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ORIGINAL ARTICLE

Population characteristics of *Macrocheles glaber* (Acari: Macrochelidae) and *Stratiolaelaps scimitus* (Acari: Laelapidae) reared on a mushroom fly *Coboldia fuscipes* (Diptera: Scatopsidae)

Mei-Fang Wen[1,2,3,4], Hsin Chi[1,2,3,4,5], Ying-Xiao Lian[1,2,3,4], Yu-Hao Zheng[1,2,3,4],
Qing-Hai Fan[1,2,3,4,6] and Min-Sheng You[1,2,3,4]

[1]State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Fujian Agriculture and Forestry University, Fuzhou, China; [2]Institute of Applied Ecology, Fujian Agriculture and Forestry University, Fuzhou, China; [3]Fujian-Taiwan Joint Centre for Ecological Control of Crop Pests, Fujian Agriculture and Forestry University, Fuzhou, China; [4]Key Laboratory of Integrated Pest Management for Fujian-Taiwan Crops, Ministry of Agriculture, Fuzhou, China; [5]Department of Plant Production and Technologies, Faculty of Agricultural Sciences and Technologies, Ömer Halisdemir University, Niğde, Turkey and [6]Plant Health & Environment Laboratory, Ministry for Primary Industries, Auckland, New Zealand

Abstract Subterranean predatory mites are important biological control agents of pests in soil. In order to understand the population characteristics of two predatory mites, *Macrocheles glaber* Müller and *Stratiolaelaps scimitus* Womersley, we studied their development, survival and fecundity data under laboratory conditions using *Coboldia fuscipes* Meigen as a food source and analyzed them with the age-stage, two-sex life table. *Macrocheles glaber* had a significantly shorter developmental time, oviposition period, longevity and lower fecundity than those of *S. scimitus*. The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), net predation rate (C_0), and finite predation rate (ω) of *M. glaber* were significantly lower than those of *S. scimitus*. Both population parameters and computer simulation implied that *S. scimitus* is a potential powerful biocontrol agent compared to *M. glaber*.

Key words biocontrol; life table; predatory mites

Introduction

The oyster mushroom fly, *Coboldia fuscipes* Meigen (Diptera: Scatopsidae), is one of the most economically important pests in mushroom cultivation. It has caused severe damage to various mushroom cultivars in many parts of the world (Cook, 1981; Luo & Zhuang, 2007; Yi *et al*., 2008; Yi *et al*., 2015). Larvae of *C. fuscipes* feed on the mushroom mycelium and transmit other pests and pathogens (Wetzel, 1981; Choi *et al*., 2000). Due to habitat diversification, short life history and high fecundity, *C. fuscipes* is capable of generating high population densities within a short period of time (Choi *et al*., 2000). Selection and application of natural enemies might turn out to be one of the efficient ways to control *C. fuscipes*.

Mites of Macrochelidae and Laelapidae have commercially been used as biocontrol agents of dipteran pests in greenhouse and mushroom cultivation (Jess & Kilpatrick, 2000; van Lenteren, 2012). The subterranean predators *Macrocheles glaber* Müller (Mesostigmata: Macrochelidae) and *Stratiolaelaps scimitus* Womersley

Correspondence: Min-Sheng You, Institute of Applied Ecology, Fujian Agriculture and Forestry University, Fuzhou 350002, China. Tel: +86 591 83789369; fax: +86 591 83768251; email: msyou@iae.fjau.edu.cn

Qing-Hai Fan, Plant Health & Environment Laboratory, Ministry for Primary Industries, Auckland 1140, New Zealand. Tel: +64 9 909 5077; email: qinghai.fan@mpi.govt.nz

(Mesostigmata: Laelapidae) are distributed world-wide (Halliday, 2000; van Lenteren, 2012). Previous works reported that *M. glaber* could be reared on various dipteran pests, such as *Lucilia* sp., *Musca domestica*, *M. vetustissima* and *Haematobia irritans exigua* (Halliday & Holm, 1987; de Azevedo *et al*., 2015). *M. glaber* could also prey on nematodes, springtails and phorid flies. Al-Dulaimi (2002) studied the predation rate and development time of *M. glaber* feeding on frozen housefly eggs. However, there are no experiments on the life table, especially the population parameters, of this species.

Stratiolaelaps scimitus is a generalist predator. It has been studied for the control of some major invertebrate pests, such as sciarid flies, phorid flies, gall midges, chrysomelid beetles (*Diabrotica* spp.), thrip, springtails and mould mites in greenhouse and mushroom cultivation factories (Enkegaard *et al*., 1997; Berndt *et al*., 2004; Jess & Bingham, 2004; Cabrera *et al*., 2005; Prischmann *et al*., 2011). A few studies have been published on the life tables, population parameters and predation ability of *S. scimitus* based on the traditional female age-specific life table (Wright & Chambers, 1994; Enkegaard *et al*., 1997; Cabrera *et al*., 2005; Wang *et al*., 2009). In addition, effectiveness of the biological control of dipteran pests by introducing *S. scimitus* along or in conjunction with other predators or parasites such as *Gaeolaelaps aculeifer* (Mesostigmata: Laelapidae), *Steinernema feltiae* (Rhabditida: Steinernematidae) on mushrooms and in glasshouses have been evaluated (Chambers *et al*., 1993; Enkegaard *et al*., 1997; Ali *et al*., 1999; Jess & Kilpatrick, 2000; Vänninen & Koskula, 2004; Freire *et al*., 2007; Castilho *et al*., 2009).

