

Article

Comparing the Life Table and Population Projection of *Gaeolaelaps aculeifer* and *Stratiolaelaps scimitus* (Acari: Laelapidae) Based on the Age-Stage, Two-Sex Life Table Theory

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Abstract: Predatory soil-dwelling mites, *Gaeolaelaps aculeifer* (Canestrini) and *Stratiolaelaps scimitus* (Womersley) (Mesostigmata: Laelapidae), are essential biocontrol agents of small soil arthropod pests. To understand the population characteristics of these two predatory mites, we investigated their development, survival, and fecundity under laboratory conditions. We used *Tyrophagus putrescentiae* (Schrank) as a food source and analyzed the data using the age-stage, two-sex life table. The duration from egg to adult for *G. aculeifer* was longer than that for *S. scimitus*, but larval duration was similar between the two species. Notably, *G. aculeifer* laid 74.88 eggs/female in 24.50 days, but *S. scimitus* laid 28.46 eggs/female in 19.1 days. Several population parameters, such as the intrinsic rate of increase, finite rate of increase, net reproductive rate, and gross reproductive rate of *G. aculeifer*, were significantly higher than those of *S. scimitus*. Using the bootstrap technique with 100,000 samples, we demonstrated that the life tables constructed based on the 2.5th and 97.5th percentiles of finite rate of increase (λ) net reproductive rate (R_0) may characterize the variability in the survival and fecundity curves, as well as predict population growth uncertainty. These data provide important information for the practical application of predatory soil mites to manage agricultural pests.

Keywords: biological control; life history traits; bootstrap technique; predatory mites; thrips control



Citation: Park, J.; Mostafiz, M.M.; Hwang, H.-S.; Jung, D.-O.; Lee, K.-Y. Comparing the Life Table and Population Projection of *Gaeolaelaps aculeifer* and *Stratiolaelaps scimitus* (Acari: Laelapidae) Based on the Age-Stage, Two-Sex Life Table Theory. *Agronomy* **2021**, *11*, 1062. <https://doi.org/10.3390/agronomy11061062>

Academic Editor: Marco Scortichini

Received: 30 April 2021

Accepted: 24 May 2021

Published: 25 May 2021

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1. Introduction

Gaeolaelaps aculeifer (Canestrini) and *Stratiolaelaps scimitus* (Womersley) are predatory, soil-dwelling mites belonging to the family Laelapidae (Acari: Mesostigmata). Typically, these two species are generalist predators and are used effectively as biological control agents of various soil pests, such as thrips pupae, fly maggots, and bulb mites [1–7]. Moreover, these two predatory mites are beneficial for controlling mushroom flies during mushroom cultivation [3,8–10], and control poultry red mite, *Dermanyssus gallinae* (De Geer) [11,12]. Recent research has shown that *G. aculeifer* and *S. scimitus* are natural enemies of *Varroa destructor* (Anderson and Trueman), the honey bee ectoparasitic mite [13]. They prey on other small soil organisms, such as Collembola, mites, nematodes, and Enchytraeidae [14–18].

The best predators should survive prey scarcity [19], and their populations should be able to survive when the target pest population density is low due to their diverse host range [20]. Furthermore, this ability facilitates rearing on factitious preys, such as the mold mite *Tyrophagus putrescentiae* (Schrank) (Acari: Sarcoptiformes: Acaridae). *T. putrescentiae* is

an important pest of stored products having a high fat or protein content [21]. *T. putrescentiae* is routinely used for experimental and commercial rearing of predatory mites [9,22]. Predators, on the other hand, face intense selection pressure for prey quality and density, oviposition-friendly habitats, and antagonist availability [23–26].

Predator fitness was evaluated using the life table tool. Two-sex life table techniques are now widely used to assess predators' fitness on prey. Two-sex life table studies assist in understanding an organism's ecology and fitness, because they take both sexes into account when constructing the population curve for future populations [27,28]. Furthermore, incorporating the life table into constructing a mass-rearing system improves the mass-rearing system's efficiency [29,30]. Traditional female age-specific life tables [31–34] ignore stage differentiation in metamorphic species and the effects caused by the male component of a population. In contrast, the age-stage, two-sex life table [35] considers both sexes and precisely describes stage differentiation; therefore, it can properly describe the developmental duration, survival, reproduction, and population growth.

