *et al.* (2004) reported the potential of *A. eharai* to control thrips.

Although many researchers tested a lot of different prey and pollen to mass-produce *A. eharai*, for example different pollens (Saito and Mori 1975; Wei *et al.* 1993; Pu *et al.* 1995), those attempts are not always successful because pollens were very difficult to collect and conserve. The detailed explanations of this species appeared in the appendix.

1.2.2. *Amblyseius swirskii* (Athias-Henriot)

McMurtry *et al.* (2013) categorized *A. swirskii* into the Type III life style: Subtype III-b, i.e. generalist predator living on glabrous leaves.

This species is a well-known biological control agent used worldwide, because it has a high efficiency to biocontrol spider mites, thrips and white flies. On the other hand, there is an unresolved problem on the introduction of this species into China, because of its supposed negative effect on native fauna. This predator was originated from east Mediterranean and distributes citrus, cotton, fig and so on. The detailed explanation of this species appeared in the appendix.

1.2.3. *Neoseiulus cucumeris* (Oudemans)

The phytoseiid mite, *N. cucumeris*, has been commercially produced by storage mite (Ramakers and Van-Lieburg 1982) for biological control of thrips and mites. In greenhouse, it has been frequently used to control *Frankliniella occidentalis* (Pergande), *Thrips tabaci* (Lindeman) and *Thrips palmi* Karny and so on (Pijnakker and Ramakers 2008; Krasavina *et al.* 2009; Kurogi *et al.* 2011). In China, it has been commercially mass-produced (Fujian Yanxuan biocontrol technology co., ltd.) and widely used in citrus, cotton and apple (Zhang *et al.* 2002; Kong *et al.* 2008; Li and Ma 2012). However, in commercial fields it had been gradually replaced by other highly efficient predators, *A. swirskii*, *Typhlodromips montdorensis* (Schicha) and *Amblydromalus* (*Typhlodromalus*) *limonicus* Garman & McGregor (Pijnakker and Ramakers 2008; Vangansbeke *et al.* 2014; Holmes and GreatRex 2011). The detailed explanation of this species appeared in the appendix.

1.2.4. *Typhlodromus bambusae* Ehara

The predator of *Stigmaeopsis* spider mites, *T. bambusae*, has the Subtype I-b: Specialized predator of web-nest producing mites (Tetranychidae) according to McMurtry *et al.* (2013). It was a dominant predator associated with the mite pests of Moso Bamboo. This subtype contains only *T. bambusae* that have adapted to attacking *Schizotetranychus*, *Stigmaeopsis* and some *Oligonychus* spider mites producing the so-called woven nests (WN-u life type). It was thought that this phytoseiid co-evolved with their prey, *Stigmaeopsis* spp. (Saito 1990 b). In fact, Gotoh and Shida (2007) reported that almost all phytoseiid mites collected in the nests of *Stigmaeopsis longus* (Saito) were *T. bambusae*. The detailed explanation of this species appeared in the appendix.

Chapter 2. General materials and methods

2.1. Mite sources and rearing

2.1.1. *Amblyseius eharai* Amitai & Swirski

The population of the native predatory mite, *A. eharai*, was originally collected from a citrus orchard in Fuzhou, Fujian Province, China on 11, October 2012. The mites were reared and maintained with *P. citri* as prey on citrus leaflets, which had been placed on water-soaked spongia in Petri dishes (Fig. 1) for at least 2 years before the present experiment. The mites were kept under 27 °C, 16:8 h (L:D) photoperiod and 80±5% RH conditions in a laboratory of the Institute of Plant Protection, Fujian Academy of Agriculture. After the discovery of alternative food (*Carpoglyphus lactis* (Linnaeus)), they were reared on black plastic sheets circled with tangle-foot, which had been placed on water-soaked plastic foam substrate in Petri dishes (Fig. 2) with this new prey.

2.1.2. *Amblyseius swirskii* (Athias-Henriot)

The exotic predatory mite, *A. swirskii*, was imported from Koppert B.V. (Berkel en Rodenrijs, Netherlands) in 2007. The mites were reared on black plastic sheets circled with tangle-foot, which had been placed on water-soaked plastic foam substrate in Petri dishes (Fig. 2) with *C. lactis* as prey in the laboratory under 27°C, 16:8 h (L:D) photoperiod and 80±5 %RH conditions.

2.1.3. *Neoseiulus cucumeris* (Oudemans)

The exotic predatory mites, *N. cucumeris*, were imported from BCP (BCP Certis®, United Kingdom) in 1996. This predatory mite had been mass produced in an ventilate acrylic bottle (Fig. 3) with *Aleuroglyphus ovatus* (Troupeau) as prey mites at the Institute of Plant Protection, Fujian Academy of Agriculture since 2000.

2.1.4. *Typhlodromus bambusae* Ehara

The native predatory mites, *T. bambusae*, were collected from *Phyllostachys pubescens* (Mazel) in the bamboo forest in Nanping City, Fujian Province, China on September 30, 2013. It was reared for at least one generation with *Stigmaeopsis nanjingensis* (Ma & Yuan) and *Stigmaeopsis miscanthi* (Saito) as prey on the undersurface of detached *P. pubescens* and *Miscanthus sp.* leaves under 25°C, 14:10 h (L:D) photoperiod and 80±5 %RH conditions in a laboratory at the Institute of Plant Protection, Fujian Academy of Agriculture. The leaves had been placed on water-soaked plastic foam substrate and spread on water soaked cotton in Petri dishes (Fig. 4).

2.1.5. *Panonychus citri* (McGregor)

The phytophagous mites (prey mite for phytoseiids), *P. citri*, were collected from the citrus orchards in Fuzhou City, Fujian Province, China on 11, October 2012. The populations of *P. citri* were maintained on citrus seedlings in a greenhouse with 25–30°C, 60–90%RH and natural photoperiod at the Institute of Plant Protection, Fujian Academy of Agriculture.

2.1.6. *Carpoglyphus lactis* (Linnaeus)

The dried fruit mites, *C. lactis*, were obtained from Fujian Agriculture and Forestry University in 2008. These mites were cultured with yeast as food in a ventilate case (Fig. 5), all cases were put into a culture box under 25°C, 14:10 h (L:D) photoperiod and 80±5 %RH in a laboratory at the Institute of Plant Protection, Fujian Academy of Agriculture.

2.1.7. *Aleuroglyphus ovatus* (Troupeau)

The acarid mites, *A. ovatus*, were collected from a food market in Fuzhou City, Fujian Province, China on 11, October 2000. The population of *A. ovatus* were cultured with wheat bran as food in an ventilate acrylic bottle (Fig. 3), all bottles were put into a culture box under 25°C, 14:10 h (L:D) photoperiod and 80±5 %RH in a laboratory at the Institute of Plant Protection, Fujian Academy of Agriculture.

2.2. Experimental apparatus

2.2.1. Leaf disk method for spider mites and predators

The experimental apparatus-1 (Fig. 1) consisted of a Petri dish (120.0 mm in diameter) with a water-soaked plastic foam substrate (110.0 mm in diameter and 1 cm thick) inside. A citrus leaflet without mite damage was placed on the plastic foam substrate with its abaxial surface facing up. An area on citrus leaf was encircled with a thin cotton wool barrier to prevent predatory mites and spider mites from escaping. The leaf stipe was twined with cotton wool strip, and cotton was put into the water for moisturizing to the leaf. The spider mites or/and predatory mites were introduced on

the area encircled with cotton wool barrier with a fine brush. If the leaves become withered and yellow, new leaves were prepared.

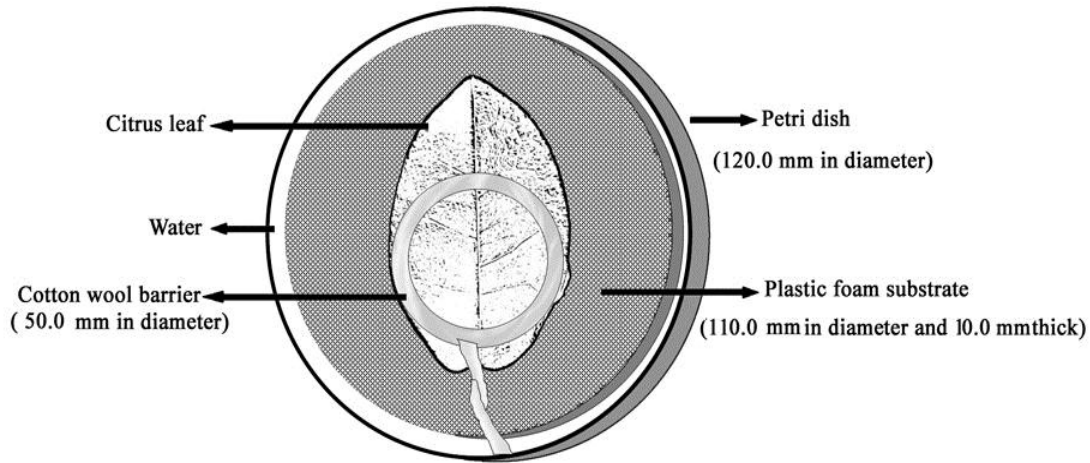


Fig. 1. Experimental apparatus-1 for predatory mites with *Panonychus citri*.

2.2.2. Plastic film disk for predators with Acarid mites

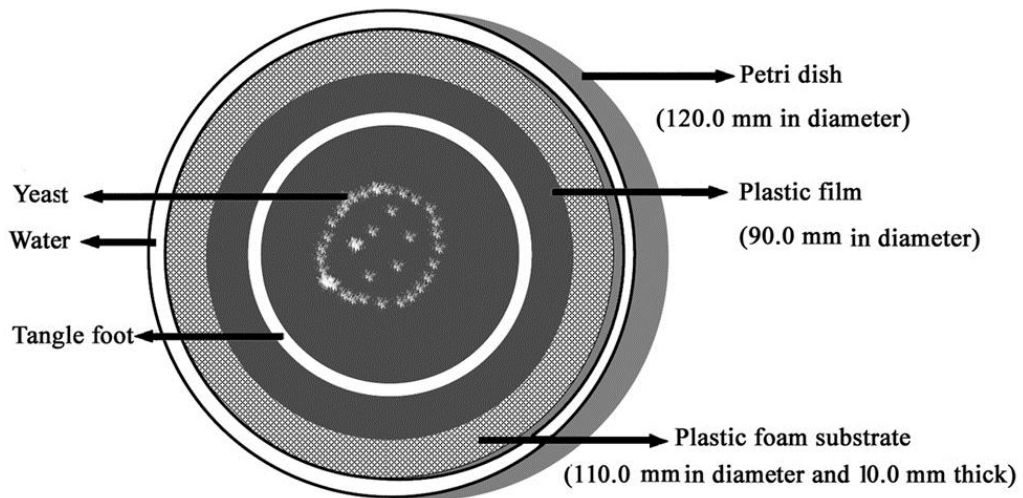


Fig. 2. The experimental apparatus-2 for predatory mites with *C. lactis* as prey.

The experimental apparatus-2 (Fig. 2) consisted of a water-soaked plastic foam substrate (110.0 mm in diameter and 1 cm thick) in a Petri dish (120.0 mm in diameter). A sheet of plastic film (90.0 mm in diameter) was placed on the plastic

foam substrate. And some yeast was put on the plastic film as the food of the mites. The margin of plastic film was encircled with tangle foot as barrier to prevent predatory mites from escaping. The acarid mites or/and phytoseiid mites was introduced on the plastic film. The yeast must be added if scarcity.

2.2.3. Mass-producing bottle of predators

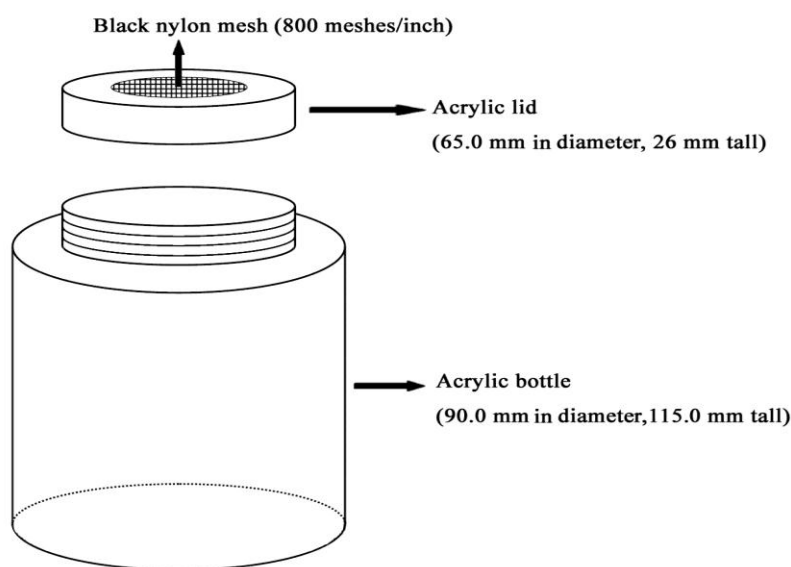


Fig. 3. The experimental apparatus-3 for mass producing of predatory mites.

The experimental apparatus-3 (Fig. 3, approximately 1 Litre) consisted of an acrylic bottle (90.0 mm in diameter and 115.0 mm tall) with a lip (65.0 mm in diameter and 26.0 mm tall). There was a hole in the middle of the lip. In addition, a sheet of black nylon screen (800 eyes, 40 mm in diameter) was melted and bonded upon the hole by heat-sealing for gas exchange.

2.2.4. Bamboo leaf disk for predators and spider mites

The experimental apparatus-4 (Fig. 4) consisted of a water-soaked plastic foam

substrate (110.0 mm in diameter and 10.0 mm thick) in a Petri dish (120.0 mm in diameter) with water. A piece cotton wool (90.0×90.0 mm) was extended over the foam. Then bamboo leaflet without mite damage was placed on the cotton wool plate with its abaxial surface facing up. Two strips of cotton wool barriers were put on both ends of the bamboo leaflet to moisturize the leaves and prevent predatory mites and spider mites from escaping.

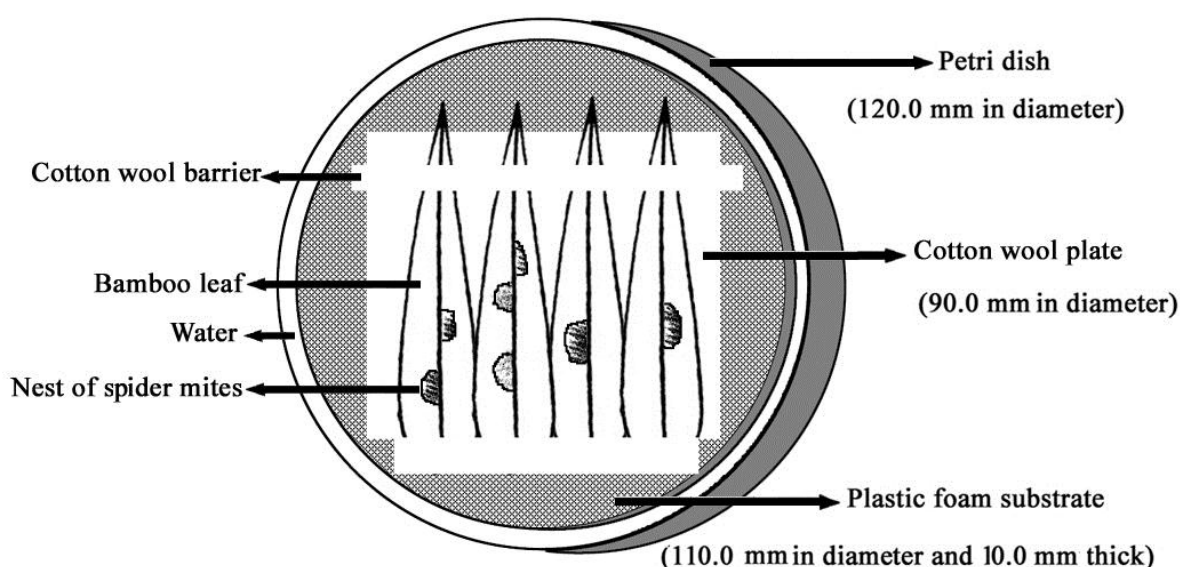


Fig. 4. The experimental apparatus-4 for *Stigmaeopsis* mites and *T. bambusae*.

2.2.5. Rearing cage for acarid mites

The experimental apparatus-5 (Fig. 5) was an acrylic case (64.8 mm in diameter and 30.0 mm tall) with a lip (65.0 mm in diameter and 15.0 mm tall). There was a hole (40.0 mm in diameter) in the middle of the lip. In addition, a sheet of black nylon screen (800 eyes, 48 mm in diameter) was melted and bonded upon the hole by heat-sealing for gas exchange. When beginning to rear *C. lactis*, a little of water was put into the case before introducing yeast and mites.

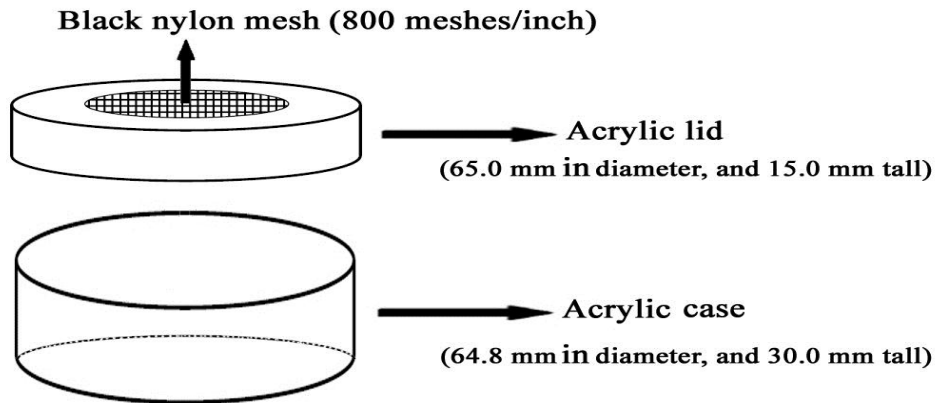


Fig. 5. The experimental apparatus-5 for *Carpoglyphus lactis*.

2.2.6. Rearing cage for mite life history study

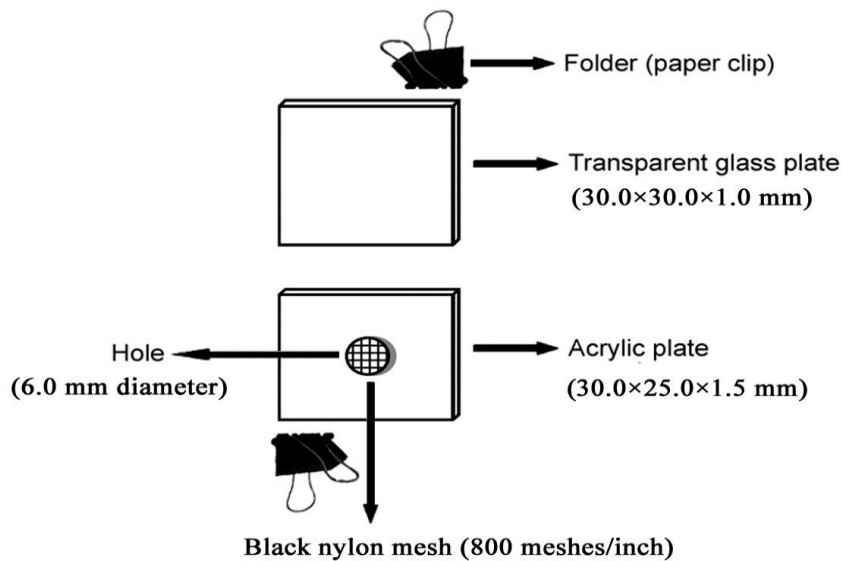


Fig. 6. The experimental apparatus-6 for life history study.

The experimental apparatus-6 (Fig. 6) consisted of an acrylic plate (30.0×25.0×1.5 mm) with a hole (6.0 mm in diameter) in the center, a transparent glass sheet (30.0×30.0×1.0 mm) and a sheet of black nylon screen (800-mesh). The nylon screen mesh was melted and bonded upon the square hole of acrylic plate by heat-sealing. The acrylic plate and the transparent glass were clamped by 2 folders at both sides of

acrylic plate to make a rearing cage for predatory mites (modified from Toyoshima & Amano 1998).

2.2.7. Rearing cage for mite's population study

The experimental apparatus-7 (Fig. 7) consisted of an acrylic plate (75.0×26.0×1.5 mm) with a square hole (40.0×20.0 mm) in its center, a transparent glass plate (75.0×26.0×1.0 mm) and a sheet of black nylon screen (800-mesh, 50.0×25.0 mm) with a small hole (1.0 mm diameter). The nylon screen mesh was melted and bonded upon the square hole of acrylic plate by heat-sealing. Before introducing mites, the acrylic plate and the transparent glass were clamped by four folders at the four corners of acrylic plate. The mites were introduced into the experimental apparatus-7 from the small hole with a fine brush. Then, a drop of glue was covered on the small hole.

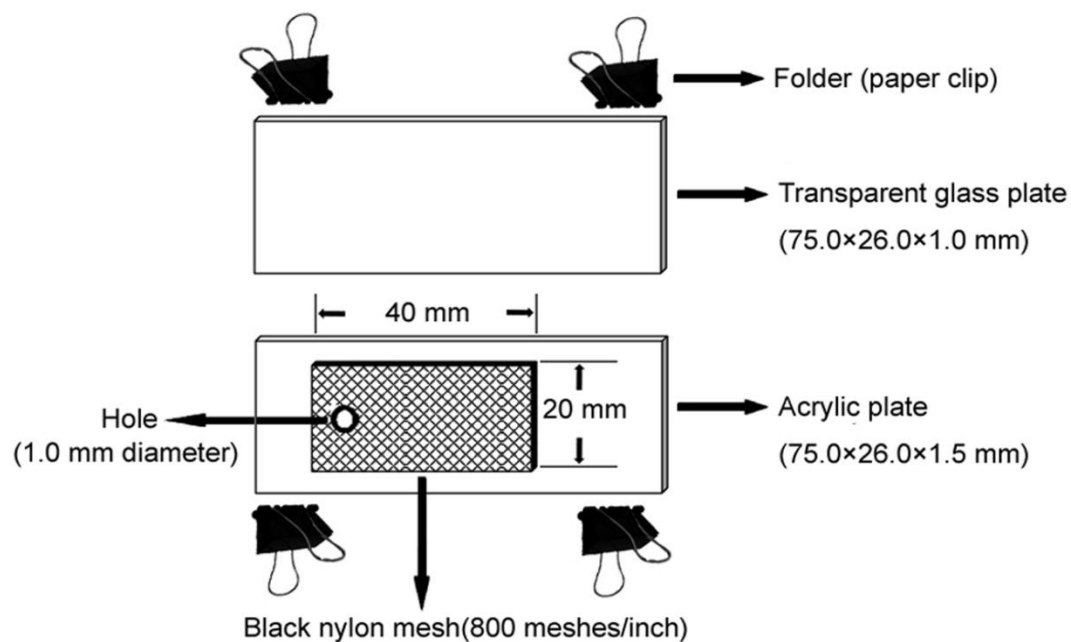


Fig. 7. The experimental apparatus-7 for mite's population study.

2.2.8. Glass tube method

The experimental apparatus-8 consisted of glass tubes (length 50 mm and inside

diameter 7 mm), water, high melting point paraffin wax (Kameyama 225G, Japan), mesh sheets (23 lm diameter mesh size polyester mesh 508, Clever, Japan) and glue (polyvinyl alcohol, Coop Clean Glue, Japan). Using this method makes it possible to maintain humidity levels inside the tubes within a certain range and to supply water (water droplets form at the interface between the wax plug and the glass wall) to the mites. Humidity inside the tubes was measured using a humidity indicator (PHI9S/5-95, PIATEC, and Japan). We learned that humidity varied from room humidity near the glass tube opening (covered by mesh) to up to 95 % near the wax surface bottom. Thus, the mites inhabiting the tube could select their preferred humidity range. Prior to beginning the experiments all materials, including the paraffin wax and the glue, were tested to see if there were any effects—either positive or negative—on phytoseiid survival. We could not determine any positive effects, but one negative effect was that mites occasionally became stuck in the glue before it had fully hardened (at least 10 min under 50 % r.h. is necessary for hardening).

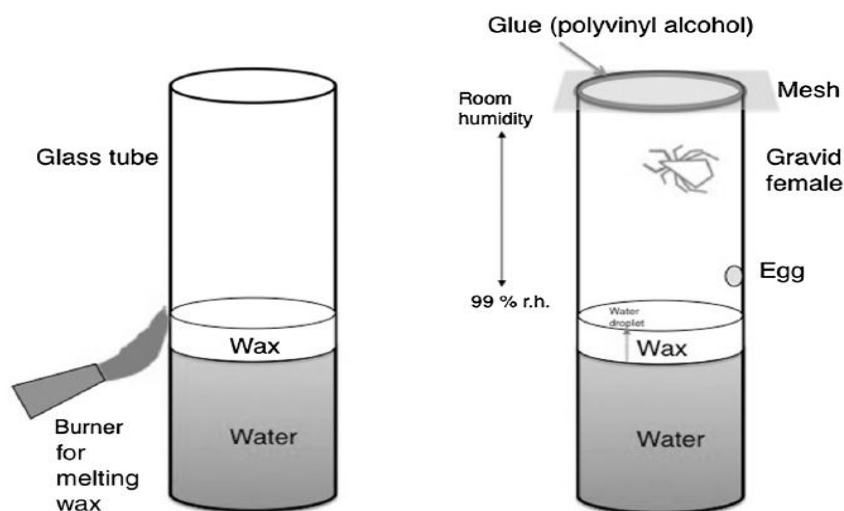


Fig. 8. The experimental apparatus-8 for observing the behavior of mites.

2.2.9. Calculation of life history parameters

Life history parameters, net reproductive rates (R_o), intrinsic rates of natural increase (r_m /female/day) were defined by Euler equation: $1 = \sum l_x m_x e^{-r_m x}$, mean generation times ($T = \ln(R_o) / r_m$) and their variances were calculated from the obtained life tables using software (bootstrap method for 10,000 trials developed by Katsura Ito according to Huang and Chi 2012; the script can be obtained by contacting the corresponding author) that runs on R (version 3.0.2, The R Foundation for Statistical Computing Platform). The differences in r_m and R_o and T were then analyzed by Anova and Tukey-Kramer HSD test using R.

Chapter 3. Method for mass-production of *A. eharai*

In this chapter, the effects of *Aleuroglyphus ovatus* Troupeau and *Carpoglyphus lactis* (linnaeus) on the development of *Amblyseius eharai* was conducted. In addition, how the initial density of *A. eharai* (1000, 2000 and 3000 mites in all stages) with different ratio of predator/prey (1:10, 1:20, 1:30 and 1:40) affect the population of *A. eharai*, to evaluate the efficiency of rearing *A. eharai* in different combinations (initial density and ratio).

3.1. Materials and methods

3.1.1. Developmental period of *A. eharai* with *A. ovatus* and *C. lactis* as prey

A single egg (in 8 hours old) of predatory mite was introduced into a cage (experimental apparatus-6, Fig. 6), after sufficient amounts of yeast and immatures of *A. ovatus* or *C. lactis* had been introduced there. There were 30 replicates for each prey mite species. All experiments were conducted in a culture box under 14:10 (L:D) photoperiod, $25 \pm 1^{\circ}\text{C}$ and $90 \pm 5\%$ R.H. conditions. The development of predatory mite was observed twice a day, at 8 am and 5 pm, and the stage of development was recorded. Sufficient amounts of yeast and *A. ovatus* or *C. lactis* were added when these foods had become scarce at the observation.

3.1.2. Method to mass-production by *C. lactis*

In this study, the experimental apparatus-3 (Fig. 3) with wheat bran that had been used for mass-production of *N. cucumeris* were tested first. Although *A. ovatus* could

increase its population on bran, *C. lactis* could not develop and live in the pure medium of bran. It was known that *C. lactis* often found in the sugar, but it was difficult to rear predatory mite with *C. lactis* as prey when this acarid mite was reared in the medium containing sugar, because sugar has very high hygroscopicity. I had tried to rear *C. lactis* on several kind of food, and then learned dry yeast was appropriate food for *C. lactis*. Dry yeast also has hygroscopicity, but it was comparatively low in comparison with sugar, and *A. eharai* (as well as *A. swirskii*) could increase its population with *C. lactis*.

Similar to the report of Ramakers and Van-Lieburg (1982), the disinfection procedures was the first step. The experimental apparatus-3 (Fig. 3) was rinsed by water to insure no insects or mites in the bottle. In addition, the wheat bran was heated 6 hours at 100°C to kill all insect, mites and fungi. The second step: 30 ml water was added into the bottle to keep the moisture, and then 30 -50 g wheat bran was put on the surface of water. Thereafter, 30 g yeast, *C. lactis* and *A. eharai* were introduced into the bottle, in sequence. Finally, approximate 200 g wheat bran was added, and then the lid was fastened down. All bottles were put into the box under 14:10 (L: D) photoperiod, 25±1°C and 80±5% R.H. conditions. The number of predator in the 0.1 g medium was checked and recorded at 10, 15, 20 and 30 days after the beginning of rearing.

In this study, the initial density of *A. eharai* (1000, 2000 and 3000 all stages) with the different ratio of predator : prey (1:10, 1:20, 1:30 and 1:40) was conducted, respectively. Every combination was replicated 3 times.

3.1.3. Data analysis

The means ($\pm$ S.E.) of developmental period were calculated using Microsoft Office Excel 2003. The means were separated using T-test for comparisons between the treatment with *A. ovatus* as prey and with *C. lactis* as prey (the data obtained in Chapter 4). The means of predator in wheat bran (0.1 g) within the same check time were analyzed using Two-Factor Analysis of Variance (ANOVA) in SPSS 13.0 version, including the interaction effects and main effect. In addition, the variation of one factor in different level of another one was compared by Tukey HSD.

3.2. Results

3.2.1. Developmental period of *A. eharai* with *A. ovatus* as prey mites

TABLE 1. The period of different stages of *Amblyseius eharai* with the prey *Aleurolyphus ovatus* and *Carpoglyphus lactis* at 25°C.