As both male and female predators can prey on the pest, studies based on the female age-specific life table could only offer limited information on the population characteristics and could not correctly evaluate the efficiency of biological control agents. In this study, we collected the life table data (i.e., the development, survival and reproduction) and predation rate of *M. glaber* and *S. scimitus* reared on *C. fuscipes*, and then analyzed and compared them by using the age-stage, two-sex life table (Chi & Liu, 1985; Chi, 1988) to assess the difference between these two predators. The information obtained in this study may serve as a basis for further studies and developing pest management program.

Table 1 Development time for the different life-stages, adult longevity, adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period, fecundity, and sex ratio of *Macrocheles glaber* and *Stratiolaelaps scimitus* fed on *Coboldia fuscipes*, and showing number of tested individuals.

Parameter	*M. glaber*		*S. scimitus*		*P*
	n	Mean ± SE	*n*	Mean ± SE	
Egg	57	1.09 ± 0.04 b	43	2.00 ± 0.17 a	< 0.0001
Larva-protonymph	53	1.85 ± 0.12 b	38	4.21 ± 0.41 a	< 0.0001
Deutonymph	52	1.48 ± 0.09 b	37	6.38 ± 0.44 a	< 0.0001
Preadult	52	4.40 ± 0.17 b	37	12.68 ± 0.67 a	< 0.0001
Adult	52	55.88 ± 4.78 b	37	76.95 ± 8.15 a	0.0258
Adult (female)	32	75.53 ± 5.23 a	28	75.11 ± 9.01 a	0.9689
Adult (male)	20	24.45 ± 2.24 b	9	82.67 ± 19.40 a	0.0039
APOP	31	7.84 ± 1.27 a	26	5.54 ± 0.53 a	0.0919
TPOP	31	12.03 ± 1.26 b	26	17.92 ± 0.68 a	0.0001
Longevity	61	52.21 ± 4.74 b	44	76.14 ± 8.18 a	0.0114
Longevity (female)	32	79.69 ± 5.22 a	28	87.50 ± 8.87 a	0.4473
Longevity (male)	20	29.25 ± 2.35 b	9	96.22 ± 18.82 a	0.0096
Oviposition days	31	18.65 ± 1.84 b	26	32.96 ± 2.04 a	< 0.0001
Fecundity (eggs/female)	32	18.94 ± 1.97 b	28	41.21 ± 3.36 a	< 0.0001
Reproductive female (%)[†]	32	96.88 ± 3.10 a	28	92.86 ± 4.89 a	0.4883
Sex ratio (% female)	52	61.54 ± 6.75 a	35	75.68 ± 7.07 a	0.1472

Mean ± SE values within the same row followed by different letters indicate significant differences in development time between two species using the paired bootstrap test (200 000 bootstraps, $P < 0.05$).

[†] The proportion of reproductive females in all female adults.