Several studies have been conducted during the past few decades on the effect of diet on the development, fecundity, and mortality of *G. aculeifer* and *S. scimitus*, such as mold mite, bulb mite, thrips, and sciarid fly [22,36–41]. To the best of our knowledge, no extensive data on the fitness of these two predators employing age-stage, two-sex life methods has ever been published. In this study, we determined the fitness traits and population parameters of *G. aculeifer* and *S. scimitus* reared on a single-species diet of *T. putrescentiae*. We also employed the age-stage, two-sex life table to examine these data, as well as population projection to show the dynamics of stage structure and population growth variability. By considering the importance of integrated pest management, the findings of this study could assist in maintaining the predation of *G. aculeifer* and *S. scimitus* on *T. putrescentiae*.

2. Materials and Methods

2.1. Insect Rearing

The laboratory populations of *G. aculeifer* and *S. scimitus* were reared separately following a simple mass-rearing method [42,43]. The two predatory mite species were maintained in two closed plastic boxes (including an inner and outer box) at 25 ± 1 °C, $90\% \pm 5\%$ relative humidity (RH), and a photoperiod of 16:8 (L:D) h.

The mold mite, *T. putrescentiae*, was used as prey for both predatory mites. The prey mites were also reared with rice bran as a food source following the same double box system [43].

The two predatory mites were collected from the stock population and reared in Petri dishes (50 mm D × 15 mm H). Cutting a 13.20-mm hole in each lid and covering the hole with a nylon mesh (0.053 mm) allowed ventilation in the Petri dishes. Rice husks (1 cc) were provided as a shelter for the mites in each Petri dish. To maintain constant humidity, water-saturated cotton was placed daily on the hole of each Petri dish (Figure 1).

2.2. Life Table Study of *G. aculeifer* and *S. scimitus*

Life table studies were initiated using the egg stages of predatory mites. More than 100 pairs of *G. aculeifer* and *S. scimitus* adults were isolated from the mite culture and maintained in the Petri dishes to obtain the egg stages. After 24 h, each newly-laid egg was separated and collected into another Petri dish. Forty-eight *G. aculeifer* eggs and 41 *S. scimitus* eggs were used for the life table study. We supplied mixed life stages of *T. putrescentiae* daily to each Petri dish as prey. The predatory mites' developmental stage and survival rate were monitored every day. Emerged male and female adults of *G. aculeifer* and *S. scimitus* were paired, and each pair was transferred to a new Petri dish with new rice husks and prey. Males from the mass-rearing colony were used to mate with females from the life table cohort, since there were more females than males. The mass-rearing colony's males were omitted from the life table analysis, and daily oviposited eggs were recorded and discarded. The survival of each adult was recorded daily until the death

of all individuals. These bioassays were conducted under laboratory conditions at the temperature and RH conditions described in Section 2.1.

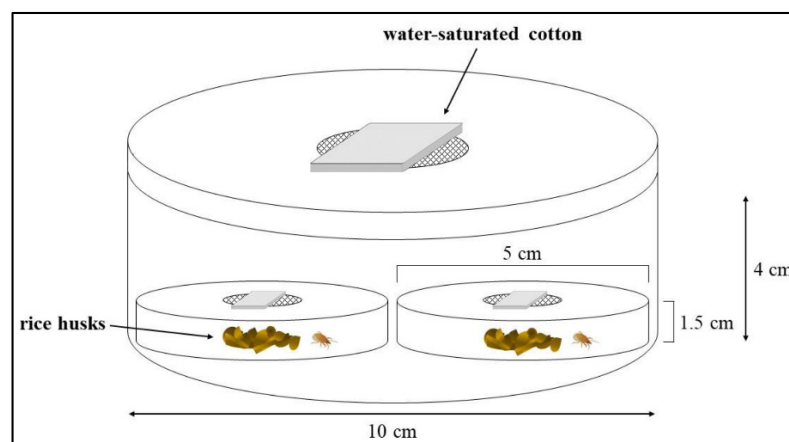


Figure 1. Experimental setup for the life table study of the two predatory mite species under laboratory conditions.