Developmental stages	<i>female</i>		<i>male</i>	
	<i>C. lactis</i>	<i>A. ovatus</i>	<i>C. lactis</i>	<i>A. ovatus</i>
Egg	1.7 $\pm$ 0.12	1.5 $\pm$ 0.09	1.4 $\pm$ 0.06	1.3 $\pm$ 0.06
Larva	0.9 $\pm$ 0.06 b	1.4 $\pm$ 0.06 a	1.0 $\pm$ 0.06	1.2 $\pm$ 0.06
Protonymph	1.1 $\pm$ 0.06	1.2 $\pm$ 0.06	1.4 $\pm$ 0.06	1.3 $\pm$ 0.09
Deutonymph	1.2 $\pm$ 0.12	1.5 $\pm$ 0.09	1.1 $\pm$ 0.06	1.3 $\pm$ 0.06
Preoviposition	1.9 $\pm$ 0.06	1.8 $\pm$ 0.12		
Generation	6.7 $\pm$ 0.12	7.4 $\pm$ 0.12	4.8 $\pm$ 0.12	5.1 $\pm$ 0.12

Means ($\pm$ s.e.) of female or male followed by different letters within same row were significantly different (t-test; $P < 0.05$), respectively.

The developmental period of *A. eharai* with *A. ovatus* as prey were listed in Table 1. There were no significant difference between the developmental period of *A. eharai* females when preying upon *A. ovatus* and when preying upon *C. lactis*, except the developmental period of *A. eharai* female larvae was significantly shorter when they preyed upon *C. lactis* than they preyed upon *A. ovatus*. Additionally, no significant difference was observed in the immature developmental period of *A. eharai* males between these two prey species.

Thus, it was suggested that these two acarid mites could be used to mass-rearing *A. eharai*. However, when I tried to conduct the life table of *A. eharai* with *A. ovatus* as prey, an unexpected phenomenon was observed. *A. eharai* males could only survive 3-5 days and were hard to mate. If mating was rarely occurred, the mated females laid approximate 15-20 eggs, which were significantly lower than those with *C. lactis* as prey. The longevity (3-5 days) of *A. eharai* males developed with *A. ovatus* was extremely shorter than that with *C. lactis* (30-40 days).

It indicated that *A. ovatus* was not an appropriate prey for mass-producing *A. eharai*. On the contrary, when *C. lactis* was supplied as prey, the fecundity or longevity of female *A. eharai* and the longevity of male *A. eharai* (the data was listed in Chapter 4, Table 7 and 8.) were exciting. Then, I conducted the experiment of mass-production of *A. eharai* with *C. lactis* as prey in this study.

TABLE 2. The produce efficiency of *A. eharai* with *C. lactis* as prey in different initial densities and predator-prey ratios under a 14:10 (L: D) photoperiod, 25 ±1 °C and 80 ±5%RH after mites were introduced.

	15 days later			20 days later			25 days later			30 days later		
	Initial density			Initial density			Initial density			Original level		
	(individuals/bottle)			(individuals/bottle)			(individuals/bottle)			(individuals/bottle)		
Ratio	1000	2000	3000	1000	2000	3000	1000	2000	3000	1000	2000	3000
1:10	4.93±0.64	10.27±1.68	16.04±2.63	10.48±1.51	15.70±2.79	13.43±2.19	15.38±2.53	18.54±2.89	11.49±1.22	3.23±0.11	13.69±1.06	6.13±0.58
1:20	6.17±0.96	13.81±1.73	14.61±1.90	21.37±2.95	36.88±5.96	31.60±5.70	22.68±3.59	32.15±5.76	25.50±2.68	14.43±1.33	22.70±2.50	19.93±2.90
1:30	9.44±1.33	14.53±1.80	16.41±2.30	18.8±2.50	21.27±3.69	26.78±4.57	16.77±2.81	26.23±4.33	21.67±2.89	8.33±0.64	20.54±2.66	12.84±2.01
1:40	10.74±1.67	17.68±2.25	18.48±2.66	18.34±3.39	22.70±4.10	31.37±5.90	16.42±2.37	20.46±3.80	23.51±2.48	5.87±0.53	18.52±2.83	17.22±2.99

Means (±s.e.) was the number of *A. eharai* (all stages) in 0.1 g wheat bran.

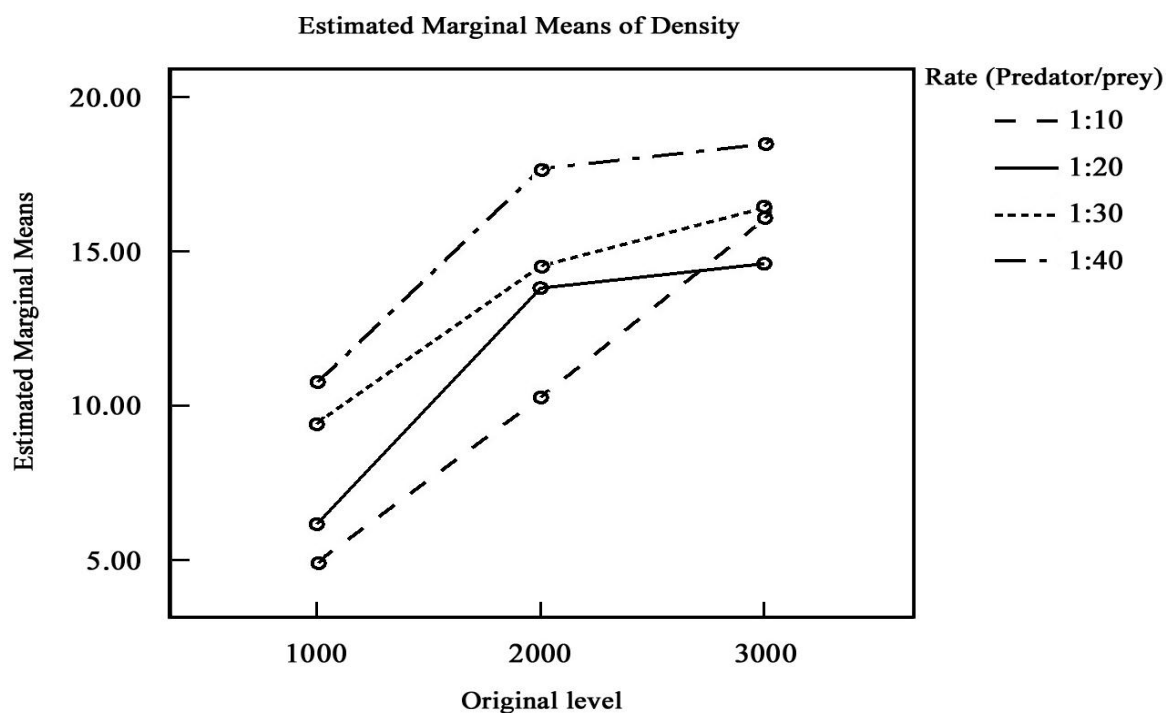


Fig. 9. The interactive effect of initial density of predator and predator-prey ratio after 15 days. The predator is *Amblyseius eharai* and the prey is *Carpoglyphus lactis*. The estimated marginal means was density of *A. eharai*.

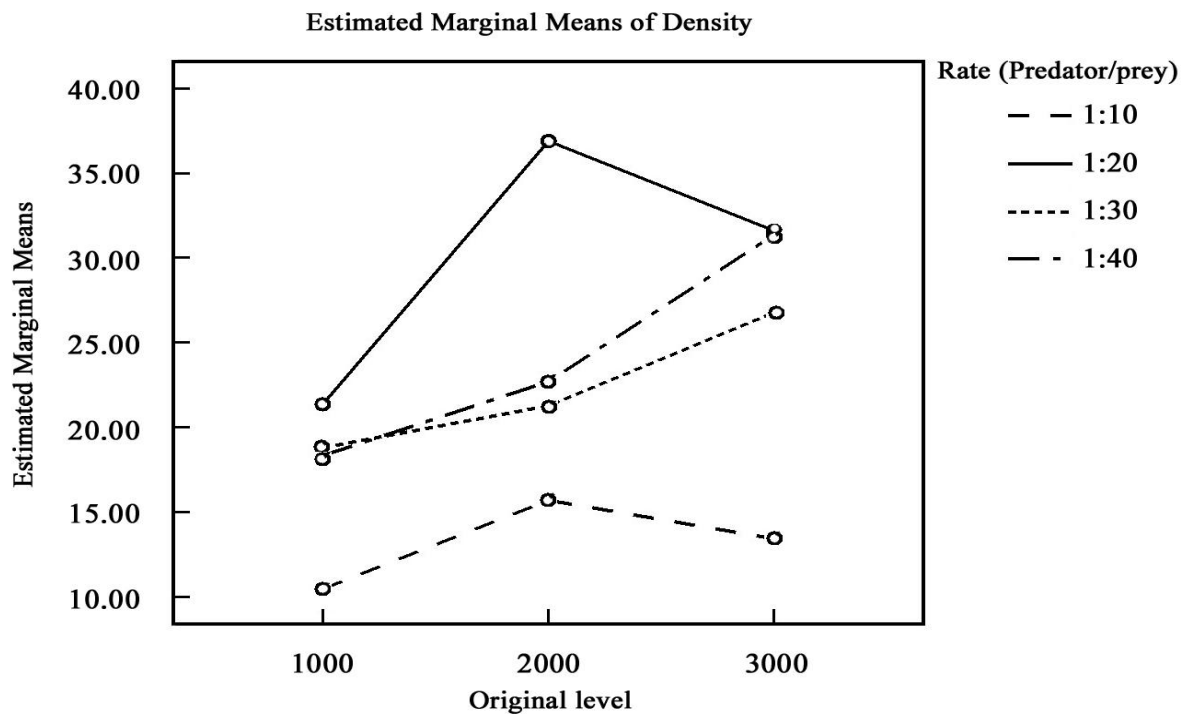


Fig. 10. The interactive effect of initial density of predator and predator-prey ratio after 20 days. The predator is *Amblyseius eharai* and the prey is *Carpoglyphus lactis*. The estimated marginal means was density of *A. eharai*.

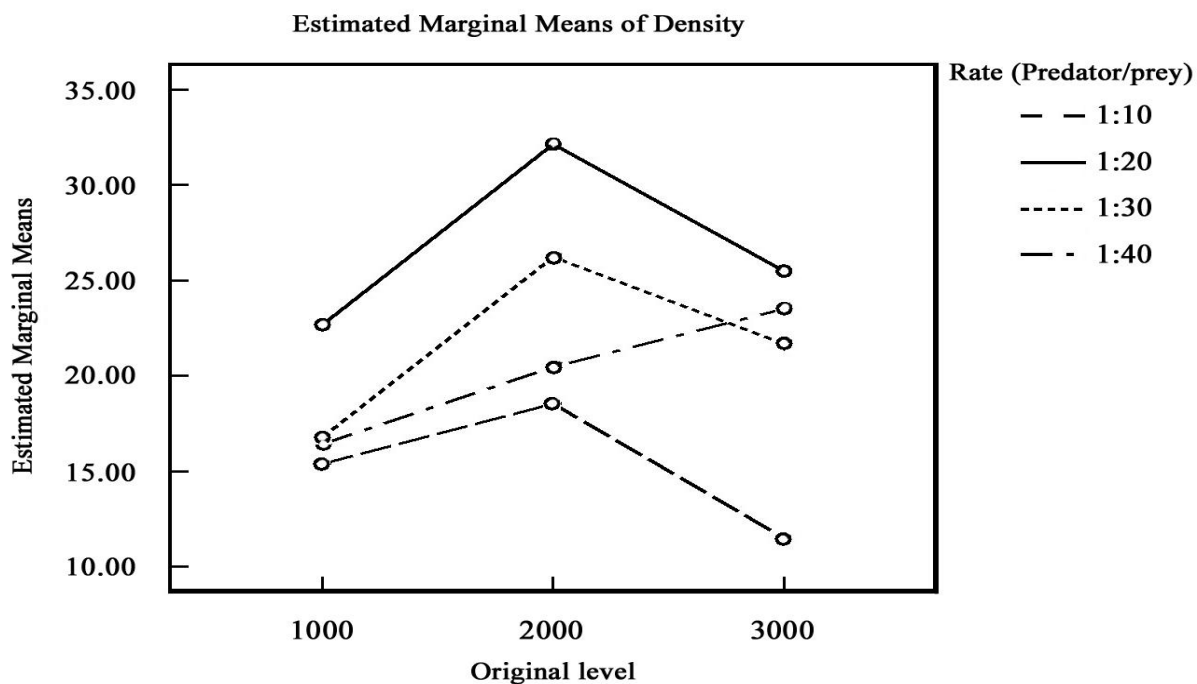


Fig. 11. The interactive effect of initial density of predator and predator-prey ratio after 25 days. The predator is *Amblyseius eharai* and the prey is *Carpoglyphus lactis*. The estimated marginal means was density of *A. eharai*.

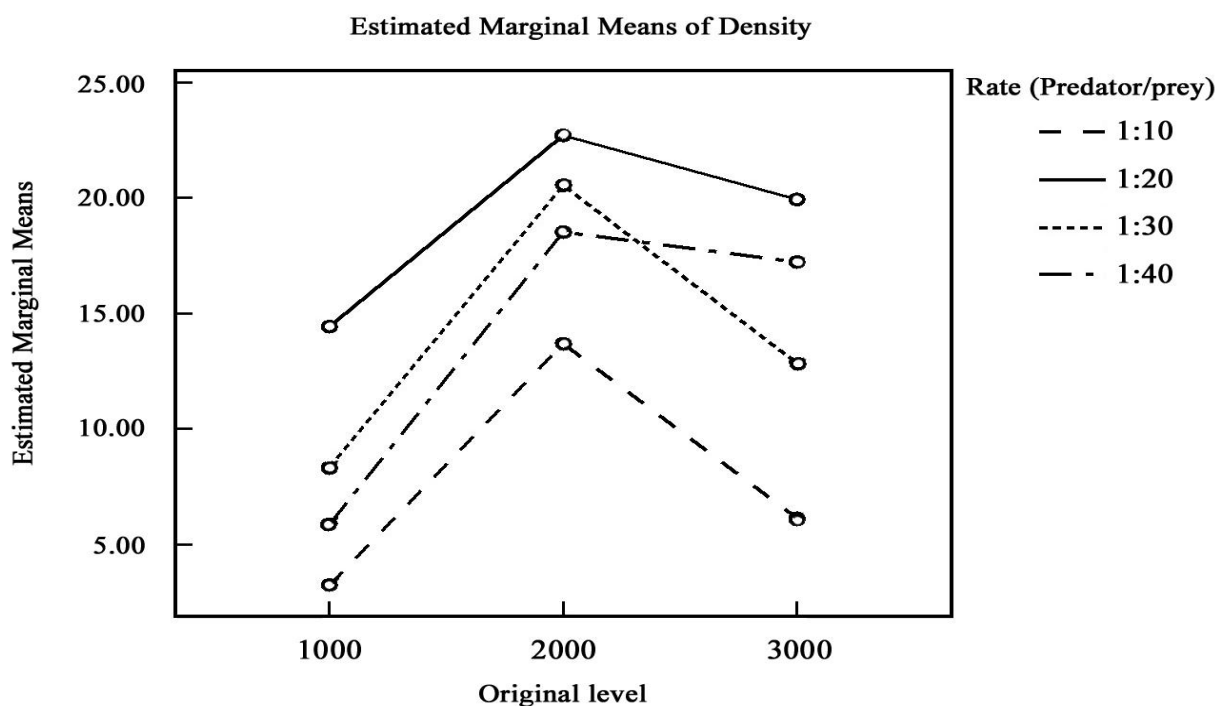


Fig. 12. The interactive effect of initial density of predator and predator-prey ratio after 30 days. The predator is *Amblyseius eharai* and the prey is *Carpoglyphus lactis*. The estimated marginal means was density of *A. eharai*.

3.2.2. The method of mass-producing *A. eharai* with *C. lactis* as prey

The populations of *A. eharai* reared from different initial densities (1000, 2000, 3000 individuals) and predator-prey ratio (predator/prey: 1:10, 1:20, 1:30 and 1:40) at 15, 20, 25 and 30 days after the start of rearing were listed in the Table 2. There were significant interaction effects between initial density and predator-prey ratio (Fig. 9, $F_{6,35} = 9.972$, $P < 0.0001$, Alpha = 0.05) after 15 days. The main effect was the initial density ($F_{2,35} = 455.293$, $P < 0.0001$). There were also significant interaction effects between initial density and predator-prey ratio (Fig. 10. $F_{6,35} = 42.411$, $P < 0.0001$) after 20 days and after 25 days (Fig. 11. $F_{6,35} = 24.842$, $P < 0.0001$) and after 25 days. The main effect was predator-prey ratio ($F_{2,35} = 386.707$, $P < 0.0001$ after 20 days; $F_{2,35} = 182.522$, $P < 0.0001$ after 25 days). Nevertheless, when those mites were introduced 30 days later, the main effect was the original level ($F_{2,35} = 251.821$, $P < 0.0001$), with the significant interaction effects (Fig. 12. $F_{6,35} = 9.976$, $P < 0.0001$) between original level and ratio (predator/prey).

TABLE 3. The results of multiple comparisons of main effect of initial density in different predator-prey ratio after introducing mites.

Initial density	N	15 days after	20 days after	25 days after	30 days after
1000	12	7.82 c	17.24 c	17.81 c	7.97 c
2000	12	14.07 b	24.14 ab	24.34 a	18.86 a
3000	12	16.38 a	25.79 a	20.54 b	14.03 b

Means for groups in homogeneous subsets were displayed. The lowercase within the same column are significantly different, Tukey HSD and Alpha = 0.05.

TABLE 4. The results of multiple comparisons of main effects of predator-prey ratio between different initial densities after introducing mites.

predator-prey ratio	N	15 days later	20 days later	25 days later	30 days later
1:10	9	10.41 d	13.20 d	15.14 d	7.69 c
1:20	9	11.53 c	29.95 a	26.78 a	19.02 a
1:30	9	13.46 b	22.29 c	21.56 b	13.91 b
1:40	9	15.63 a	24.13 b	20.13 c	13.87 b

Means for groups in homogeneous subsets were displayed. The lowercase within the same column are significantly different, Tukey HSD and Alpha = 0.05.

3.3. Discussion

The significant interactions between initial density and prey-predator ratio were observed (Fig. 9-12). These indicated that both the initial density and predator-prey ratio were important factors to mass-production of *A. eharai*. Then, *post hoc* multiple comparisons were made to analyze the main effect on the mass-production efficiency at the different level of the other factor. The results showed that 3000 individuals as the initial density was better than 1000 or 2000 individuals within 15 days rearing period (Table 3), though the yield of predacious mites was low (only 14.61-18.48 individuals per 0.1 g bran). If the longer rearing (storage) period was necessary, 2000 individuals as the initial density was the better choice. Similarly, the mass-producing efficiency in the predator-prey ratio, 1:40 was best for 15 days mass production (Table 4). On the other hand, if we intend to obtain a sufficient number of the predator after 20-30 days, the ratio of predators to prey should be 1:20. Because a longer storage period is desirable for the industry standard, I suggest the combination of 2000

individuals and 1 : 20 as an optimal combination.

Anyhow, the present results showed that *C. lactis* was a suitable prey mite for mass-production of *A. eharai*. However, *C. lactis* was not successfully reared with pure wheat bran, and dry yeast was necessary. Dry yeast is not so cheap, so that the mass production by the present method becomes a little bit costly relative to *N. cucumeris* that can be mass-produced with *A. ovatus* as prey mites in pure wheat bran.

Chapter 4. The life histories of three predators with *C. lactis* as prey

In the previous chapter, I found that *Amblyseius eharai* can increase in population when confined with the prey, *Carpoglyphus lactis*. In this chapter, the life histories of *Amblyseius swirskii*, *Neoseiulus cucumeris* and *A. eharai* were observed in the laboratory with *C. lactis* as prey. Then, the effectiveness of this prey for mass-production was discussed. The experimental apparatus-6 (Fig. 6) was used.

4.1. Materials and methods

4.1.1. Development

An egg (in 8 hours old) of each predatory mite was introduced into an experimental apparatus-6 with yeast and *C. lactis* immatures. There were 30 replicates for each predatory mite species. All experiments were conducted in a culture box kept under a 14:10 (L: D) photoperiod, $25 \pm 1^\circ\text{C}$ and $90 \pm 5\%$ R.H conditions. The development of each predatory mite was observed twice a day, at 8 am and 5 pm, and the stage of development was recorded. Sufficient amounts of yeast and *C. lactis* were added when these food had become scarce at the observation.

4.1.2. Oviposition

A newly emerged female of each predatory mite obtained from the development experiment was allowed to mate with an unmated male (3 days old) for 1 day in the experimental apparatus-6. In the following day, the male was removed. Five days

after that, the female was again allowed to mate with another unmated male (3 days old) for 1 day. Predators were provided sufficient *C. lactis* every day. The oviposition and survival of the predatory mite females were observed once a day until their death. The offspring sex ratio was determined by rearing all predators eggs deposited by the females to adulthood with *C. lactis* as prey. All experiments were kept in a culture box under a photoperiod of 14:10 (L: D) h, $25 \pm 1^\circ\text{C}$ and $90 \pm 5\%$ R.H. conditions. The experiment of each species was repeated for 15 times.

4.1.3. Data analysis

Mites that died accidentally during development were not included in the development analysis. The means ($\pm$ s.e.) of developmental periods were calculated using Microsoft Office Excel 2003. The means were separated using Tukey test for multiple comparisons in SPSS (13th edition). Life history parameters were calculated and separated (ANOVA) by using the method that was shown in Chapter 2. The means of life history parameters were separated using *t*-test for comparisons ($P < 0.05$) if the treatment indicated a significant effect.

4.2. Results

4.2.1. Development

Both males and females of three predator species could develop to adult with the prey *C. lactis* (Table 5, 6). There was no significant difference in the periods of larval stage and preoviposition between the females of three predator species (Table 5). However, the egg period of *N. cucumeris* females was significantly longer than that of *A.*

swirskii, but was similar to that of *A. eharai* ($F_{2, 29}=3.343$, $P < 0.05$). The periods of protonymph stage ($F_{2, 29}=11.284$, $P < 0.05$) and deutonymph stage ($F_{2, 29}=4.395$, $P < 0.05$) of *N. cucumeris* females were significantly longer than those of *A. eharai*, but was similar to that of *A. swirskii*. Furthermore, the development period (egg to egg) of *N. cucumeris* females was significantly longer than that of *A. eharai* or *A. swirskii* ($F_{2, 29}=15.712$, $P < 0.05$).

TABLE 5. Period of different developmental stages of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* females with *Carpoglyphus lactis* at 25°C.

Developmental stages	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>
Egg	1.7±0.13 ab	1.6±0.1 b	2.0±0.11 a
Larva	0.9±0.07	0.7±0.08	0.7±0.08
Protonymph	1.1±0.05 b	1.6±0.09 a	1.5±0.09 a
Deutonymph	1.2±0.13 b	1.3±0.11 ab	1.7±0.13 a
Preoviposition	1.9±0.08	2.0±0.09	1.9±0.13
Egg to adult	4.9±0.11 b	5.1±0.07 b	5.9±0.15 a
Generation (egg to egg)	6.7±0.11 b	7.1±0.14 b	7.7±0.13 a

Means (±s.e.) followed by different letters within same line are significantly different (Tukey test; $P < 0.05$)

The durations of egg stage of *A. eharai* and *A. swirskii* males were similar, and were significantly shorter than that of *N. cucumeris* males ($F_{2, 29}=7.415$, $P < 0.05$). In larval stage, the duration of *A. eharai* male was the longest among three predator species ($F_{2, 29}=12.000$, $P < 0.05$). No significant difference was observed in the duration of male protonymph between the three predator species. However, the

duration of deutonymph stage of *A. swirskii* males was significantly longer than that of *A. eharai* ($F_{2, 29} = 3.742$, $P < 0.05$). The significantly shortest developmental duration was observed in the treatment of *A. swirskii* males ($F_{2, 29} = 3.886$, $P < 0.05$).

TABLE 6. Durations of developmental stages of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* males with the prey *Carpoglyphus lactis* at 25°C.

Developmental stages	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>
Egg	1.4±0.07 b	1.3±0.22 b	1.9±0.13 a
Larva	1.0±0.05 a	0.7±0.08 b	0.6±0.05 b
Protonymph	1.4±0.08	1.3±0.08	1.4±0.07
Deutonymph	1.1±0.07 b	1.5±0.12 a	1.3±0.08 ab
Generation	4.8±0.13 ab	4.6±0.15 b	5.1±0.10 a

Means (±s.e.) followed by different letters within same row are significantly different (Tukey test; $P < 0.05$)

4.2.2. Oviposition

TABLE 7. Longevity and fecundity of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* with the prey *Carpoglyphus lactis* at 25°C.

	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>
Mean longevity (days)	47.6±2.50 b	45.7±2.15 b	67.3±3.76 a
Mean oviposition duration (days)	20.5±1.95	26.7±1.56	25.6±2.13
Postoviposition duration (days)	20.4±2.43 a	12.0±2.78 b	33.4±4.62 a
Fecundity (eggs/female)	51.1±4.52	45.9±1.93	53.3±4.84
Oviposition rate (eggs/female/day)	2.5±0.12 a	1.8±0.07 b	2.1±0.09 b

Means (±s.e.) followed by different letters within the same row of each species were significantly different (Tukey test; $P < 0.01$).

The mean oviposition duration and the fecundity of three predatory speices did not differ when feeding upon *C. lactis* (Table 7). The mean longevity of *A. swirskii* and *A. eharai* were shorter than that of *N. cucumeris* ($F_{2, 29}=17.176$, $P<0.0001$). Significant differences were observed among postoviposition duration of three species ($F_{2, 29}=9.968$, $P<0.001$). Although there were no differences in total fecundity between three predatory speices, the number of eggs per day in *A. eharai* was significantly higher than that in the other two species ($F_{2, 29}=16.892$, $P < 0.0001$).

TABLE 8. Life history parameters of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* with the prey *Carpoglyphus lactis* at 25°C.

Parameters	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>
net reproductive rate (R_0)	33.849±2.798 b	36.598±1.450 a	31.052±2.711 c
mean generation time (T)	13.9±0.5 b	15.5±0.2 a	16.2±0.4 a
intrinsic rate of increase (r_m)	0.253±0.005 a	0.232±0.003 b	0.212±0.003c
Percent of female offspring (%)	66.24	79.74	58.54

Means (±s.e.) followed by different letters within the same row of each species were significantly different (*t*-test; $P < 0.01$).

4.2.3. Life history parameters

The life history parameters of *A. swirskii*, *A. eharai* and *N. cucumeris* feeding upon *C. lactis* were shown in Table 8. Although *A. swirskii* had significantly higher R_0 (*t*-test, $P < 0.001$) than two other predators, its r_m was lower (*t*-test, $P < 0.05$) than that of *A. eharai* due to its higher T (*t*-test, $P < 0.001$). In addition, the r_m of *N. cucumeris* was lowest among three predators because it has the lowest R_0 and highest T .

4.3. Discussion

The life history parameters of *A. swirskii*, the famous predator for whitefly and thrips, were evaluated by several researchers with different prey, for example whitefly, thrips, mites, pollen (Onzo *et al.* 2012; Fouly *et al.* 2011; Duc *et al.* 2013; Lee and Gillespie, 2011). However, the dried fruit mite *C. lactis* has been used as the prey mite of *A. swirskii* in commercialized production; there have been no studies on life history of *A. eharai* and *N. cucumeris* when *C. lactis* was given as prey. This study is the first report on the parameters.

The r_m of *A. eharai* was 0.286 females/female/day when feeding upon *T. urticae* Koch and 0.247 females/female/day when feeding upon *P. citri* at 25°C (Saito and Mori, 1981; Ji *et al.* 2013 c mentioned in Chapter 5). The present result showed that the r_m was 0.253 females/female/day when feeding upon *C. lactis*. This value was higher than that of *A. swirskii* and *N. cucumeris* (two commercialized predators), suggesting *A. eharai* has a good potential to use as a biological control agent by mass-production.

However, several problems about *A. eharai* have to be overwhelmed. *A. eharai* is extremely ferocious. It ordinarily performs cannibalism although extraguild prey was present (Chapters 7 and 8). One approach to overcome this problem is to provide wide and complicated habitat with sufficient number of *C. lactis*. We had developed an appropriate mass-producing system based on the present results in previous Chapter 3.

Several studies reported the life history parameters of *A. swirskii* with various foods. When it preyed upon *Typha latifolia* pollen, the immature *Bemisia tabaci*

(Gennadius) and *P. citri* at 25°C, the r_m values were 0.135, 0.213 and 0.249 females/female/day, respectively (Park *et al.* 2011; Lee and Gillespie, 2011; Nomikou *et al.* 2001; Ji *et al.* 2013 c mentioned in Chapert 5). Duc *et al.* (2013) reported the r_m of *A. swirskii* with *C. lactis* was 0.175 females/female/day at 23 °C. The r_m value, 0.232 females/female/day at 25°C obtained in the present study must well correspond to their result.

N. cucumeris had been commercially produced by using *Acarus farris* (Oudemans), a storage mite (Ramakers and Van-Lieburg, 1982) as food. Afterward, *Tyrophagus putrescentiae* (Schrank) has been more widely used as the prey mite in mass-production (Workman *et al.* 1994). However *C. lactis* must be a more perfect prey for *N. cucumeris*, because it led *N. cucumeris* females to survive longer: The longevity and oviposition duration (67.3 days and 25.6 days, respectively in the present paper) provided with *C. lactis* was longer than that provided with *T. putrescentiae* (30.2 days and 20.4 days, respectively) (Muhammad *et al.* 2009). The intrinsic rate of increase (0.212 females/female/day) when feeding upon *C. lactis* is higher than when feeding upon other prey or food, such as the pollen of Horse-chestnu, *Tetranychus urticae* Koch and *Dermatophagoides farinae* (0.180, 0.174 and 0.203 females/female/day, respectively) (Ranabhat *et al.* 2013; Marisa and Sauro 1990; Castagnoli 1989).