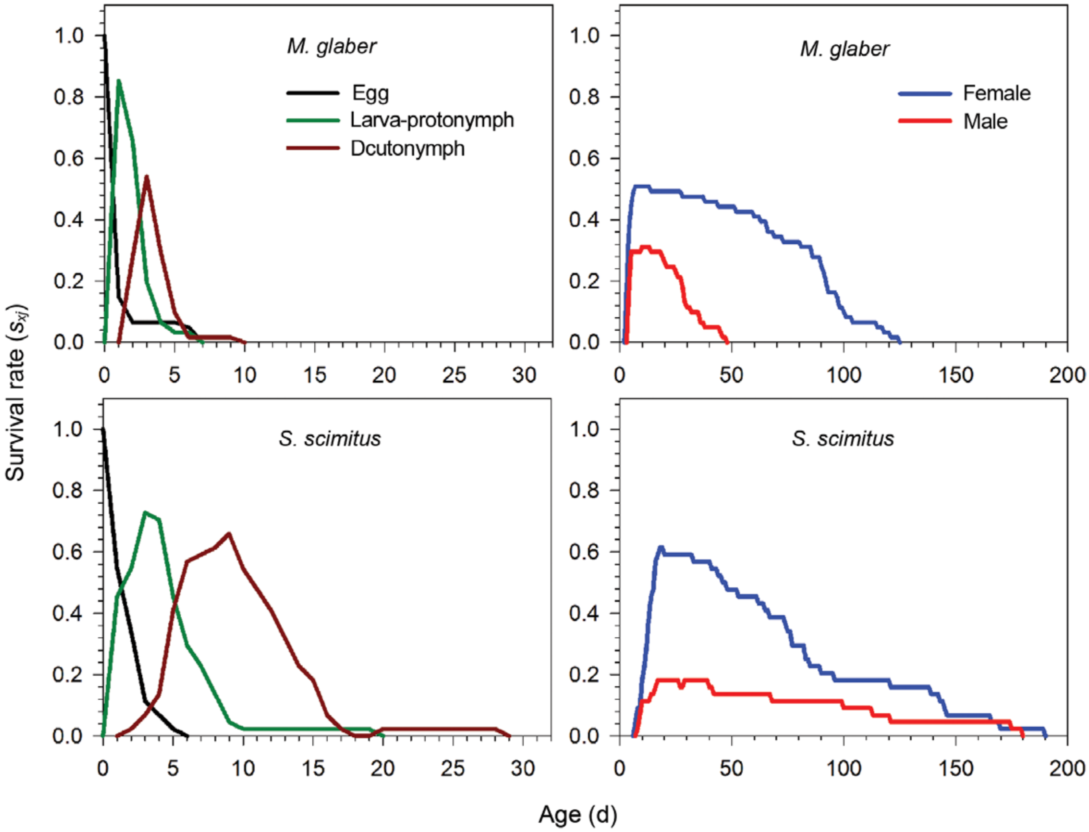

Fig. 1 Age-stage specific survival rate (s_{xj}) for immature stage (left) and adult-stage (right) of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes*.

Materials and methods

The experiments were conducted in climatic chambers maintained at 25 ± 1°C, 90% ± 10% relative humidity (RH), and no lighting.

Coboldia fuscipes *mass rearing*

Coboldia fuscipes was originally collected from the mushroom (*Agrocybe cylindracea*) in a farm in Gu Tian County (Jiaxin Cooperative, Ningde, China) on 10 October 2014 and then reared on small cubes (320–640 mm^3) of fresh yam bought from a market. Fresh yam cubes were used as egg-laying substrate, and then were transferred to new plastic pots every two weeks.

Macrocheles glaber *and* Stratiolaelaps scimitus *colonies*

Initial populations of *M. glaber* and *S. scimitus* were collected from taro (*Colocasia esculenta*) and ginger (*Zingiber officinale*) fields on 27 February 2014 and 25 July 2013, respectively, in Xingquan Town (Longyan, Fujian, China) and kept in closed plastic pots (200 mm diameter × 80 mm depth). On the lid, there was a hole (60-mm in diameter) covered with nylon mesh (200 mesh) for ventilation and to prevent mites escaping. The larvae of *C. fuscipes* were supplied as prey. Before the life table study, the laboratory colonies of both predatory mites were established and maintained for more than three generations.

Life table and predation rate studies

For life table studies, the adult predator and prey were transferred into a hollow arena of a glass clip-cell (6 mm in diameter and 1 mm depth) individually by using a fine moistened paintbrush. The bottom of the cell was covered with nylon mesh (300 mesh) to balance humidity and temperature of the hollow arena. The glass clip-cell consisted of a plastic board (25 × 20 × 1 mm^3), covered with a glass slide (same size as the plastic board), and fasten by clips at both sides. The clip-cell was placed onto a water-saturated sponge in a lidless plastic container (80 × 100 × 50 mm^3). The plastic container was surrounded by saturated salt (NaCl) water in a closed plastic container (180 × 120 × 60 mm^3) to maintain constant humidity (95% ± 5% RH).

Before the life table studies, the populations of *M. glaber* and *S. scimitus* were reared on *C. fuscipes* under aforementioned conditions for three generations. Fifty pairs of immature *M. glaber* and *S. scimitus* were randomly selected and each pair was kept in a clip-cell. After 24 h, each new-laid egg was transferred into a clean clip-cell. In total, 61 eggs of *M. glaber* and 44 eggs of *S. scimitus* were used for the life table study. Because newly hatched larvae did not feed, we supplied 10 larvae of the 1st or 2nd instar of *C. fuscipes* daily to each individual of protonymph and deutonymph, and 15–20 larvae to adult until death. Newly emerged adults were paired until the female mite laid eggs. In case of a male mite dying earlier before the female produced eggs, another male was recruited from the mass-rearing colony and paired with the surviving individual. The data of the recruited male were excluded for life table analysis. Because once a female is successfully mated it can lay eggs until its death, no male was recruited from the mass-rearing colony after the death of the male.

To calculate the finite predation rate (ω), the finite rate (λ), the stable age-stage distribution (SASD) and the age-stage predation rate (c_{xj}) are acquired (Yu *et al.*, 2013). We collected the daily predation rate of protonymphs, deutonymphs, female adults, and male adults by using 20 newly emerged individuals, respectively. We provided 20 individuals of the 1st or 2nd instar of *C. fuscipes* to each individual of predatory mites. After 24 h, the number of *C. fuscipes* consumed was recorded. As the collection of predation rate is very time- and labor-consuming, we collected only the predation rate of adult stage for the first 4 days. Because the proportion of adults in the stable age-stage distribution is minor, this practice has only minor effect on the calculation of the finite predation rate.

