

## Temperature-Dependent Demography of Two Closely Related Predatory Mites *Neoseiulus womersleyi* and *N. longispinosus* (Acari: Phytoseiidae)

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### Abstract

Temperature has significant effects on the development, survival, and reproduction of ectothermic organisms. In this study, we examined the effect of temperature on the demographic characteristics of two predatory mite species, *Neoseiulus womersleyi* (Schicha) and *N. longispinosus* (Evans), reared on *Tetranychus urticae* Koch. The developmental and reproductive traits of both species were examined at 10 constant temperatures between 15 °C and 37.5 °C. The preadult development time of *N. womersleyi* and *N. longispinosus* decreased with increasing temperature until 32.5 °C and 35 °C, respectively. The lower developmental threshold ( $T_0$ ) and thermal constant ( $K$ ) estimated by using a linear model were 11.61 °C and 69.36 DD for *N. womersleyi* and 11.92 °C and 61.5 DD for *N. longispinosus*, respectively. Total preoviposition period and total longevity of females and males of *N. womersleyi* and *N. longispinosus* decreased with increasing temperature. The mean generation time ( $T$ ) first decreased with temperature until 32.5 and 35 °C for *N. womersleyi* and *N. longispinosus*, respectively, and then increased at higher temperatures. The  $R_0$  and  $r$  values first increased with temperature until 32.5 and 30 °C for *N. womersleyi* and *N. longispinosus*, respectively, and then decreased at higher temperatures. The  $R_0$  and  $r$  values for *N. longispinosus* at 37.5 °C were 0.3 offspring and  $-0.143 \text{ d}^{-1}$ , respectively. These results show that *N. longispinosus* is less fit than *N. womersleyi* at 37.5 °C.

**Key words:** life table parameter, temperature, distribution, adaptation, Phytoseiidae

Temperature has significant effects on many processes such as development, survival, and reproduction of ectothermic organisms such as insects and mites, and these effects can vary based on daily or hourly temperature either on individuals or populations (Bale et al. 2002; Gotoh et al. 2004, 2010; Logan et al. 2006; Yang and Rudolf 2010; Ullah et al. 2011, 2012; Ullah and Lim 2015). A change of temperature can have a number of consequences on the above life history parameters, which may eventually cause a change in the population dynamics (Ladányi and Horváth 2010). As results of such changes, arthropods may experience variations in population growth rates, increase in the number of generations, extension of the development season and may change in geographical distribution and interspecific interactions (Bale et al. 2002, Hance et al. 2007).

The genus *Neoseiulus* is one of the largest phytoseiid genera with 355 valid described species (Demite et al. 2014). Most members of

the genus have high economic importance owing to their role in controlling spider mites and other small insects. Of the many species of *Neoseiulus*, reproductive interference occurs between *N. womersleyi* (Schicha) and *N. longispinosus* (Evans), and they have different but overlapping distribution patterns in some places (Ho et al. 1995; Ullah et al. 2017). *Neoseiulus womersleyi* has a longitudinal distribution from Russia to Australia along the Pacific coast region of east and the Southeast Asia and Oceania. On the other hand, *N. longispinosus* has a latitudinal distribution around the globe in regions between 30° S and 30° N, including Japan, China, Taiwan, Philippines, Indonesia, Malaysia, India, Pakistan, Thailand, Australia, New Zealand, Papua New Guinea, and Hawaii (Ho et al. 1995; Ehara 2002a,b; Kongchuensin et al. 2005).