Chapter 5. The life histories of *A. eharai* and *A. swirskii* with *P. citri* as prey

It has been pointed out that *Neoseiulus cucumeris* cannot establish its population in citrus orchards in China. Thus, the life histories of *Amblyseius swirskii* and *Amblyseius eharai* feeding upon *Panonychus citri* were studied to know whether they are effective natural enemies in citrus orchards. The possibility of competition between *A. swirskii* and *A. eharai* was discussed as a part of the invasion risk evaluation by comparing in biology and life history of these two predators with *P. citri* as prey, if *A. swirskii* was released into the citrus orchard where *A. eharai* is dominated.

5.1. Materials and methods

5.1.1. Development and predation

The experimental apparatus-1 (Fig. 1) was used in this study. Thirty adult females of *A. swirskii* or *A. eharai* were introduced into each of the thirty citrus leaves respectively. The following day, only one egg of those predatory mites was kept on every leaf. All experiments were conducted in a culture box with a 16:8 (L: D) photoperiod, $25 \pm 1^{\circ}\text{C}$ and $80 \pm 5\%$ relative humidity. The development of each predatory mite was observed twice a day, at 8 am and 5 pm, and the stage of development was recorded. Thirty eggs of *P. citri* were supplied as a food source for the developing mites each day, and the number of eggs consumed was recorded per day. There were 30 replicates in each treatment.

5.1.2. Life history

A newly emerged female of *A. swirskii* or *A. eharai* in the above experiment was allowed to mate with an unmated male (3 days old) for 1 day on a clean citrus leaf as above. The following day, the male was removed. And 5 days later, the female was allowed to mate with another unmated male (3 days old) for 1 day (Ji *et al.* 2007). Fifteen adult females of *P. citri* were provided as prey each day. The oviposition and survival of the predatory mites were observed once every day until their death. The offspring sex ratio was determined by rearing all eggs deposited by the predators to adulthood in separate citrus leaf arenas with *P. citri* as prey. All experiments were conducted in a culture box with a photoperiod of 16:8 (L: D) h, $25 \pm 1^\circ\text{C}$ and $80 \pm 5\%$ relative humidity. The experiment was repeated for 10 females of *A. swirskii* or *A. eharai*.

5.1.3. Data analysis

Mites that died during development were not used in the analysis. The means ($\pm$ s.e.) of developmental duration or predations were calculated using Microsoft Office Excel 2003. The means were tested using T-test ($P < 0.05$) if the treatment indicated a significant effect. Life parameters were calculated by using the method that was shown in Chapter 2. The differences in intrinsic rates of natural increase (r_m), net reproductive rates (R_o) of *A. swirskii* and *A. eharai* were then analyzed by *t*-test (the bootstrap method guarantees the normality of estimated values).

5.2. Results

5.2.1. Developmental duration

The two predators, *A. eharai* and *A. swirskii*, develop into adult females successfully with the prey eggs of *P. citri*. The duration of every immature stage of *A. swirskii* tended to be shorter than that of *A. eharai*, but no significant difference was observed (Table 9, $P > 0.05$) except for the larval stage ($P < 0.05$). The durations of larval stage and the development from egg to egg of *A. swirskii* were significantly shorter than that of *A. eharai* ($P < 0.05$). There was no significant difference in preoviposition duration between these two predator species ($P > 0.05$).

5.2.2. Predation

TABLE 9. The duration of developmental stages of *Amblyseius eharai* and *Amblyseius swirskii* with the prey *Panonychus citri* at 25°C.

Developmental stages	<i>A. eharai</i>	<i>A. swirskii</i>
Egg	2.2 ± 0.03	1.9 ± 0.03
Larva	1.2 ± 0.03 a	0.6 ± 0.03 b
Protonymph	1.8 ± 0.03	1.5 ± 0.06
Deutonymph	1.3 ± 0.03	1.2 ± 0.03
Preoviposition	2.9 ± 0.06	2.7 ± 0.03
Generation	9.7 ± 0.06 a	7.9 ± 0.12 b

Means (±s.e.) followed by different letters within same row are significantly different (t-test).

The larvae of *A. swirskii* did not feed any prey, but those of *A. eharai* fed upon *P. citri*.

The protonymphs, deutonymphs of *A. swirskii* showed higher feeding rates (number

of eggs consumed/day) than those of *A. eharai*, and then there were the significant differences between species (Table 10, $P < 0.05$). The larvae of *A. swirskii* developed to protonymphs without feeding even though there were 30 eggs of *P. citri*, whereas feeding is obligatory for *A. eharai* larvae.

TABLE 10. Consumption rate (eggs/day) of *Panonychus citri* eggs by immature stages of *Amblyseius eharai* and *Amblyseius swirskii* at 25°C.

Stage of phytoseiid mite	<i>A. eharai</i>	<i>A. swirskii</i>
Larva	1.12 ±0.03	--
Protonymph	1.33 ±0.07 b	3.20 ±0.06 a
Deutonymph	5.33 ±0.13 b	7.20 ±0.25 a
Immature total	7.77 ±0.20 b	10.38 ±0.23 a

Means (±s.e.) followed by different letters within the same row are significantly different (*t*-test).

5.2.3. Life history parameters

The calculated life history parameters, r_m , Ro , and T at 25°C, were shown in Table 11. The result showed that the mean generation time (T) and the net reproductive rate (Ro) of *A. swirskii* was significantly shorter/lower than that of *A. eharai* ($P < 0.001$). However, there was not significant difference in the intrinsic rate of increase (r_m) of *A. eharai* and *A. swirskii* (Table 11).

The longevity and fecundity of *A. eharai* and *A. swirskii* were listed in Table 12. The mean longevity and postoviposition duration of *A. swirskii* were significantly longer than *A. eharai* ($P < 0.05$). However, *A. eharai* had the higher fecundity and oviposition rate than *A. swirskii* did ($P < 0.05$). In addition, there was not difference in the mean oviposition duration between two predators.

TABLE 11. Life history parameters of *Amblyseius eharai* and *Amblyseius swirskii* with the prey adult females of *Panonychus citri* at 25°C.

Parameters	<i>A. eharai</i>	<i>A. swirskii</i>
net reproductive rate (R_o)	68.90 ±1.46 a	55.10 ±0.99 b
mean generation time (T)	22.35 ±0.30 a	21.47 ±0.23 b
intrinsic rate of increase (r_m)	0.247 ±0.002	0.249 ±0.001
finite rate of increase (λ)	1.2802	1.2827
doubling time for population (dt)	2.81	2.78
Sex ratio (♀ : ♂)	1.97	1.65

Means (±s.e.) followed by different letters within the same row are significantly different (*t-test*).

TABLE 12. Longevity and fecundity of *Amblyseius eharai* and *Amblyseius swirskii* with adult females of *Panonychus citri* as prey at 25°C.

	<i>A. eharai</i>	<i>A. swirskii</i>
Longevity range (days)	40–46	44–48
Mean longevity (days)	43.5 ±0.22 b	46.4 ±0.13 a
Oviposition duration range (days)	24–28	24–28
Mean oviposition duration (days)	26.3 ±0.70	25.8 ±0.63
Postoviposition duration (days)	7.8 ±0.19 b	13.8 ±0.28 a
Fecundity (eggs/female)	67.70 ±0.42 a	54.90 ±0.38 b
Oviposition rate (eggs/female/day)	2.59 ±0.001 a	2.13 ±0.006 b

Daily fecundity: Eggs per female per day of *Amblyseius swirskii* or *Amblyseius eharai*. Means (±s.e.) followed by different letters within the same row are significantly different (*t-test*).

5.3. Discussion

The results showed that the larvae of *A. swirskii* might be the type of non-feeding larvae, and the larvae of *A. eharai* was the type of obligatory feeding larvae according to the classification of Zhang and Croft (1994).

A recent review about the risks of exotic phytoseiids (Palevsky *et al.* 2013) showed that on a number of crops including citrus, exotic phytoseiids have in general a positive role in biological control without negatively affecting indigenous species of natural enemies. For example, 20 phytoseiid species were introduced into California, USA, to control *P. citri* of citrus (McMurtry 1989), the only negative case is for *Euseius stipulatus* (Athias- Henriot) on citrus: it displaced *Euseius hibisci* (Chant) in a limited region of coastal California, but the latter considered to be an inferior biocontrol agent of *P. citri*.

In this chapter, I showed that *A. eharai* can easily maintain its population relative to *A. swirskii* when the prey *P. citri* were scarce in the citrus orchard, because that the immatures of *A. eharai* just consumed fewer prey to develop into adults. However, the intrinsic rate of increase (r_m) of *A. eharai* was same as that of *A. swirskii* when the prey was sufficient. Thus, which of *A. eharai* and *A. swirskii* is a better competitor even cannot be determined.

Even though *A. swirskii* might be a worse competitor relative to *A. eharai*, it could still play an important role in biocontrol of citrus pest mites through using augmentative releases early in the growing season, because *A. eharai* or other indigenous predators cannot control populations of citrus pest mites due to their low

density at that time (Ji *et al.* 2012).

Anyhow, the result of competition would be influenced by many other factors, for example the ability to endure starvation, alternative prey in ecosystem and intraguild predation, reproductive interference, predation preference and so on. In a previous study, that showed *A. swirskii* was a better competitor relative to *N. cucumeris* in greenhouses, because *A. swirskii* preferred to prey upon *N. cucumeris* larvae rather than the natural prey thrips (Messelink *et al.* 2005; Buitenhuis *et al.* 2010). Therefore, these results provided only a part of information about the invasion risk. I had to address other problems in the later chapters one by one.

Chapter 6. Effects of starvation and humidity on *A. swirskii* and *A. eharai*

In this chapter, I compared the effect of starvation and humidity on the development and survival of *A. swirskii* and *A. eharai*. Then, their survival ability was evaluated under some adverse conditions as a part of the invasion risk evaluation.

6.1. Materials and methods

The experimental apparatus-6 (Fig. 6) was used in this study. The cages of method 6 were placed into culture boxes with a 16:8 (L: D) photoperiod, $25 \pm 1^\circ\text{C}$ and subjected to five different relative humidity treatments: $60 \pm 5\%RH$, $70 \pm 5\%RH$, $80 \pm 5\%RH$, $90 \pm 5\%RH$ and $100\%RH$ by using certain super-saturated salt solutions and water. There were 10 replicates in each treatment. The development and survival of every mite were observed twice a day, at 8 am and 5 pm.

6.1.1. Development of eggs

A single egg (in 8 hours old) of each species was accommodated in the rearing cage, and then their developmental durations were recorded.

6.1.2. Development and survival duration of larvae

A single egg (in 24 hours old) of each species was accommodated in the rearing cage (method 6). When those eggs developed into larval stage, the developmental (*A. swirskii* larvae develops to protonymph without food) and survival durations of those

larvae were recorded.

6.1.3. Survival duration of protonymphs

A single larva of *A. swirskii* or *A. eharai* (it had preyed on enough eggs of *P. citri*) was accommodated in the rearing cage. When those larvae developed into the protonymph stage, the survival duration of these protonymphs were recorded.

6.1.4. Survival duration of deutonymphs

A single protonymph of *A. swirskii* or *A. eharai* was accommodated in the rearing cage. Moreover, those phytoseiid protonymphs had preyed enough eggs of *P. citri*. Just after the protonymphs developed into deutonymphal stage, the survival duration of those deutonymphs under no food conditions were recorded.

6.1.5. Survival duration of virgin females

A single deutonymph of *A. swirskii* or *A. eharai* was accommodated in the rearing cage. Moreover, those phytoseiid deutonymphs had preyed on enough eggs of *P. citri*. When they developed into adult females stage, the survival duration of those virgin females under no food conditions were recorded.

6.1.6. Survival duration of gravid females

A single female of the each species was accommodated in the rearing cage. The females had successfully mated and oviposited for 2 days before experiments. The survival duration of those gravid females were recorded under no food condition. Most females deposited one or two eggs even under no food conditions. Thus, all eggs

deposited by them in the rearing cages were removed every observation time.

6.1.7. Data analysis

The means ($\pm$ s.e.) of developmental durations or survival durations were calculated using Microsoft Office Excel 2003. The means were separated using *t*-test for comparisons ($P < 0.05$) if the treatment indicated a significant effect.

6.2. Results

6.2.1. Development of eggs

At 60%RH, only two eggs of *A. eharai* developed into larva stage, whereas, all eggs of *A. swirskii* developed into larvae (Table 13). In the range of 70–100%RH, all eggs of the two predatory mites developed into larvae. No significant differences were observed between developmental durations of *A. swirskii* and *A. eharai* in the range of 70–90%RH, excepting at 100%RH (Table 13. $P < 0.05$).

TABLE 13. Egg durations of *Amblyseius eharai* and *Amblyseius swirskii* under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Egg durations of <i>A. eharai</i> (days)	--	2.1 $\pm$ 0.06	1.9 $\pm$ 0.06	2.1 $\pm$ 0.03	2.3 $\pm$ 0.09 a
Egg durations of <i>A. swirskii</i> (days)	2.7 $\pm$ 0.16	2.7 $\pm$ 0.09	1.9 $\pm$ 0.06	1.9 $\pm$ 0.06	1.9 $\pm$ 0.09 b

Means ($\pm$ s.e.) followed by different letters within same column are significantly different (*t*-test; $P < 0.05$).

6.2.2. Developmental or survival durations of larvae

Larval *A. eharai* could not develop into protonymphs without prey, but *A. swirskii*

could do (Table 14).

TABLE 14. Developmental or survival durations of larvae of *Amblyseius eharai* and *Amblyseius swirskii* without food under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Survival durations of <i>A. eharai</i> (days)	2.0±0.13	1.9±0.13	3.1±0.16	3.1±0.06	3.2±0.19
Developmental duration of <i>A. swirskii</i> (days)	1.0±0.06	0.8±0.09	0.7±0.03	0.7±0.06	0.8±0.09

6.2.3. Survival duration of protonymphs

All protonymphs of two species died of starvation in a few days (Table 15), whereas, the survival durations of *A. swirskii* were significantly longer than those of *A. eharai* in all tests (Table 15). In addition, the survival duration of *A. eharai* in the range of 60–80%RH were shorter than those in the range of 90–100%RH. Similarly, the duration of *A. swirskii* at 60%RH was shorter than in the range of 70–100%RH.

TABLE 15. The survival durations of protonymphs of *Amblyseius eharai* and *Amblyseius swirskii* without food under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Survival durations of <i>A. eharai</i> (days)	1.4±0.09 b	1.5±0.16 b	1.9±0.06 b	2.4±0.16 b	2.6±0.19 b
Survival durations of <i>A. swirskii</i> (days)	1.8±0.13 a	2.8±0.09 a	3.6±0.19 a	3.5±0.22 a	3.3±0.16 a

Means (±s.e.) followed by different letters within same column are significantly different (*t*-test; *P* < 0.05).

6.2.4. The survival duration of deutonymphs

In the range of 60–100%RH, there was no significant difference between the survival durations of deutonymphs of the two phytoseiid mites without prey (Table 16). Being

similar to the protonymphs, at 60%RH, the survival durations of deutonymph of *A. swirskii* and *A. eharai* were very shorter than those in the range of 80–100%RH.

TABLE 16. Survival durations of deutonymphs of *Amblyseius eharai* and *Amblyseius swirskii* without food under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Survival durations of <i>A. eharai</i> (days)	2.0±0.13	2.0±0.09	3.5±0.25	3.4±0.16	3.6±0.16
Survival durations of <i>A. swirskii</i> (days)	1.8±0.09	2.2±0.09	3.7±0.32	3.6±0.25	3.5±0.22

6.2.5. The survival duration of virgin females

In the range of 60–70%RH, the survival duration of virgin females of *A. swirskii* without prey was significantly longer than that of *A. eharai*. No significant difference was observed in the survival duration of virgin females between the two phytoseiid mites in the range of 80–100%RH (Table 17).

TABLE 17. Survival durations of virgin females of *Amblyseius eharai* and *Amblyseius swirskii* without food under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Survival durations of <i>A. eharai</i> (days)	2.4±0.16 b	2.5±0.13 b	3.3±0.19	3.5±0.16	3.7±0.25
Survival durations of <i>A. swirskii</i> (days)	2.8±0.09 a	3.5±0.22 a	3.5±0.19	3.6±0.22	3.6±0.25

Means (±s.e.) followed by different letters within same column are significantly different (*t*-test; *P* < 0.05).

6.2.6. The survival duration of gravid females

The survival durations of gravid females of *A. swirskii* without prey were significantly longer than those of *A. eharai* in the range of 60–100%RH. In addition, the survival

durations of *A. swirskii* (4.0 days) and *A. eharai* (3.1 days) at 60%RH were very shorter than those at 100%RH (8.0 days and 5.4 days, respectively, Table 18).

TABLE 18. Survival durations of gravid females of *Amblyseius eharai* and *Amblyseius swirskii* without food under five relative humidity conditions.

Relative humidity	60%	70%	80%	90%	100%
Survival durations of <i>A. eharai</i> (days)	3.1±0.16 b	3.4±0.19 b	3.3±0.16 b	3.5±0.19 b	5.4±0.41 b
Survival durations of <i>A. swirskii</i> (days)	4.0±0.35 a	5.4±0.16 a	7.6±0.41 a	7.3±0.38 a	8.0±0.44 a

Means ($\pm$ s.e.) followed by different letters within same column are significantly different (*t*-test; $P < 0.05$).

6.3. Discussion

The ability to endure unfavorable environment is very important for natural enemies to maintain their population and exert their effectiveness for biological control (Greco *et al.* 2006; Wei *et al.* 1994; Chant & Fleschner 1960). If a natural enemy has stronger ability to endure starvation, it will exist longer relative to other natural enemies (Wei *et al.* 1994). In fact, the ability may have contributed to the dominance of *T. pyri* on apple seedlings in greenhouse, because unfed adult females or immatures of *T. pyri* lived longer than the corresponding stages of *Euseius (Seiulus) finlandicus* Oudemans and *Kampimodromus aberrans* (Oudemans) (Schausberger 1998, 1999). In addition, the favourable humidity is a key factor for the survival of natural enemies (McMurtry & Scriven 1965), whereas the humidity is not always favorable in an ecosystem. Sometimes, the humidity may be very low because of some reasons, e.g. drought. Obviously, a natural enemy, which can adapt lower humidity or has stronger ability to survive without prey, might win the competition in interspecific competition.

The fact that starvation can affect the longevity and development of predatory mites had been confirmed (Momen 1994; Elsayi and Abou-Awad 1992). The abilities of predatory mites to survive without food were different between species, for example, adult females and protonymphs of *Neoseiulus californicus* (McGregor) survived longer than the corresponding stages of *Phytoseiulus persimilis* (Athias-Henriot) (Walzer and Schausberger 1999). Williams *et al.* (2004) had also showed that the female of *P. persimilis* and *Amblyseius* (*Iphiseius*) *degenerans* (Berlese) had a low ability to survive (5 days or 4 days) when they were starved even with access to water, but both *N. californicus* and *N. cucumeris* could survive for 8–10 days (Williams *et al.* 2004). Whereas, if without prey and water, the female *N. californicus* survived for only 4.3 days at 20°C and 85% RH (Toyoshima *et al.* 2009). In addition, feeding is obligatory for larval *A. eharai* and *Galendromus* (*Typhlodromus*) *occidentalis* (Nesbitt) (Zhang and Croft 1994; Chittenden and Saito 2001; Ji *et al.* 2013 c mentioned in Chapter 5). Unfed larvae of *A. eharai* could survive for 1.9–3.2 days in range of 60–100%RH and 25°C, and unfed larvae of *G. occidentalis* died within 2–3 days at 95%RH and 20°C (Croft and Croft 1993).

This study showed that all protonymphs, deutonymphs and females of *A. swirskii* and *A. eharai* were gradually fainting with starvation and died, but some significant differences were observed among them. When the prey was absent, in protonymph or gravid female stage, the survival duration of *A. swirskii* was significantly longer than that of *A. eharai* under all humidity conditions. In the lower humidity range (60–70%RH), a similar case was observed between the virgin females of the two phytoseiid mites. Those indicated that the ability to endure starvation or low humidity

of *A. swirskii* was stronger than those of *A. eharai*.

In conclusion, *A. swirskii* might be a better competitor than *A. eharai* when the prey was absent. In addition, most eggs of *A. eharai* failed to develop at low humidity (60%RH), whereas, *A. swirskii* could do. Furthermore, larval *A. eharai* could not develop into protonymph stage without prey, but *A. swirskii* could do. Therefore, because of the high abilities of eggs and larvae to adapt to low humidity, *A. swirskii* might be also a strong competitor.

Nevertheless, the result of competition should be influenced by a series of factors, for example, intraguild predation, cannibalism, reproductive interference, predation preference, social behavior and so on. Therefore, the results of this study were also just a part of the invasion risk evaluation, and more studies should be conducted.

Chapter 7. Intraguild predation among three predatory mites

In this chapter, the intraguild predations among *Amblyseius swirskii*, *Neoseiulus cucumeris* and *Amblyseius eharai* were observed. Their developmental durations and the parameters of life history when they performed intraguild predation were compared to evaluate whether intraguild predation would occur and the possibility for them to maintain their population only by intraguild predation when the extraguild prey was absent.

7.1. Materials and methods

7.1.1. Development of three predatory mites with heterospecific eggs

The experimental apparatus-6 (Fig. 6) was used in this study. An egg (at most 8 h old) of *A. swirskii*, *A. eharai* or *N. cucumeris* was introduced into an experimental apparatus as mentioned above. After the larva hatched from the egg, 10 heterospecific eggs (*A. eharai*, *A. swirskii* or *N. cucumeris* eggs at most 8 h old) were supplied as food, these eggs were replaced twice a day, at 8 a.m. and 5 p.m., and the developmental stage of the predator was recorded at that time. When supplying prey eggs, new apparatus with prey eggs had been prepared, and the predator mite individual being tested was moved from the old apparatus to the new one using a fine brush. All experiments were performed in an incubator ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 16:8). The experiments were replicated 30 times for each species.

7.1.2. Oviposition of *A. eharai* and *A. swirskii*, *N. cucumeris* with heterospecific eggs

A newly emerged *A. swirskii*, *A. eharai* or *N. cucumeris* female obtained in the above development experiments was allowed to mate with a conspecific male (3 days old) for 1 day in the apparatus. Six days and 11 days after the first male introduction, the female was allowed to mate again with another male (3 days old) for 1 day (Ji *et al.* 2007). A sufficient number of heterospecific eggs (15 eggs per female) were supplied daily. When supplying prey eggs, new apparatus with prey eggs had been prepared, and then the tested female was picked up from old apparatus and introduced into the new one using a fine brush. The oviposition and survival of each female was observed once a day until its death. Offspring sex ratios were determined by rearing all the eggs laid by females during the experiments to adulthood on experimental apparatus-2 (Fig. 2) with *C. lactis* supplied as prey. The experiments were replicated 16-20 times for each species. All experiments were performed in incubators ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 16:8).

7.1.3. Data analysis

Mites that died accidentally during development (at most 10% of replicates) were not included in the analysis. Differences in mean developmental durations, in the numbers of eggs laid, in mean longevities and in mean oviposition durations of *A. swirskii*, *N. cucumeris* or *A. eharai* when supplied heterospecific eggs as prey were analyzed using the *t*-test for comparisons. Life history parameters were calculated by the method shown in Chapter 2; *t*-test was used to compare the difference of the mean parameters between these two predators.

7.2. Results

7.2.1. The development of three predatory mites

TABLE 19. Development of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* females when they were supplied with heterospecific eggs as prey at 25 °C (mean $\pm$ S.E.)

Predator and prey	Development duration (days)					
	Egg	Larva	Protonymph	Deutonymph	Preoviposition	Egg to egg
<i>A. eharai</i>						
<i>Prey=A. swirskii</i> (n=14)	1.89 $\pm$ 0.08	0.87 $\pm$ 0.06	3.08 $\pm$ 0.16	1.80 $\pm$ 0.13	3.30 $\pm$ 0.23	10.95 $\pm$ 0.16
<i>Prey=N. cucumeris</i> (n=10)	1.86 $\pm$ 0.10	0.89 $\pm$ 0.07	2.88 $\pm$ 0.18	1.85 $\pm$ 0.21	3.22 $\pm$ 0.17	10.26 $\pm$ 0.51
<i>A. swirskii</i>						
<i>Prey=A. eharai</i> (n=16)	1.83 $\pm$ 0.06	0.82 $\pm$ 0.08	1.80 $\pm$ 0.12	1.45 $\pm$ 0.13	3.35 $\pm$ 0.35a	9.25 $\pm$ 0.43a
<i>Prey=N. cucumeris</i> (n=10)	1.75 $\pm$ 0.04	0.75 $\pm$ 0.03	1.92 $\pm$ 0.12	1.67 $\pm$ 0.05	2.58 $\pm$ 0.48b	8.58 $\pm$ 0.53b
<i>N. cucumeris</i>						
<i>Prey=A. eharai</i> (n=15)	2.10 $\pm$ 0.05	0.60 $\pm$ 0.05	1.60 $\pm$ 0.05	1.80 $\pm$ 0.07b	1.80 $\pm$ 0.07	7.90 $\pm$ 0.08
<i>Prey=A. swirskii</i> (n=15)	2.00 $\pm$ 0.09	0.58 $\pm$ 0.01	1.80 $\pm$ 0.11	2.10 $\pm$ 0.05a	1.60 $\pm$ 0.10	8.10 $\pm$ 0.13

Means ($\pm$ s.e.) followed by different letters within the same column of each stage of each species between two diets were significantly different (*t*-test; $P<0.05$). Numerals in parentheses are numbers of replicates.

All females of three phytoseiid species successfully develop into adulthood when supplied with heterospecific eggs as prey (Table 19). There was no significant difference in *A. eharai* immature development between the intraguild prey species (two diets) (Table 19). In *A. swirskii*, there were significant differences ($P<0.05$) in the

preoviposition and developmental (egg to egg) durations between the two diets: *A. swirskii* developed faster when it ate *N. cucumeris* eggs than when ate *A. eharai* eggs. In *N. cucumeris*, there were significant differences ($P<0.05$) in the protonymphal and deutonymphal developmental durations between the intraguild prey species: These were longer when it ate *A. swirskii* eggs than when it ate *A. eharai* eggs. On the other hand, the larval and protonymphal developmental durations of all species were not different between the intraguild prey species.

TABLE 20. Development of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* males when they were supplied with heterospecific eggs as prey at 25°C (mean $\pm$ S.E.)

Predator and prey	Development duration (days)				
	Egg	Larva	Protonymph	Deutonymph	Egg to egg
<i>A. eharai</i>					
<i>Prey=A. swirskii</i> eggs (n=11)	1.65 $\pm$ 0.14	0.80 $\pm$ 0.08	2.40 $\pm$ 0.16	1.20 $\pm$ 0.11	6.05 $\pm$ 0.26
<i>Prey=N. cucumeris</i> eggs (n=10)	1.68 $\pm$ 0.10	0.85 $\pm$ 0.08	2.16 $\pm$ 0.24	1.55 $\pm$ 0.07	6.35 $\pm$ 0.30
<i>A. swirskii</i>					
<i>Prey=A. eharai</i> eggs (n=11)	1.85 $\pm$ 0.07	0.80 $\pm$ 0.11	2.90 $\pm$ 0.06	1.55 $\pm$ 0.19	7.10 $\pm$ 0.28
<i>Prey=N. cucumeris</i> eggs (n=10)	1.75 $\pm$ 0.06	0.75 $\pm$ 0.07	2.68 $\pm$ 0.10	1.65 $\pm$ 0.18	6.88 $\pm$ 0.28
<i>N. cucumeris</i>					
<i>Prey=A. eharai</i> eggs (n=15)	1.85 $\pm$ 0.11	0.75 $\pm$ 0.07	2.10 $\pm$ 0.10	1.55 $\pm$ 0.11	6.25 $\pm$ 0.23
<i>Prey=A. swirskii</i> eggs (n=15)	1.80 $\pm$ 0.09	0.90 $\pm$ 0.05	2.00 $\pm$ 0.11	1.55 $\pm$ 0.07	6.25 $\pm$ 0.23

Numerals in parentheses are numbers of replicates.

All male predatory mite species could develop into adulthood when supplied with

heterospecific eggs as prey (Table 20). No significant differences were observed in the developmental durations of all stages in *A. eharai*, *A. swirskii* and *N. cucumeris* males between the two diets (Table 20).

7.2.2. Oviposition of three predatory mites

TABLE 21. Longevity, oviposition duration and fecundity of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* when they were supplied with heterospecific eggs as prey at 25 °C (mean $\pm$ S.E.).

Predator and prey	Longevity	Oviposition duration	Fecundity	Sex ratio (♀/♂)
<i>A. eharai</i>				
<i>Prey=A. swirskii</i> eggs (n=15)	34.20 $\pm$ 3.74b	14.20 $\pm$ 2.47	13.73 $\pm$ 0.94b	2.58
<i>Prey=N. cucumeris</i> (n=10)	41.53 $\pm$ 4.91a	20.13 $\pm$ 2.38	36.33 $\pm$ 3.77a	2.16
<i>A. swirskii</i>				
<i>Prey=A. eharai</i> eggs (n=15)	31.27 $\pm$ 2.56b	16.33 $\pm$ 1.57b	15.07 $\pm$ 1.71b	2.45
<i>Prey=N. cucumeris</i> eggs (n=10)	55.73 $\pm$ 3.21a	36.33 $\pm$ 2.63a	48.26 $\pm$ 1.62a	2.33
<i>N. cucumeris</i>				
<i>Prey=A. eharai</i> eggs (n=15)	52.69 $\pm$ 4.20	37.67 $\pm$ 2.93a	36.27 $\pm$ 3.36	1.55
<i>Prey=A. swirskii</i> eggs (n=15)	61.93 $\pm$ 3.12	32.13 $\pm$ 1.43b	42.60 $\pm$ 1.59	1.33

Numerals in parentheses are numbers of replicates. Means ($\pm$ s.e.) followed by different letters within the same column of each species between two diets were significantly different (*t*-test; $P < 0.05$).

In *A. eharai* there were significant differences in the longevity and fecundity between the two intraguild prey eggs (Table 21, $P < 0.05$). There were significant differences in the longevity, oviposition duration and fecundity of *A. swirskii* between the two

intraguild prey eggs (Table 21, $P < 0.05$). On the other hand, there were significant differences in the oviposition duration of *N. cucumeris* between the two diets (intraguild prey eggs).