Statistical analysis

Life table analysis The life history raw data of *M. glaber* and *S. scimitus* individuals were analyzed based upon age-stage, two-sex life table theory (Chi & Liu, 1985; Chi, 1988, Huang & Chi, 2012) using the computer program TWOSEX-MSChart (Chi, 2016b). The age-stage specific survival rate (s_{xj}, the probability that a new-laid egg will survive to age x and stage j), the age-specific survival rate (l_x, the probability that a new-laid egg will survive to age x), the age-stage fecundity of female (f_{x4}, the mean fecundity of female adults at age x) (female adult stage 4), the age-specific fecundity (m_x, the mean fecundity of individuals at age x), and the population parameters, the intrinsic rate of increase (r), the finite rate (λ), the net reproductive rate (R_0), the mean generation time (T) were calculated by using the following equations (Chi & Liu, 1985):

The age-specific survival rate (l_x) and the age-specific fecundity (m_x) were calculated as:

$$l_x = \sum_{j=1}^{k} s_{xj},$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}},$$

where k is the number of life stages. The net reproductive rate (R_0) is the total number of offspring that an individual could produce during its life time and is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x.$$

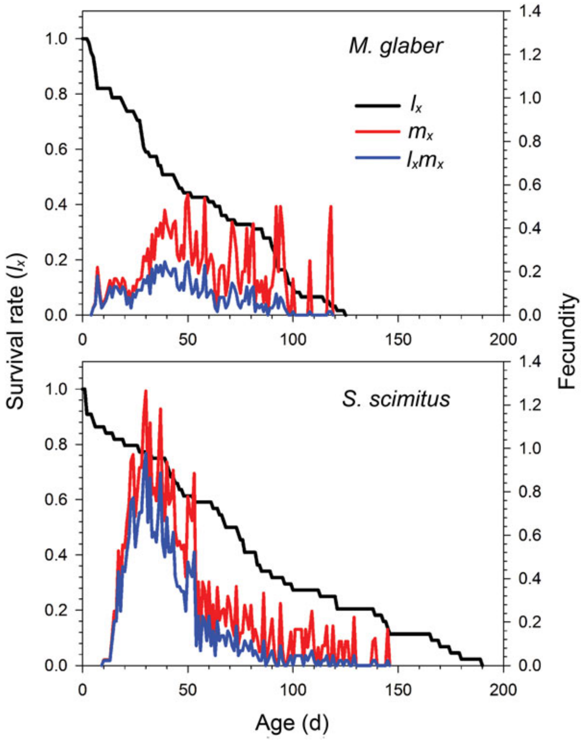

Fig. 2 Age-specific survival rate (l_x), fecundity (m_x), and net maternity (l_xm_x) of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes*.

The intrinsic rate of increase (r) was estimated by the Euler-Lotka formula with age indexed from 0 (Goodman, 1982) as:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1.$$

The finite rate of increase (λ) was calculated as:

$$\lambda = e^{r}.$$

The mean generation time (T) is the length of time that a population needs to increase to R_0-fold of its size when the population reaches the stable age-stage distribution. It was calculated as:

$$T = \frac{\ln R_0}{r}.$$

The age-stage life expectancy (e_{xj}) is the length of time that an individual of age x and stage j is expected to survive and it was calculated according to Chi and Su (2006):

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} s'_{iy},$$

where s'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y and is calculated by assuming $s'_{xj} = 1$. The age-stage reproductive value (v_{xj}) is the contribution of an individual of age x and stage j to the future population (Fisher, 1930). The reproductive value (v_{xj}) in the age-stage, two-sex life table (Huang & Chi, 2012; Tuan *et al.*, 2016) is calculated as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{k} s'_{iy} f_{iy}.$$

The finite predation rate was calculated as:

$$\omega = \lambda\psi = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{k} a_{xj} c_{xj},$$

where λ is the finite rate of a predator with a stable age-stage distribution, ψ is the stable predation rate ($\psi = \sum\sum a_{xj} c_{xj}$), and a_{xj} is the proportion of individuals belonging to age x and stage j in a stable age-stage distribution.

