

Article

Effects of Prey Switching at Different Stages on Life Parameters of *Neoseiulus bicaudus*

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Abstract: The phenomenon of prey switching is prevalent in the natural world and represents a strategic adaptation of predators to their environment. *Neoseiulus bicaudus*, a native predatory mite found in Xinjiang, serves as a natural enemy to numerous small pests. The utilization of *Tyrophagus putrescentiae* as an alternative prey for the mass breeding of *N. bicaudus* is employed to fulfill the demands of enhanced breeding efficiency and cost-effectiveness. Following the introduction of mass breed *N. bicaudus* into the agricultural ecosystem, there was a switching in the prey of *N. bicaudus* from *Ty. putrescentiae* to *Tetranychus turkestani*. The objective of this study was to investigate the impact of prey switching at various stages on *N. bicaudus*. This study employed the age-stage, two-sex life table to assess the life parameters of *N. bicaudus* undergoing prey switching at different stages. The results showed that the survival rate of *N. bicaudus* was significantly decreased, the developmental period was significantly prolonged, the fecundity was improved during prey switching, and the intrinsic rate of increase of *N. bicaudus* was significantly decreased. The negative effects of prey switching in larva and deutonymph stages were greater than those in protonymph and adult stages. The stage and age of *N. bicaudus* undergoing prey switching were positively correlated with the male ratio, and negatively correlated with the total preoviposition period and the mean generation time. The comprehension of prey switching effects on *N. bicaudus* can enhance our understanding of the predator adaptation to environmental changes and contribute to the artificial rearing and application of natural enemy.



Citation: Nie, Z.; Zuo, L.; Tang, S.; Fang, C.; Ma, Y.; Li, X.; Zhang, J.; Su, J. Effects of Prey Switching at Different Stages on Life Parameters of *Neoseiulus bicaudus*. *Agriculture* **2024**, *14*, 728. <https://doi.org/10.3390/agriculture14050728>

Academic Editor: Jinzhi Niu

Received: 25 March 2024

Revised: 1 May 2024

Accepted: 6 May 2024

Published: 8 May 2024



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Keywords: age-stage; two-sex life table; Pearson correlation analysis; Phytoseiidae; prey switching

1. Introduction

The phenomenon of prey switching refers to a predator's inclination towards preying on species with higher abundance in the prey population [1]. This phenomenon is widely observed in nature and represents the adaptation of predators to their environment [2–4], which contributes to the stability of predator populations [5]. The fecundity, survival, and development of predators can be adversely affected by prey switching on predators [2,6,7]. However, the relatively limited attention given to the short life cycle of arthropod predators is noteworthy among researchers.

Natural enemies play an important role in integrated pest management [8]. The utilization of natural enemies for agricultural pest control is commonly achieved through the preservation of natural enemy insect habitats, attraction of natural enemies, and deliberate release of artificial populations to enhance their numbers [9,10]. Commonly, various types of natural enemies, including ladybugs, lacewings, parasitic wasps, pirate bugs, and predatory mites, are frequently employed for agricultural pest control [11–15], for example, *Aphelinus certus* has a substantial impact on decreasing the population size of *Aphis glycines*, and *Amblyseius swirskii* can prey on *Tetranychus urticae* and *Bemisia tabaci* [16,17], etc.

In their natural habitat, natural enemies primarily rely on their preferred prey for sustenance [18]. In the absence of a main prey, natural enemies undergo a prey switching

to ensure survival [5]. In the case of commercially propagated natural enemies, artificial rearing often involves using economically advantageous alternative prey species [19]. These alternative prey species differ from the target pests and can lead to passive prey switching of natural enemies. The process of prey switching is typically not accomplished swiftly, and the adaptation to new prey can often exert detrimental effects on both individual and population levels, such as deaths caused by insufficient nutrient intake [20]. *Orius sauteri*, which is commercially bred and fed on *Corcyra cephalonica* eggs for reproduction, is commonly employed as a biological control agent against aphids. However, the predation efficacy of the *O. sauteri* on aphids during the early phase of prey switching is suboptimal. Unfortunately, these negative consequences associated with prey switching are frequently overlooked but could contribute to failures in agricultural biological control [21].

Neoseiulus bicaudus (Mesostigmata: Phytoseiidae) was discovered in 2013 by Shihezi University in Ili, Xinjiang. This indigenous predatory mite is endemic to Xinjiang Uygur Autonomous Region [22]. The predatory mite *N. bicaudus* has demonstrated a broad prey spectrum, making it an effective agent in the management and control of *Te. truncatus*, *B. tabaci*, *Thrips tabaci*, and *Te. turkestanii* [23–25]. Among them, the *Te. turkestanii*, is one of the dominant species in cotton [26]. Severe damage caused by *Te. turkestanii* can lead to leaf wilting and subsequent detachment, resulting in major economic losses [26]. The alternative prey (*Ty. putrescentiae*) utilizes *N. bicaudus* for mass breeding, similar to the majority of commercial Phytoseiidae. It takes a few days for a predator mite fed on *Ty. putrescentiae* to gradually increase its predation ability when it switches to *Te. turkestanii* [27]. Therefore, the impact of prey switching on predator mites deserves further investigation.

Predatory mite populations typically exhibit overlapping generations. Consequently, predatory mites undergo prey switching during each available feeding stage. Furthermore, it is worth further clarifying the impact of prey switching occurring at different stages of *N. bicaudus*. The age-stage, two-sex life table prioritizes the male individuals in a population and is capable of describing the unique and important feature of stage differentiation (i.e., metamorphosis) that is a defining characteristic of insects and mites [28–30]. Hence, this study employs a comprehensive analysis of the age-stage, two-sex life table to investigate the influence of prey switching at different stages on individuals and populations. The aim of this study is to improve the understanding of the effects of prey switching on predators. The present study holds the potential to enhance the practicality of artificial breeding and biological-control strategies for predatory mites and other natural enemies.