7.2.3. Life history parameters of three predatory mites

TABLE 22. Life history parameters of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* and when they were supplied with heterospecific eggs as prey at 25°C (Mean±SE) calculated by bootstrap method (no.of repeats=10,000)

Predator and prey	Parameters of life table		
	R_0	r_m	T
<i>A. eharai</i>			
Prey= <i>A. swirskii</i> eggs (n=15)	7.56±1.04b	0.124±0.009b	15.46±0.30b
Prey= <i>N. cucumeris</i> eggs (n=10)	27.03±1.32a	0.186±0.003a	16.74±0.62a
<i>A. swirskii</i>			
Prey= <i>A. eharai</i> eggs (n=15)	10.07±1.23b	0.134±0.006b	17.23±0.47
Prey= <i>N. cucumeris</i> eggs (n=10)	28.67±0.63a	0.196±0.008a	17.32±0.31
<i>N. cucumeris</i>			
Prey= <i>A. eharai</i> eggs (n=15)	22.03±1.97	0.177±0.004b	17.43±0.25
Prey= <i>A. swirskii</i> eggs (n=15)	24.34±0.88	0.191±0.004a	16.69±0.31

Different letters within the same column (between treatments and between species) were significantly different (*t*-test with the sequential Bonferroni adjustment: $P < 0.01$). R_0 =Net reproductive rate; r_m =Intrinsic rate of increase; T =Mean generation time.

The life history parameters, R_0 , r_m , and T of *A. swirskii*, *N. cucumeris* and *A. eharai* with heterospecific eggs as prey were shown in Table 22. When *A. eharai* ate *N.*

cucumeri eggs, the r_m was very high when it ate *A. swirskii* eggs. There were significant differences in the R_0 , r_m and T of *A. eharai* between two intraguild prey (Table 22, *t*-test with Bonferroni adjustment: $P < 0.05$). In *A. swirskii*, there were significant differences in the R_0 and r_m between the two diets ($P < 0.05$). On the other hand, there were not large differences in these parameters of *N. cucumeris*, even though a small significant difference appeared in the r_m between the two diets.

7.3. Discussion

It must be an important discovery that three predatory mites reproduce successfully when they performed intraguild predation. Thus, we could not define which one was intraguild predators and intraguild prey in the intraguild predation. For *A. swirskii* and *N. cucumeris*, Buitenhuis *et al.* (2010) reported their development when they performed intraguild predation each other. Their data are very similar to the present results. Anyhow, their abilities to prey on intraguild prey must be very important elements to understand the invasion risk of these predators in fields. Further discussion would be made in the next chapter in relation to their cannibalistic nature.

Chapter 8. Cannibalism in three predatory mites

In this chapter, the cannibalism of *Amblyseius swirskii*, *Neoseiulus cucumeris* and *Amblyseius eharai* was observed, because it was thought to be an element of competition between intraguild species. Then, their reproduction and the parameters of life table when they performed cannibalism were compared to evaluate whether the cannibalism occurred to maintain their population when the extraguild prey was absent.

8.1. Materials and methods

8.1.1. Development of *A. eharai*, *A. swirskii* and *N. cucumeris* by cannibalism

The experimental apparatus-6 (Fig. 6) was used in this experiment. A new egg (at most 8 h old) of *A. eharai*, *A. swirskii* or *N. cucumeris* was introduced into an experimental apparatus. After the larva hatched from the egg, 10 eggs (at most 8 h old) of conspecific eggs were supplied as food. These eggs were replaced twice a day, at 8 a.m. and 5 p.m., and the developmental stage of the predator was recorded at that time. When supplying prey eggs, new apparatus with prey eggs had been prepared, and the predator mite individual being tested was moved from the old apparatus to the new one using a fine brush. All experiments were performed in an incubator ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L: D = 16:8). The experiments were replicated 30 times for each species.

8.1.2. Oviposition of *A. eharai*, *A. swirskii* and *N. cucumeris* by cannibalism

A newly emerged *A. swirskii*, *N. cucumeris* or *A. eharai* female obtained in the above development experiments was allowed to mate with a conspecific male (3 days old) for 1 day in the rearing space. Six days and 11 days after the first male introduction, the female was allowed to mate again with another male (3 days old) for 1 day (Ji *et al.* 2007). A sufficient number of conspecific eggs (15 eggs per female) were supplied daily. When supplying prey eggs, new apparatus with eggs had been prepared, and then the tested female was picked up from old apparatus and introduced into the new one using a fine brush. The oviposition and survival of each female was observed once a day until its death. Offspring sex ratios were determined by rearing all the eggs laid by tested females during the experiments to adulthood on experimental apparatus-2 with *C. lactis* supplied as prey. The experiments were replicated 16-20 times for each species. All experiments were performed in incubators ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 16:8).

8.1.3. Data analysis

Mites that died accidentally during development (at most 10% of replicates) were not included in the analysis. Differences in mean developmental durations, in the numbers of eggs laid, in mean longevities and in mean oviposition durations of *A. swirskii*, *N. cucumeris* or *A. eharai* when supplied conspecific eggs as prey were analyzed using the Tukey test for multiple comparisons by SPSS® (Version 13). Life history parameters were calculated by the method shown in Chapter 2 and were analyzed using *t*-test for comparisons.

8.2. Results

8.2.1. The development of three predatory mites

TABLE 23. Development of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* females with conspecific eggs as prey at 25°C (mean $\pm$ S.E.)

Predatory mites	<i>A. eharai</i> (n=16)	<i>A. swirskii</i> (n=15)	<i>N. cucumeris</i> (n=15)
Egg	1.95 $\pm$ 0.12	1.85 $\pm$ 0.06	2.10 $\pm$ 0.05
Larva	0.85 $\pm$ 0.06 a	0.80 $\pm$ 0.05a	0.60 $\pm$ 0.05 b
Protonymph	2.95 $\pm$ 0.21 a	3.00 $\pm$ 0.12 a	1.85 $\pm$ 0.10 b
Deutonymph	1.85 $\pm$ 0.17	2.15 $\pm$ 0.12	1.95 $\pm$ 0.11
Preoviposition	2.40 $\pm$ 0.18 b	8.50 $\pm$ 0.22 a	2.5 $\pm$ 0.11 b
Egg to egg	9.70 $\pm$ 0.33 b	16.30 $\pm$ 0.32 a	9.00 $\pm$ 0.09 b

Means ($\pm$ s.e.) followed by different letters within the same row of each species were significantly different (Tukey test; $P < 0.05$)

Three predatory mites species (female and male) developed to adulthood only by cannibalism (Tables 23 and 24). The larval developmental duration of *A. eharai* and *A. swirskii* females were more longer than that of *N. cucumeris* ($F_{2,29} = 5.24$, $P = 0.012$). Similar phenomemon had occurred in the protonymphs of three predatory mite females ($F_{2,29} = 13.037$, $P < 0.0001$). There was no significant difference among the developmental durations of deutonymph of three predatory mite females ($F_{2,29} = 0.810$, $P = 0.455$). However, the preoviposition duration of *A. swirskii* was significantly longer than that of the other two species ($F_{2,29} = 265.718$, $P < 0.0001$), so that the whole developmental duration (egg to egg) of *A. swirskii* females was longest among three predatory species ($F_{2,29} = 150.201$, $P < 0.0001$).

No significant differences between the larval developmental durations of three predatory mite males were observed ($F_{2,29}=0.130$, $P=0.878$). The total developmental duration of *A. swirskii* males was longer than that of *A. eharai* males ($F_{2,29}=3.580$, $P=0.042$), and there was no significant difference in total development duration (egg to egg) between *A. eharai* and *N. cucumeris*.

TABLE 24. Development of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* males when they were supplied with conspecific eggs as prey at 25°C (mean $\pm$ S.E.)

Predatory mites	<i>A. eharai</i> (n=12)	<i>A. swirskii</i> (n=10)	<i>N. cucumeris</i> (n=10)
Egg	1.50 $\pm$ 0.15	1.80 $\pm$ 0.08	1.75 $\pm$ 0.11
Larva	0.80 $\pm$ 0.08	0.85 $\pm$ 0.08	0.80 $\pm$ 0.08
Protonymph	2.25 $\pm$ 0.08 b	2.78 $\pm$ 0.14 a	1.90 $\pm$ 0.07 b
Deutonymph	1.75 $\pm$ 0.08 b	1.70 $\pm$ 0.21 b	2.40 $\pm$ 0.07 a
Egg to egg	6.30 $\pm$ 0.19 b	7.13 $\pm$ 0.29 a	6.85 $\pm$ 0.13 ab

Means ($\pm$ s.e.) followed by different letters within the same row of each species were significantly different (Tukey test; $P < 0.05$).

8.2.2. Oviposition and longevity of three predatory mites by cannibalism

The longevity of *N. cucumeris* was longest among three species (Table 25, $F_{2,29}=13.497$, $P<0.0001$). The oviposition duration of *N. cucumeris* was similar to that of *A. eharai*, and they were longer than that of *A. swirskii* ($F_{2,29}=18.769$, $P<0.0001$). *A. eharai* had the highest fecundity among three species, and then the fecundity of *N. cucumeris* was higher than that of *A. swirskii* when they performed cannibalism ($F_{2,29}=146.738$, $P<0.0001$). The most offspring of *A. eharai* and *A. swirskii* were

female; on the contrary, *N. cucumeris* laid more male offspring when they preyed on conspecific eggs.

TABLE 25. Longevity, oviposition duration and fecundity of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* with conspecific eggs as prey at 25 °C (mean $\pm$ S.E.).

Predatory mites	<i>A. eharai</i> (n=15)	<i>A. swirskii</i> (n=15)	<i>N. cucumeris</i> (n=15)
Longevity	34.73 $\pm$ 1.13 b	34.27 $\pm$ 1.91 b	47.53 $\pm$ 2.77 a
Oviposition duration	23.80 $\pm$ 1.198 a	13.07 $\pm$ 2.10 b	29.67 $\pm$ 2.33 a
Fecundity	37.20 $\pm$ 2.19 a	5.13 $\pm$ 0.78 c	10.67 $\pm$ 0.75 b
D ($\text{♀}/\text{♂}$)	1.56	2.00	0.24

Numerals in parentheses are numbers of replicates. Means ($\pm$ s.e.) followed by different letters within the same row of each species were significantly different (Tukey test; $P < 0.05$). A=Mean longevity (days); B=Mean oviposition duration (days); C=Fecundity per female (eggs/female); D=Offspring sex ratio ($\text{♀}/\text{♂}$).

8.2.3. Life table parameters of three predatory

TABLE 26. Life history parameters of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris* when they were supplied with conspecific eggs as prey at 25°C (Mean $\pm$ SE) calculated by bootstrap method (no.of repeats=10,000)

Predatory mites	<i>A. eharai</i> (n=15)	<i>A. swirskii</i> (n=15)	<i>N. cucumeris</i> (n=15)
R_o	20.13 $\pm$ 2.02 a	3.07 $\pm$ 0.51b	2.03 $\pm$ 0.14 b
r_m	0.202 $\pm$ 0.008 a	0.050 $\pm$ 0.007 b	0.033 $\pm$ 0.003 b
T	14.82 $\pm$ 0.19 b	22.26 $\pm$ 0.56 a	21.65 $\pm$ 0.83 a

Different letters within the same row (between treatments and between species) were significantly different (t -test with the sequential Bonferroni adjustment: $P < 0.01$). R_o =Net reproductive rate; r_m =Intrinsic rate of increase; T =Mean generation time.

The life history parameters of *A. eharai*, *A. swirskii* and *N. cucumeris* with conspecific

eggs as prey were shown in Table 26. The R_0 of *A. swirskii* and *N. cucumeris* were similar and lower than that of *A. eharai* with higher r_m (*t*-test with Bonferroni adjustment, $P < 0.001$). On the other hand, *A. swirskii* and *N. cucumeris* had a significantly higher T when they cannibalized conspecific eggs, relative to *A. eharai*.

8.3. Discussion

It is noticeable that the reproduction of *A. eharai* was significantly higher when it preyed upon conspecific eggs ($r_m = 0.202$ female/female/day in Table 26) than when it preyed upon heterospecific eggs ($r_m = 0.124$ female/female/day feeding upon *A. swirskii* and 0.186 female/female/day preying on *N. cucumeris* in Table 22). Previous researches indicated that when extraguild prey is scarce phytoseiid predators prefer attacking intraguild prey to conspecific prey (Montserrat *et al.* 2006; Schausberger & Croft, 2000, 2001), possibly because the intraguild prey may be of a higher quality (Montserrat *et al.* 2006). Although we got precisely this result for *A. swirskii* and *N. cucumeris* in the present study (Tables 22 and 26), *A. eharai* provided a contrary result, suggesting that the quality of heterospecific prey is not always higher than that of conspecific prey. Furthermore, we had learned that *A. swirskii* could still reproduce, albeit at a much lower rate, when feeding solely upon conspecific eggs. This result differs from that of Momen & Abdel-khalek (2009) in which *A. swirskii* females supplied with only conspecific prey all died within a short time without producing any eggs.

The reports on the life history of *A. eharai* are scarce. Saito and Mori (1981) reported that the r_m of *A. eharai* (*Amblyseius deleoni* Muma et Denmark in their report

is a synonym of *A. eharai*) when feeding upon *Tetranychus urticae* Koch was 0.286 female/female/day at 25°C. In chapter 5, an r_m of 0.249 female/female/day when feeding upon *Panonychus citri* was obtained. The r_m value (0.202 female/female/day) when feeding upon conspecific eggs is not so different from the value obtained when feeding upon *P. citri*.

Several studies have examined the life history parameters of *A. swirskii*. The r_m was 0.135 female/female/day at 25°C when feeding upon *Typha latifolia* pollen, (Lee & Gillespie 2011), and 0.20 female/female/day at 25-27°C with maize pollen (Zannou & Hanna 2011). When feeding upon immature *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) at 25°C, the r_m was 0.213 female/female/day and 0.208 female/female/day for two different Mediterranean strains (Nomikou *et al.* 2001). Also in the present study, an r_m of 0.247 female/female/day for this species was obtained when it fed upon *P. citri* at 25°C. In comparison with these previous data, the r_m of 0.134 female/female/day when feeding upon *A. eharai* eggs and that of 0.196 female/female/day when feeding upon and *N. cucumeris* obtained in the present study at 25°C are similar to the result gotten with *T. latifolia* pollen and maize pollen, respectively. On the other hand, if it preyed upon conspecific eggs, the r_m of 0.050 female/female/day was much lower than in any of the other previous cases. Therefore, we conclude that conspecific egg predation, i.e. cannibalism is not a good option for *A. swirskii*.

There were so many reports about the life history parameters of *N. cucumeris*. For example, under 25°C conditions, the intrinsic rate of increase of *N. cucumeris* when preying upon the pollen of Horse-chestnut, *T. urticae* Koch and *Dermatophagoides*

farinae Hughes was 0.180, 0.174 and 0.203 female/female/day, respectively (Ranabhat *et al.* 2013; Marisa and Sauro, 1990; Castagnoli, 1989). Zhang *et al.* (2005) reported that when *N. cucumeris* prey on *P. citri* at 25°C, 80-85% RH and 15L:9D, the intrinsic rate of increase was $r_m=0.1826$ female/female/day. In addition, Li *et al.* (2003) showed that the intrinsic rate of natural increase (r_m) when feeding upon *Polyphagotarsonemus latus* (Banks) was 0.1765 female/female/day under 25°C conditions. Furthermore, Marisa and Sauro (1990) reported: With *Quercus* spp. pollen or *T. urticae* as prey, the intrinsic rate of increase of *N. cucumeris* was 0.193 and 0.174 female/female/day, respectively at 25 °C.

The r_m values of *N. cucumeris* (0.177 female/female/day feeding upon *A. eharai* eggs and 0.191 female/female/day upon *A. swirskii* eggs) obtained in the intraguild predation experiment (Chapter 7, Table 22) were very similar to the above reports. On the other hand, $r_m=0.033$ female/female/day when it cannibalized conspecific eggs was quite low, suggesting that cannibalism is also not good option for this species.

By the way, the present data shows the high quality of conspecific eggs for *A. eharai*; how can we interpret this to understand what happens to *A. eharai* in the field? If conspecific eggs are suitable as prey for *A. eharai* females, how can *A. eharai* maintain and increase its population is a key question that must be addressed. If strong kin-cannibalism avoidance mechanisms exist, as reported in *Phytoseiulus persimilis* Athias-Henriot (Schausberger 2005), they may at least preclude any loss of inclusive fitness through sib cannibalism. However, this does not seem to be the case here, as we recently showed that *A. eharai* females frequently prey upon their offspring under no extra-guild prey conditions (Zhang *et al.* 2014). Therefore, we

have to assume that there is some other yet undetermined mechanism(s) preventing the predator mites from engaging in cannibalism in the field. One plausible trait is that *A. eharai* females tend to lay their eggs sparsely (Chittenden and Saito 2001). If they always move widely across their habitats and lay eggs sparsely, then the probability of mothers encountering their eggs should be low. Such habits may help to protect this species from the deleterious effects of kin cannibalism as hypothesized by Schausberger (2003). A hint at the answer may lie in our frequent observations that *A. eharai* females lay their eggs on the tips of leaf hairs. Females always lay their eggs singly, never in clumped masses. This egg laying behavior may also help them avoid cannibalism.

Chapter 9. Competition among three predatory mites

Competition between species having the same ecological niche has received a great deal of attention in animal ecology. The earliest work by Gause (1934) showing two closely related species having the same ecological niche do not coexist was based on laboratory competition experiments with *Paramecium aurelia* Ehrenberg and *P. caudatum* Ehrenberg. This phenomenon known as Gause's "competitive exclusion principle" is frequently referred to in ecology textbooks. Hardin (1960) further elaborated on this principle by proposing that two completely competitive species could not coexist in the same ecological niche, unless they underwent an evolutionary or behavioral shift towards a differentiation in ecology.

Clear evidence supporting Gause's principle has been uncovered in wild squirrels (Wauters *et al.* 2002), in aphids (Tapia *et al.* 2008) and in coral reef fishes (Sale 1977). Interestingly however, many ecological studies also exist that have failed to prove the principle (Hardin 1960). In fact, because supporting evidence for this principle is not always forthcoming, many counter arguments have been put forward, the competitive coexistence principle (Neill *et al.* 2009) and the neutral theory (Hubbell 2005) are two such examples.

In any case, competition between species is thought to be an important driving factor of evolution (Hubbell and Foster 1986). However, precisely how such a driving force operates between individuals of two confronting species is not fully understood.

Phytoseiid mites (Phytoseiidae) are an important predacious mite group commonly used as natural control agents in agricultural situations (McMurtry *et al.*

2013). They are frequently introduced into countries from abroad (Palevsky *et al.* 2013). Although biological control is usually considered to be better for the environment than chemical control, it can have potentially negative effects if not employed cautiously, e.g. competitive displacement of native fauna by introduced predators (Palevsky *et al.* 2013). Many recent researches have addressed the cannibalistic and intra-guild predatory traits of several phytoseiid species (Schausberger and Croft 2000, Zhang *et al.* 2014; Ji *et al.* submitted). Therefore, evaluating whether introduced predators can potentially affect native predator fauna is an urgent theme that must be undertaken before the predators are released into the field.

Gotoh *et al.* (2014) reported that the introduced phytoseiid predator *Neoseiulus* (*Amblyseius*) *californicus* (McGregor) displaced the native species *Neoseiulus womerslyi* (Schicha) in the central part of Japan. They then observed the possibility that the former excluded the latter under experimental conditions. They concluded that the mechanism behind the displacement of *N. womerslyi* is most likely one-sided intraguild predation by *N. californicus*, because the latter can develop by feeding upon the former, but not vice versa. This is regarded as an example of competitive exclusion through intraguild prey-predator interaction. If we analyze the competitive displacement of predators, we have to simultaneously focus on at least two different kinds of competition, namely intraguild predation and competition other than predation, such as reproductive interference (Kuno 1992; Gotoh *et al.* 2014), competition for food and space, and so on.

However, it is not always easy to establish how strong competition and predation

need to be in order to result in species displacement. As shown by Gotoh (2014), it is not difficult to say that one-sided intraguild predation must cause the displacement of one species. If there is mutual intraguild predation in the species being focused on, as is known in several phytoseiid species (Momen and Abdel-Khalek 2009; Buitenhuis *et al.* 2010; Ji *et al.* under submission), then it must be very difficult to predict which species will win. Therefore, if we intend to address such phenomena, theoretical models that can show the existence of competition and/or intra-guild predation may help our understanding. As such, competition coefficients and intraguild predation coefficients (as defined in this report) under the assumption of Lotka-Volterra equations of competition and predation (Lotka 1925; Volterra 1926) should be considered useful tools.

In this chapter, I then observed the interactions between these three species, under conditions with sufficient extraguild prey common to these species.. Furthermore, we estimated the rate of population increase (r) and carrying capacity (K) of each species from the single species population dynamics under the same experimental conditions. Based on these parameters, I attempted to estimate the competition and/or intraguild predation coefficients between these three phytoseiid species using numerical calculations based on Lotka-Volterra equations.

9.1. Materials and methods

9.1.1. Population dynamics

Prior to the introduction of phytoseiid mites, 0.05 g yeast and approx. 200 female *C. lactis* had been placed on the nylon mesh screens inside the experimental apparatus-7

(method 7 in Fig. 7), and the acrylic plates and the transparent glass sheets were clamped with the 4 clips. Then, using a fine brush, a certain number of phytoseiid females were introduced into each experimental cage through the hole in the nylon screen mesh. When all mites had been introduced, the holes were covered with a drop of glue. The phytoseiids used in the experiments were gravid (mated for 48 h with a newly emerged male) females aged five days after emergence.

The experimental designs were as follows:

Control (single species dynamics)

1. 5-female Control: Five females of each phytoseiid species (*A. eharai*, *A. swirskii* and *N. cucumeris*) were introduced in each experimental cage. This experiment was terminated at the day of extinction of either species in experiments 3 to 5 (mentioned hereafter).

2. 10-female Control: Ten females of each phytoseiid species (*A. eharai*, *A. swirskii* and *N. cucumeris*) were introduced in each experimental cage. This experiment was continued until the populations reached a plateau that allowed the calculation of r and K .

Interaction between two species

3. *A. eharai* vs. *A. swirskii* (known as Ae-As systems hereafter): Five females each (total=10) of both *A. eharai* and *A. swirskii* were introduced in the experimental cages.

4. *A. eharai* vs. *N. cucumeris* (Ae-Nc systems hereafter): Five females each (total=10) of both *A. eharai* and *N. cucumeris* were introduced in the experimental cages.

5. *A. swirskii* vs. *N. cucumeris* (As-Nc systems hereafter): Five females each (total=10) of both *A. swirskii* and *N. cucumeris* were introduced in the experimental cages.

The above 3 to 5 experiments were continued until one of the species went extinct (namely the female population of one species = 0).

All the experiments consisted of five replicates, and were performed in small climate-controlled chambers (25 ± 1 °C, $90 \pm 5\%$ RH and L : D = 14 : 10). The female phytoseiid populations were counted at two days interval after anesthetizing for 8 minutes in an airtight cup filled with CO₂. At that time, sufficient numbers of *C. lactis* were supplied to maintain a predator: prey ratio of approx. 1:20 during the experiments.

These predator species develop from egg to adult in approx. 4.9-5.9 days with *C. lactis* as prey (Table 5), thus 4 days after female introduction was an appropriate duration to approximate stable age distribution (a necessary condition of r definition, see text below). We considered four days after the first female predator introduction as the population dynamics “start day” (there were many eggs and other immature stages).

9.1.2 Estimation of r and K from population data

The carrying capacity (K) and the rate of population increase (r - here we discriminate “ r ” as estimated from population dynamics from “ r_m ” estimated from Euler equation mentioned above) are formulated as the following Lotka-Volterra equation for a single species population, i.e. logistic equation, as:

$$\frac{dN_t}{dt} = rN_t(1 - \frac{N_t}{K}),$$

and thus

$$\frac{d(\ln N_t)}{dt} = r(1 - \frac{N_t}{K})$$

Then, we could get the following linear relationship, using the approximation of

$$\frac{d(\ln N_t)}{dt} \approx \frac{\ln N_{t+\Delta t} - \ln N_t}{\Delta t} = \frac{\ln \frac{N_{t+\Delta t}}{N_t}}{\Delta t} = r(1 - \frac{N_t}{K}) = r - \frac{r}{K} N_t, \quad (1)$$

where N_t is the female population at time t and Δt is the census interval.

The number of females at time t , N_t and $\ln \frac{N_{t+\Delta t}}{N_t}$ was obtained using the data from the

10-female control (experiment 2). $\Delta t = 2$. Therefore, r can be estimated when $N_t = 0$

and K can be obtained when $\ln \frac{N_{t+\Delta t}}{N_t} = 0$ from the regression of equation 1. These

parameters and statistics were calculated using JMP ver. 9.0[®].

9.1.3 Estimation of competition and intra-guild predation coefficients

In order to simulate the population dynamics of all the experiments, we adopted the r and K values obtained earlier. To calculate the population dynamics the Lotka-Volterra equations for competition and predation were modified (joined) as follows:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1 + a_{2,1} N_2}{K_1}) - b_{2,1} N_1 N_2 \dots \dots \dots (2)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2 + a_{1,2} N_1}{K_2}) - b_{1,2} N_1 N_2 \dots \dots \dots (3)$$

where N_1 , r_1 , $a_{2,1}$, K_1 and $b_{2,1}$ were the number of females, population increase rate, competition coefficient (from species 2 to species 1), carrying capacity and intraguild predation coefficient (from species 2 to species 1) for species 1, respectively, and N_2 , r_2 , $a_{1,2}$ (from species 1 to species 2), K_2 , $b_{1,2}$ (from species 1 to species 2) were

those for species 2. There was sufficient extra guild prey for both predators, such that there is no term "predator increase rate with prey consumption" in the original Lotka-Volterra predation model.

Because there were four unknown parameters ($a_{1,2}, a_{2,1}, b_{1,2}, b_{2,1}$) with two differential equations (2) and (3), there was no way to estimate them simultaneously.

As such we separated the equations as follows:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + a_{2,1} N_2}{K_1}\right) \dots \dots \dots (4)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + a_{1,2} N_1}{K_2}\right) \dots \dots \dots (5)$$

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - b_{2,1} N_1 N_2 \dots \dots \dots (6)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - b_{1,2} N_1 N_2 \dots \dots \dots (7)$$

Then we attempted to estimate the competition coefficients ($a_{1,2}$ and $a_{2,1}$) other than predation in equations (4) and (5), and the intraguild predation coefficients ($b_{1,2}$ and $b_{2,1}$) in equations (6) and (7) by a numerical calculation program. Given provisional values of $a_{1,2}$ and $a_{2,1}$ (or $b_{1,2}$ and $b_{2,1}$), we calculated the populations by a program for numerical calculation. When the calculated value of one population (the winner) reached the observed value within ± 1 from the time when the population of the other species (the loser) became extinct (population < 0.1), then we considered the set of coefficient values were solution.

For these calculations, we used a program assembled by Nobuyuki Tsuji using Mathematica version 10.0[®].

9.2. Results

9.2.1. Population dynamics of each species and estimations of r and K

9.2.1.1. *A. eharai*

When supplied with ample quantities of extraguild prey *C. lactis*, the *A. eharai* female population had increased to 209 ± 6.1 (average $\pm$ SD) after 24 days and appeared to reach a plateau at 20 days in the 10-female experiment (Fig. 13). The female population increased in parallel in the 5-female experiment and had reached 87 ± 30.1 after 16 days (this control experiment was terminated when one of the populations became extinct in the competition experiments mentioned hereafter).

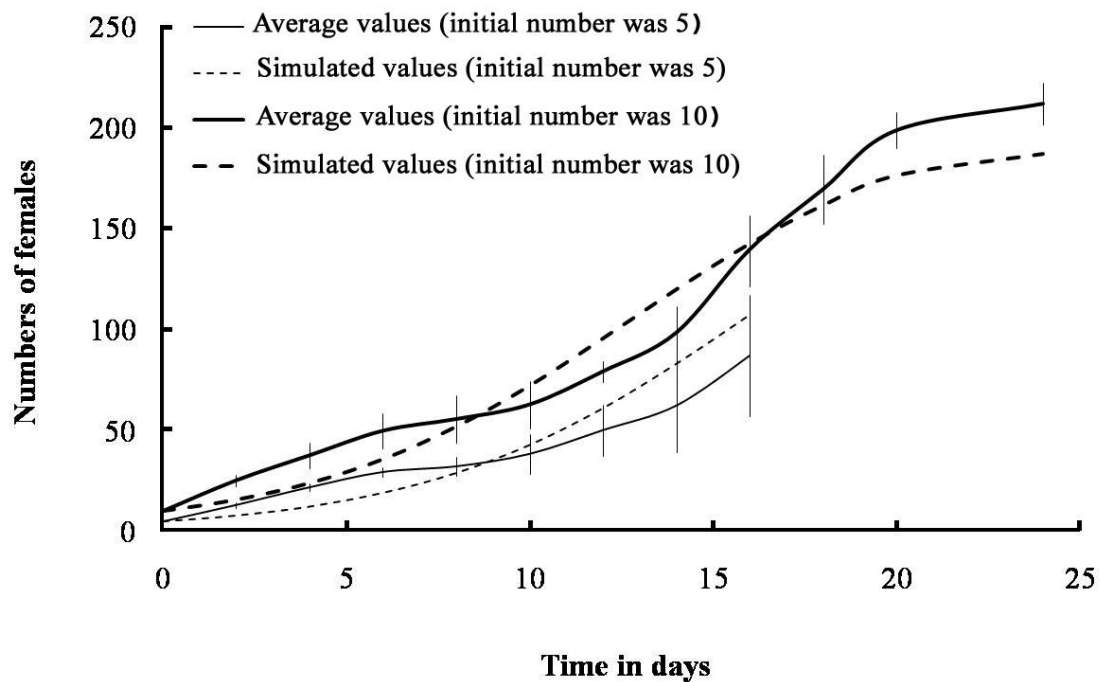


Fig. 13. Population dynamics of *A. eharai* under experimental conditions. The initial number of females introduced (before 4 days, see text) are 10 for the thick solid line and 5 for the thin solid line. Vertical lines showed standard deviations. Thick broken line (initial number = 10) and thin broken (initial number = 5) line showed the simulated values based on the r and K estimated by the procedure in Fig. 14.