2.3. Life Table Data Analysis

The population parameters, including the intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), mean generation time (T), age-stage-specific survival rate (s_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), adult preoviposition period (APOP) and the total preoviposition period (TPOP), reproductive days (R_d), age-specific maternity ($l_x m_x$), age-stage life expectancy (e_{xj}), and reproductive value (v_{xj}), were calculated, according to the age-stage, two-sex life table approach [35,44–46] using TWOSEX-MSChart [47]. Population parameter variances and standard errors were calculated following the 100,000 random resampling bootstrap technique [48]. The differences in population parameters between *G. aculeifer* and *S. scimitus* were evaluated using a paired bootstrap test, based on the confidence intervals implemented in the TWOSEX-MSChart [46,47,49]. All graphs were generated using SigmaPlot v.12.5 (Systat Software Inc., San Jose, CA, USA, 2013).

2.4. Population Projection

The potential population growth of *G. aculeifer* and *S. scimitus* on *T. putrescentiae* was projected according to Chi [50] by incorporating the life table data into TIMING-MSChart [51]. The variability of population growth was projected as described by Huang et al. [49] using life tables representing the 2.5th and 97.5th percentiles, i.e., the 2500th and 97,500th sorted bootstrap results of the net reproductive rate (R_0) and finite rate of increase (λ).

3. Results

3.1. Survival and Developmental Characteristics of *G. aculeifer* and *S. scimitus*

We observed that the two predatory mite species could complete development and produce offspring when fed on *T. putrescentiae*. Table 1 shows the developmental times of each stage, preadult duration, adult longevity, reproductive days, and fecundity of females for the two species. The mean developmental time of the egg stage for *G. aculeifer* and *S. scimitus* was 3.71 and 2.89 d, respectively (Table 1). The duration of the egg stage was significantly different between the two species ($p < 0.0001$). However, no significant differences were observed in the duration of larva ($p = 0.2783$), protonymph ($p = 0.3577$), and deutonymph ($p = 0.6078$) between *G. aculeifer* and *S. scimitus*. The preadult duration was significantly longer for *G. aculeifer* (11.51 d) than for *S. scimitus* (10.69 d). However, there were no significant differences in preadult survival rate (s_a) between the two species. Female

longevity was significantly higher ($p = 0.0165$) for *G. aculeifer* (80.31 d) than *S. scimitus* (69.71 d). However, there were no significant differences in male longevity between the two species ($p = 0.1242$) (Table 1). Significant differences were observed in APOP and TPOP between the two predatory mites. The maximum number of reproductive days was recorded for *G. aculeifer* (24.5 d), which was significantly higher than that for *S. scimitus* (19.12 d) ($p = 0.0288$). The fecundity of *G. aculeifer* (74.88 offspring/female) was also significantly higher than that of *S. scimitus* (28.46 offspring/female) ($p = 0.0285$).

Table 1. Development time for the different life stages, total preadult duration, adult longevity, adult preoviposition period (APOP), total preoviposition period (TPOP), reproductive days, and fecundity of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

Biological Parameters	Developmental Time (days)				<i>p</i>
	<i>Gaeolaelaps aculeifer</i>		<i>Stratiolaelaps scimitus</i>		
	N	Mean ± SE	N	Mean ± SE	
Egg (d)	41	3.71 ± 0.11 a	36	2.89 ± 0.096 b	<0.0001
Larva (d)	41	1.05 ± 0.034 a	36	1.11 ± 0.053 a	0.2783
Protonymph (d)	41	3.32 ± 0.101 a	36	3.06 ± 0.112 a	0.3577
Deutonymph (d)	41	3.44 ± 0.093 a	36	3.64 ± 0.15 a	0.6078
Preadult (d)	41	11.51 ± 0.18 a	36	10.69 ± 0.25 b	0.0064
Adult longevity (d)	41	66.24 ± 2.20 a	36	57.19 ± 2.61 b	0.0072
Female adult	26	80.31 ± 2.75 a	24	69.71 ± 3.08 b	0.0165
Male adult	15	73.33 ± 3.55 a	12	64.25 ± 4.78 a	0.1242
Total longevity (d)	41	77.76 ± 2.21 a	36	67.89 ± 2.61 b	0.0035
APOP (d)	26	3.23 ± 0.19 a	24	6.04 ± 0.47 b	0.0035
TPOP (d)	26	14.88 ± 0.34 a	24	16.42 ± 0.60 b	0.0285
Oviposition days (d)	26	24.50 ± 0.73 a	24	19.12 ± 1.29 b	0.0288
Fecundity (offspring/individual)	26	74.88 ± 2.25 a	24	28.46 ± 2.00 b	0.0285
Fecundity (eggs/day)	26	3.06 ± 0.07 a	24	1.49 ± 0.04 b	<0.0001

Standard errors (SEs) were estimated using 100,000 bootstraps. Mean values followed by the same letters in rows are not significantly different between the two species as assessed using the paired bootstrap test at the 5% significance level.