Because climatic factors, especially extreme temperatures, are the main factors in defining distribution of both tropical and

**Table 1.** Mean durations and standard errors (in parentheses) of each developmental stage of female (F) and male (M) *N. womersleyi* at different temperatures [number of hatched eggs/number of total eggs of the parent cohort]

Stage	Sex	Temp (°C)									
		15.0 [39/63]	17.5 [50/68]	20.0 [60/69]	22.5 [36/41]	25.0 [65/73]	27.5 [53/57]	30.0 [41/45]	32.5 [41/43]	35.0 [59/59]	37.5 [45/64]
Preadult survival (%)	All	97.4 (2.5)a	92.0 (3.9)a	96.7 (2.3)a	91.7 (4.6)a	95.4 (2.6)a	96.2 (2.6)a	97.6 (2.4)a	95.1 (3.4)a	52.5 (6.5)b	44.7 (7.4)c
Egg	F	9.0 (0.1)a	5.1 (0.1)b	3.5 (0.0)c	3.1 (0.1)d	2.0 (0.0)e	1.7 (0.0)f	1.6 (0.0)gh	1.4 (0.0)i	1.7 (0.1)fg	1.5 (0.1)ghi
Larva		2.5 (0.1)a	1.7 (0.1)b	1.1 (0.0)c	0.9 (0.0)d	0.6 (0.0)e	0.4 (0.0)f	0.4 (0.0)f	0.5 (0.0)f	0.6 (0.0)e	0.5 (0.0)f
Protonymph		5.7 (0.1)a	3.2 (0.1)b	1.9 (0.1)c	1.4 (0.1)d	1.0 (0.0)e	1.0 (0.0)e	0.9 (0.0)fg	0.8 (0.0)fg	1.0 (0.0)e	1.1 (0.1)ef
Deutonymph		4.8 (0.1)a	2.9 (0.1)b	2.0 (0.1)c	1.6 (0.1)d	1.2 (0.0)e	0.9 (0.0)g	1.0 (0.0)f	1.0 (0.0)f	0.9 (0.0)fg	0.9 (0.1)fg
Total preadult		21.9 (0.3)a	12.9 (0.1)b	8.5 (0.1)c	7.1 (0.1)d	4.7 (0.0)e	3.8 (0.1)f	3.9 (0.0)f	3.7 (0.1)f	4.2 (0.1)ef	4.0 (0.2)f
Adult duration		31.3 (1.9)a	34.8 (5.2)a	28.6 (2.3)ab	21.8 (2.7)bcd	28.6 (2.6)ab	26.8 (3.1)abc	17.2 (2.2)de	20.8 (2.0)cd	14.2 (1.8)ef	10.4 (1.1)f
N		19	31	41	18	44	37	27	28	13	11
Egg	M	9.8 (0.2)a	5.6 (0.1)b	3.7 (0.1)c	2.9 (0.1)d	2.0 (0.1)e	1.6 (0.1)f	1.5 (0.0)g	1.6 (0.1)g	1.5 (0.1)g	1.5 (0.1)g
Larva		2.8 (0.1)a	1.7 (0.1)b	1.1 (0.0)c	0.7 (0.1)d	0.6 (0.1)de	0.4 (0.0)gh	0.4 (0.0)h	0.5 (0.1)fgh	0.5 (0.0)efg	0.5 (0.0)f
Protonymph		5.9 (0.2)a	3.1 (0.1)b	1.7 (0.1)c	1.5 (0.1)d	1.1 (0.1)e	0.8 (0.1)f	0.8 (0.0)f	0.8 (0.1)f	0.9 (0.0)f	1.2 (0.1)e
Deutonymph		4.3 (0.2)a	2.5 (0.1)b	1.7 (0.1)c	1.4 (0.1)d	1.1 (0.1)e	0.9 (0.1)f	0.8 (0.1)f	0.7 (0.1)f	0.8 (0.0)f	1.1 (0.0)e
Total preadult		22.7 (0.3)a	12.9 (0.2)b	8.2 (0.1)c	6.5 (0.2)d	4.8 (0.1)e	3.7 (0.1)f	3.6 (0.1)f	3.5 (0.1)f	3.7 (0.1)f	4.2 (0.1)ef
Adult duration		30.0 (5.5)a	22.0 (5.5)abc	22.9 (3.4)ab	21.3 (3.8)abc	15.4 (1.8)cd	14.8 (2.3)f	9.9 (1.7)f	11.8 (2.5)def	17.1 (1.5)bcd	7.4 (1.6)f
N		19	15	17	15	18	14	13	11	18	9

Means in the same row followed by different letters denote significant differences between temperatures (paired bootstrap test,  $P < 0.05$ ).