From the population dynamics of the 10-female experiment, the regression of Y ($= \frac{\ln \frac{N_{t+\Delta t}}{N_t}}{\Delta t}$) to N_t , was conducted and a significant linear relationship was obtained ($Y = 0.235 - 0.00113 N_t$, $P < 0.0001$ by Anova). Then, using the equation of Y and N_t , we estimated $r = 0.235$ (intercept when $N_t = 0$) and $K = 207$ (the intercept when $Y = 0$) for *A. eharai* (Fig. 14). The obtained r value guaranteed that our monitoring method (anesthetizing with CO₂) had little (if any) negative effects on the mite population dynamics adopted in this study, because the r_m value ($= 0.253$ in Table 8) - estimated separately from the life table - corresponded well with the r value of *A. eharai* with the same extraguild prey.

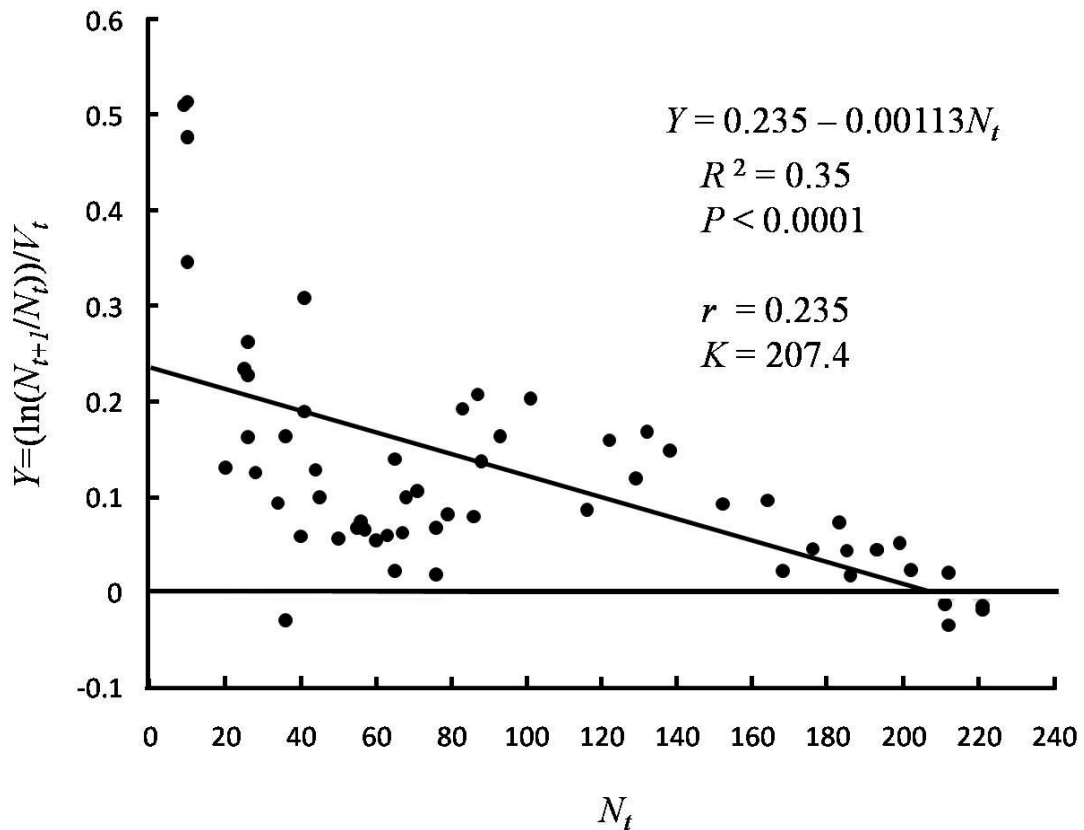


Fig. 14. Estimation of *A. eharai* population parameters. r is population increase rate and K is carrying capacity estimated from the regression line.

Based on the estimated r and K values, we calculated the population growth of *A.*

charai using the differential equation, $\frac{dN_t}{dt} = rN(1 - \frac{N_t}{K})$ for both 5-female and 10 female experiments in Fig. 13. In both experiments the calculated female populations were lower in the early period of population growth, and a little higher in the middle period, perhaps reflecting some deviation in the initial populations between the actual and theoretical ones. Anyhow, there were not any great discrepancies between the simulated and the actual dynamics as a whole (Fig. 13).

9.2.1.2. *A. swirskii*

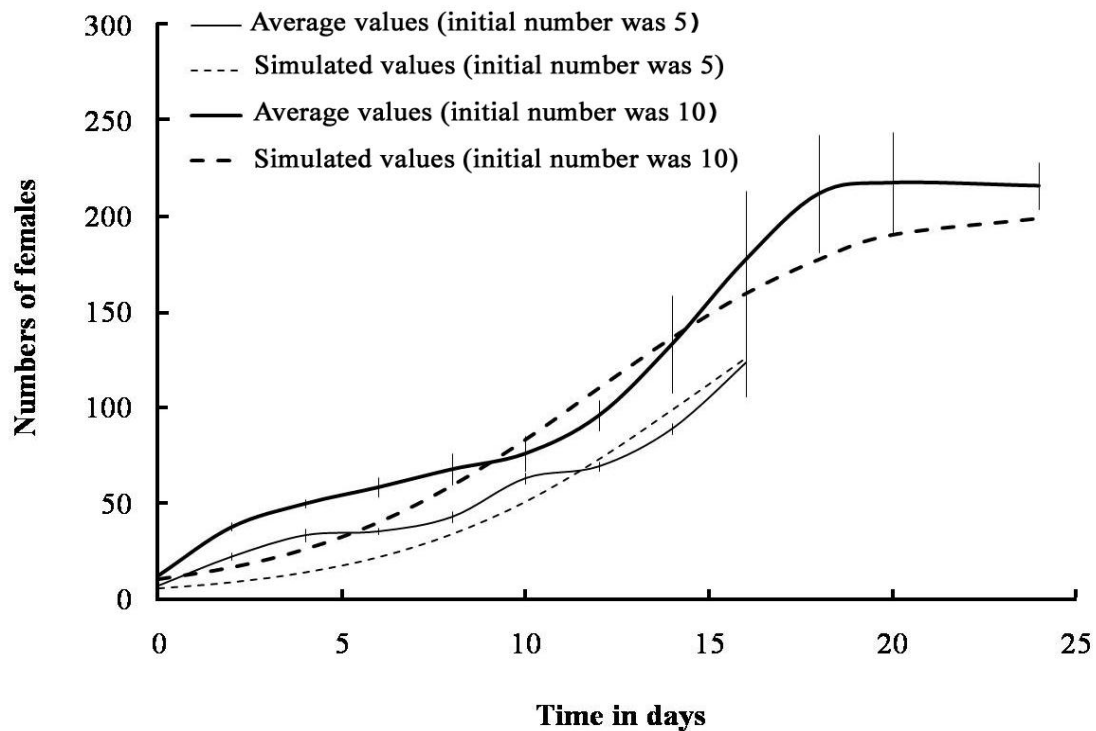


Fig. 15. Population dynamics of *A. swirskii* under experimental conditions. The initial number of females introduced (before 4 days, see text) are 10 for the thick solid line and 5 for the thin solid line. Vertical lines showed standard deviations. Thick broken line (initial number = 10) and thin broken (initial number = 5) line showed the simulated values based on the r and K estimated by the procedure in Fig. 16.

The *A. swirskii* female population increased to 215.2 ± 16.5 (average $\pm$ SD) at 24 days with the extraguild prey *C. lactis*, and appeared to reach a plateau at 18 days in the

10-female experiment (Fig. 15). The female population in the 5-female experiment increased in a similar manner and reached 123.2 ± 17.7 at 16 days.

From the population dynamics of the 10-female experiment, the regression of Y to N_t showed a significant linear relationship ($Y = 0.256 - 0.0012N_t$, $P < 0.0001$ by Anova). Then from the equation of Y and N_t , we estimated $r = 0.256$ and $K = 213$ for *A. swirskii* (Fig. 16). This r value guaranteed that any negative effects of the monitoring method on mite population dynamics adopted in this study were negligible, because the r_m value ($= 0.232$ in Table 8) separately estimated from the life table corresponded well to the r value of *A. swirskii* with the same extra guild prey.

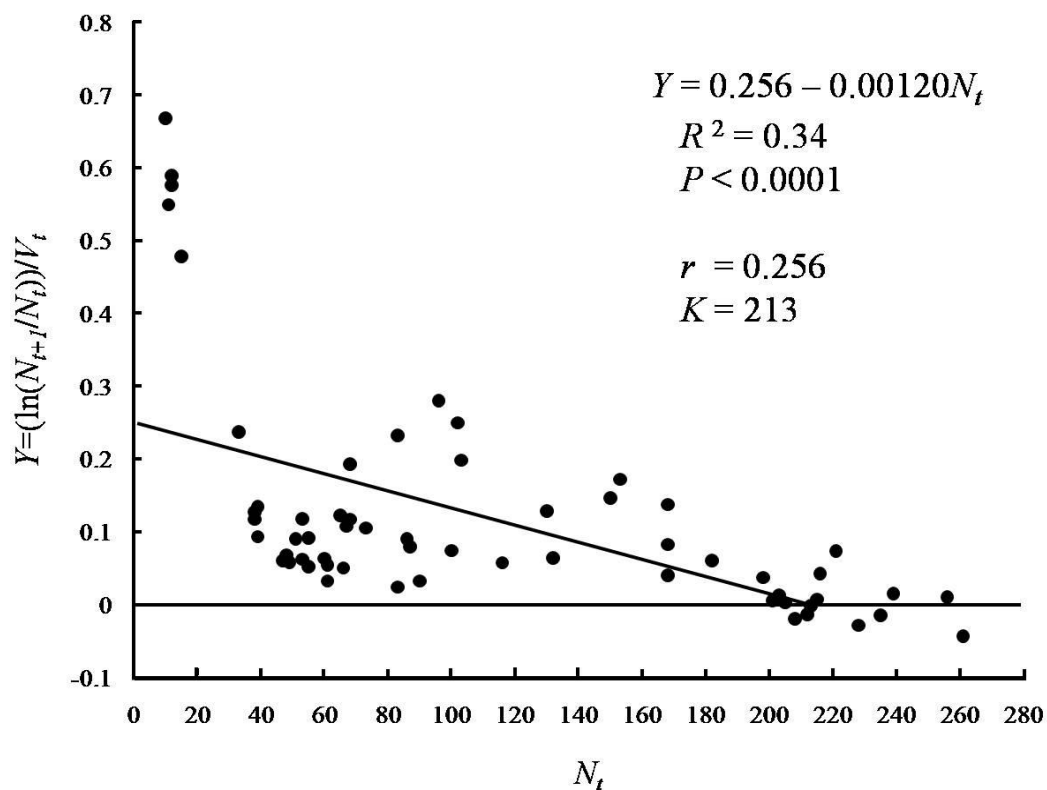


Fig. 16. Estimation of *A. swirskii* population parameters. r is population increase rate and K is carrying capacity estimated from the regression line.

By using the estimated r and K values, we calculated the population growth of *A. swirskii* by differential equation for both the 5-female and 10 female experiments in

Fig. 15. The estimated female populations of both experiments were lower than the observed ones in the early period of population growth, and a bit higher in the middle period as in *A. eharai* (Fig. 13), but there were no great discrepancies between the calculated and the actual dynamics (Fig. 15).

9.2.1.3. *N. cucumeris*

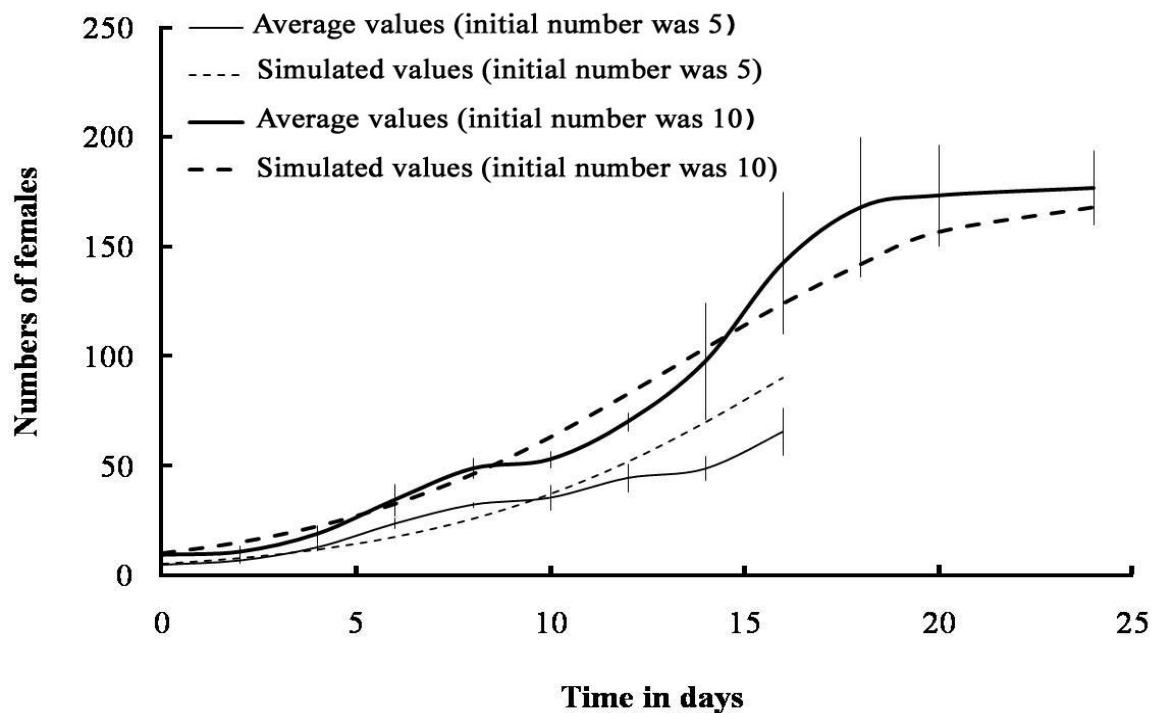


Fig. 17. Population dynamics of *N. cucumeris* under experimental conditions. The initial number of females introduced (before 4 days, see text) are 10 for the thick solid line and 5 for the thin solid line. Vertical lines showed standard deviations. Thick broken line (initial number = 10) and thin broken (initial number = 5) line showed the simulated values based on the r and K estimated by the procedure in Fig. 18.

The population of *N. cucumeris* females increased to 174 ± 10.0 (average $\pm$ SD) with extraguild prey *C. lactis*, and appeared to have reached a plateau at 18 days in the 10-female experiment (Fig. 17). As expected, the female population in the 5-female experiment increased in parallel manner and reached 48.6 ± 5.5 at 16 days.

From the population dynamics of the 10-female experiment, a regression of Y to

N_t was conducted and a significant linear relationship was obtained ($Y = 0.218 - 0.00113N_t$, $P < 0.0001$ by Anova). From the equation of Y and N_t , we then estimated $r = 0.218$ and $K = 193$ for *N. cucumeris* (Fig. 18). This r value also assured that the monitoring method adopted in this study had little (if any) negative effects, because the r_m value ($= 0.212$ in Table 8) separately estimated from the life table corresponded well to the r value of *A. swirskii* with the same extra guild prey.

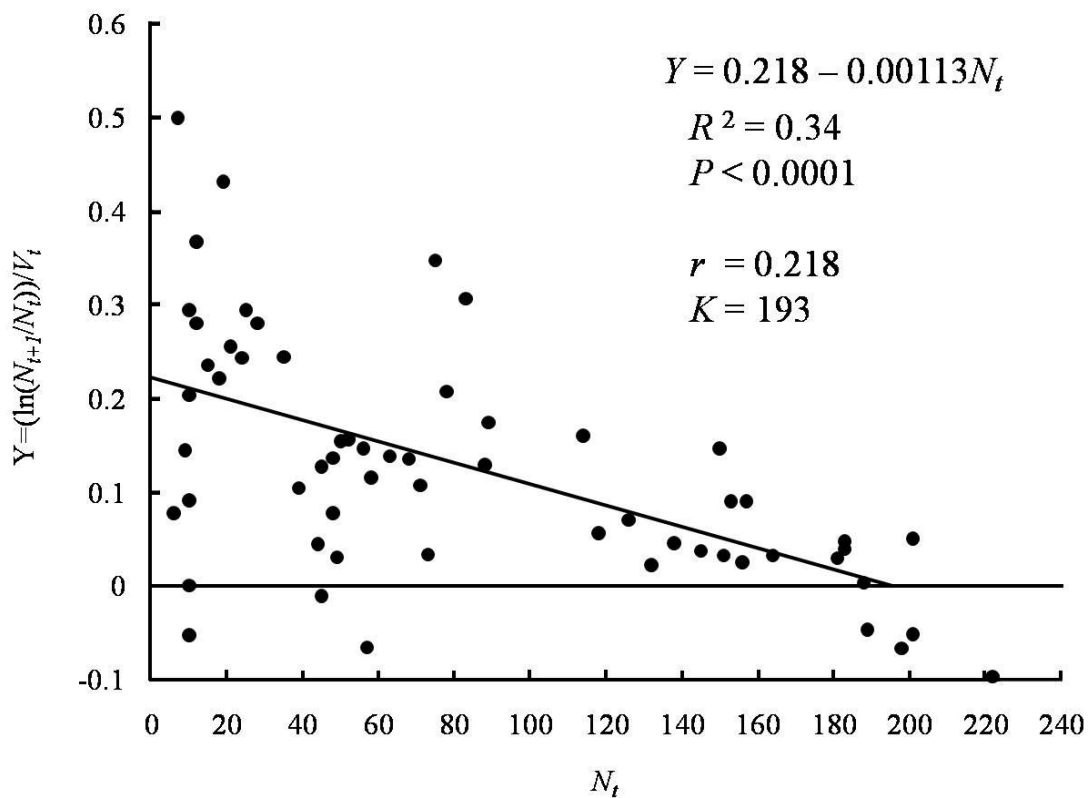


Fig. 18. Estimation of *N. cucumeris* population parameters. r is population increase rate and K is carrying capacity estimated from the regression line.

Based on the estimated r and K values, the population growth patterns of *N. cucumeris* by the differential equation for both the 5-female and 10 female experiments were calculated as in Fig. 17. The calculated female population of the 10 female experiment fitted well to the actual dynamics, while that of the 5-female experiment was lower than the observed one in the later period of population growth

(Fig. 17).

9.2.2. Population dynamics in interacting systems and their simulation

9.2.2.1. *A. eharai* -*A. swirskii* systems

TABLE 27. Sets of two coefficients (competition, $a_{1,2}$ and $a_{2,1}$ or predation, $b_{1,2}$ and $b_{2,1}$) evaluated under equations (4) and (5) or under (6) and (7), when calculated population of winning species reached the observed population within ± 1 at the time when loser population became extinction (< 0.1).

<i>A. eharai</i> (N_1)				
Coefficient	$a_{1,2}$	$a_{2,1}$	$b_{1,2}$	$b_{2,1}$
<i>A. swirskii</i> (N_2)	29.8	31.8	0.05	0.051
<i>A. eharai</i> (N_1)				
Coefficient	$a_{1,2}$	$a_{2,1}$	$b_{1,2}$	$b_{2,1}$
<i>N. cucumeris</i> (N_2)	17	10	0.02	0.012
<i>A. swirskii</i> (N_1)				
Coefficient	$a_{1,2}$	$a_{2,1}$	$b_{1,2}$	$b_{2,1}$
<i>N. cucumeris</i> (N_2)	9	0	0.01	0

In the *A. eharai* (N_1) and *A. swirskii* (N_2) interacting systems, the *A. eharai* female population became extinct and the *A. swirskii* female population increased to an average of 21.6 at 16 days. In order to explain the dynamics of these species, we calculated these two populations under the assumption of sets of equations (4) and (5), or (6) and (7) by giving provisional coefficient values. The female population of one species (winning female population) calculated with a set of values ($b_{1,2}$ and $b_{2,1}$ or $a_{1,2}$ and $a_{2,1}$) reached the observed female population within ± 1 of the time when the other species females (losing female population) became extinct (population < 0.1) was considered to be the solution. To calculate, we obtained the solution, $a_{1,2}=29.8$

and $a_{2,1}=31.8$ under the equation (4) and (5), and $b_{1,2} = 0.050$ and $b_{2,1} = 0.051$ under equation (6) and (7) (Table 27). In Fig. 19 the calculated dynamics of these two species in the latter case ($b_{1,2} = 0.050$ and $b_{2,1} = 0.051$) are depicted.

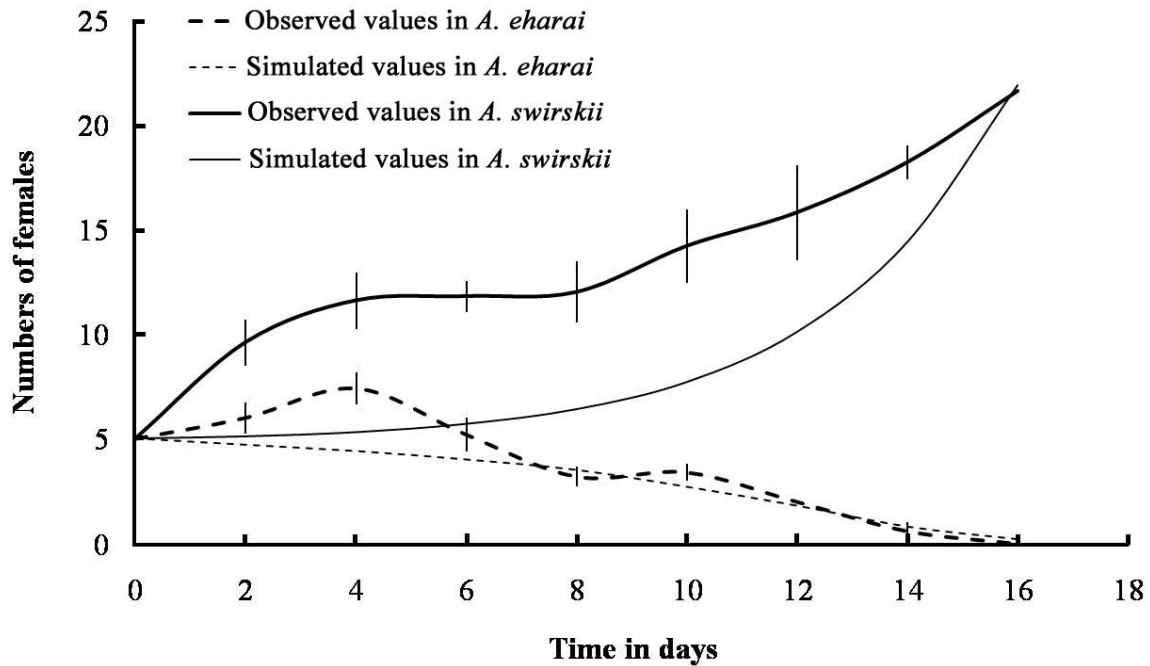


Fig. 19. Population dynamics of *A. eharai* and *A. swirskii* interacting in a cage with sufficient extra-guild prey. Thick and solid line showed observed values in *A. swirskii* and thick and broken line in *A. eharai*. Vertical lines show standard deviations. Thin and solid line showed calculated values in *A. swirskii* and thin and broken line in *A. eharai*, when $b_{1,2} = 0.051$, $b_{2,1} = 0.050$ under the equations (6) and (7) (see text).

9.2.2.2. *A. eharai* -*N.cucumeris* systems

In the *A. eharai* (N_1) and *N. cucumeris* (N_2) interacting systems, the *A. eharai* female population reached 45.2 at 14 days whereas the *N. cucumeris* female population had become extinct at that time. By calculation, $a_{1,2}=17$ and $a_{2,1}=10$ under the assumption of sets of equations (4) and (5) was the solution. On the other hand, $b_{1,2}=0.02$ and $b_{2,1}=0.012$ under equations (6) and (7) was the solution. In Fig. 20 the calculated dynamics of the latter case are depicted. The calculated population trend of *N.*

cucumeris was similar to the actual data, but that of *A. eharai* was different from the actual data.

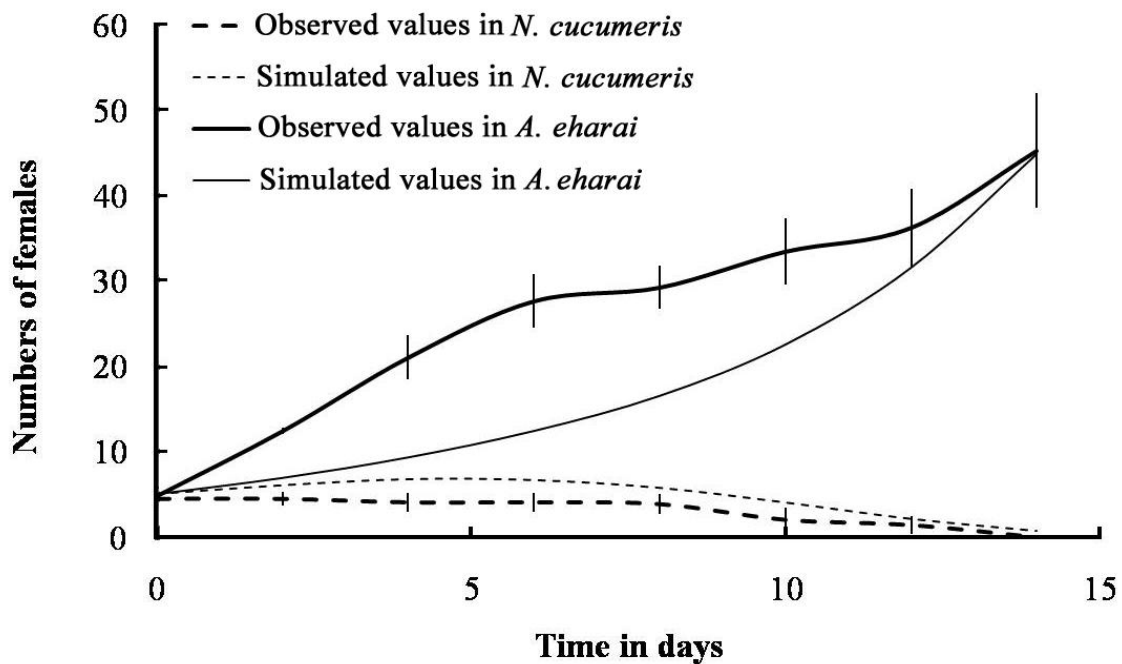


Fig. 20. Population dynamics of *A. eharai* and *N. cucumeris* interacting in a cage with sufficient extra-guild prey. Thick and solid line showed observed values in *A. eharai* and thick and broken line in *N. cucumeris*. Vertical lines showed standard deviations. Thin and solid line showed calculated values in *A. eharai* and thin and broken line in *N. cucumeris*, when $b_{1,2}=0.012$, $b_{2,1}=0.020$, under the equations (6) and (7) (see text).. The length of vertical axis was decreased to $\frac{1}{2}$ of Fig. 19.

9.2.2.3. *A. swirskii* -*N. cucumeris* systems

In the *A. swirskii* (N_1) and *N. cucumeris* (N_2) interacting systems, the *A. swirskii* female population reached 130 at 16 days (Fig. 21), which was more than the value when there was no competitor (123.2 see Fig. 14). *N. cucumeris* females on the other hand, had become extinct by that time. Thus, the competition and predation coefficients from *N. cucumeris* that affect *A. swirskii* could be assumed to be zero. Then we evaluated the *N. cucumeris* parameters as $a_{1,2}=9$ when $a_{2,1}=0$ under the equations (4) and (5), or $b_{1,2}=0.01$ and $b_{2,1}=0$ under the equations (6) and (7) (Table

27). In Fig. 21 the calculated dynamics of these two species in the latter case are depicted. The simulated population trend for *A. swirskii* was similar to the actual data, but that of *N. cucumeris* was consistently higher than that of the observed data. The result showed that the effect of *A. swirskii* on *N. cucumeris* through competition and/or predation was almost completely one-sided.

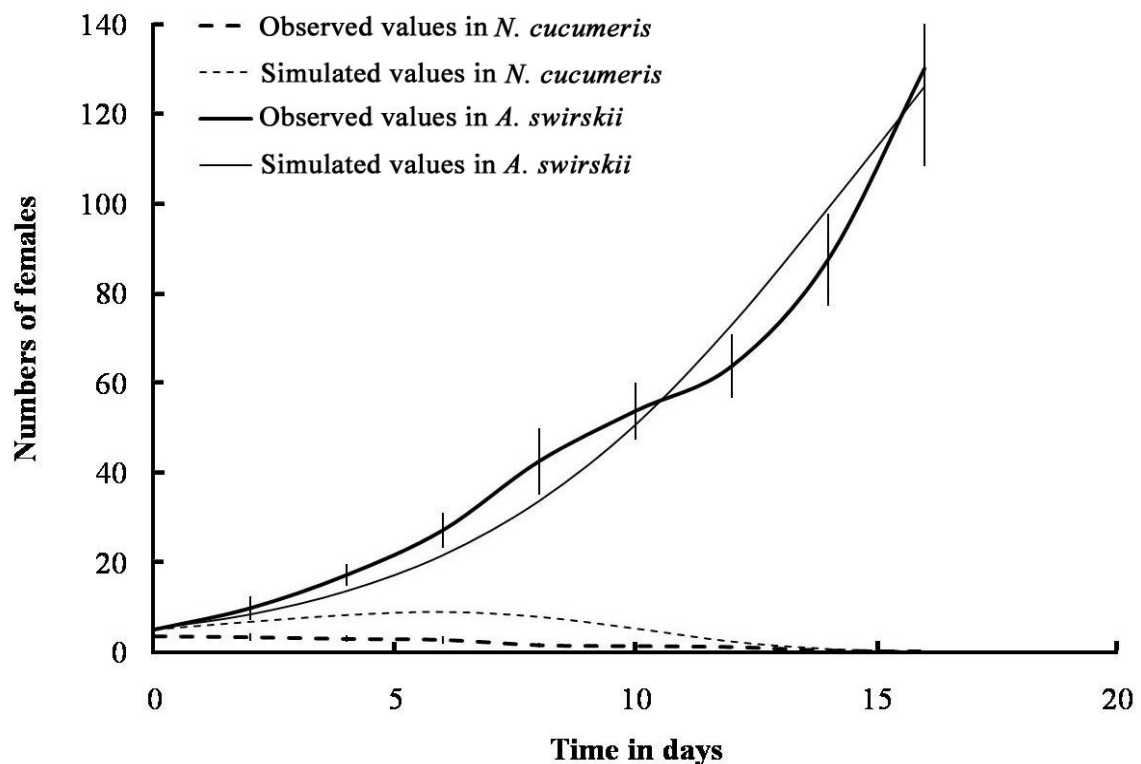


Fig. 21. Population dynamics of *A. swirskii* and *N. cucumeris* interacting in a cage with sufficient extra-guild prey. Thick and solid line showed observed values in *A. swirskii* and thick and broken line in *N. cucumeris*. Vertical lines showed standard deviations. Thin and solid line showed calculated values in *A. swirskii* and thin and broken line in *N. cucumeris*, when $b_{1,2} = 0$, $b_{2,1} = 0.01$ under the equations (6) and (7) (see text). The length of vertical axis was decreased to 1/2 of Fig. 18.