2. Materials and Methods

2.1. Mite Cultures

Ty. putrescentiae was obtained from the Key Laboratory of Entomology and Pest Control Engineering College of Plant Protection, Southwest University in 2015. The mite colony of *Ty. putrescentiae* was fed with bran, supplemented with yeast powder at a weight ratio of 25%. The room temperature was maintained at 26 ± 1 °C, with a humidity level of $65 \pm 5\%$, and a photoperiod of 16:8 (L:D) hours.

Te. turkestanii was collected from a cotton field near Huayuan, Shihezi City, Xinjiang Uygur Autonomous Region, China in 2010. The spider mite colony of *Te. turkestanii* was maintained on potted sword bean (*Semen canavaliae* Gladiatae) seedlings under controlled conditions in a feeding room with a temperature of 26 ± 1 °C and humidity of $65 \pm 5\%$. The photoperiod follows a 16:8 (L:D) hour cycle.

N. bicaudus was collected from forest trees in Ili, Xinjiang Uygur Autonomous Region in 2013. The predatory mite colony of *N. bicaudus* was reared under controlled conditions in a dedicated feeding facility, with temperature and humidity maintained at 26 ± 1 °C and $65 \pm 5\%$, respectively, while maintaining a photoperiod of 16:8 (L:D) hours. The *N. bicaudus* colony was reared on *Ty. putrescentiae* for more than 1 year [25].

2.2. Experimental Setup

As illustrated in Figure 1, *N. bicaudus* undergoes five distinct developmental stages: egg, larva, protonymph, deutonymph, and adult. To account for the absence of prey consumption during the egg stage in *N. bicaudus*, four experimental treatment groups were established: *N. bicaudus* with prey switching at the larva stage (PSL); *N. bicaudus* with prey switching at the protonymph stage (PSP); *N. bicaudus* with prey switching at the deutonymph stage (PSD); and *N. bicaudus*, which underwent prey switching during adult (PSA). Additionally, a control group without any prey switching was included: *N. bicaudus* was continuously provided *Ty. putrescentiae* (F-Ty). For instance, mites of PSP treatment are being fed on *Ty. putrescentiae* from the moment the eggs hatch, and when the protonymph stage starts, we stop providing *Ty. putrescentiae* and start providing *Te. turkestanii*. Relevant processing operations adopt a similar approach.

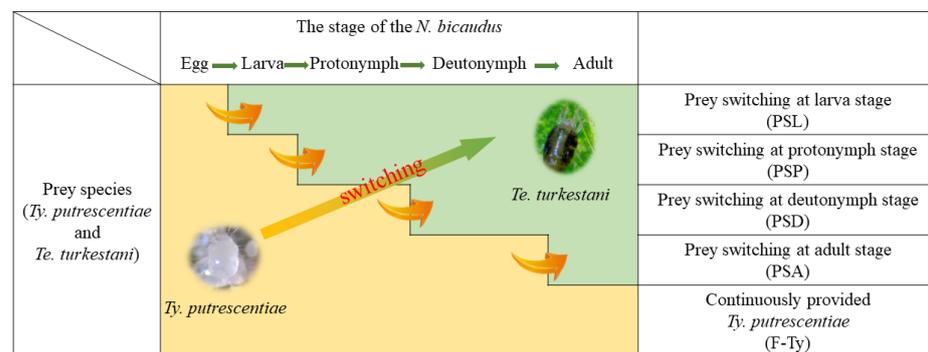


Figure 1. Developmental stages of *Neoseiulus bicaudus* and experimental treatments for prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

The experiment was conducted in acrylic chambers, each composed of three acrylic sheets (Figure 2). The dimensions of the acrylic sheet were 3 cm in length, 2 cm in width, and 0.3 cm in height. One of the acrylic plates featured a centrally located circular hole with a diameter of 1 cm. The chamber structure, from top to bottom, consisted of an acrylic plate, an acrylic plate with a hole, the leaves, a filter paper strip, another acrylic plate, and two clips on the left and right for securing the chamber [25]. Each egg was transferred to a separate chamber as a repeat. F-Ty, PSL, PSP, PSD, and PSA were set to 97, 86, 95, 94, and 101 replicates, respectively.

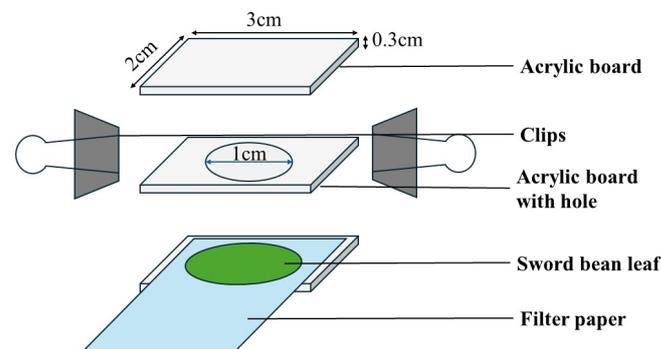


Figure 2. The photographs of the plexiglass chambers.