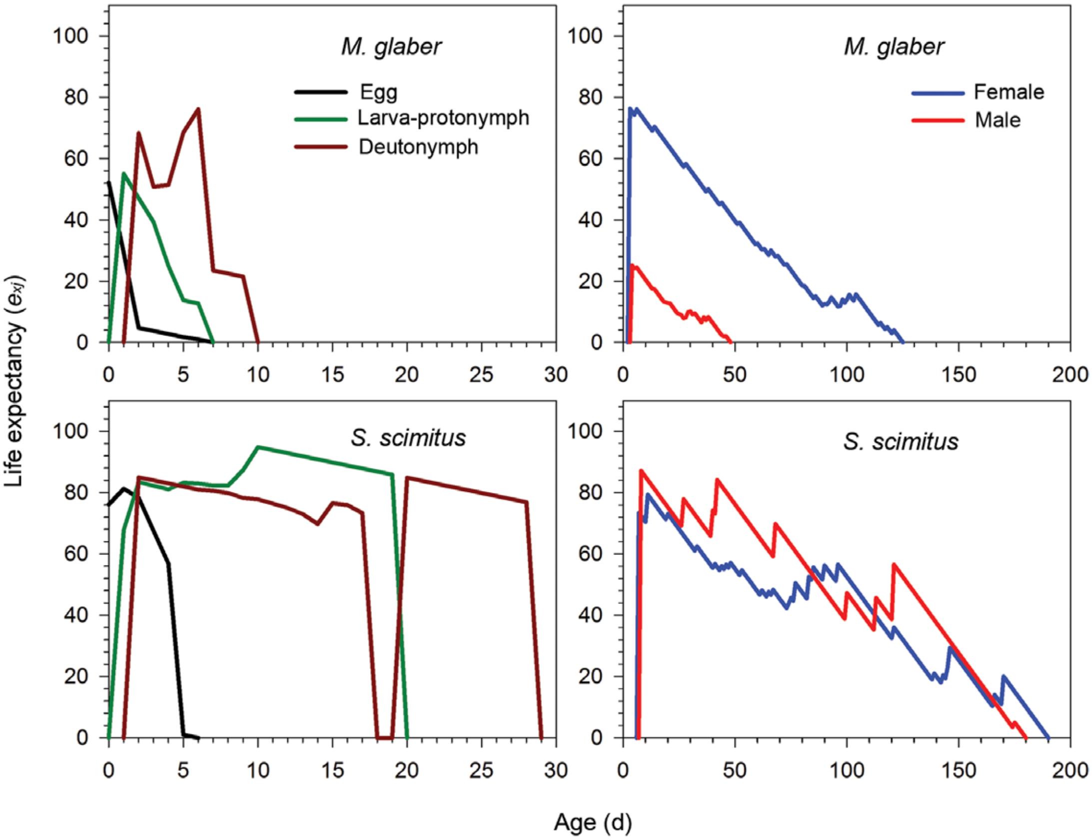

Fig. 3 Age-stage-specific life expectancy (e_{xj}) of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes*.

The variances and standard errors of the development time, longevity, fecundity and population parameters were analyzed by the bootstrap method with 200 000 bootstraps (Efron & Tibshirani, 1993; Polat-Akköprü *et al.*, 2015; Tuan *et al.*, 2017). The differences between two predator mites were compared by the paired bootstrap test (Efron & Tibshirani, 1993; Polat-Akköprü *et al.*, 2015).

Population projection The data of survival rate, developmental rate and fecundity of age-stage, two-sex life table were used to simulate the population growth by using the program TIMING-MSChart (Chi, 2016a). An initial population of 10 new-laid eggs were used for the population projection of both predatory mites (Chi & Liu, 1985; Chi, 1990). The predation rates of both predatory mites observed were used to project the predation potential of both predators. These predation rates were used to project the predation potential of both mites.

Results

Survival and developmental characteristics of M. glaber *and* S. scimitus

The two predator species were able to complete development and produce offspring when reared on *C. fuscipes*. Significant differences were observed in the developmental time of each immature stage as well as adult longevity (Table 1). Although *M. glaber* had a significant shorter development time and total longevity from egg to adult than that of *S. scimitus*, there were no significant differences in the female adult duration and longevity; however, both duration and longevity in male *M. glaber* were considerably shorter than those in *S. scimitus*. There were no significant differences observed for the adult preoviposition period (APOP) between the two predatory mites; however, the total preoviposition period (TPOP) was significantly shorter in *M. glaber*, due to the reduced length of immature stages in this species. The number of oviposition periods was also remarkably fewer in *M. glaber* compared to *S. scimitus*.