3.2. Life Table of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*

The age-stage survival rate (s_{xj}) depicts the probability of whether a newly hatched individual would survive to age x and stage j (Figure 2). Due to differences in developmental rate among individuals, there was an obvious stage overlap during the developmental period (Figure 2). The female and male adults emerged at 8 and 10 d, respectively, for *S. scimitus* (Figure 2). In contrast, female and male adults appeared at 9 and 10 d, respectively, for *G. aculeifer* (Figure 2). The longer longevity of female adults compared to males could be observed in Figure 2.

Figure 3 shows the age-specific survival rate (l_x), female age-specific fecundity (f_{x5}) (the female adult being in the fifth life stage), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) for *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*. The l_x curve of *G. aculeifer* was significantly decreased from age 50 d, whereas that of *S. scimitus* decreased from age 37 d (Figure 3). The parameter, f_{x5} , is the mean number of fertilized eggs produced by the female adult at age x . The highest peak of f_{x5} was observed for *G. aculeifer* fed on *T. putrescentiae* at age 18 d ($f_{18,5} = 4.8$ eggs). Based on the curve, m_x , the highest peaks occurred at age 18 d (with 3.04 offspring) for *G. aculeifer*, and at age 24 d (with 0.86 offspring) for *S. scimitus* (Figure 3). Based on both l_x and m_x , the maximum $l_x m_x$ value of 3.04 offspring was recorded for *G. aculeifer* at age 18 d, whereas its value of 0.86 offspring was recorded for *S. scimitus* at age 24 d (Figure 3).

Life expectancy (e_{xj}) indicates the length of time an individual of age x and stage j is expected to survive. The curves of e_{xj} of the egg, larva, protonymph, deutonymph, and adult of *G. aculeifer* fed on *T. putrescentiae* were higher than those of *S. scimitus* (Figure 4).

The life expectancy values of a newly-laid egg of *G. aculeifer* and *S. scimitus* were 67.33 and 60.34 d, respectively (Figure 4).

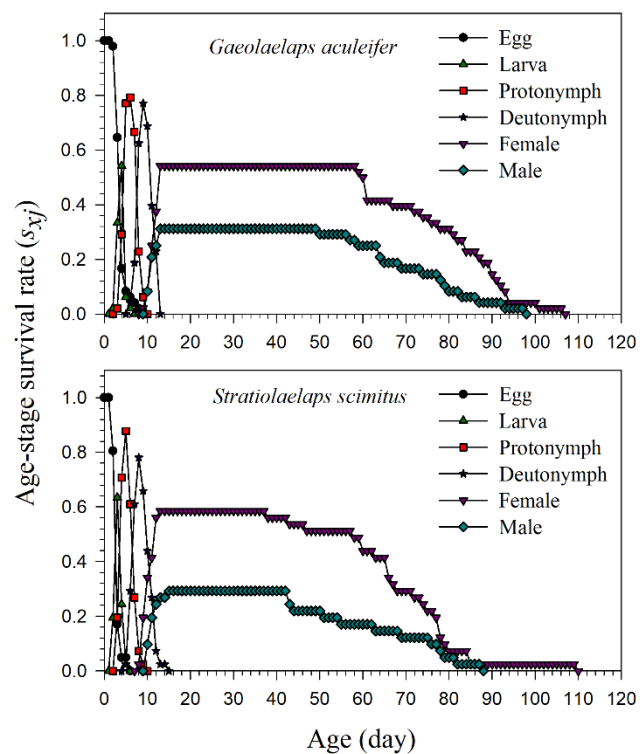


Figure 2. Age-stage-specific survival rate (s_{xj}) of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