All eggs were laid by F-Ty females within a 12 h period. During the incubation period from egg to larva stage of *N. bicaudus*, the chamber leaves remained unchanged. Once *N. bicaudus* reached the larva stage, the chamber leaves were replaced daily. If *N. bicaudus* was to reach a specific mite stage, immediate replacement of its prey would be required. The survival and mite stage of *N. bicaudus* were recorded every 12 h. Female adult *N. bicaudus* individuals that reached maturity were paired, and their survival and egg production

were recorded every 12 h. However, male adult mites only needed to have their survival recorded every 12 h. Additionally, there was an excessive daily supply of prey [31].

2.3. Statistical Analysis

2.3.1. Life-Table Analysis

The original life-table data of *N. bicaudus* were analyzed using the age-stage, two-sex life-table theory [29,32] and the computer program TWISEX-MSChart [33].

The survival rate (l_x), age-stage survival rate (s_{xj}), age-specific fecundity of females (f_{xj}), and age-specific fecundity of the total population (m_x) are important parameters in the life table and were calculated using the daily-life-history raw data. The formula for calculating the values of s_{xj} , l_x , and m_x is as follows:

$$s_{xj} = \frac{n_{xj}}{n_{01}} \tag{1}$$

$$l_x = \sum_{j=1}^{\beta} s_{xj} \tag{2}$$

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{3}$$

where n_{01} is the number of eggs used at the beginning of the life-table study, n_{xj} is the number of individuals surviving to age x and stage j , and β is the number of stages.

The net reproductive rate (R_0), the intrinsic rate of increase (r), the finite rate of increase (λ), and the mean generation time (T) are important parameters for describing population characteristics. The formula for calculating the values of R_0 , r , λ , and T is as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{4}$$

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{5}$$

$$\lambda = e^r \tag{6}$$

$$T = \frac{\ln R_0}{r} \tag{7}$$

The R_0 is the total number of offspring produced during the survival period of an individual in a population, the r is the maximum instantaneous growth rate of the population under relatively stable environmental conditions when the population has a stable age structure, the λ is the daily growth rate of the population without resource constraints, and T is the period that population requires to increase to R_0 -fold of its size as time approaches infinity and the population settles down to a stable age-stage distribution. The multiplication of l_x and m_x gave us the age-specific maternity ($l_x m_x$), named age-specific net reproductive rate of population.

The age-stage life expectancy (e_{xj}) is the duration that an individual of age x and stage j is expected to survive after age x , following the method of Chi and Su [34], and is calculated as follows:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s'_{iy} \tag{8}$$

The s'_{iy} represents the probability that the individual of age x and stage j will survival to age i and stage y and is calculated by assuming $s'_{xj} = 1$ [29].

The age-stage reproductive value (v_{xj}) is the contribution that an individual of age x and stage j to the future population and is calculated as follows:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{\beta} s'_{iy} f_{iy} \tag{9}$$

The means and standard errors of population parameters were calculated by using the bootstrap method with 100,000 replications [35]. A paired bootstrap test was used to detect differences by the program TWOSEX-MSChart.

The mean fecundity of females (F) is the mean number of eggs (offspring) produced by each female during its adult stage. N_f/N , N_m/N and N_m/N_f are the female ratio, male ratio and male–female ratio. The N_f represents the number of female adults. The N_m represents the number of male adults. N represents the number of beginning of life table study. The adult preoviposition period (APOP) and total preoviposition period (TPOP) are the adult pre-oviposition period of female adult and the total pre-oviposition period of female counted from birth, respectively.

2.3.2. Pearson Correlation Analysis

Because of the different stages differentiation in the colonies of *N. bicaudus*, the ages at which they underwent prey switching were also different. Therefore, it is particularly important to explore the relationship between switching age/stage and life-table parameters of *N. bicaudus*. In this study, Pearson correlation analysis was used to explain the influence of the age/stage of prey switching on the life parameters of *N. bicaudus* [36]. All data was obtained using the bootstrap method with 100,000 replications, including the switching age and life-table parameters. The switching stage was converted to a number for analysis according to the mite stage (the larva, protonymph, deutonymph, and adult stage were 1, 2, 3, and 4, respectively). Computer software Origin (Version number: 10.050156) (Northampton, MA, USA) was utilized to perform Pearson correlation analysis on the data, clarifying the correlation relationship between the switching stage/age at switching day with the life-table parameters [37].

3. Results

3.1. Survival of *Neoseiulus Bicaudus* during Prey Switching from *Tyrophagus putrescentiae* to *Tetranychus turkestani* in Each Stage

The total number of collected eggs amounted to 473. Each treatment yielded varying quantities of eggs, with F-Ty, PSL, PSP, PSD, and PSA producing 97, 86, 95, 94, and 101 eggs, respectively.

The survival rate of *N. bicaudus* is shown in Table 1. The survival rate of larva was significantly higher for F-Ty (0.990) compared to PSL (0.919). Similarly, F-Ty exhibited a significantly higher survival rate at the deutonymph stage (0.989) in comparison to PSD (0.886). Additionally, the preadult stage survival rate for PSD (0.830) was significantly lower than that of F-Ty (0.928).

Table 1. Mean (\pm SE) of survival rate of the *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestani* in each stage.