9.3. Discussion

When 10 females of each phytoseiid species were reared in cages with *C. lactis*, the populations of all species plateaued (Figs. 13, 15 and 17), meaning that there was a

carrying capacity (K) for each of the species examined in this experimental environment. After calculating the K of each species from the population data, we attempted to calculate the population growth patterns by a logistic model (Lotka-Volterra model). The calculated dynamics were not so different from the observed ones, suggesting that some density dependent factors were operating in the present systems.

One factor appeared to be related to the cannibalistic nature of these species (Ji *et al.* 2014; Ji *et al.* submitted; Zhang *et al.* 2014). The ability of these three species to reproduce with conspecific eggs was recently observed (Ji *et al.* submitted), and although there is no data about preferences for conspecifics or for *C. lactis*, it must be plausible that any such cannibalistic habit may be more strongly manifested under high-density conditions, and is thus density dependent. Because the experimental spaces were limited, the carrying capacities observed for each species were thought to be partially caused by this factor.

In all the various combinations of the three phytoseiid mites, one species always went extinct (with the other winning the competition) and these trends were consistent within 5 replications for each combination. Among the three species, *A. swirskii* was the strongest under the present experimental conditions. The native species, *A. eharai* was second and the weakest was *N. cucumeris* (Figs. 19-21). We consider the present results to have been caused by at least two factors: Intraguild predation and competition other than predation between two species.

By introducing competition or predation coefficients into the modified Lotka-Volterra equations one by one, we were not able to, however, get any nice fit

between the observed and simulated dynamics for the Ae-As and Ae-Nc systems (Figs. 19 and 20). Although we were unable to definitively identify any reason(s) for this from within the study, there are several potential explanations. For example, in Ae-As systems, the observed populations of the two species increased rapidly during the early periods. One reason for this must be the discrepancy in initial population structure between the observed and simulated dynamics. The model used in the calculation was primarily defined under the stable age distribution of individuals. Even if we tried to approximate the initial populations to the stable age distribution by moving the starting day of the observation to 4 days after the actual females release (as described in the materials and methods), some biased age distribution may inevitably influence the initial trend of the observed population increase. This appeared to be supported from the population dynamics of single species (Figs. 13, 15 and 17), all of which showed excess populations in the observed values compared to the calculated ones during the early phases. However, it could not be excluded that there were some other factors reducing the interaction intensity during the initial population dynamics phase of these species.

In any case, we think that our attempts to evaluate the intensity of competition and predation coefficients were necessary in order to know the relative importance of these two factors. We learned from Table 27 that intraguild predation overwhelms the competition. Although we had no strict way of joining these two kinds of coefficients, i.e. synergistic effect of competition and intraguild predation as supposed in equation (2), the possibility of predation occurring must be more likely than competition, because the former showed more realistic values in all combinations (Table 27): If

there is no competition other than intraguild predation (equations (6) and (7)), the predation coefficients, $b_{2,1}=0.051$, $b_{1,2}=0.05$ satisfied to approximate the final results of the Ae-As population dynamics. These values correspond to that one adult female of *A. swirskii* eating 0.17 *A. eharai* females when there are 3.4 *A. eharai* females and 14.2 *A. swirskii* females ($((0.051*N_1*N_2)/ N_2)$) on day 10 in Fig. 19 (observed data). Although the adult females of either species are not known to eat adult females of the other species, the intraguild predation of females on younger stages (Ji *et al.* unpublished) can substitute such a predation effect in this system.

On the other hand, the competition coefficients, for example $a_{1,2}=29.8$ (negative effect from *A. eharai* to *A. swirskii*) and $a_{2,1}=31.8$ (that from *A. swirskii* to *A. eharai*) estimated by calculations using the Ae-As systems when the predation coefficients were zero (equations (4) and (5)), are so large that it is difficult to imagine them as the actual competition mechanisms between these two predators, because $a_{2,1}=31.8$ means that a single *A. swirskii* female reduces *A. eharai* carrying capacity (K) by 31.8 (converting into number of *A. eharai* females) per unit of time, a dubiously high figure.

Furthermore, it must be noted that even a small difference between the predation coefficients of two species can mean the difference between victory and defeat (Fig. 19, Table 27). We should pay attention to the population levels of the two predator systems where one species went extinct. For example, *A. swirskii*, the winner in Ae-As system did not increase its population of up to 21.6 females at that time, even though the K of this species without a competitor was 213 (Fig. 13). Ji *et al.* (submitted) observed that there is strong intraguild predation between *A. eharai* and *A.*

swirskii, i.e. they can reproduce feeding only upon the eggs of the other species. There was no statistically visible difference in the intensity of intraguild predation between these species (Ji *et al.* unpublished data), indirect support for the observation that a small amount of difference in the intensity of intraguild predation may separate the winner and loser.

From the view of field applications, these three species are very important biological control agents (Buitenhuis *et al.* 2014; Messelink *et al.* 2006; Ji *et al.* 2013 a, b, c). Among them, *A. swirskii* and *N. cucumeris* are introduced predators in China and Japan. In the present study, *A. swirskii* always displaced *N. cucumeris* and the native species *A. eharai* in closed cages even though sufficient extraguild prey was supplied. The risks associated with introducing *A. swirskii* have previously been pointed out, e.g. Buitenhuis *et al.* (2010) noted that *A. swirskii* had a high predation rate and a preference for *N. cucumeris* juveniles over thrips. Although it is still unknown whether *A. swirskii* can eliminate *A. eharai* under field conditions, more attention must be paid to such a possibility, because a nice example of displacement of *N. womersleyi* by *N. californicus* through intraguild predation exists from Japan (Gotoh *et al.* 2014).

Another factor that may cause competitive displacement was not addressed in the present study, i.e. reproductive interference between species (Kuno 1992; Takafuji *et al.* 1997; Sato *et al.* 2014; Gotoh *et al.* 2014). Kuno (1992) theoretically showed that this process has a rather mild effect on competitive exclusion. We have studied this factor between several phytoseiid mite species and learned that there is some one-sided reproductive interference from *A. swirskii* to *A. eharai* (Ji *et al.*

unpublished). We expect that this will have some effect on the dynamics of *A. swirskii* and *A. eharai* systems. However, just how this factor affected the present results is still undetermined. We have to address it in a future study.

Chapter 10. Reproductive interference between three predatory mites

In this chapter, the reproductive interference among *Amblyseius swirskii*, *Neoseiulus cucumeris* and *Amblyseius eharai* was observed in the laboratory, in order to understand the factors caused species displacement in Chapter 8. The competition mechanism among three predators was discussed.

10.1. Materials and methods

10.1.1. Between *A. eharai* and *A. swirskii*

The design of experiments was as follows:

Treatment 1: single *A. swirskii* deutonymph + two *A. swirskii* males,

Treatment 2: single *A. swirskii* deutonymph + two *A. eharai* males,

Treatment 3: single *A. swirskii* deutonymph + 1 *A. eharai* males + 1 *A. swirskii* males.

Treatment 4: single *A. eharai* deutonymph + two *A. eharai* males,

Treatment 5: single *A. eharai* deutonymph + two *A. swirskii* males,

Treatment 6: single *A. eharai* deutonymph + 1 *A. eharai* males + 1 *A. swirskii* males.

In all the treatments, the mites were accommodated into the experimental apparatus-6 (method 6 in Fig. 6). Before the introduction of predatory mites, a sufficient number of prey mites (30 individuals of *C. lactis*, all stage) were introduced in experimental apparatus. All unmated males were 3 days old (after molting to adult). The preoviposition duration of each female were observed, and the oviposition and survival of each female were observed and recorded once a day in 10 days after the

female began to oviposit. When supplying additional prey mites, new experimental apparatus with prey mites had been prepared, and the tested female and male were picked up from the old one and introduced into the new one using a fine brush. If the male died, the same male was added. The offspring development and sex ratio were determined by rearing all the offspring eggs laid to adulthood on experimental apparatus-2 (Fig. 2) with *C. lactis* as prey. The experiments were replicated 10 times for each treatment. All experiments were performed in incubators ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 14:10).

The reproductive interference between *A. swirskii* and *N. cucumeris* and between *N. cucumeris* and *A. eharai* were conducted by the same design mentioned above.

10.1.2. Data analysis

The means ($\pm$ s.e.) of oviposition, survival rate and offspring sex ratio were calculated using Microsoft Office Excel 2003. In addition, the means were separated by Tukey test for comparisons using SPSS (13th edition) if the treatment indicated a significant effect.

10.2. Results

10.2.1. Between *A. eharai* and *A. swirskii*

The average fecundity, preoviposition duration, offspring sex ratio and survival rate of *A. eharai* and *A. swirskii* mated with heterospecific or conspecific males were listed in the Table 28. Both *A. swirskii* and *A. eharai* did not oviposit when they were accommodated into a closed cage with the males of different species (treatments 2

and 5), although the mating behavior was sometimes observed.

TABLE 28. The fecundity of *A. eharai* and *A. swirskii* mated heterospecific or conspecific male at 25°C, 85±5%RH and 14:10 L:D in 10 days after the female began to oviposit.

Treatments	Average fecundity (eggs)	Preoviposition Duration (days)	Offspring sex ratio (♀/♂)	Survival Rate (%)
1♀ <i>A. eharai</i>				
Treatment 1 (2 ♂ <i>A. eharai</i>)	27.70±1.39 a	1.85±0.08	1.94	90.25
Treatment 2 (2 ♂ <i>A. swirskii</i>)	0	0	0	0
Treatment 3 (1 ♂ <i>A. eharai</i> + 1 ♂ <i>A. swirskii</i>)	20.70±1.71 b	2.04±0.33	1.91	97.10
1♀ <i>A. swirskii</i>				
Treatment 4 (2 ♂ <i>A. swirskii</i>)	19.90±0.41 b	1.95±0.09	2.93	90.95
Treatment 5 (2 ♂ <i>A. eharai</i>)	0	0	0	0
Treatment 6 (1 ♂ <i>A. eharai</i> + 1 ♂ <i>A. swirskii</i>)	21.40±0.48 b	1.90±0.07	3.17	93.46

Means (±s.e.) followed by different letters within the same column of different combinations were significantly different (Tukey test; $P < 0.01$).

When a single female *A. eharai* was put into a closed cage with a conspecific male and a heterospecific male (treatment 3), the oviposition was significantly lower than that with two conspecific males (treatment 1) ($F_{3,39} = 9.688$, $P < 0.0001$). On the other hand, no significant differences were observed between the combination of 1 *A. swirskii*♀ with 2 *A. swirskii*♂ (treatment 4) and that of 1 *A. swirskii*♀ with 1 *A. eharai*♂ + 1 *A. swirskii*♂ (treatment 6). In addition, there were no significant differences ($P > 0.05$) in the preoviposition duration, and survival rate between *A. eharai* and *A. swirskii*. The offspring sex ratio was similar between two combinations

of *A. swirskii* females, and between two combinations of *A. eharai* females ($P > 0.05$).

10.2.2. Between *A. eharai* and *N. cucumeris*

TABLE 29. The fecundity of *A. eharai* and *N. cucumeris* mated heterospecific or conspecific male at 25°C, 85±5%RH and 14:10 L:D in 10 days after the female began to oviposit.

Treatments	Average fecundity (eggs)	Preoviposition Duration (days)	Offspring sex ratio (♀/♂)	Survival Rate (%)
1♀<i>A. eharai</i>				
Treatment 1 (2 ♂ <i>A. eharai</i>)	27.70±1.39 a	1.85±0.08	1.94	90.25
Treatment 2 (2 ♂ <i>N. cucumeris</i>)	0	0	0	0
Treatment 3 (1 ♂ <i>A. eharai</i> + 1 ♂ <i>N. cucumeris</i>)	27.10±0.74 ab	1.90±0.16	1.72	86.35
1♀<i>N. cucumeris</i>				
Treatment 4 (2 ♂ <i>N. cucumeris</i>)	23.60±1.08b	1.85±0.13	1.55	95.87
Treatment 5 (2 ♂ <i>A. eharai</i>)	0	0	0	0
Treatment 6 (1 ♂ <i>A. eharai</i> + 1 ♂ <i>N. cucumeris</i>)	24.10±0.85 ab	2.30±0.17	1.53	93.36

Means (±s.e.) followed by different letters within the same column of different combinations were significantly different (Tukey test; $P < 0.01$).

The average fecundity, preoviposition duration, offspring sex ratio and survival rate of *A. eharai* and *N. cucumeris* mated heterospecific or conspecific were listed in the Table 29. Both *N. cucumeris* and *A. eharai* did not lay any eggs when they were accommodated with the males of different species into a closed cage (treatments 2 and 5), but the mating behavior was sometimes observed too.

There were no significant differences in the fecundity, offspring sex ratio and

offspring survival rate between the treatments 1 and 3, and between 4 and 6, suggesting that there were no reproductive interference between *A. eharai* and *N. cucumeris*.

10.2.3. Between *A. swirskii* and *N. cucumeris*

TABLE 30. The fecundity of *A. swirskii* and *N. cucumeris* mated heterospecific or conspecific male at 25 °C, 85±5%RH and 14:10 L:D in 10 days after the female began to oviposit.

Treatments	Average fecundity (eggs)	Preoviposition Duration (days)	Offspring sex ratio (♀/♂)	Survival Rate (%)
1♀<i>A. swirskii</i>				
Treatment 1 (2 ♂ <i>A. swirskii</i>)	19.90±0.41 b	1.95±0.09	2.93	90.95
Treatment 1 (2 ♂ <i>N. cucumeris</i>)	0	0	0	0
Treatment 1 (1♂ <i>A. swirskii</i> + 1 ♂ <i>N. cucumeris</i>)	20.30±0.37 b	1.85±0.08	2.38	93.10
1♀<i>N. cucumeris</i>				
Treatment 1 (2 ♂ <i>N. cucumeris</i>)	23.60±1.08a	1.85±0.13	1.55	95.87
Treatment 1 (2 ♂ <i>A. swirskii</i>)	0	0	0	0
Treatment 1 (1♂ <i>A. swirskii</i> + 1 ♂ <i>N. cucumeris</i>)	22.80±0.57 ab	1.90±0.07	1.53	98.68

Means (±s.e.) followed by different letters within the same column of different combinations were significantly different (Tukey test; $P < 0.01$).

The average fecundity, preoviposition duration, offspring sex ratio and survival rate of *A. swirskii* and *N. cucumeris* mated heterospecific or conspecific were listed in the Table 30. Both *A. swirskii* and *N. cucumeris* did not lay any eggs when they were accommodated with the males of different species into a closed cage (treatments 2

and 5).

There were no significant differences in the fecundity, offspring sex ratio and offspring survival rate between the treatments 1 and 3, and between 4 and 6, suggesting that there were no reproductive interference between *A. swurskii* and *N. cucumeris*.

10.3. Discussion

Reproductive interference is defined as a negative interspecific sexual interaction that adversely affects the fitness of males and females of at least one of the species involved and that is caused by incomplete species recognition, during reproductive process (Gröning and Hochkirch 2008; Kishi *et al.* 2009). Moreover, reproductive interference results in species exclusion that primarily depends on not only the positive frequency-dependent effect also the initial population ratio of two species (Kishi *et al.* 2009), usually, the ratio of males in population plays a key role. In other words, the density-dependence and asymmetry was the mainly mechanism of reproductive interference (Gröning and Hochkirch 2008).

The reproductive interference frequently occurred among many animals (Gröning and Hochkirch 2008). Especially, it had been frequently observed between two congeneric species. For example between two congeneric damselfly species (Van Gossum *et al.* 2007), between bean weevil *Callosobruchus chinensis* and cowpea beetle *Callosobruchus maculatus* (Kishi *et al.* 2009), between *Tetranychus evansi* and *Tetranychus urticae* (Sato *et al.* 2014) and between *Tetranychus turkestani* and *Tetranychus urticae* (Ben-David *et al.* 2009), and so on. Nevertheless,

reproductive interference also had been detected between different biological types of the same species, for example between cryptic species Middle East-Asia and Mediterranean of the whitefly *Bemisia tabaci* (Sun *et al.* 2014).

Gröning and Hochkirch (2008) distinguish seven types of reproductive interference: signal jamming, heterospecific rivalry, misdirected courtship, heterospecific mating attempts, erroneous female choice, heterospecific mating, and hybridization. In this chapter, however I concerned only the results of reproductive interference.

No females of three phytoseiid mites could lay eggs, when they were accommodated into a closed cage with two males of different species. Moreover, no reproductive interference was observed between *A. eharai* and *N. cucumeris* and between *A. swirskii* and *N. cucumeris*. Gotoh *et al.* (2014) also indicated that there was no reproductive interference between *Neoseiulus womersleyi* and *N. californicus*.

However, significant reproductive interference between *A. eharai* and *A. swirskii* was observed. Although there was no interference between *A. swirskii* females and *A. eharai* males, *A. eharai* females decreased their oviposition when they cohabited with *A. swirskii* male. It implies that the reproductive interference is asymmetric.

It was a little bit difficult to know the mechanism that induced *A. swirskii* males to disturb *A. eharai* female oviposition within this study, even though the mating behavior was frequently observed between *A. eharai* female and *A. swirskii* male. A hypothesis that *A. swirskii* males could sometimes put their spermatopore into the spermatheca of *A. eharai* female could be proposed. Then the sperms from *A. swirskii* occupied the partial space of spermatheca of *A. eharai* females, which may disturb the oviposition of *A. eharai*.

Anyhow, such a one-way reproductive interference must an important role in the competition between *A. eharai* and *A. swirskii* observed in chapter 8.

Chapter 11. Predation preference of three Phytoseiid mites

In this chapter, I conducted the experiment of prey preference of *Amblyseius eharai*, *Amblyseius swirskii* and *Neoseiulus cucumeris*. I intend to know whether the intraguild predation and cannibalism will occur when the extraguild prey, conspecifics and intraguild prey were present. According to the results, I discussed about the competition mechanism among three predators.

11.1. Materials and methods

11.1.1. Predation preference of three predators

An young gravid female (5 days old after molting to adult) of *A. swirskii* (or *A. eharai* or *N. cucumeris*), 10 conspecific eggs, 10 heterospecific eggs and 30 extraguild preys (nymphs of *C. lactis*) were accommodated into the experimental apparatus-6 (methd 6 in Fig. 6). The tested females had been starved 24 h. All tested prey eggs were 8 h old. When supplying the prey eggs, I marked the eggs with the mixture (containing 800-mesh carbon powder, starch and water with the rate 0.05/1/2 g) using a fine brush under the microscope. The conspecific eggs were marked on the middle of eggs, and the heterospecific eggs were marked on the end of eggs. Then, the species and number of consumed eggs could be distinguished from the new eggs laid by the tested females. There were 10 replicates for all species. All experimental apparatus were kept in incubators ($25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 14:10). Then, the consumption of eggs was observed after 24 h.

11.1.2. Preference of *A. eharai* and *N. cucumeris* to hetero- or conspecific larvae

An emerged gravid *A. eharai* or *N. cucumeris*, 10 conspecific larvae, 10 heterospecific larvae and 30 *C. lactis* nymphs were accommodated into the experimental apparatus-6 (Fig. 6). All tested larvae were 8 h old and all tested females had been starved 24 h. There are 10 replicates. All experimental apparatus were kept in incubators ($25 \pm 1^\circ\text{C}$, $90 \pm 5\%$ RH and L:D = 14:10). Because it was very difficult to distinguish species of larval mites, the live larvae or pronymphs in every experimental apparatus were individually reared to adulthood with *C. lactis* as prey in the experimental apparatus-6. After that, their species were distinguished under the microscope.

11.1.3. Data analysis

The means ($\pm$ S.E.) of consumption were calculated using Microsoft Office Excel 2003. In addition, the means were separated using *t-test* if the treatment indicated a significant effect.

11.2. Results

11.2.1. Predation preference of three phytoseiid mites to eggs

The preference of three predators to conspecific or heterospecific eggs was shown in Table 31, when the extraguild prey *C. lactis* were present. It must be very important that they preyed upon the prey eggs, irrespective of conspecific or heterospecific eggs, under abundant extraguild prey existing conditions.

The results showed that *A. swirskii* consumed more heterospecific eggs than

conspecific eggs ($P < 0.001$), though there were sufficient extraguild prey *C. lactis* were present. On the contrary, *A. eharai* and *N. cucumeris* did not show any preference for conspecific and heterospecific eggs (all $P > 0.05$).

TABLE 31. The preference predation of *Amblyseius swirskii*, *Amblyseius eharai* or *Neoseiulus cucumeris* to three prey types, conspecific eggs, heterospecific eggs and extraguild prey, nymph of *Carpoglyphus lactis*, at $25 \pm 1^\circ\text{C}$, $90 \pm 5\%$ RH and L:D = 14:10.

Prey combination and predators	Consumption (eggs/24 h)	
	conspecific eggs	heterospecific eggs
Prey: <i>A. swirskii</i> + <i>A. eharai</i> eggs		
<i>A. swirskii</i>	0.20 ± 0.13 b	2.40 ± 0.81 a
<i>A. eharai</i>	0.50 ± 0.22	0.90 ± 0.41
Prey: <i>A. eharai</i> + <i>N. cucumeris</i> eggs		
<i>A. eharai</i>	0.40 ± 0.22	0.50 ± 0.31
<i>N. cucumeris</i>	0.30 ± 0.15	0.20 ± 0.13
Prey: <i>A. swirskii</i> + <i>N. cucumeris</i> eggs		
<i>A. swirskii</i>	0.21 ± 0.18 b	0.98 ± 0.22 a
<i>N. cucumeris</i>	0.33 ± 0.11	0.40 ± 0.23

Means ($\pm$ s.e.) followed by different letters within the same row of different combinations were significantly different (*t*-test).

11.2.2 Predation preference of *A. eharai* and *N. cucumeris* to larvae

The results (Table 32) indicated that *N. cucumeris* did not show any preference for con- or heterospecific larvae as observed in the egg cases. However, *A. eharai* preferred heterospecific larvae to conspecific larvae ($P < 0.001$).

TABLE 32. The preference predation of *Amblyseius eharai* or *Neoseiulus cucumeris* to three prey types, consepecific eggs, heterospecific eggs and extraguild prey, nymph of *Carpoglyphus lactis*, at $25 \pm 1^{\circ}\text{C}$, $90 \pm 5\%$ RH and L:D = 14:10.

Prey combination and predators	Consumption (eggs/24 h)	
	consepecific larvae	heterospecific larvae
Prey: <i>A. eharai</i> + <i>N. cucumeris</i> larvae		
<i>A. eharai</i>	$6.00 \pm 0.37\text{b}$	$9.00 \pm 0.49\text{ a}$
<i>N. cucumeris</i>	5.60 ± 0.54	5.10 ± 0.38

Means ($\pm$ s.e.) followed by different letters were significantly different (*t-test*).

11.3. Discussion

Prey vulnerability is a major factor influencing predator preferences (Provost *et al.* 2006). The predators firstly prey upon the phytophagous pests in general, due to their natural feeding habits. However, when there were not only one pest species in the habitat, the predator should make a choice, which one was more delicious or easier to prey upon. Many studies had been conducted to show the preference of different predators. Xu and Enkegaard (2010) showed that the prey preference of *A. swirskii* between the spider mites *Tetranychus urticae* and *Frankliniella occidentalis*. Their results indicated that *A. swirskii* clearly preferred thrips to both spider mite protonymphs and deutonymphs.

If two predator species coexist in a habitat, the predators should make a choice between another predator (intraguild predation) and pests (extraguild prey). For example, the bug *Orius laevigatus* should attack and kill large numbers of *Phytoseiulus persimilis* and *Tetranychus urticae* when they coexist in cucumber plants

in a greenhouse, in spite of the population of spider mites was even controlled (Venzon *et al.* 2001). Buitenhuis *et al.* (2010) indicated *A. swirskii* was an important intraguild predator of *N. cucumeris* immatures due to a high predation rate and a preference for *N. cucumeris* immatures over thrips, though *N. cucumeris* also preyed upon *A. swirskii* immatures. It suggested that intraguild prey was an equally good or better food source than thrips (extra-guild prey) for both the predators, because of high oviposition rates and fast development. Such a negative interaction between *A. swirskii* and *N. cucumeris* suggested that these two species should not use together in biological control of thrips.

In the present study, I obtained the similar result. *A. swirskii* consumed more *N. cucumeris* eggs than conspecific eggs. On the contrary, *N. cucumeris* equally preyed upon both conspecific and heterospecific eggs. In addition, *A. swirskii* has an obvious preference for *A. eharai* eggs and *N. cucumeris*. The predation rate of female *A. swirskii* to *N. cucumeris* eggs was ten times compared with the predation rate to conspecific eggs when the extraguild prey *C. lactis* was present. This must be very important to interpret the competition results of *A. swirskii*-*A. eharai* systems, and of *A. swirskii*-*N. cucumeris* systems observed in Chapter 8.

In the combination of *A. eharai* and *N. cucumeris*, both predators all preyed equally upon the conspecific and heterospecific eggs. However, *A. eharai* preferred *N. cucumeris* to conspecific larvae, while *N. cucumeris* had no such preference. This must be also important to understand the results of *A. eharai* and *N. cucumeris* competition observed in Chapter 8.

Chapter 12. Female performance towards offspring under starved conditions in four phytoseiid species

In this chapter, my interest was establishing whether there are any differences in kin cannibalism between four phytoseiid species, *Amblyseius swirskii*, *Amblyseius eharai*, *Neoseiulus cucumeris* and *Typhlodromus bambusae*, having different life styles, by comparing phytoseiid female performance towards their own offspring under extremely starved conditions.

12.1. Materials and methods

12.1.1. Female and offspring survival under starved conditions

A small amount of glue was applied to the edges of each glass tube opening (Fig. 8). A gravid phytoseiid female (3–5 days old after adult emergence) was then arbitrarily picked up from one of the cultures using a fine brush, and released into the glass tube (method 8 in Fig. 8). Immediately after release, a mesh sheet was used to close off the tube opening. All but one of the eggs laid by the female during a 24-h duration were removed from the tube. The mites inside the tubes (the female and its single offspring) were observed every day until their death. The trials (called 1-offspring trials) were replicated 30 times for each phytoseiid species. As a control for the above experiment, female survival without any food was observed by removing all the offspring produced by the female. Control trials (non-offspring trials) were replicated 20 times for each phytoseiid species.

12.1.2. Immature survival under no mother and no food conditions

In addition to the above experiment, one egg deposited during a 1-day interval was arbitrarily picked up from each phytoseiid culture then placed into the glass tube using a fine brush. The opening was closed in the same way as mentioned above. The survival durations (longevity) of the immature mites under the no-prey and no-female conditions were then observed. The trials were replicated 21–24 times for each phytoseiid species. All glass tubes were placed into a temperature-controlled chamber kept at 25°C, 60–80 % r.h., and 14:10 (L:D) photoperiod.

12.1.3. Statistics

I adopted Kaplan–Meier survival analysis for all survival data using the software JMP 9.0 (SAS Institute) on PC. Furthermore, Fisher’s exact probability test was applied to compare the death sequences of females and their offspring. Most cases were considered to be post hoc multiple comparisons, such that I adjusted the probabilities (P) depending upon the number of comparisons by the sequential Bonferroni method (Rice 1989).

12.2. Results

12.2.1. Female longevity with their offspring

Even under “without extraguild prey” conditions (but with their own offspring available as food), most phytoseiid females had laid at least one egg by the second day after introduction. Those females that did not oviposit were eliminated from the present analysis.

TABLE 33. Results of Kaplan–Meier survival analyses (logrank test) for adult females of four phytoseiid species between 1-offspring and non-offspring (control) trials (degree of freedom of each comparison is 1).

Species	1-offspring ^a	Non-offspring ^a	χ^2	Probability
<i>Amblyseius eharai</i>	8.29 ± 0.53 (19)	8.10 ± 0.86 (13)	0.082	>0.99
<i>Amblyseius swirskii</i>	9.46 ± 0.47 (23)	9.28 ± 0.63 (16)	0	>0.99
<i>Neoseiulus cucumeris</i>	13.95 ± 1.65 (20)	15.28 ± 0.93 (20)	0.054	>0.99
<i>Typhlodromus bambusae</i>	4.14 ± 0.42 (28)	4.12 ± 0.30 (13)	0.048	>0.99

^a Number of eggs observed in parentheses and average days ± SE. Probability (*P*) was adjusted by the sequential Bonferroni test for post hoc multiple comparisons.

TABLE 34. Results of Kaplan–Meier survival analyses (logrank test) for gravid female survivorships of four phytoseiid species with one offspring.

	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>	<i>T. bambusae</i>
<i>Amblyseius eharai</i>	-	0.117	0.009	<0.001
<i>Amblyseius swirskii</i>	2.46	-	0.001	<0.001
<i>Neoseiulus cucumeris</i>	13.13	11.98	-	<0.001
<i>Typhlodromus bambusae</i>	23.73	34.17	27.06	-

Above the diagonal probabilities are shown and below the diagonal χ^2 values. Degree of freedom is 1 in each comparison. Probability (*P*) was adjusted by the sequential Bonferroni test for post hoc multiple comparisons.

There was no significant difference in female survivorship between 1-offspring and nonoffspring experiments in any species (Table 33), showing that a single egg or immature, if a female fed upon it, has no effect on the female survival. In these comparisons between species, all probabilities were adjusted by the sequential Bonferroni test for six post hoc comparisons.