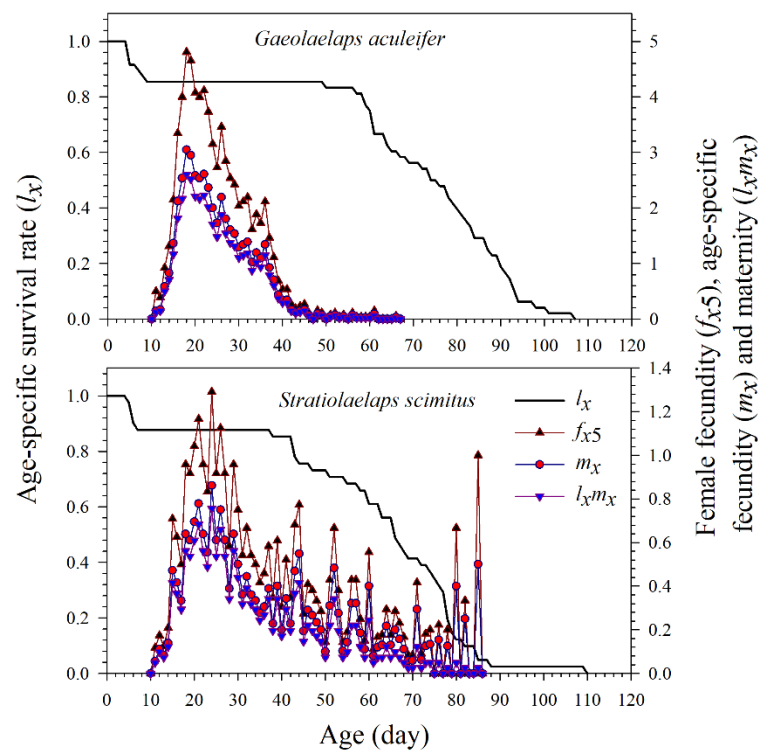


Figure 3. Age-specific survival rate (l_x), female age-specific fecundity (f_{x5}), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

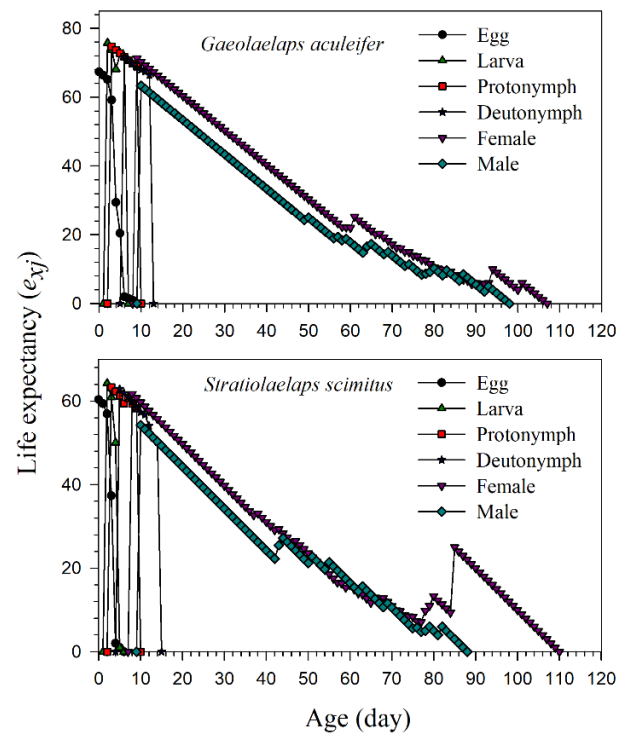


Figure 4. Age-stage-specific life expectancy (e_{xj}) of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

The reproductive value (v_{xj}) indicates the expected contribution of an individual of age x and stage j to the future population. The reproductive value gradually increased with an increase in age and stage, whereas the reproductive value of the female stage dramatically increased when they began to oviposit. The highest reproductive values for *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae* were recorded at age 17 d ($v_{17,5} = 24.11 \text{ d}^{-1}$) and 18 d ($v_{18,5} = 8.61 \text{ d}^{-1}$), respectively (Figure 5).