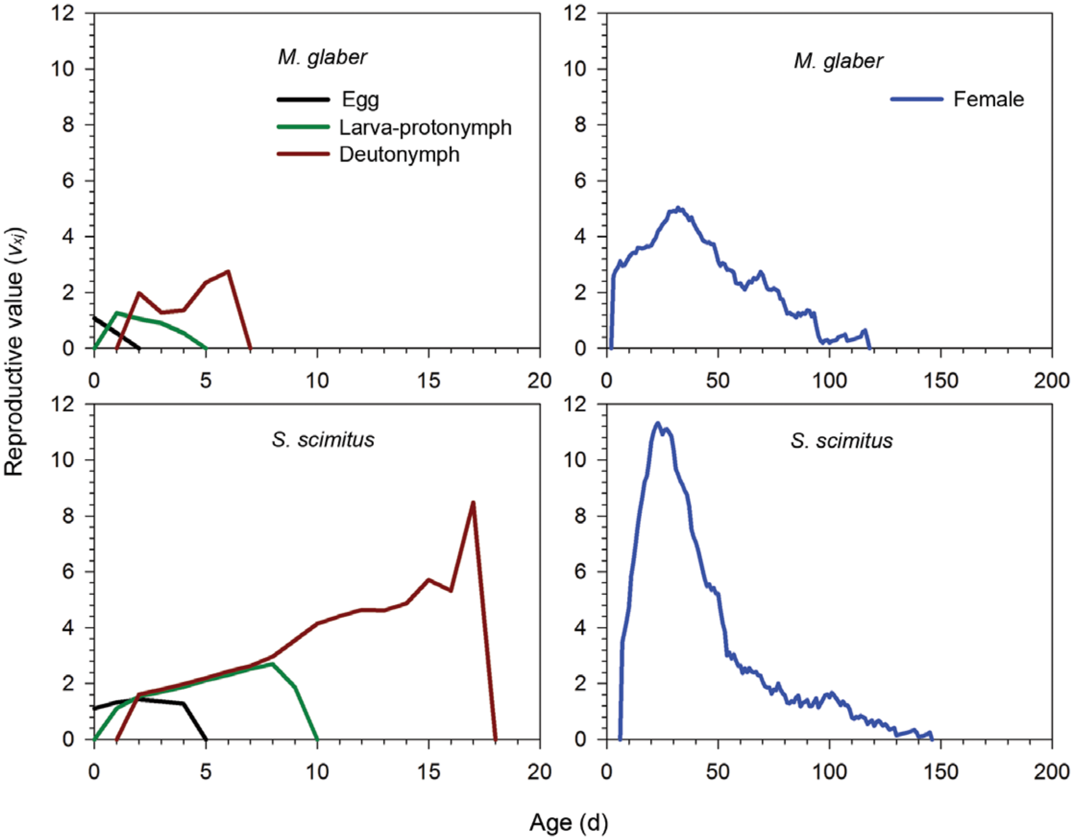

Fig. 4 Age-stage-specific reproductive value (v_{xj}) of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes*.

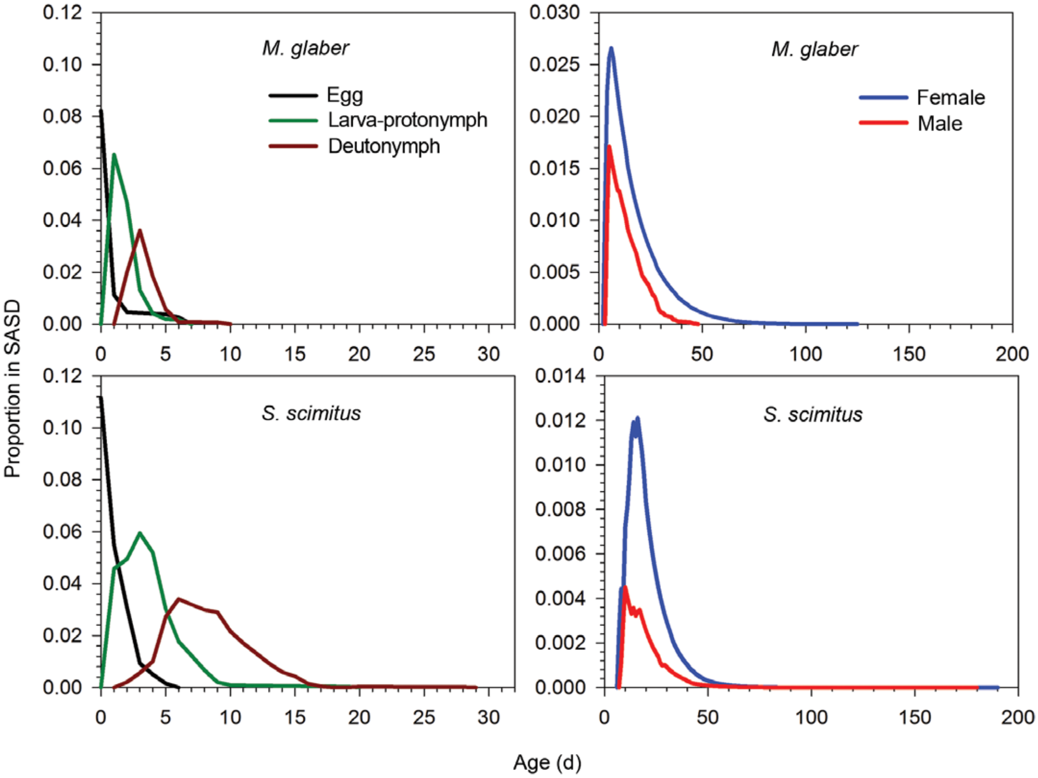

Fig. 5 The stable age-stage distribution (SASD) of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes*.

The mean fecundity of females of *M. glaber* was significantly lower than that of *S. scimitus*, but no significant difference was found in the proportion of reproductive females. Although females outnumbered males, there was no significant difference between species.

Age-stage survival rate curves (s_{xj}) show obvious overlapping between successive life-stages, demonstrating variable developmental rates among individuals (Fig. 1). Most *M. glaber* developed more rapidly but lived shorter than *S. scimitus*. There were significant differences in the adult survival curves between male and female *M. glaber*. Males lived considerably shorter than females ($P < 0.0001$). However, the adult survival rates of male and female *S. scimitus* were not significantly different ($P = 0.7242$).

The age-specific survival rate (l_x) demonstrates a simplified overview of the survival rate (Fig. 2). The oviposition patterns for the two species of predatory mites were remarkably different. The age-specific fecundity (m_x) of *M. glaber* was mostly lower than that of *S. scimitus*. The age-specific net maternity ($l_x m_x$) in *S. scimitus* increased dramatically at early adulthood and decreased gradually as it aged.