Stage	F-Ty		PSL		PSP		PSD		PSA	
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE						
Larva survival	97	0.990 \pm 0.010 a	86	0.919 \pm 0.030 b	95	0.968 \pm 0.018 ab	97	0.968 \pm 0.018 ab	101	0.990 \pm 0.010 a
Protonymph survival	96	0.948 \pm 0.023 a	79	0.924 \pm 0.030 a	92	0.924 \pm 0.028 a	91	0.967 \pm 0.019 a	100	0.980 \pm 0.014 a
Deutonymph survival	91	0.989 \pm 0.011 a	73	1.000 \pm 0 a	85	0.988 \pm 0.012 a	88	0.886 \pm 0.034 b	98	0.990 \pm 0.010 a
Preadult survival rate (sa)	97	0.928 \pm 0.026 ab	86	0.849 \pm 0.039 bc	95	0.884 \pm 0.033 bc	94	0.830 \pm 0.039 c	101	0.960 \pm 0.020 a

The standard errors were estimated by using bootstrap technique with 100,000 resampling. The same letter within a row indicates no significant difference between treatments based on a paired bootstrap test at the 5% significance level.

The age-stage specific survival rate (s_{xj}) of *N. bicaudus* is shown in Figure 3. Due to variations in individual development time, there was an overlap in the age-stage specific survival rates across different stages. All F-Ty mites reached adult stage within 6.5 days, while both PSD and PSA mites achieved adult stage by day 7.5. Similarly, PSL and PSP

mites attained adult stage at day 8.5. The survival curve for female adult PSD mites exhibited a minimum peak at 0.457, in contrast to the maximum peak observed in male adult PSA mites at 0.406.

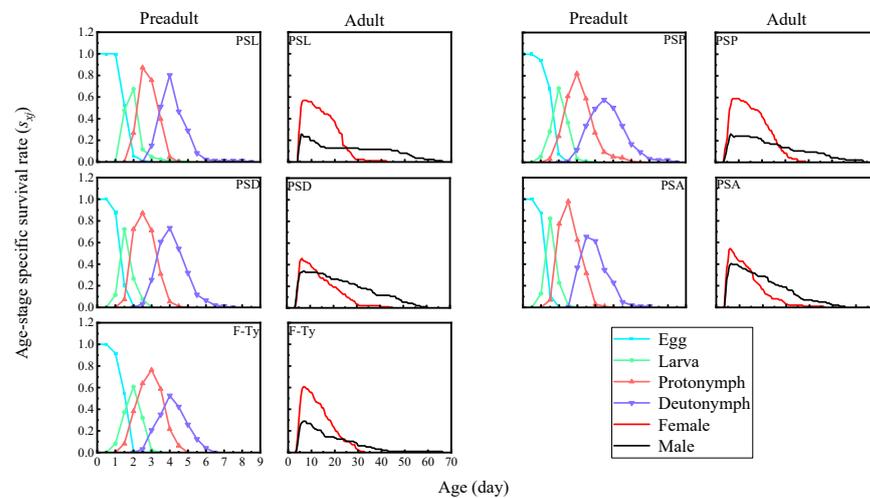


Figure 3. Age-stage specific survival rate (s_{xj}) of *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestani* in each stage.

3.2. Development Duration, Longevity, and Fecundity of the *Neoseiulus bicaudus* during Prey Switching from *Tyrophagus putrescentiae* to *Tetranychus turkestani* in Each Stage

The developmental duration, longevity, and fecundity of *N. bicaudus* are presented in Table 2. The protonymph duration of PSL was notably shorter at 1.253 d compared to F-Ty, which had a duration of 1.373 d. Conversely, PSL, PSP, and PSD exhibited significantly longer deutonymph durations (1.397 d, 1.512 d, and 1.391 d, respectively) compared to F-Ty's duration of 1.044 d. Furthermore, the preadult duration was significantly prolonged in PSP (5.435 d) as opposed to F-Ty (4.850 d). As for adult longevity, PSL, PSP, and PSD displayed significantly longer durations (18.979 d, 20.649 d, and 20.404 d, respectively) than F-Ty's duration of 14.472 d. Notably, PSP demonstrated significantly greater longevity lasting 23.568 d compared to F-Ty's longevity of 18.211 d.

PSL displayed a notably extended adult preoviposition period (APOP) of 3.044 d, compared to F-Ty's shorter duration of 2.088 d. Additionally, both PSL and PSP exhibited significantly longer total preoviposition periods (TPOP) of 8.100 d and 7.768 d, respectively, in contrast to F-Ty's TPOP of 6.974 d. Furthermore, the oviposition period was significantly prolonged in PSL (10.411 d) and PSP (11.750 d) compared to F-Ty (8.072). Lastly, PSP demonstrated significantly higher fecundity, with a value of 33.912, compared to F-Ty's fecundity of 24.361.

The values for age-specific fecundity of female (f_{xj}), age-specific fecundity of population (m_x), and age-specific net reproductive rate of population ($l_x m_x$) of the *N. bicaudus* are shown in Figure 4. PSL and PSA both reached their highest peak values of f_{xj} at 1.789, although PSL peaked later at 17th day compared to PSA's 13th day. Conversely, PSD had the lowest peak value of f_{xj} at 1.667, occurring on the 12th day, while PSP reached a peak value of 1.697 on the 22nd day, and F-Ty peaked at 1.727 on the 9th day. Concerning the peak value of $l_x m_x$, F-Ty had the highest at 0.979 on the 9th day, while PSD had the lowest at 0.596, also on the 9th day. PSL reached a peak value of 0.791 on the 10th and 17th days, PSP peaked at 0.863 on the 11th day, and PSA peaked at 0.713 on the 10th and 10.5th days. Additionally, the peak values of m_x for PSL, PSP, PSD, PSA, and F-Ty were 1.388, 1.12, 0.859, 0.932, and 1.173, respectively, aligning with the occurrence times of f_{xj} .