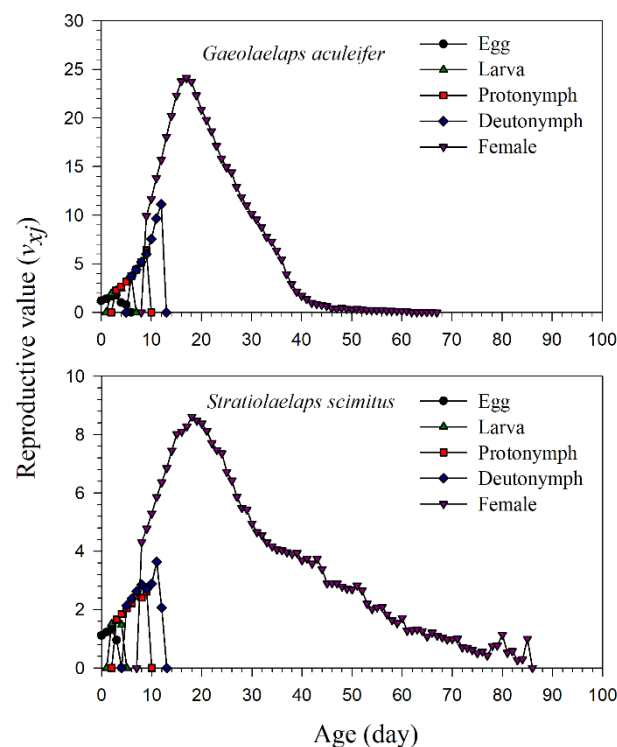


Figure 5. Age-stage-specific reproductive value (v_{xj}) of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

3.3. Population Parameters

Table 2 shows the population parameters of *G. aculeifer* and *S. scimitus*. The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and gross reproduction rate (GRR) of *G. aculeifer* fed on *T. putrescentiae* were 0.1733 d^{-1} , 1.1893 d^{-1} , 47.49 offspring, and 47.53 offspring, respectively. These parameters were significantly higher ($p < 0.0001$) than the values obtained for *S. scimitus* (0.1079 d^{-1} , 1.1139 d^{-1} , 18.97 offspring, and 22.03 offspring, respectively) (Table 2). In contrast, the mean generation time (T) obtained for *G. aculeifer* (22.27 d) was significantly shorter ($p < 0.0001$) than that for *S. scimitus* (27.29 d) (Table 2).

Table 2. Population parameter of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

Population Parameters ^a	Bootstrap (Mean $\pm$ SE ^{b,c})		<i>p</i>
	<i>Gaeolaelaps aculeifer</i>	<i>Stratiolaelaps scimitus</i>	
$r \text{ (d}^{-1}\text{)}$	$0.1733 \pm 0.0071 \text{ a}$	$0.1079 \pm 0.0071 \text{ b}$	<0.0001
$\lambda \text{ (d}^{-1}\text{)}$	$1.1893 \pm 0.0084 \text{ a}$	$1.1139 \pm 0.0068 \text{ b}$	<0.0001
R_0 (offspring/female)	$47.49 \pm 5.80 \text{ a}$	$18.97 \pm 2.59 \text{ b}$	<0.0001
$T \text{ (d)}$	$22.27 \pm 0.44 \text{ a}$	$27.29 \pm 0.83 \text{ b}$	<0.0001
GRR (offspring/female)	$47.53 \pm 5.81 \text{ a}$	$22.03 \pm 3.12 \text{ b}$	<0.0001

^a r , intrinsic rate of increase; λ , finite rate of increase; R_0 , net reproductive rate; T , mean generation time (offspring/individual); GRR, gross reproduction rate. ^b Standard errors (SEs) were estimated using the bootstrap technique with 100,000 re-samplings. ^c Mean values followed by the same letters in rows are not significantly different between the two species as assessed using the paired bootstrap test at the 5% significance level.

3.4. Population Projection

The growth capacities of *G. aculeifer* and *S. scimitus* were projected using life table data to demonstrate the increase in the pest population and stage structure during population growth on *T. putrescentiae*. The population growth and stage structure of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae* are depicted in Figure 6; the changes in the stage structure can be observed. The fastest population growth was observed for *G. aculeifer* fed on *T. putrescentiae*. Starting with 10 eggs, the population of *G. aculeifer* increased faster than that of *S. scimitus* fed on *T. putrescentiae*, which increased slowly (Figure 6). According to the simulation, after 30 d, the total number of eggs, larvae, protonymphs, deutonymphs, female, and male adults of *G. aculeifer* was 112, 18, 55, 68, 46, and 29, respectively (Figure 6).

Figure 7 shows the total population sizes of the original cohort and those based on the 2.5th and 97.5th bootstrap percentiles of the finite rate and net reproductive rate, which helps understand the variability of population growth. The population growth rates of *G. aculeifer* and *S. scimitus* on *T. putrescentiae* were different. This could be attributed to differences in developmental time, viability, and fertility among individuals (Figure 7). The total population size of *G. aculeifer* and *S. scimitus* reached 76.76 and 27.93 individuals on day 30 when fed on *T. putrescentiae*, respectively (Figure 7).