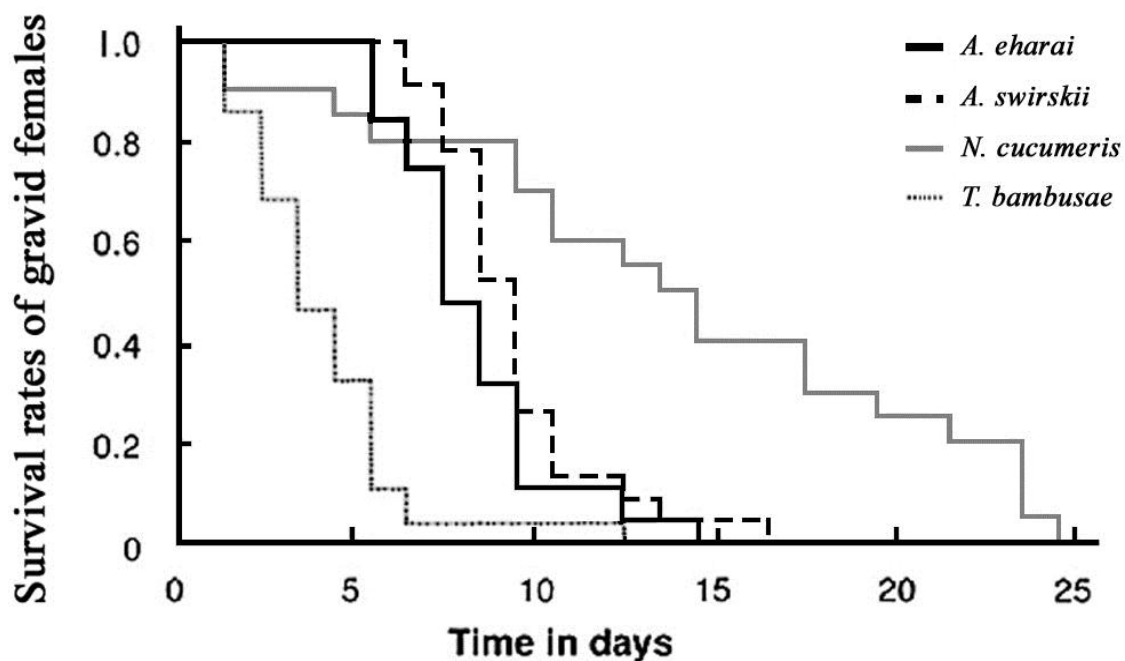


Fig. 22. Survivorship of gravid females in four species: *Amblyseius eharai* (AE), *Amblyseius swirskii* (AS), *Neoseiulus cucumeris* (NC) and *Typhlodromus bambusae* (TB) under no prey (but offspring available as prey), free-water available and humidity selectable conditions. Number of replicates, average survivorship and SE of each species appear in Table 33.

In all species tested, it was sometimes observed that mothers ate their offspring. However, it was difficult to determine whether the bodies on which they were feeding were alive or dead. When the females lived with one offspring under starved conditions, there was a significant difference in female survivorship among the four phytoseiid mite species by Kaplan–Meier survival analysis (Fig. 22, logrank, $df = 3$, $\chi^2 = 76.53$, $P < 0.0001$). The survival duration of *T. bambusae* was very short (4.14 days on average) and significantly differed from that of the other three species (Table 34). Among the three latter species, significant differences occurred between *N. cucumeris* and *A. swirskii*, and between *N. cucumeris* and *A. eharai*. There was no significant difference between *A. eharai* and *A. swirskii* (Table 34). In these comparisons between species, all probabilities were adjusted by the sequential

Bonferroni test for six post hoc comparisons.

12.2.2. Effect of mother presence on offspring survival

When mothers cohabited with their offspring (hereafter called mother-presence), the survival duration of offspring varied among phytoseiid species (Fig. 23, logrank, $df = 3$, $\chi^2 = 36.05$, $P < 0.0001$). The survival duration of immature *A. eharai* was the shortest and significantly differed from the other three species (Table 35). Furthermore, there was a difference between *T. bambusae* and *N. cucumeris*. However, there were no significant differences between *T. bambusae* and *A. swirskii* or between *N. cucumeris* and *A. swirskii* (Table 35). In these comparisons between species, all probabilities have been adjusted by the sequential Bonferroni test for six post hoc comparisons.

In the above immature survival analyses, it was difficult to determine whether the observed differences were caused by the effects of mother presence and/or species-specific tolerance to starvation. The survival durations of immature stages when they were left alone (hereafter called mother-absence) in the tubes were then observed.

There was a significant difference among the survival patterns of the four species (logrank, $df = 3$, $\chi^2 = 85.37$, $P < 0.0001$) when the immature stages lived alone (mother-absence). Paired comparisons between species showed that there were significant differences between all species combinations (Table 36), showing that there is species-specific tolerance to starvation.

Next, we compared the immature survival rates between the mother-presence and

mother-absence experiments (Fig. 24a–d). In *A. eharai*, *N. cucumeris* and *A. swirskii*, there were significant differences between mother-presence and mother-absence conditions, indicating a negative effect of mother presence on offspring survival (Table 37). However, there was no difference in immature survival between mother-presence and mother-absence conditions in *T. bambusae* (Table 37). In the above between species comparisons, all probabilities have been adjusted by the sequential Bonferroni test for six post hoc comparisons.

TABLE 35. Results of Kaplan–Meier survival analyses (logrank test) for offspring (immatures) survivorships of four phytoseiid species under mother presence conditions (Fig. 23).

	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>	<i>T. bambusae</i>
<i>Amblyseius eharai</i>	-	<0.001	<0.001	<0.001
<i>Amblyseius swirskii</i>	22.57	-	>0.90	0.16
<i>Neoseiulus cucumeris</i>	18.33	0.88	-	0.04
<i>Typhlodromus bambusae</i>	13.31	3.03	4.22	-

Above the diagonal probabilities are shown and below the diagonal χ^2 values. Degree of freedom is 1 in each comparison. Each probability (*P*) was adjusted by the sequential Bonferroni test for post hoc multiple comparisons

Finally, the mortality sequence of mothers and their offspring in the mother-presence experiments was analyzed (Table 38). *T. bambusae* females tended to die before their offspring, showing that they have little responsibility for the death of their offspring under starved conditions. However, offspring tended to die before their mothers' death in each of the other phytoseiid species, suggesting that mothers may have a role in the deaths of their offspring (mother's death before offspring death

versus mother's death after offspring death, Fisher's exact probability test: between *T. bambusae* and the other three species at $P < 0.001$; Among the other three phytoseiids, at least $P > 0.20$ with the sequential Bonferroni adjustment for post hoc comparisons.

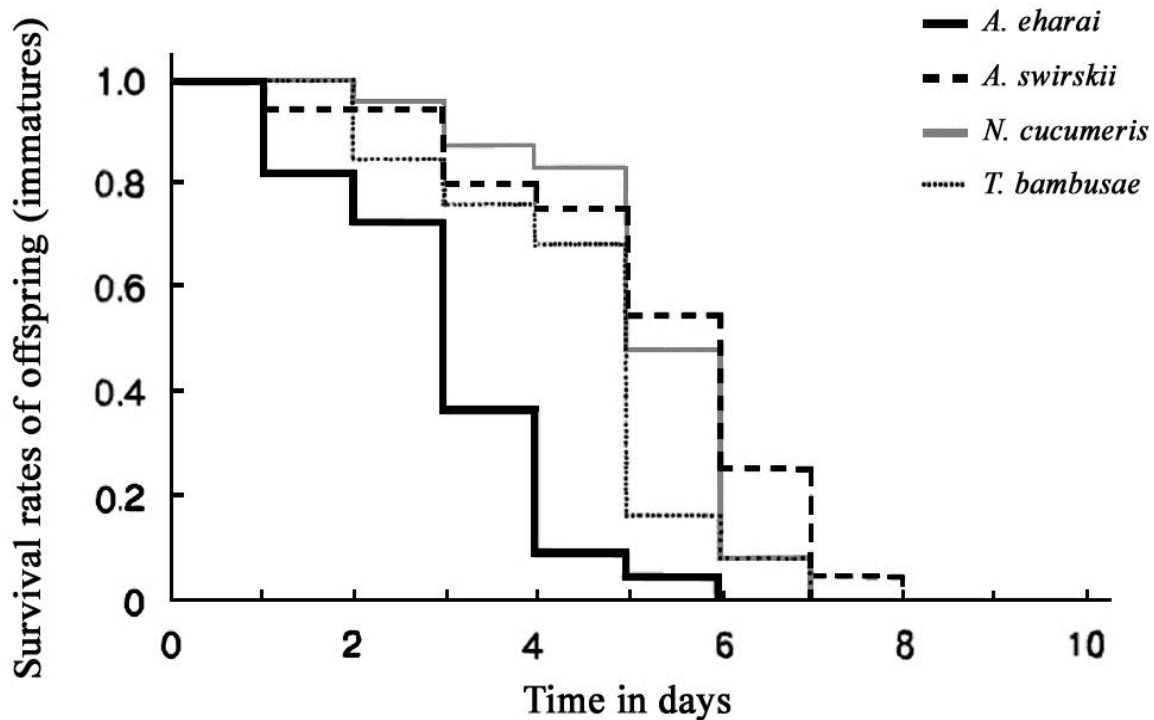


Fig. 23. Offspring survivorship in four species under mother-presence, no prey, free water available and humidity-selectable conditions. Number of replicates, average survivorship and SE of each species appear in Table 37.

TABLE 36. Results of Kaplan–Meier survival analyses (logrank test) for immatures of four phytoseiid species living alone (mother-absence) under no prey conditions

	<i>A. eharai</i>	<i>A. swirskii</i>	<i>N. cucumeris</i>	<i>T. bambusae</i>
<i>Amblyseius eharai</i>	-	<0.001	<0.001	<0.001
<i>Amblyseius swirskii</i>	34.06	-	<0.001	=0.001
<i>Neoseiulus cucumeris</i>	43.16	15.97	-	<0.001
<i>Typhlodromus bambusae</i>	19.69	10.97	32.39	-

Above the diagonal probabilities are shown and below the diagonal χ^2 values. Degree of freedom is 1 in each comparison. Probability (P) was adjusted by the sequential Bonferroni test for post hoc multiple comparisons

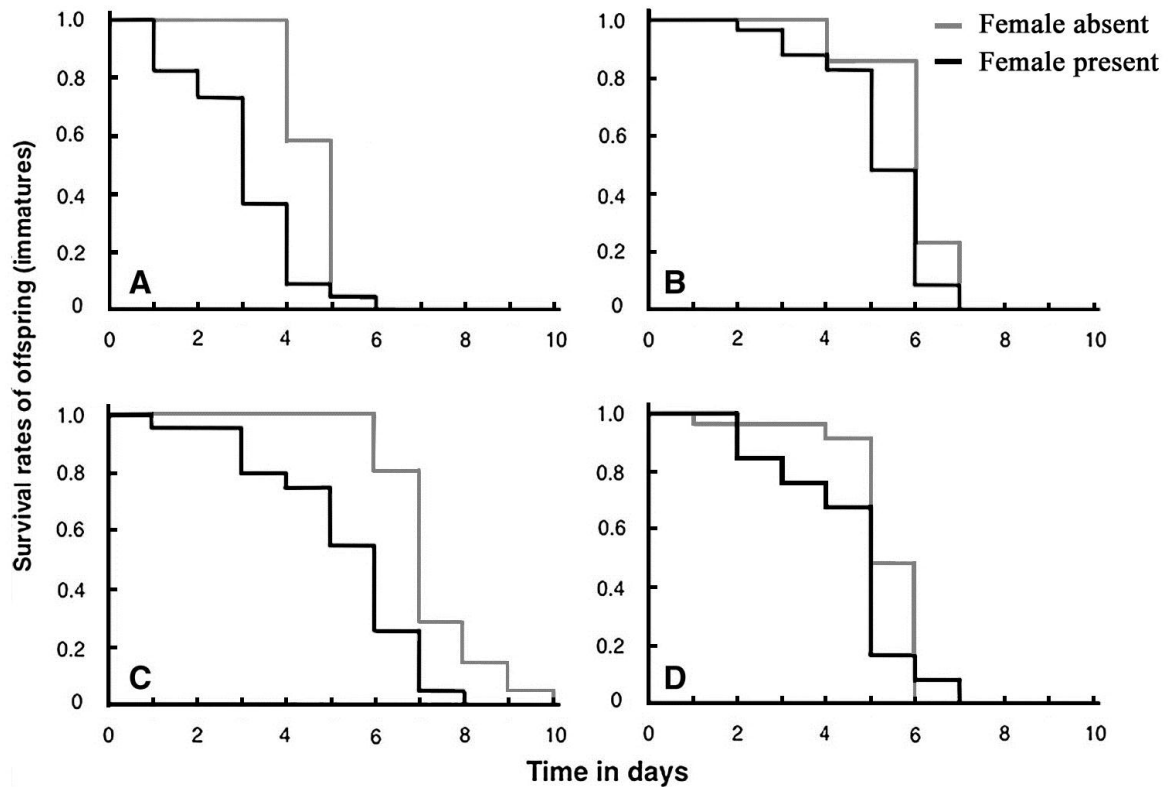


Fig. 24. Comparison of immature survival curves between mother-presence and mother-absence experiments under no prey other than its offspring and free-water available conditions. a *Amblyseius eharai*; b *Amblyseius swirskii*; c *Neoseiulus cucumeris*, and d *Typhlodromus bambusae*.

TABLE 37. Results of Kaplan–Meier survival analyses (logrank test) for immatures of four phytoseiid species between mother-presence and mother-absence (degree of freedom of each comparison is 1).

	Mother-presence ^a	Mother-absence ^a	χ^2	Probability
<i>Amblyseius eharai</i>	3.05 ± 0.28 (22)	4.631 ± 0.12 (24)	18.18	<0.001
<i>Amblyseius swirskii</i>	5.22 ± 0.26 (23)	6.05 ± 0.18 (21)	7.08	0.016
<i>Neoseiulus cucumeris</i>	5.30 ± 0.39 (20)	7.29 ± 0.23 (21)	15.24	<0.001
<i>Typhlodromus bambusae</i>	4.52 ± 0.18 (25)	5.26 ± 0.23 (23)	3.54	0.060

^a Number of eggs observed in parentheses and average days ± SE. Probability (*P*) was adjusted by the sequential Bonferroni text for post hoc multiple comparisons

TABLE 38. Comparisons between longevity of mothers and their offsprings under starved conditions by Fisher's exact probability test, 2-tailed, $df = 1$

	Offspring survived longer than their mothers	Offspring survived shorter than their mothers	Difference from <i>Typhlodromus bambusae</i>
<i>Amblyseius eharai</i>	0	22	<0.001
<i>Amblyseius swirskii</i>	0	23	<0.001
<i>Neoseiulus cucumeris</i>	2	18	<0.001
<i>Typhlodromus bambusae</i>	17	7	-

There are no significant differences ($P>0.20$) between the other combinations. Each probability (P) was adjusted by the sequential Bonferroni test for post hoc multiple comparisons.

12.3. Discussion

There is an important difference between cannibalism between unrelated individuals and between a mother and its offspring, because the former can be defined as a form of intraspecific competition, but the latter affects the inclusive fitness of individuals. Thus, we must discriminate between these two kinds of cannibalism. Most previous studies on cannibalism (Croft and Croft 1996; Walzer and Schausberger 1999; Schausberger 2003; Williams *et al.* 2004; Zannoui *et al.* 2005; Momen and Abdel-Khalek 2009) have addressed the former phenomenon. We conducted the present study in such a way so as to identify the maternal response(s) towards offspring under no other prey conditions. This is not an unrealistic situation for phytoseiid species, because most females together with their offspring must confront starvation when prey and/or alternative food sources become scarce. In such situations, mothers can select one of two paths, i.e. kin cannibalism or dispersal without feeding

to maintain their lives and/or gain inclusive fitness through the survival of their offspring, although feeding upon a single offspring did not prolong female longevity in any species in the present study.

The presence of *A. eharai* females deeply affected the survival of their offspring, suggesting strong maternal cannibalism. According to McMurtry *et al.* (2013), this species is considered to be a typical generalist (Type III-b in McMurtry *et al.* 2013), with a diet that includes a wide variety of prey (Cao *et al.* 1998; Ji *et al.* 2013 a), such as *P. citri*, *Phyllocoptruta oleivora* (Ashmead) and pollen (*Amblyseius largoensis* in Saito and Mori 1975 and *A. deleoni* 1981 are synonyms of *A. eharai*). Furthermore, females of this species are known to deposit their eggs in a scattered fashion (Chittenden and Saito 2001). Therefore, this species may have no mechanism to avoid kin cannibalism other than its egg deposition pattern. The absence of any kin cannibalism avoidance behavior seems to be related to its solitary and generalist life style, as discussed in Schausberger (2003). In addition, we should note here that several larvae of this species developed into protonymphs in the mother-absence (with no food) experiment, although previous studies reported that this species has obligatory feeding larvae (Chittenden and Saito 2001; Ji *et al.* 2013 c). Whether this phenomenon was caused by the different maternal diet (*Tetranychus* prey was supplied to mothers in the previous two studies, but *C. lactis* in the present study) or by a different strain is still unknown.

Momen and Abdel-Khalek (2009) reported that *A. swirskii* females (Type III-b in McMurtry *et al.* 2013) did not eat conspecific eggs or protonymphs, but did eat larvae at very low frequencies. This species is used extensively to control thrips and

whiteflies in greenhouses (McMurtry *et al.* 2013). The present results showed that mother presence significantly affected offspring survival, indicating possible maternal cannibalism. Thus, there appears to be some disagreement between Momen and Abdel-Khalek (2009) and the present study. However, the difference (0.83 days) in immature survivorship between mother-presence and mother-absence was small, showing that kin cannibalism is relatively low. In any case, *A. swirskii* does not appear to have a fail-safe kin cannibalism avoidance mechanism. Under the severe starvation conditions set in the present study, females may have been obliged to decrease their offspring survival.

McMurtry *et al.* (2013) categorized *N. cucumeris* into Type III-e. This species is also an important biological control agent, mass-produced for commercial supply. It can prey upon various mite and insect pests, e.g. spider mites, western flower thrips, broad mites (McMurtry *et al.* 2013) and the Asian citrus psyllid (Zhang *et al.* 2011; Fang *et al.* 2013). Schausberger (2003) has already reported on female cannibalism. The present study also suggests a tendency for maternal cannibalism of offspring in this species. However, whether female response differs between related and unrelated individuals is unknown, and must be observed using choice experiments (Schausberger 2004).

The phytoseiid *T. bambusae* (Type I-b in McMurtry *et al.* 2013) is a specialist predator of *Stigmaeopsis* spider mites that live aggregately within self-woven nests (WN-c life types, Saito 1983, 2010; Zhang 2002, the WN-u listing that appears in McMurtry *et al.* (2013) may be erroneous) on the undersides of bamboo or Chinese silver grass leaves (Saito 1990 a, 2010). They also live aggregately in *Stigmaeopsis*

nests and often cohabit with their offspring (Saito 1990 b). Furthermore, several *Stigmaeopsis* species possess a highly developed cooperative sociality that includes strong counter-attack behavior against phytoseiid predators (Saito 1986; Zhang 2002; Mori and Saito 2005; Yano *et al.* 2011; Saito *et al.* 2011). These may have required *T. bambusae* to evolve some special adaptation(s) to allow it to handle such dangerous prey, e.g. defending offspring against prey counter-attack and to cohabit safely with many offspring. If specialization on highly aggregated prey species can bring about the adaptation of special kin-cannibalism avoidance mechanisms, as hypothesized by Schausberger (2003) in *P. persimilis*, we can expect to find similar kin cannibalism avoidance mechanisms in *T. bambusae*. As predicted in Saito (2010), *T. bambusae* females seldom ate their offspring and tended to die earlier in the present study. During the experiments however, we occasionally observed instances where mothers of this species were eating their offspring (whether they were living or dead bodies is unknown). Furthermore, survival in the initial period tended to be lower in the mother-presence than in the mother-absence, although there was no significant difference in survivorship between them. From the view of avoiding kin cannibalism, the phenomenon that mothers tended to die before their offspring appears to be important, because it inevitably decreases the probability of cannibalism by mothers. Therefore, the short longevity of mothers is one of the reasons why there is no significant difference in immature survival between the mother-presence and mother-absence experiments. In any case, we think that *T. bambusae* females seldom have any opportunities to cannibalize their offspring even under extreme starvation conditions.

Williams *et al.* (2004) showed that the diet-specialist (Type I-a in McMurtry *et al.* 2013) *P. persimilis* females and the diet-generalist (Type III-c in McMurtry *et al.* 2013) *Iphiseius degenerans* (Berlese) females both have poor survivability without food (5 and 4 days, respectively). They considered such shortened female longevity under no food conditions as to be extraordinarily in phytoseiids. Furthermore, these two species have kin discrimination ability to avoid kin cannibalism (Faraji *et al.* 2000; Schausberger and Croft 2001). As shown in the present study, *T. bambusae* females also have very short survivability without food (4.12 days). This may indirectly function as a kin cannibalism avoidance mechanism. Thus these three species have a common set of characteristics, i.e. poor starvation tolerance and an ability to avoid kin cannibalism, even though they are categorized into three different life styles (McMurtry *et al.* 2013). What factors are related to the evolution of such common characteristics in these three species?

Schausberger (2003) postulated a hypothesis for why diet-specialist, *P. persimilis* discriminates between kin and non-kin prey, but not between con- and hetero-specific prey. He said that a specialist that exploits a patchily distributed prey entails an aggregated egg distribution. For the threat of decreasing inclusive fitness by kin cannibalism, species with aggregated egg distribution are likely to be selected for kin discrimination. In contrast, if generalist females spread out their eggs as a consequence of the overall random distribution of their different food sources, the offspring of such species will encounter each other less often. Thus they may use this cruder mechanism to reduce the risk of cannibalizing kin.

While I basically agree with his hypothesis on kin cannibalism and kin

discrimination mechanisms, Schausbergers (2003) never addressed the linkage between the avoidance of kin cannibalism and the short longevity of starved females. I think that determining precisely which factors can explain such a linkage(s) will be a fascinating and crucial topic for future studies.

Chapter 13. General discussion and conclusion

13.1. Aspects from biological control

In this thesis, I addressed the biology of two native and two introduced phytoseiid mites in relation to their peculiarities as biological control agents. On the reflection of the decrease use of chemicals in agricultural fields in China, biological control has been considered as an alternative method for pest control. Especially phytoseiid mites that can control small insects and mites are now getting great attention (Helle and Sabelis 1985; Lindquist *et al.* 1996; Sabelis and Van Rijn 1997; McMurtry and Croft 1997; Gerson *et al.* 2003). However, if we intend to use these natural enemies in agricultural fields, there are several unresolved problems, such as actual efficiency as natural enemy, mass-production systems for commercial use, impact of introduced predators on native fauna and so on.

Therefore, I studied on the following three subjects. The first was how to mass-produce *A. eharai*, an indigenous predatory mites; The second was to estimate the invasive risk of *A. swirskii*, the exotic predatory mites, if introducing this predator into the citrus orchards in China; The third subject was why *N. cucumeris* did not successfully colonize the citrus orchard in China? Although this predator had been used over ten years in some citrus orchards.

Then I attempted to develop a rearing method of native phytoseiid, *A. eharai* (Chapters 3 and 4) that is a very important native species regulating citrus pests in China. Despite small arthropods and nematodes are known mainly as the prey of predators, most phytoseiids also have other feeding habits, consuming food items

such as fungi, plant exudates, pollen, etc. Some are able to feed upon extract liquid from leaf cells, for example *Euseius scutalis* (Athias-Henriot). The commercially important predatory mites mainly come from the list of genus, *Phytoseiulus*, *Amblyseius*, *Neoseiulus*, *Typhlodromus* and *Metaseiulus*. Some specialized mite predators, which only prey spider mites, for example *Phytoseiulus persimilis*, are mass reared only with spider mites as prey mite. Despite the higher efficiency to control spider mites are known by farmer, the high costs are difficult to be accepted. The method of predatory mite mass production using alternative prey mites (storage mites, for example *Acarus farris* (Oudemans)) made a tremendous contribution in biocontrol of pest, invented by Ramakers & Van-Lieburg (1982). Hereafter, several species of predatory mites were successfully mass reared with this method, for example *Neoseiulus cucumeris*, *Neoseiulus barkeri*, *Amblyseius swirskii* and *Neoseiulus californicus*.

For mass production of *A. eharai*, *Aleurolyphus ovatus*, *Tyrophagus putrescentiae* and *Carpoglyphus laticollis* were the candidates, since they were widely used to rear different predatory mites. However, *T. putrescentiae* was firstly eliminated because *A. eharai* showed high mortality. On the other hand, male *A. eharai* could not survival only with *A. ovatus* as prey, although female performed very well. *A. eharai* showed perfect performance when feeding on *C. lactis* than feeding upon a targeted pest mite prey, *Panonychus citri*, i.e. higher fecundity and faster development. Therefore, *C. lactis* was a suitable prey for the mass production of *A. eharai*. Thus, I could add a new species that can be mass produced by *C. lactis*, if some rearing environment, such as mite density and ratio (predator:prey) can be optimized as shown in chapter 3.

Even if there are several unresolved problems to apply *A. eharai* for commercial use, for example the refrigeration condition, it can be said that I take a new step toward utilization of native natural enemy in Chinese citrus orchards.

When we introduce exotic species for biological control, it is an important pre-requisite whether the introduced species affect native fauna or not (Gotoh *et al.* 2014). In this thesis, I attempted to evaluate the impact of introduced predators on native predator species from several criteria, such as comparisons of intrinsic rates of natural increase, tolerance to starvation low humidity conditions, introguild predations, cannibalistic responses, and competitions between exotic and native species.

In the 20th century, *N. cucumeris* had been introduced into China from England. Then, this predator, as an augmentative biocontrol agent, had been widely used to control pest mites in citrus, cotton, pear, bamboo, tea and greenhouse plants and so on (Zhang *et al.*, 2002; Kong *et al.* 2008; Li and Ma 2012). However, it was known that *N. cucumeris* could not always colonize citrus orchards, based on a long-term survey over ten years (Ji *et al.* 2012). As an alternative of *N. cucumeris*, *A. swirskii* had been introduced into China from Koppert Company. Despite its high efficiency in the biocontrol, this predator has not been used in agricultural system of China, considering the invasive risks.

In fact, there are many indigenous predatory mites; some of them have high efficiency in the biocontrol of pest, for example *Neoseiulus longispinosus*, *Amblyseius eharai*, *Euseius nicholsi* and *Amblyseius orientalis*. However, there had been no sufficient method of mass production, such that these predatory mites have not been widely used in the biocontrol of pest in China. They are believed to be important

regulation agents of phytophagous mites and insects in natural fields. Therefore, we must pay our attention to their conservation when we apply the mass-produced exotic predatory mites in the fields.

In the present study, I discovered that *N. cucumeris* used widely in China is not so dangerous exotic species in China, because it is very difficult to establish its population in citrus orchards in China (Ji *et al.* 2012). Furthermore, the present study revealed that this species was weakest in the competition with *A. eharai* and *A. swirskii*.

On the other hand, it was learned that *A. swirskii* has very strong ability to compete with the native phytoseiid mite *A. eharai* under experimental conditions. Then, there is a risk of replacement of *A. eharai* that was the dominant predatory mites in most citrus orchards of China: It was confirmed that *A. swirskii* was an efficient predator for *P. citri* through the study of life history (Chapter 5). However, *A. eharai* appeared more advantage than *A. swirskii*, due to fewer prey for the development of immature, when the extraguild prey *P. citri* was sufficient.

Next, I compared the ability to endure starvation and low humidity between *A. swirskii* and *A. eharai*. As a result, *A. swirskii* might be a better competitor relative to *A. eharai* when their prey was absent, because the former has stronger ability to endure starvation and low humidity. Moreover, *A. swirskii* larvae could develop to protonymph either at low humidity (60 % R.H.) or without prey, but *A. eharai* larvae could not.

Which would win the competition between them? It had been still unclear. So that, I conducted the intraguild predation and cannibalism among *A. swirskii*, *A. eharai* and

N. cucumeris (Chapter 7 and 8). However, the conclusion was still difficult to obtain, because the three predatory mites, either female or male, could develop into adulthood when they preyed upon intraguild prey. Moreover, either in combination of *A. swirskii* and *N. cucumeris* or *A. swirskii* and *A. eharai*, every species had the similar r_m when they ate intraguild prey.

Furthermore, it was revealed that three predatory mites species (female or male) all could develop to adulthood by cannibalism only. However, it was worth noting that *A. swirskii* obviously increase its development duration, and that *A. eharai* had very high fecundity and intrinsic rate of increase when they performed cannibalism. This meant an extraordinary phenomenon that *A. eharai* could obtain more advantage by cannibalism rather than by intraguild predation in a closed habitat. However, these results still gave no conclusion about species displacement.

Then, I conducted direct competition experiments between these three phytoseiid species (Chapter 9). In all the combinations between the three phytoseiid mites, one species always became extinction and the other won in the competition, when supplying sufficient extraguild prey *C. lactis*. Among three predatory mites, the exotic *A. swirskii* was the strongest under the present experimental conditions. The native *A. eharai* was second and the weakest species was *N. cucumeris*.

What factors were responsible to the above competitive exclusions? This question has been not always completely resolved, because every species can prey upon the other two species, and every species could perform cannibalism to complete their life history when the extraguild prey was absent. Then I addressed several factors, such as reproductive interference, prey preference and the effects of intraguild predation.

The numerical calculations by the models based on Lotka (1925) and Volterra (1926) suggested that a main factor that caused species displacement was "a very small difference" in the ability of intraguild predation between two predator species, but not the intensity of competition other than intraguild predation.