Table 2. Mean (\pm SE) of development time, longevity, adult preoviposition period (APOP), total preoviposition period (TPOP), and fecundity (F) of the *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

Stage	F-Ty		PSL		PSP		PSD		PSA	
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE
Egg (d)	97	1.737 \pm 0.033 b	86	1.797 \pm 0.034 ab	95	1.853 \pm 0.035 a	94	1.548 \pm 0.030 c	101	1.490 \pm 0.024 c
Larva (d)	96	0.698 \pm 0.027 a	79	0.633 \pm 0.025 ab	92	0.701 \pm 0.026 a	91	0.577 \pm 0.019 b	100	0.590 \pm 0.021 b
Protonymph (d)	91	1.373 \pm 0.042 a	73	1.253 \pm 0.038 b	85	1.382 \pm 0.051 a	88	1.421 \pm 0.050 a	98	1.418 \pm 0.046 a
Deutonymph (d)	90	1.044 \pm 0.055 b	73	1.397 \pm 0.064 a	84	1.512 \pm 0.075 a	78	1.391 \pm 0.058 a	97	1.180 \pm 0.061 b
Preadult (d)	90	4.850 \pm 0.078 bc	73	5.034 \pm 0.078 b	84	5.435 \pm 0.116 a	78	4.904 \pm 0.079 b	97	4.670 \pm 0.071 c
Adult (d)	90	14.472 \pm 1.016 c	73	18.979 \pm 1.640 ab	84	20.649 \pm 1.276 a	78	20.404 \pm 1.601 ab	97	17.196 \pm 1.158 bc
Longevity (d)	97	18.211 \pm 1.027 b	86	20.942 \pm 1.591 ab	95	23.568 \pm 1.341 a	94	21.798 \pm 1.529 ab	101	21.153 \pm 1.175 ab
APOP (d)	57	2.088 \pm 0.116 b	45	3.044 \pm 0.264 a	56	2.339 \pm 0.088 b	41	2.366 \pm 0.219 b	53	2.245 \pm 0.138 b
TPOP (d)	57	6.974 \pm 0.158 c	45	8.100 \pm 0.293 a	56	7.768 \pm 0.165 ab	41	7.354 \pm 0.222 bc	53	6.906 \pm 0.146 c
Oviposition day (d)	57	8.702 \pm 0.569 c	45	10.411 \pm 0.522 ab	56	11.750 \pm 0.611 a	41	9.378 \pm 0.879 bc	53	8.575 \pm 0.728 c
F (eggs per female)	61	24.361 \pm 1.785 b	49	28.245 \pm 1.874 b	57	33.912 \pm 2.017 a	44	26.091 \pm 2.620 b	56	25.286 \pm 2.227 b

The standard errors were estimated by using bootstrap technique with 100,000 resampling. The same letter within a row indicates no significant difference between treatments based on a paired bootstrap test at the 5% significance level.

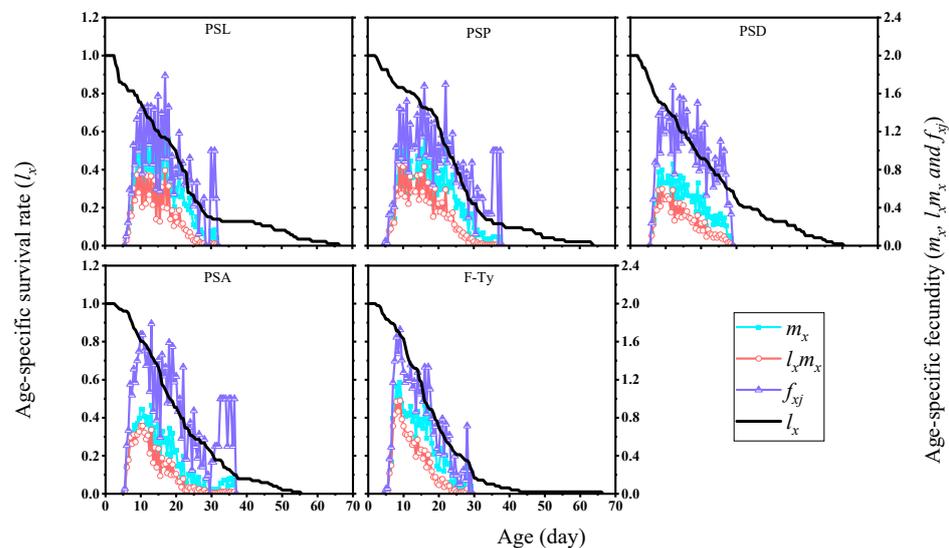


Figure 4. Age-specific survival rate (l_x), female age-specific fecundity (f_{xj}), age-specific fecundity of the total population (m_x), and age-specific maternity ($l_x m_x$) of *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

3.3. Population Parameters of *Neoseiulus bicaudus* during Prey Switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in Each Stage

The population parameters of *N. bicaudus* are presented in Table 3. The r values of the PSL ($r = 0.218 \text{ d}^{-1}$) and PSD ($r = 0.204 \text{ d}^{-1}$) were notably lower compared to F-Ty ($r = 0.250 \text{ d}^{-1}$). Similarly, the λ values of the PSL ($\lambda = 1.243 \text{ d}^{-1}$) and PSD ($\lambda = 1.226 \text{ d}^{-1}$) were significantly lower than that of the F-Ty ($\lambda = 1.283 \text{ d}^{-1}$). Furthermore, the T values of the PSL ($T = 12.75 \text{ d}$), PSP ($T = 13.321 \text{ d}$), and PSD ($T = 12.283 \text{ d}$) were significantly longer compared to F-Ty ($T = 10.936 \text{ d}$).