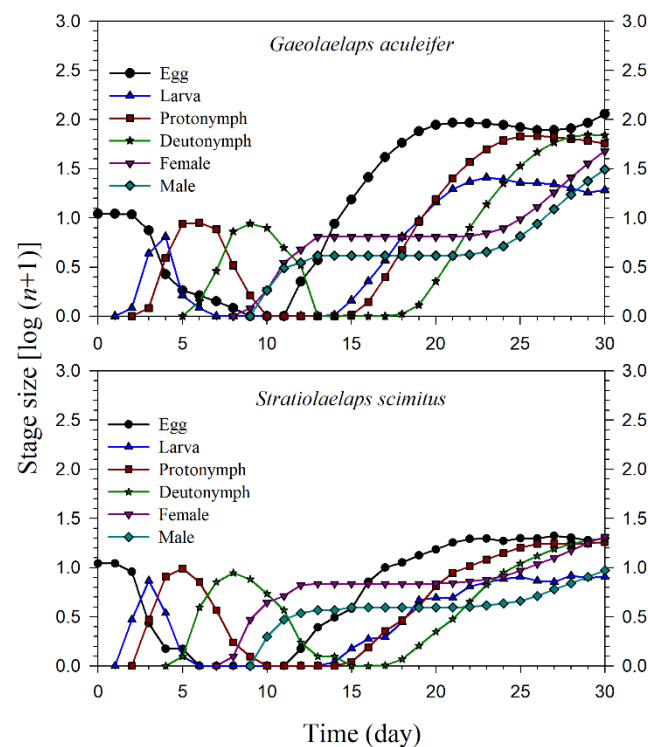


Figure 6. Population growth and stage structure of *G. aculeifer* and *S. scimitus* fed on *T. putrescentiae*.

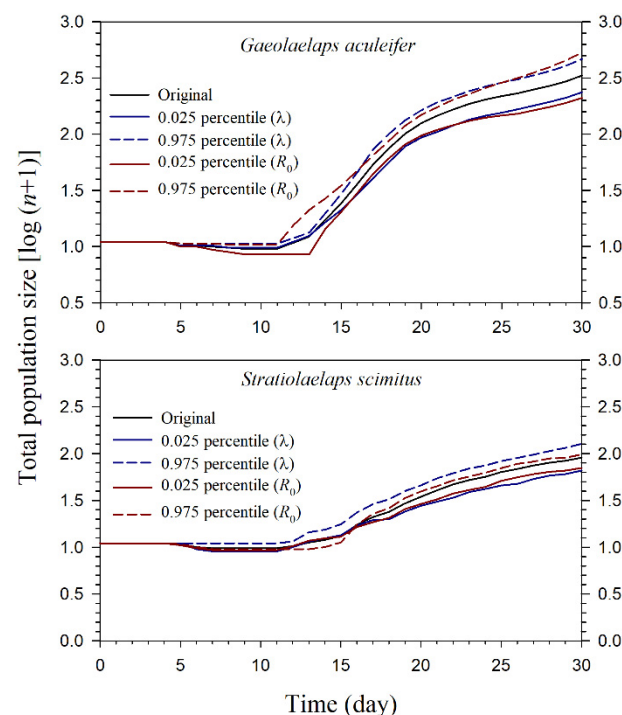


Figure 7. Population projection of *G. aculeifer* and *S. scimitus* using life tables of the original cohort; the cohorts were constructed based on the 2.5% and 97.5% percentiles of finite rate of increase (λ) and net reproductive rate (R_0).

4. Discussion

This study has shown that *G. aculeifer* had higher fecundity, intrinsic rate of increase, finite rate of increase, and shorter mean generation time than *S. scimitus* when fed on *T. putrescentiae*. Preadult survival and reproduction rates of insects on a prey that are higher

indicate that the prey is more suitable [52]. Although this prey mite species has been used commercially for rearing *G. aculeifer* and *S. scimitus* [9,22], we used the age-stage, two-sex life table technique to compare the fitness traits of these two predatory mite species that feed on *T. putrescentiae*. The predator–prey interaction, population development, survival, and reproduction can all be assessed using life table parameters [53,54].