The life expectancies of immature and adult stages of *S. scimitus* were mostly higher than those in *M. glaber* (Fig. 3). Because of the constant rearing conditions, the life expectancy decreased gradually as they aged. The life expectancy of a new-laid egg of *M. glaber* was 52.2 d, which was shorter than that of *S. scimitus* (76.1 d). For a new-laid egg, the reproductive value is exactly the finite rates of increase, that is, *M. glaber* 1.0724/d and *S. scimitus* 1.1090/d, respectively (Fig. 4). When female individuals emerged, the reproductive value jumped to the highest value of *M. glaber* (5.1/d) at age 33 d, which occurred late and lower than that of *S. scimitus* (11.3/d at age 23 d) (Fig. 4).

The stable age-stage distributions of *M. glaber* and *S. scimitus* are plotted in Figure 5. The proportion of preadults in the stable age-stage distribution of *S. scimitus* was about 74% and that of protonymphs and deutonymphs was 54%; while the proportion of preadults in the stable age-stage distribution of *M. glaber* was about 33% and that of protonymphs and deutonymphs was 21.6%.

Population parameters

Population parameters were significantly different between the two predatory mites (Table 2). The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), net predation rate (C_0) and finite predation rate

Table 2 Population parameters of *Macrocheles glaber* and *Stratiolaelaps scimitus* fed on *Coboldia fuscipes*.

Parameter	*M. glaber*		*S. scimitus*		P
	n	Mean ± SE	n	Mean ± SE	
Predation rate					
Protonymph + Deutonymph	20	4.55 ± 0.76	20	3.35 ± 0.30	0.1451
Female adult (first 4 d)	20	4.12 ± 0.39	20	4.10 ± 0.40	0.9637
Male adult (first 4 d)	20	1.49 ± 0.15	20	2.13 ± 0.15	0.0027
Population parameter					
Intrinsic rate of increase, r (d^{-1})	61	0.0699 ± 0.0074 b	44	0.1034 ± 0.0060 a	<0.001
Finite rate of increase, λ (d^{-1})	61	1.0724 ± 0.0080 b	44	1.1090 ± 0.0066 a	<0.001
Net reproductive rate, R_0 (offspring)	61	9.93 ± 1.58 b	44	26.23 ± 3.66 a	<0.001
Mean generation time, T (d)	61	32.84 ± 1.97 a	44	31.59 ± 1.05 a	0.5516
Net predation rate, C_0 (prey)	61	17.51 ± 0.79 b	44	29.19 ± 1.81 a	<0.001
Finite predation rate, ω (d^{-1})	61	1.148 ± 0.013 b	44	1.445 ± 0.016 a	<0.001

Mean ± SE values within the same row followed by different letters represent significant difference between species based on the paired bootstrap test (200 000 bootstraps, $P < 0.05$).

(ω) for *M. glaber* were all significantly lower than those for *S. scimitus* (Table 2), while the mean generation time (T) of *M. glaber* did not differ significantly from that of *S. scimitus*. These population parameters showed that the *S. scimitus* cohort could not only increase faster, but also killed more prey than *M. glaber*.

Population projection

As the age-stage, two-sex life table can take the stage differentiation into consideration, the stage structure of a population could be revealed in population projection. Our simulation results showed that *S. scimitus* increased much faster than *M. glaber* (Fig. 6). Beginning with 10 eggs, the total population of *S. scimitus* could increase to 1714 individuals and the total predation rate could be 2508 larvae/d (3.40 in log scale), while the total population of *M. glaber* could increase to 357 individuals and the daily total predation rate could be 411 larvae (2.62 in log scale) of *C. fuscipes*.

Discussion

The biological control of mushroom pests has been an important subject as mushrooms are usually produced in closed spaces similar to a greenhouse. However, little is known about the mite predators of *Coboldia fuscipes*. This study is the first to demonstrate that both *M. glaber* and *S. scimitus* could successfully develop and reproduce when they fed on *C. fuscipes*. The developmental time of *M. glaber* was similar to the stage duration of *M. glaber* under laboratory conditions at 28°C, 90% RH on frozen housefly eggs (Al-Dulaimi, 2002); however, the female longevity was much longer (nearly three times) and the number of eggs produced was slightly lower. This might be due to the different laboratory rearing conditions. The developmental time of *S. scimitus* was similar to that in previous research (Wright & Chambers, 1994; Enkegaard *et al*., 1997; Cabrera *et al*., 2005; Wang *et al*., 2009). The longevity of female adult *S. scimitus* was shorter than that found by Wright and Chambers (1994) who reported that with sufficient food supply, 60% of individuals could survive for 142 d. The longevity of male *S. scimitus* was slightly longer than that of females. This is significantly longer than that reported by Enkegaard *et al*. (1997).