The age-stage-specific life expectancy (e_{xj}) of *N. bicaudus* is presented in Figure 5. F-Ty showed the shortest life expectancy at age zero (e_{01}), with a value of 18.211 d, while PSP exhibited the longest, with an e_{01} expectancy of 23.568 d. PSL, PSD, and PSA had e_{01} life expectancies of 20.942 d, 21.798 d, and 21.153 d, respectively, aligning with the mean longevity of all individuals in the life table. The peak life expectancy for female mites in PSA was slightly lower than that in F-Ty, recorded at 13.901 d and 14.178 d, respectively. PSL, PSP, and PSD reached peak life expectancies of 16.857 d, 19.802 d, and 15.656 d, respectively. The overall peak life expectancy values for PSL, PSP, PSD, PSA, and F-Ty were 35.864 d, 28.217 d, 29.018 d, 23.939 d, and 18.657 d, respectively. Notably, *N. bicaudus* exhibited a phenomenon of prey switching prior to adult stage, leading to significant declines in life

expectancy. Specifically, on the 3rd day of PSL, the larval stage experienced a sharp drop, followed by a valley value of 17.573 on the 3.5th day for protonymph. Subsequent declines occurred on the 5th day of PSP for protonymph and the 6th day of PSD for deutonymph, reaching valley values of 5.485 and 9.736, respectively.

Table 3. Population parameters of *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

Population Parameters	F-Ty	PSL	PSP	PSD	PSA
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Intrinsic rate of increase (r) (d^{-1})	0.250 ± 0.010 a	0.218 ± 0.011 b	0.226 ± 0.009 ab	0.204 ± 0.012 b	0.231 ± 0.011 ab
Finite rate of increase (λ) (d^{-1})	1.283 ± 0.013 a	1.243 ± 0.013 bc	1.254 ± 0.012 abc	1.226 ± 0.015 c	1.260 ± 0.014 abc
Net reproductive rate (R_0) (offspring/individual)	15.320 ± 1.640 ab	16.093 ± 1.845 ab	20.347 ± 2.090 a	12.213 ± 1.812 b	14.02 ± 1.755 b
Mean generation time (T) (d)	10.936 ± 0.190 c	12.75 ± 0.290 ab	13.321 ± 0.286 a	12.283 ± 0.316 b	11.42 ± 0.274 c

The standard errors were estimated by using bootstrap technique with 100,000 resampling. The same letter within a row indicates no significant difference between treatments based on a paired bootstrap test at the 5% significance level.

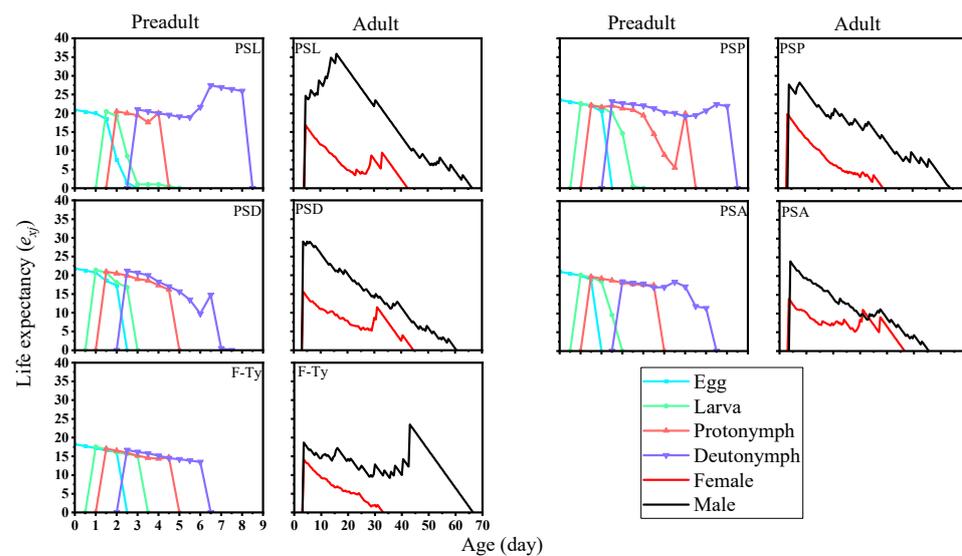


Figure 5. Age-stage-specific life expectancy (e_{xj}) of *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

The reproductive value (v_{xj}) of *N. bicaudus* is presented in Figure 6. The reproductive value of the PSD at age zero (v_{01}) was shortest ($1.226 d^{-1}$), while the reproductive value of the F-Ty at age zero (v_{01}) was longest ($1.283 d^{-1}$). The reproductive values of the PSL, PSP, and PSA at age zero (v_{01}) were $1.243 d^{-1}$, $1.254 d^{-1}$, and $1.260 d^{-1}$, respectively. These reproductive values were exactly the same as the finite rates. The peak reproductive value of PSL ($9.556 d^{-1}$) females was lower than that of F-Ty ($9.649 d^{-1}$). The peak reproductive values of PSP, PSD, and PSA females were higher than those of F-Ty, which were $9.851 d^{-1}$, $9.885 d^{-1}$, and $10.446 d^{-1}$, respectively. The peak reproductive values of PSL, PSP, PSD, and PSA females all manifested on Day 9, while the peak reproductive value of F-Ty females appeared on Day 7.5.