In a predator–prey relationship, predator fitness is extremely important. It is affected by many factors, such as prey size and density [55,56], environmental factors, i.e., temperature, humidity [57,58], habitat complexity, and internal state of the predator [54,59]. Changes in the developmental rate, survival rate, fecundity, and reproductive age can all be attributed to these factors [60,61]. Our study showed that *G. aculeifer* and *S. scimitus* could complete their development and reproduction when fed on *T. putrescentiae*, but the fitness of these two species differed due to differences in survival, development, and fecundity. *S. scimitus* was found to be less suited to *T. putrescentiae* than *G. aculeifer* due to its prolonged TPOP and preadult length, as well as its lower fecundity and reproductive value. On the other hand, *G. aculeifer* is more suited and susceptible when fed on *T. putrescentiae*, because it has longer adult longevity, and life expectancy, higher fecundity, and population parameters (Tables 1 and 2).

Preys have been found to have an impact on the survival and development of numerous insects in previous studies [26,52,62]. Ajvad et al. [41] reported that female and male longevity of *G. aculeifer* fed on sciarid larvae was 67.7 and 60.3 d, respectively. Kakimoto et al. [63] revealed that the longevity of *Orius similis* Zheng females and males was 27.2 d and 13.2 d, respectively, compared with that of *Orius sauteri* (23.8 d and 14.5 d, respectively) when fed with *Ephestia kuehniella* Zeller. In another study, Asgari et al. [52] reported that male adult longevity (14.46 d) of *Amblyseius swirskii* Athias-Henriot was shorter than female adult longevity (16.61 d) when fed on *T. putrescentiae*. The same trend was observed in this study, where the total longevity of female and male adults (80.31 d and 73.33, respectively) of *G. aculeifer* was increased when fed on *T. putrescentiae*. Alternatively, the total longevity of females and males of *S. scimitus* was lower (69.71 d and 64.25 d, respectively) than *G. aculeifer*. This could be due to the nutritional content or quality of the specific diet/prey, decreased food pressure throughout development, physical defense or response of the prey, more feeding resources [62,64,65], predator preference behavior toward laying eggs [66,67], and complete physiological reactions in the insect body under selection pressure [68].

The life parameters, particularly r and λ , represent the various population features such as the developmental rate, fecundity, survival rate, and the population growth rate together to evaluate the population fitness. This theory supported the present study and showed that *G. aculeifer* showed higher R_0 , r , λ , and GRR values when fed on *T. putrescentiae* under our test conditions.

A population projection based on the age-stage, two-sex life table can reveal the change in stage structure during population growth. Understanding stage structure is vital to pest management, because predatory mites' dispersal and damage capability vary with stage. This study demonstrated that such a life table could provide a comprehensive description of predatory mite population's fitness on a given prey. The predicted population growth through time according to the age-stage, two-sex life table data can be described using the stages, as shown in Figure 6. Due to the incapability of traditional female age-specific life tables [31,32,34], to describe the stage differentiation, it would not be possible to show the stage structure, as shown in Figure 6.

We also demonstrated the variability of population growth using computer projections based on the bootstrap percentile confidence intervals. It is the first study to use the life tables of *G. aculeifer* and *S. scimitus* to depict the population growth range that is lower and upper 2.5th and 97.5th percentile to the most appropriate level of range for simulation (Figure 7). The findings revealed that insect populations have a lot of fluctuation and that including the life table variability into population projections is critical.

5. Conclusions

In conclusion, our study's life table parameters and population prediction analysis demonstrated that *G. aculeifer* has greater efficiency as a natural enemy than *S. scimitus*. The obtained results support Hwang et al.'s study [43] indicating that the *G. aculeifer* population increased to a higher density than that of *S. scimitus* using a simple mass-rearing method. We strongly promote the use of age-stage, two-sex life table in pest management programs at the age stage to anticipate population growth, stage structure, and possible damage by including stage-specific consumption rates in their control strategies.

Author Contributions: Conceptualization: J.P., M.M.M., and K.-Y.L.; methodology: J.P., M.M.M., H.-S.H., D.-O.J., and K.-Y.L.; software: M.M.M.; formal analysis: M.M.M.; investigation: K.-Y.L.; resources: K.-Y.L.; data curation: K.-Y.L.; writing—original draft preparation: J.P. and M.M.M.; writing—review and editing: M.M.M. and K.-Y.L.; supervision: K.-Y.L.; project administration: K.-Y.L.; funding acquisition: K.-Y.L. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by a research fund (PJ01336201) from the Rural Development Administration.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: There is no supplementary information to reveal; all information is contained in this manuscript.

Acknowledgments: We would like to thank Hsin Chi (Department of Entomology, National Chung Hsing University, Taichung 402, Taiwan) for his support and invaluable advice.

Conflicts of Interest: The authors declare no conflict of interest.

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