The intrinsic rate of increase and finite rate of increase of *S. scimitus* fed *C. fuscipes* are comparable to those provided by Cabrera *et al*. (2005) for *S. scimitus* fed *Lycoriella* sp. and potworms (Enchytraeidae). However, the net reproductive rate (R_0) and generation time (T) (Table 2) are much greater than those in Cabrera *et al*. (2005). The differences may be due to Cabrera *et al*. (2005) using the traditional female age-specific life table which could not take the male population and the stage differentiation into account. Moreover, they estimated the standard errors with jackknife method which was considered inappropriate for the life table analysis (Huang & Chi, 2012). Using the age-stage, two-sex life table, we could analyze the survival, development, fecundity, sex ratio, and population parameters of two predatory mites with the bootstrap technique and compare them by using the paired bootstrap test.

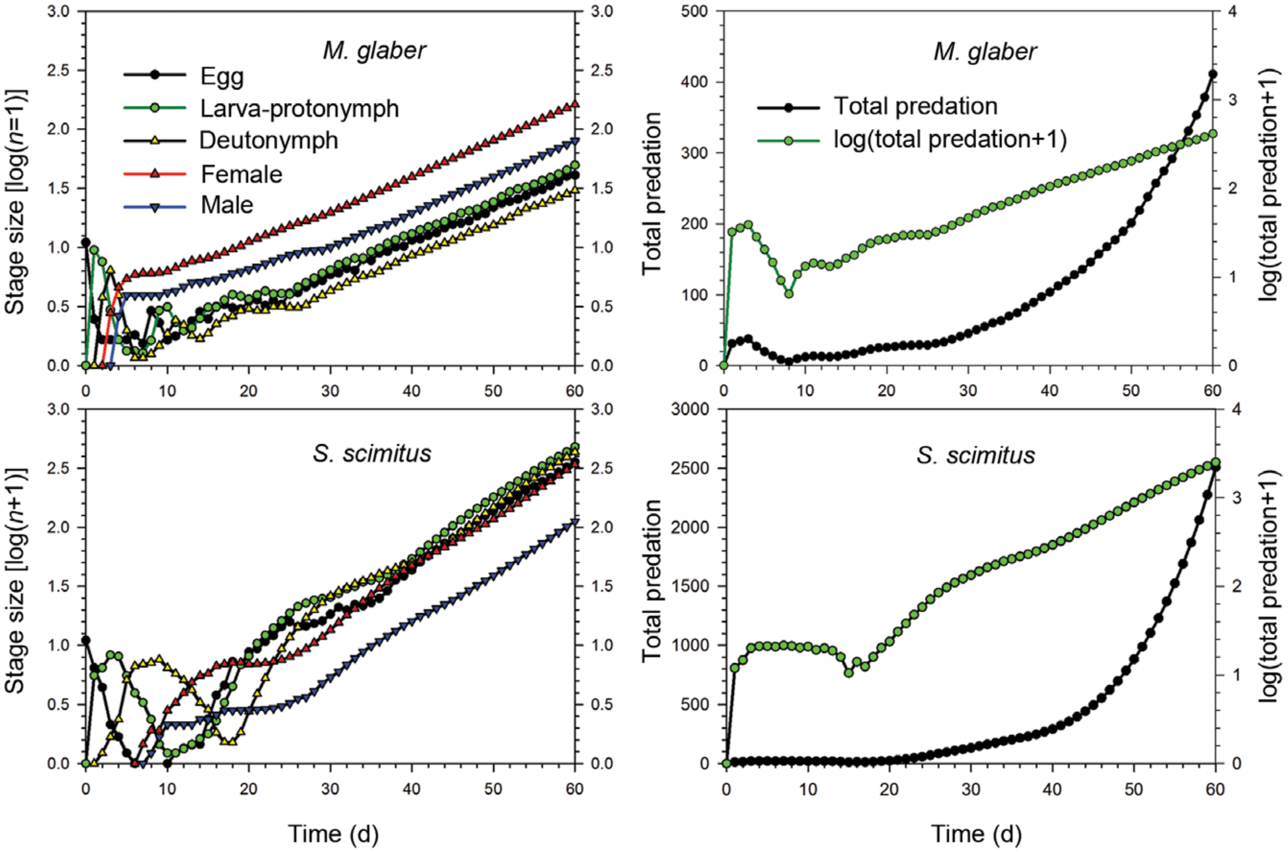

Fig. 6 Simulated population growth of *Macrocheles glaber* and *Stratiolaelaps scimitus* reared on *Coboldia fuscipes* with an initial population of 10 eggs. Left figures show the stage size in log scale. Right figures show the total predation in both regular and log scale.

The developmental time of different stages of *S. scimitus* was significantly prolonged. Furthermore, the oviposition period of *S. scimitus* was significantly longer and the number of offspring produced was higher. It showed that *S. scimitus* had high potential in establishing a population (Fig. 2). The higher net reproductive rate and intrinsic rate of increase could reinforce the advantages of *S. scimitus*. The longer life expectancy (Fig. 3) and greater reproductive value (Fig. 4) showed the potential of *S. scimitus* in biological control. The higher net predation rate, finite predation rate, population projection showed *S. scimitus* could build a higher population and has the potential to be a more effective biological agent than *M. glaber* (Figs. 5 and 6).

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Disclosure

The authors are not involved in any potential conflicts of interest, including financial or otherwise.

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