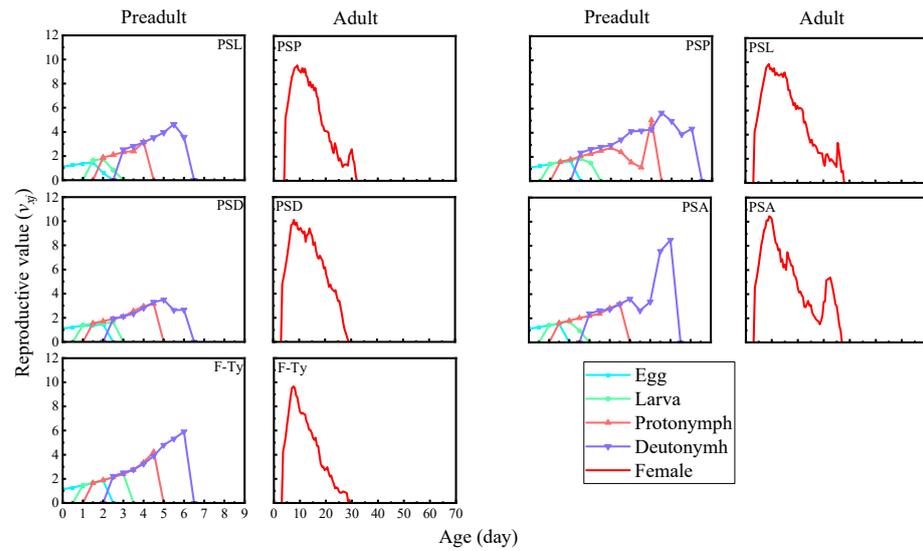


Figure 6. Reproductive value (v_{xj}) of *Neoseiulus bicaudus* during prey switching from *Tyrophagus putrescentiae* to *Tetranychus turkestanii* in each stage.

3.4. Correlation between the Switching Stage/Age of the Prey Switching with Life-Table Parameters

The relationship between switching stage/age and life-table parameters is presented in Figure 7. A positive correlation ($R = 0.71$) was observed between the switching stage and the ratio of males, while a negative correlation ($R = -0.90$) was found between the switching stage and the TPOP. Additionally, the switching stage showed a negative correlation ($R = -0.75$) with the mean generation time. Similarly, the switching age exhibited positive correlations with the ratio of males ($R = 0.72$), negative correlations with the TPOP ($R = -0.90$), and negative correlations with the mean generation time ($R = -0.78$).

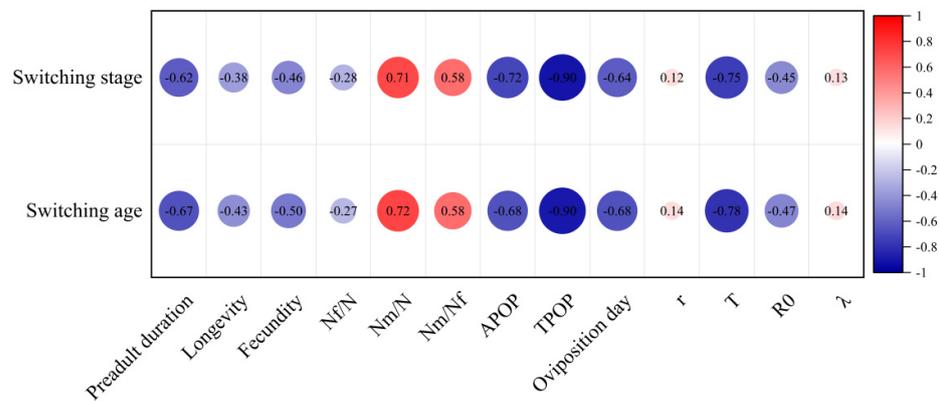


Figure 7. Pearson's correlation heatmap between switching stage/age and life-table parameters.

4. Discussion

The results show that the influence of prey switching on *N. bicaudus* is multifaceted. The survival rate of *N. bicaudus* exhibited a decrease, during prey switching, while the developmental period was prolonged. Additionally, there was an increase in fecundity and a reduction in the intrinsic rate of increase.

The reduced survival rate of *N. bicaudus* during prey switching was comparable to that observed in *Meiacanthus atrodorsalis*, which also exhibited a significant decline in survival during prey switching [38]. The decreased survival rate of *N. bicaudus* may be attributed to two factors: (a) fast prey switching does not guarantee sufficient food for predators in the short term [20]; (b) the cobweb formation habit of *Te. turkestanii* can impede unexperienced predators [39], and in this study, it could even trap small *N. bicaudus*.

The results of this study indicate that the adult preoviposition period (APOP) of F-Ty was 2.088 d, which aligns with the findings of Su et al. [31]. The developmental duration of *N. bicaudus* during prey switching was prolonged, such as deutonymph duration and adult duration. Similarly, the preadult duration of *A. orientalis* undergoing prey switching from *Carpoglyphus lactis* to *Te. urticae* also was prolonged [40]. This phenomenon may be attributed to a decrease in the availability of the most suitable prey during the prey-switching phase, coupled with the significant impact of adapting to new prey on predator performance [20], resulting in reduced prey consumption and subsequent effects on predator growth.

The findings of this study suggest that the fecundity of *N. bicaudus* undergoing prey switching demonstrated an increase compared to F-Ty (24.361). Similarly, compared with the absence of pollen, the fecundity of *A. swirskii* (3.55) with pollen was increased [41]. The findings imply that the adoption of prey switching could potentially enhance the fecundity of Phytoseiidae. It is plausible that this enhanced fecundity can be attributed to the predator consuming a more diverse range or a higher quality of food sources [42].