As one of the possible factors, the reproductive interference was observed in the three combinations among three predatory mites. The asymmetric interaction of *A. swirskii* to *A. eharai* was observed. *A. swirskii* male could mate *A. eharai* female and decrease the fecundity of the latter. On the contrary, *A. eharai* male could not do so. On the other hand, there was no reproductive interference between *A. eharai* and *N. cucumeris*, or *A. swirskii* and *N. cucumeris*. Thus, the displacement of *A. eharai* by *A. swirskii* might cause partially by this factor. However, as shown by the sensitivity analyses by Lotka-Volterra models (Chapter 9), the competition coefficient other than intraguild predation (reproductive interference can be regarded as an element of competition) cannot always explain the immediate extinction of *A. eharai* in the *A. swirskii* and *A. eharai* competition systems, because the competitive effect must be rather mild (Kuno 1992).

About intraguild predation, it was learned that *A. swirskii* females more preferred *A. eharai* eggs or *N. cucumeris* egg to conspecific eggs, when supplying those eggs simultaneously. This must be very important because such a preference strongly enhance the frequency of intraguild predation by *A. swirskii*.

A. swirskii had higher r_m when preying on *C. lactis* than *N. cucumeris* and higher predation rate to *N. cucumeris* eggs than *N. cucumeris*, relative to their conspecific eggs. Those resulted in that *A. swirskii* won the competition with *N. cucumeris*.

Lastly, *A. eharai* had higher r_m when preying on *C. lactis* than *N. cucumeris* and higher predation rate to the larvae of *N. cucumeris*, relative to *N. cucumeris* was indiscriminate.

Base on the present study, we conclude that *A. swirskii* was a high-risk exotic species to citrus orchards ecosystem of China. However, the results were obtained according to the data of laboratory; more and further researches should be conducted in the isolated field, for example closed greenhouse or island.

Anyhow, the exotic predatory mite *A. swirskii* has a high invasive risk due to its high ability to exclude the native *A. eharai*. Since the latter was the dominant predatory mite in most citrus orchards of China and must play a key role in citrus ecosystem. If it was excluded by the exotic *A. swirskii*, the native food chain of citrus ecosystem should be altered, and that may result in some unpredictable consequences. In addition, one of the reasons why introduced *N. cucumeris* could not colonize citrus orchards may be that it failed in the competition with *A. eharai*.

I suggested *A. swirskii* should be forbid in biocontrol of citrus pest. However, this predator appeared high efficient in biocontrol of whitefly, for example *Bemisia tabaci*. Moreover, it was rather cheaper for farmer than other natural enemies, for example *Encarsia formosa* Gahan, *Delphastus catalinae* (Horn) or lacewing and so on. Therefore, since it cannot be recommended in citrus, it was still an alternative nice natural enemy for biocontrol of whitely. Of cause, the risk must be firstly estimated before actually using.

13.2. Aspects of phytoseiid mite ecology

Huffaker *et al.* (1963) first showed that there is a typical predator-prey interaction between phytoseiid and tetranychid mites. This study is now a very famous and standard knowledge that appears so many ecological textbooks. There are several reasons why these animals showed such a typical predator-prey interaction. One of them is that phytoseiid and tetranychid mites are very easy to rear under experimental conditions. Another is there is a very specialized relationship between the predator and prey. Furthermore, the body sizes of these animals are very similar, such that numerical and functional responses of them were easy to observe. After his pioneer work, there have been so many studies by use of these animals from applied and ecological viewpoints. The former have been addressed before. Then here I addressed some ecological aspects of phytoseiids.

Although there had been so many studies on phytoseiid predators and tetranychid prey interaction studies before 1980s (Sabelis 1985), there were few studies that addressed the interaction between different species of phytoseiids, i.e. intraguild predation (Polis 1981; Polis *et al.* 1989). In other words, it can be said that no one believed the phenomena of intraguild predation of phytoseiids before that. After 1980, many researchers began to observe on the intraguild predation of phytoseiids, however most studies on this theme have been restricted to biological control, i.e. the introduction problems of multiple phytoseiid species.

Furthermore, before Croft and Croft (1996) first observed frequent cannibalism in phytoseiids, such cannibalism was considered as an anomaly, with most researchers

tacitly believing that such predators evolved avoidance mechanisms.

Now we recognized that the intraguild predation and cannibalism must be inevitable phenomena in predacious phytoseiid species. Thus, so many studies have been conducted for so many species (Schausberger and Croft 2000; Schausberger 2003; Zhang *et al.* 2014). From these studies, we learned that intraguild predation and cannibalism are usual phenomena in phytoseiids, while there is much variation in the traits of intraguild predation and cannibalism among phytoseiid species.

In the present study, I compared the abilities (or traits) of intraguild predation among three phytoseiid species and cannibalistic habits of four phytoseiid mites. Then I learned that there was a difference between specialized predator and generalistic predators (in the sense of McMurtry *et al.* 2013) in sib-cannibalism, which must be related to the social interaction between individuals of respective species. Furthermore, I could suggest that the abilities of intraguild predation are closely related to the result of the competition between phytoseiid species, as also suggested by Gotoh *et al.* (2014). Thus, it can be said that these traits evolved through strong interactions between these phytoseiids sharing common extraguild prey in nature.

Although it has not been fully resolved why there is such variation in these traits among phytoseiid species, I believed that these findings provide new perspectives for studying these animals in the future.

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Appendix

Detailed introductions of four phytoseiid mites used in this study

1. *Amblyseius eharai* Amitai & Swirski

1.1. Feeding habits

Its prey includes spider mites, eggs or nymph of whitefly, eggs of scale insect and different pollens (Zhang and Luo 1990; Pu *et al.*, 1995). However, there is less information about the types of its food. The food had been reported as follow: *Panonychus citri* (McGregor), *Panonychus mori* Yokoyama, *Tetranychus urticae* Koch, *Tetranychus kanzawai* Kishida, *Eutetranychus orientalis* (Klein), *Brevipalpus phoenicis* (Geijskes), eggs or younger nymph of *Dialeurodes citri* (Ashmead) or *Bemisia tabaci* (Gennadius) and different pollens and so on.

1.2. Development

This predatory mite have six developmental stages, egg, larva, pronymph, deutonymph, preoviposition, adult, respectively. At 25°C and 75-85% RH with *P. citri* as prey, the developmental duration of egg, larval, protonymph and deutonymph of female *A. eharai* was 2.01, 0.96, 1.02 and 1.14 days, respectively. That of different stage of male was 2.00, 0.82, 1.00 and 1.10 days, respectively (Zhang and Luo 1990). However, when preying on eggs of *Bemisia tabaci* at 25°C, that of different stage of female was 1.7, 2.1, 1.9 and 2.2 days, respectively (Ji *et al.* 2013 c). Saito and Mori (1981) reported the developmental duration of egg, larva to adult and preoviposition

was 1.8, 3.1 and 1.4 days, respectively.

In addition, 20 different plant pollens had been tested, and the pollen of cucumber, lantana, canna, jasmine, castor, carambola, luffa and rice was suitable to development and oviposition of *A. eharai*. The duration from egg to adult and preoviposition was 3.6-4.2 days and 1.1-2.7 days at 27 °C and 75-85% RH (Pu *et al.* 1995).

1.3. Fecundity and predation

The larva of *A. eharai* is the type of obligatory feeding larvae according to the classification of Zhang and Croft (1994). A new female can immediately mate with a male. However, mating is obligatory for its reproduction. The mating duration is various. And the maximum is above 2 hours (Zhang and Luo 1990). Female or male can mate repeatedly.

Adult females of this predator can lay average 41.7 eggs/female at 25 °C with *P. citri* as prey. Average longevity was 55.5 days for female and 39.9 days for male (Zhang and Luo 1990).

The total fecundity of *A. eharai* was 33.1-54.1 eggs/female with the daily 1.7-3.4 eggs/female in oviposition period of 16.4-20.1 days when supplying the pollen of cucumber, lantana, canna, jasmine, castor, carambola, luffa and rice, at 27 °C and 75-85% RH (Pu *et al.* 1995).

1.4. Effect of environment

This predatory mite species like high humidity, whereas the high temperature has some negative effect to its survival, such as 30°C (Jiang *et al.* 1988). Especially,

when the temperature is over 32°C, the population of the predator will be reduced rapidly (Zhang and Luo 1990).

Lower humidity than 75%RH can prolong egg of *A. eharai* incubation and decreased hatchability from 78% at 75%RH to 4% at 53%. The suitable of humidity range is 85-95%RH. As well as, female survival and reproduction have been decreased from 100% at 75%RH to 0% at 53%RH and from 1.1 eggs/female/day at 85%RH to 0.23 eggs at 75%RH, respectively (Zeng *et al.* 1992). In addition, if the predator can obtain water from environment, it can increase the survival ability (Wei *et al.* 1994).

1.5. Life table

The net reproductive rate (R_0), mean generation time (T) intrinsic rate of increase (r_m) finite rate of increase (λ) of *A. eharai* was 24.93, 11.25, 0.286 and 1.331, respectively, when with *T. urticae* as prey at 25°C (Saito and Mori 1981). However, when the food was pollen of canna at 30°C, those parameters were 22.41, 12.39, 0.322 and 1.380, respectively (Wei *et al.* 1993). Those studies about *A. deleari* were not referenced in this paper.

2. *Amblyseius swirskii* (Athias-Henriot)

2.1. Feeding habits

This predator can prey on different thrips, whiteflies, spider mites, tarsonemid mite, eriophyid mite, egg or larva of scale insect, and also pollen or acarid mite and so on. For example, *F. occidentalis*, *T. tabaci* and *T. palmi*, *Gynaikothrips uzeli* Zimm,

Bemisia tabaci (Gennadius), *Trialeurodes vaporariorum* Westwood, *Tetranychus kanzawai* Kishida, *Tetranychus truncatus* Ehara *T. urticae*, *Eutetranychus orientalis* Klein, *P. latus* (Banks), *Aceria ficus* (Cotte) and *Rhyncaphytoptus ficifoliae* Keifer and so on.

Goleva and Zebitz (2013) reported that *A. swirskii* can feed on 19 pollens and develop into adult with 18 various pollen sources as food, including highly suitable: *Schlumbergera hybrid*, *Crocus vernus*, *Echinocereus* sp., *Paulownia tomentosa*, *Aesculus hippocastanum*, and suitable: *Ricinus communis*, *Betula pendula*, *Zea mays*, *Tulipa gesneriana*, *Abutilon* sp., *Calla palustris*, *Phoenix dactylifera* L. These pollen sources were nice for its development and oviposition, and also, eggs of the Maskell scale insect *Insulaspis pallidula* (Green) and the red date scale insect *Phoenicococcus marlatti* Cockerell (Goleva and Zebitz 2013; Abou-Ellella *et al.* 2013).

And many species of acarid mites can be used to mass produce the predator, for example, *Carpoglyphus lactis* Linne, *Thyreophagus entomophagus* (Laboulbene), but only the former is frequently-used.

2.2. Development

This predatory mite have six developmental stages, egg, larva, pronymph, deutonymph, preoviposition, adult, respectively.

The average female life cycle and life span of *A. swirskii* was 6.26 and 43.20 days, respectively, supplying *T. urticae* as prey at 28 °C (Osman *et al.* 2010). In addition, Ali and Zaher (2007) had reported the average developmental durations was 18.5, 14.3, 10.8, 9.0, 7.7, 6.8 and 6.1 days, respectively, at 15, 20, 25, 28, 30, 32 and 35 °C,

when preying on *E. orientalis* immatures. However, when the astigmatid mite *Suidasia medanensis* (Oudemans) was supplied as prey mites, the developmental duration of *A. swirskii* was 5.1 days at 25 °C, 70 % RH and 16L:8D (Midthassel *et al.* 2013). In addition when with thrips as prey, the developmental time (egg to adult) of *A. swirskii* was 7.8 days with either preyed upon first larval instars of *F. occidentalis* and *T. tabaci* at 25 °C (Wimmer *et al.* 2008). At 25 °C and 70% RH, the developmental time of female *A. swirskii* fed on *Aculops lycopersici* (Massee) or on cattail pollen was 4.97 and 6.16 days, respectively (Park *et al.* 2010).

2.3. Fecundity and predation

There were many studies about of the fecundity of *N. cucumeris* were conducted, for example, different thrips, ararid mites, spider mites and so on.

Tarsonemid mite: When preying on the female adult of *P. latus*, the average number of eggs/female/day was 2.36 and 1.69, respectively, at 28°C and 19 °C (Abou-Awad *et al.* 2014).

Thrips: The oviposition rates of *A. swirskii* was 0.92 and 0.99 eggs/female/day, when with *F. occidentalis* and *T. tabaci* as prey, respectively, at 25°C (Wimmer *et al.* 2008).

Ararid mites: When *S. medanensis* was supplied as prey at 25°C, *A. swirskii* can lay 1.71 eggs/female/day (Midthassel *et al.* 2013).

Spider mites: During the life span, female *A. swirskii* can feed on 345.66 with a daily rate 8.00 individual of *T. urticae* immatures at 28 °C (Osman *et al.* 2010). And the total oviposition of *A. swirskii* was 33.75 and 24.19 eggs, respectively, when

preying on *P. citri* at 20 °C and 30°C (Elmoghazy 2010). However, *E. orientalis* may be a perfect prey for *A. swirskii*, because the female fecundity of *A. swirskii* was 12.0 eggs/female in 10 days at 25 °C and 85% RH (Zaher *et al.* 2007), and the total fecundity is 38.0 eggs/female (Ali and Zaher 2007).

Eriophyid mite: When feeding on 144.4 individuals/female *Eriophyes olivit* per day, *A. swirskii* can lay 44.4 eggs/female at 27°C and 60-80% RH (El-Laithy 1998). Park *et al.* (2010) reported that *A. swirskii* had a higher daily oviposition rate (2.0 eggs/day) on tomato russet mite *Aculops lycopersici* than on pollen (1.5 eggs/day) in the first 10 days after developing into adult female.

Whitefly: There were many papers involved the life history and fecundity of *A. swirskii* to the whitefly. When this predator prey on the *B. tabaci*, the average oviposition ratio was 1.6-1.7 eggs/female/day (Nomikou *et al.* 2001).

2.4. Effect of environment

Zaher *et al.* (2007) had reported that when *Eutetranychus orientalis* was supplied as prey at 70 to 85% RH, the low temperature (5 and 9 °C) prolonged egg of *A. swirskii* incubation and decreased hatchability as well as female survival. After one to four weeks, egg hatchability ranged decreased from 90 to 50% and from 100 to 64% at 5 and 9 °C, respectively. And the female survival decreased from 50 to 0% and from 80 to 10% at 5 and 9 °C, respectively.

In addition, the host plants of different leaf texture can affect female fecundity, the average fecundity of *A. swirskii* was 15.8 eggs/female in 10 days after emerging on smooth leathery leaf of grape fruit, while coarse reticulated leaf of guava resulted

in the least number of deposited eggs (10.8 eggs/female in 10 days) (Zaher *et al.* 2007).

2.5. Life table

The temperature is very important for this predator increasing its population. The intrinsic rate of increase (r_m) of *A. swirskii* was 0.139 and 0.170 individuals/female/day, respectively, at 28 °C and 19 °C with female adult of *P. latus* as prey (Abou-Awad *et al.* 2014). And Elmoghazy (2010) reported the generation period and adult female longevity of *A. swirskii* were 10.59 days and 31.72 days at 20°C, also were 7.81 days and 21.72 days at 30 °C with *T. urticae* immatures as prey. However, r_m was 0.14 and 0.18 at both degrees respectively.

In spite of *A. swirskii* had gradually replaced *N. cucumeris* in biocontrol of different thrips, Wimmer *et al.* (2008) indicated that superiority of *A. swirskii* was not due to its population growth capacity with thrips as prey, because of its relatively low intrinsic rates of increase (r_m) (0.056 and 0.024 per day with *F. occidentalis* and *T. tabaci*, respectively). However, the famous predator due to its high efficiency in biocontrol of whitefly *B. tabaci*, Nomiko *et al.* (2001) reported that when this predator collected from cotton fed on *B. tabaci* immatures, the r_m was 0.208-0.213 and the λ was 1.03-1.17 at 27 °C and 16:8L:D.

In addition, when *A. swirskii* preying upon *S. medianensis* 25°C, 70 % RH and 16L: 8D, The intrinsic (r_m) and finite (λ) rates of increase were 0.222 and 1.249, respectively, with average oviposition rate of 1.71 eggs/female/day (Midthassel *et al.* 2013). So, this acarid mite may be a nice prey mite for mass producing *A. swirskii*.

3. *Neoseiulus cucumeris* (Oudemans)

3.1. Feeding habits

Except different thrips, the predator is known to feed on the pest mites of *Polyphagotarsonemus*, *Tetranychus*, *Stigmaeopsis*, *Aponychus*, *Panonychus*, *Eotetranychus*, *Oligonychus*, *Acaphylla*, *Stigmaeopsis*, and also pollen, acarid mite and fungi and so on. For example, *O. coffeae* Nietner, *O. ununguis* (Jacobi), *E. sexmaculatus* (Riley), *A. corpusae* Rimando, *A. theae* (Watt), *P. latus* (Banks), *Phytonemus pallidus* (Banks), *T. urticae*, *S. nanjingensis* (Ma & Yuan) (Gerson *et al.* 2003; Weintraub *et al.* 2003; Zhang *et al.* 2000; Ji *et al.* 2001; Ranabhat *et al.* 2013). Also including pollen of tulip (*Tulipa* sp.) (Liliaceae), apple (*Malus domestica* Borkh.) (Rosaceae), Christmas cactus (*Schlumbergera* sp.) (Cactaceae), horse-chestnut (*Aesculus hippocastaneum* L.) (Sapindaceae), maize (*Zeamays* L.) (Poaceae), and birch (*Betula pendula* Roth) (Ranabhat *et al.* 2013). In addition, *N. cucumeris* can prey many species of acarid mites had been reported, in fact, commercialized production of *N. cucumeris* currently used some kind of this group as prey mites, for example, *T. putrescentiae*, *A. farris*, *Dermatophagoides farinae* Hughes and *A. ovatus* (Zhang *et al.* 2002; Ramakers and Van–Lieburg 1982; Koppert or Biobest Company).

Muhammad *et al.* (2009) reported that the significant differences were observed for the types of prey diet used, *T. putrescentiae* was the most suitable prey closely followed by *T. urticae*; then *F. occidentalis* diet.

3.2. Development

This predator have six developmental stages, egg, larva, pronymph, deutonymph, preoviposition, adult, respectively. The eggs of *N. cucumeris* could not hatch at or over 32°C. The lower developmental thresholds, upper developmental thresholds and the optimum developmental temperature were 12.77°C, 33.50°C and 23.87 °C, respectively (Li *et al.* 2003). *N. cucumeris* reproduced normally at 15 and 18°C, but all individuals of some train entered diapause when night temperatures were 12°C at the photoperiod of L:D 11:13 (Rodriguez-Reina *et al.* 1994). But, commercialized *N. cucumeris* had not diapause habit on short photoperiod or low temperature.

With *P. latus* as prey, the generation period of *N. cucumeris* was 13.02, 9.61, 5.96, 5.26, 4.65, 4.78, and 5.80 days at 18, 20, 23, 25, 28, 30, and 31°C, respectively (Li *et al.* 2003). In addition, *N. cucumeris* completed its development in 11.09, 8.74 and 6.25 days at 20, 25 and 30°C, respectively, when this predator preyed upon *F. occidentalis* (Gillespie and Ramey 1988). Nevertheless, Castagnoli *et al.* (1990) reported its generation was 9.48 days with the same prey at 25°C, significantly longer than the report of Gillespie and Ramey (1988). However, when *T. tabaci* was supplied as prey, the development of the predator from egg to adult took 8.22 days and mortality gradually decreased from 13.63% in the 1st generation to 11% in the 3rd at 25°C (Castagnoli *et al.* 1990). Obviously, different food affects the development of *N. cucumeris*. Further evidences were that the development period of *N. cucumeris* was 8.9, 8.5 and 7 days at 25 °C when supplying *T. palmi*, *T. urticae* and *D. farinae* Hughes as prey, respectively (Cuellar *et al.* 2002; Castagnoli 1989).

3.3. Fecundity and predation

There were many studies about of the fecundity of *N. cucumeris* were conducted, for example, different thrips, ararid mites, spider mites and so on. When supplying *A. ovatus* as prey, female *N.cucumeris* allowed to mate with a second or third male at 5-day intervals produced 39 eggs on average, but those mated with a single male produced 28 eggs on average. Matings with additional males 5 or 10 days after the first male increased the duration of the oviposition period of these females by 5-7 days and at the same time reduced the post-oviposition period by about 10 days. Overall, females with additional matings by one or two different males at 5-day intervals survived a few days shorter than females without additional males. Mating with a different female each day, a male of *N.cucumeris* could mate with 5-8 females, which produced a total of 85-116 eggs: females mated with a male during days 1 and 2 in its adulthood and with a male of the last 2 days of life (days 7 and 8) produced about half as many eggs as females mated with a male during 3-6 days of its adulthood. Females mated with males that are too young or too old had a shorter oviposition period and a longer post-oviposition period and longevity than females mated with middle-aged males.

Thrips: The fecundity of *N. cucumeris* was 25.2 eggs per female at 25 °C, when consumed 65.3 first instar larvae of *T. palmi* and 18.7 second instar larvae during its life cycle (Cuellar *et al.* 2002). And when supplying *T. tabaci* or *F. occidentalis* as prey, *N. cucumeris* laid 2 eggs/female/day or 1.88/ female/day at 25°C (Castagnoli *et al.* 1990), Gillespie and Ramey (1988) had reported the similar result, in which the

mean fecundity was 1.5 eggs/female per day with *F. occidentalis* as prey at 25°C. However, Muhammad *et al.* (2009) reported a higher 2.2 eggs/female/day when fed thrips with the oviposition periods 13.4 days at 25°C.

Ararid mites: When *D. farinae* was supplied as prey at 25°C, that the average fecundity were 53.46 eggs/female was observed with about the daily fecundity of 1.87 eggs/female/day (Castagnoli 1989). When supplying *A. ovatus* as prey, multiple mating females produced 39 eggs on average (Ji *et al.* 2007). However, Muhammad *et al.* (2009) also reported the higher fecundity, when feeding upon *T. putrescentiae* the fecundity of *N. cucumeris* were 3.8 eggs/female/day in the oviposition period (20.4 days) at 25°C.

Spider mites: Muhammad *et al.* (2009) reported that the daily fecundity *N. cucumeris* was 3.4 eggs/female/day and the oviposition period was 18.0 days when feeding *T. urticae* at 25°C. However, *N. cucumeris* laid 28.9 eggs/female in the average oviposition period (22.2 days) with *A. corpuzae* as prey at 25°C (Zhang *et al.* 2003). In addition, with *S. nanjingensis* as prey at 27-28°C, *N. cucumeris* started to lay eggs at the age of 3 days with 2.2 days/female/day over a period of 7-18 days, and a total fecundity of 35.8 (14-47) eggs was observed (Zhang *et al.* 2000).

Eriophyid mite: Ji *et al.* (2001) reported that the fecundity of *N. cucumeris* was 38.97 eggs/female with the daily 2.19 eggs/female when preying upon adult of *A. theae*, and 79.78 eriophyid mites was consumed per day at 25°C.

In addition, Fang *et al.* (2013) reported that *N. cucumeris* can prey *D. citri*, but only eggs, and could lay eggs when feeding exclusively on eggs of *D. citri*.

Neoseiulus cucumeris shows the lifestyle, Type III lifestyle—Generalist predators-Subtype III-e—Generalist predator from soil/litter habitats according to McMurtry *et al.* (2013) and , it periodically move up onto low-growing plants from soil or litter and moved from the aerial to the ground habitat. In natural, they are tan colored mites and can be often found on the underside of leaves along the veins or inside mature flowers. This predator ordinarily overwintered in litter or soil (Putman 1959).

3.4. Effect of environment

The egg mortalities of *N. cucumeris* were less than 3% at 75-80% RH at 20 °C. The mean life span of *N. cucumeris* was 28 days when food was available continuously. In the absence of both food and water, the survival of adult female mites was reduced to 2-4 days. Survival time was at least doubled when free water was available in the absence of food. Mean survival of adult female mites with water but without food was only 10 days for *N. cucumeris*. Survival of adult female *N. cucumeris* was increased to 20 when fungal hyphae were present along with water but in the absence of other food (Williams *et al.* 2004).

3.5. Life table

The intrinsic rate of increase of *N. cucumeris* when preying upon the pollen of Horse-chestnut, *T. urticae* Koch and *D. farinae* was 0.180/day, 0.174/day and 0.203/day, respectively (Ranabhat *et al.* 2013; Marisa and Sauro, 1990; Castagnoli 1989).

Zhang *et al.* (2005) reported that when *N. cucumeris* prey on *P. citri* at 25°C, 80-85% RH and 15L:9D, the net reproductive rate, mean generation duration and the time for population double increase of *N. cucumeris* were $R_0=21.8750$, $T=16.8943$, $t=3.7954$, respectively, and the intrinsic rate of increase and finite rate of increase of were $r_m=0.1826$, $\lambda=1.2004$, respectively.

In addition, Li *et al.* (2003) showed that the highest value of the total fecundity, fecundity rate, net reproductive rate (R_0), intrinsic rate of natural increase (r_m) and finite rate of increase (λ) of *N. cucumeris* were, near to 28.0952, 0.7892, 14.2380, 0.1765, 1.1930, respectively, had been observed at 25 °C, when with *P. latus* as prey. The longevity and ovipositing periods were 31.9 and 30.5 days in average.

Marisa and Sauro (1990) reported: With *Quercus* spp. pollen or *T. urticae* as prey, the intrinsic rate of increase of *N. cucumeris* was 0.193 and 0.174/day, respectively at 25 °C. Significantly, when rearing *N. cucumeris* only with *T. tabaci* as prey in 3 successive generations, *N. cucumeris* can improve its reproductive capacity, the intrinsic rate of increase was 0.154, 0.164 and 0.178/day for the 1st, 2nd and 3rd generations, respectively.

4. *Typhlodromus bambusae* Ehara

4.1. Feeding habits

This predator only prefer prey upon the spider mites in web-nest of bamboo or miscanthus, for example, *S. nanjingensis*, *S. celarius*, *Aponychus corpuzae* Rimando, *Schizotetranychus bambusae* Reck, *Stigmaeopsis* (*Schizotetranychus*) *longus* (Saito), *Stigmaeopsis* (*Schizotetranychus*) *miscanthi* (Saito), also prey on *Aculus*

bambusae Kuang when the predator move from a web-nest to another. *T. bambusae* is a highly specialized predator for the long-seta form of *Stigmaeopsis*.

4.2. Development

The eggs of *T. bambusae* could not hatch at 36°C. The total fecundity of *T. bambusae* ranged from 31.26 at 24 °C to 9.20 at 32 °C (Liu *et al.* 2004).

This predatory mite has six developmental stages, egg, larva, pronymph, deutonymph, preoviposition, adult, respectively. Laboratory studies showed that females of *T. bambusae* completed a full egg-egg cycle in 7.5 days at 22-30 °C with a diet of *S. nanjingensis* (Zhang *et al.* 1999). However, when with *S. celarius* as prey mites, the egg-adult of female or male *T. bambusae* was 7.3 and 6.1 days, respectively, and the generation developmental duration of female was 8.9 days with 2.0 days of preoviposition period at 25°C, 60-80% RH and 15 : 9 L: D (Saito1990 b).

4.3. Fecundity and predation

There were few studies about of the fecundity of *T. bambusae* were conducted.

When *T. bambusae* preying upon the spider mites, *S. celarius*, the total fecundity of *T. bambusae* was 28.5 eggs/female with daily oviposition 1.7 eggs/female in 16.7 days of oviposition period at 25°C, 60-80% RH and 15: 9 L: D (Saito1990 b). In addition, when *S. recki* or *A. corpuzae* was supplied as prey, *T. bambuse* can consume 5.32 or 8.92 eggs of prey, respectively, and lay 1.46 and 1.54 eggs in 48 hours (Saito1990 b). The oviposition of *T. bambusae* with spider mite *S. bambusae* as prey had been conducted at different, the total fecundity was 11, 30.86, 31.26, 29.35 and

9.2 eggs/female with daily oviposition ratio 0.63, 1.28, 2.23, 2.33 and 1.74 eggs/female/day, respectively, at 16, 20, 24, 28 and 32°C (Liu *et al.* 2004).

4.4. Effect of environment

Temperature significantly affected fecundity and longevity of *T. bambusae*. Percentage of survival was the highest (92.50 %) at 20°C, and lowest (67.50%) at 32°C. The oviposition period was the longest (24.43d) at 20°C, whereas the shortest (5.14d) at 32°C. The developmental threshold temperatures for egg, lava, protonymph, deutonymph, from egg to adult, and pre-oviposition were 10.21, 10.67, 10.94, 10.76, 10.44 and 13.36 °C , respectively .The developmental effective accumulated temperatures for egg, lava, protonymph, deutonymph, from egg to adult, and female adult pre-oviposition were 36.18, 12.61, 21.46, 21.63, 93.71 and 39.43 DD, respectively (Liu *et al.* 2004).

The polyculture bamboo forest planted with other plants benefit remain the population of *T. bambusae*, rather than monoculture bamboo forest, due to the *T. bambusae* could obtain alternative food when they had consumed the bamboo pest mites on the leaves of bamboo, for example, *S. miscanthi* on the leaves of miscanthus, which often growing beside bamboo forest (Zhang *et al.* 2004 b).

Saito (1986) had indicated that the female *S. celarius* can kill its specific phytoseiid predator, the larvae of *T. bambusae*.

4.5. Life table

The generations survival rate of *T. bambusae* were 95.23, 100.00, 87.10, 80.48% and

average fecundity of female *T. bambusae* were 44.50 46.80, 41.15, 20.10 at 25 °C when feeding on *S. nanjingensis*, *S. bambusae*, *Aponychus corpuzae*, and *Aculus bambusae* (Zhang *et al.* 2004 a).

The net reproductive rate (R_0), mean generation time (T) intrinsic rate of increase (r_m) finite rate of increase (λ) of *T. bambusae* was 14.20, 16.21, 0.164 and 1.19, respectively, when with *S. celarius* as prey at 25°C, 60-80%, and 15: 9 L: D (Saito1990 b). However, Zhang *et al.* (2004 a) reported that the intrinsic rate of increase (r_m) of *T. bambusae* was 0.155, 0.152 and 0.148, respectively, with different prey, *S. nanjingensis*, *S. bambusae*, *A. corpuzae*, at 25°C. However, when preying on *Aculus bambusae*, the (r_m) was very lower than above those mentioned.