The intrinsic rate of increase (r) of F-Ty was 0.250 d^{-1} in this study. The result was similar to that obtained by Su et al. [31], whose research showed that the intrinsic rate of increase (r) of *N. bicaudus*, which preys on *Ty. putrescentiae*, was 0.278. *N. bicaudus* experienced a decline in its intrinsic rate of increase upon prey switching, similar to the observed decrease also seen in *N. cucumeris*' intrinsic rate of increase following prey switching [43]. The intrinsic rate of increase serves as a crucial parameter for evaluating and comparing pest population dynamics; it is also influenced by mortality and developmental duration factors [44]. In this study, the reduction in the intrinsic rate of increase may be attributed to increased mortality rates and prolonged development of *N. bicaudus* during prey switching. This suggests that prey switching is an obstacle to the growth of predatory mite populations.

The research findings suggest that the impact of prey switching on different age stages of predatory mites exhibits inconsistency. It is hypothesized that this phenomenon primarily stems from variations in hunting ability and nutritional requirements across different age stages. The larval stage, characterized by limited mobility due to the larvae possessing only three pairs of legs, renders it vulnerable to entrapment by spider mite webs [45]. Many animal species undergo critical learning periods during which their learning efficiency is heightened, leading to long-term effects on subsequent behavior [46–48]. The survival rate of protonymph does not significantly decrease during prey switching. Moreover, PSP's reproductive capacity exhibited a noticeable increase. We postulate that the protonymph stage may represent a critical period for predatory mites to acquire knowledge about their prey, as feeding experiences during this developmental phase have been shown to significantly enhance mites' efficiency in utilizing prey. In contrast to the protonymph, the deutonymph demonstrates a higher nutritional demand but experiences a substantial decline in survival rate during the prey-switching phase. Hence, we hypothesize that the deutonymph lacks efficient learning abilities at this stage. The adult mite stage is characterized by extensive body ossification and a robust resistance to hunger. Additionally, it possesses the ability to navigate through spider mite webs for successful predation, rendering it highly adaptable to prey switching [45].

This study revealed a negative correlation between the age of prey switching and the female ratio, while an opposite trend was observed for males. We hypothesize that this discrepancy arises from the distinct nutritional demands of male and female predatory mites. Specifically, the nutritional requirements of females escalate significantly with age [23,24], leading to higher mortality rates during the adaptation period caused by prey switching. Males exhibit accelerated development and lower nutritional needs [24,27]. Unlike females, male individuals gradually enhance their ability to adapt to prey conversion as they mature.

The nutritional profile of the flour mite is characterized by a low protein content, whereas the leaf mite has a high protein content [49,50]. The nutrient content of the two

prey species is different, and the switching of prey species also causes changes in nutrient supply, which can also affect the development and reproductive capacity of the predator mite. We believe that the nutritional intake of predator mites is not only influenced by differences in food quality, but also by feeding intensity. Predatory mites undergo physiological metabolic changes in their acquisition of nutrients. Therefore, the nutrient accumulation, digestive enzyme activity, and metabolic changes of predator mites after prey switching deserve further study.

To optimize the artificial rearing and application of predatory mites, it is recommended to avoid relying solely on a single alternative prey (non-target prey) for feeding and direct release in biological control efforts. In agricultural settings, targeting specific pests, and introducing multiple prey species during the artificial rearing process, can enhance the feeding experiences of predatory mites on pests, thereby mitigating the potential negative impacts associated with prey switching.

5. Conclusions

The impact of prey switching on the life parameters of different stages of *Neoseiulus bicaudus* is intricate, as evidenced by its effects on the survival rate, developmental period, longevity, fecundity, and population dynamics at both individual and collective levels. The influence of prey switching on different mite stages is not completely consistent. Prey switching during the larva and deutonymph stages leads to a decrease in the intrinsic rate of increase and prolongs the mean generation time. Prey switching during the protonymph stage also contributes to a prolonged mean generation time. However, when prey switching occurs during the adult stage, its negative impact is relatively minor. Overall, prey switching can significantly decrease the survival rate of *N. bicaudus* during the switching stage, prolong the deutonymph and adult duration of the predatory mites, significantly prolong the mean generation time, and reduce both the intrinsic rate of increase and the finite rate of increase. Additionally, the later the prey switching takes place, the higher the male ratio, and the shorter the total preoviposition period and mean generation time of *N. bicaudus*. The utilization of natural enemies for biological control is widely prevalent in agricultural systems. The phenomenon of prey switching often accompanies the release of natural enemies for artificial propagation. The impact of prey switching on natural enemies deserves more consideration to ensure the effectiveness of agricultural biological control.

Author Contributions: Conceptualization, J.Z. and J.S.; Data curation, Z.N. and L.Z.; Formal analysis, Z.N., S.T. and C.F.; Funding acquisition, J.S.; Investigation, Z.N., Y.M. and X.L.; Methodology, J.S.; Project administration, J.S.; Resources, J.Z. and J.S.; Software, J.S.; Supervision, J.Z. and J.S.; Visualization, J.Z. and J.S.; Writing—original draft, Z.N.; Writing—review and editing, J.Z. and J.S. All authors have read and agreed to the published version of the manuscript.

Funding: This search was funded by the Guiding Science and Technology Plan Project of Xinjiang (2022ZD053), Key Research and Development Project of Autonomous Region (2022B02043), Major Science and Technology Projects in Xinjiang Uygur Autonomous Region (2022A020053), and National Key Research and Development Program of China (2022YFD1400300).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: All data analyzed in this study are included in this article, and available from the corresponding author with a reasonable request.

Acknowledgments: We are grateful to Hsin Chi for the instruction of his creative ecology software based on MSChart (Version 2023.05.13).

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

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