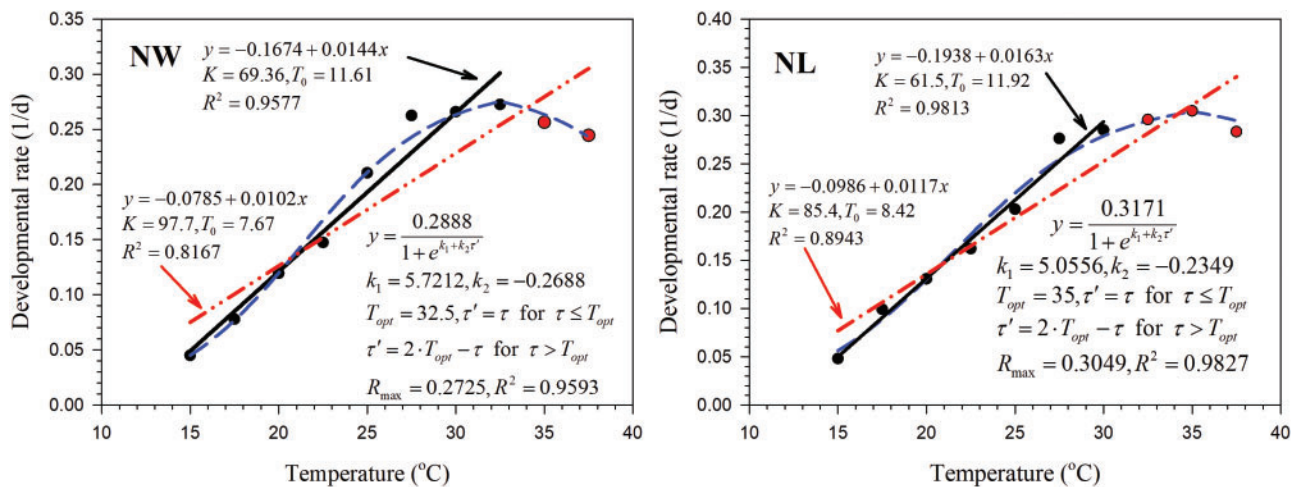
N: Number of individuals survived to the adult stage.

**Table 2.** Mean durations and standard errors (in parentheses) of each developmental stage of female (F) and male (M) *N. longispinosus* at different temperatures [number of hatched eggs/number of total eggs of the parent cohort]

Stage	Sex	Temp (°C)									
		15.0 [27/47]	17.5 [51/54]	20.0 [48/48]	22.5 [64/64]	25.0 [80/83]	27.5 [54/54]	30.0 [40/42]	32.5 [48/57]	35.0 [50/50]	37.5 [167/167]
Preadult survival (%)	All	96.3 (3.6)a	94.1 (3.3)a	95.8 (2.9)a	92.2 (3.4)a	91.3 (3.2)a	94.4 (3.1)a	90.4 (2.4)a	93.8 (3.5)a	58.0 (7.0)b	4.8 (1.6)c
Egg	F	8.3 (0.1)a	4.1 (0.1)b	3.3 (0.1)c	2.6 (0.0)d	2.1 (0.0)e	1.5 (0.0)f	1.4 (0.0)g	1.3 (0.0)h	1.3 (0.0)h	1.3 (0.0)h
Larva		2.1 (0.1)a	1.2 (0.1)b	1.1 (0.0)c	0.9 (0.1)d	0.6 (0.0)e	0.5 (0.0)fg	0.5 (0.0)fg	0.4 (0.0)g	0.4 (0.0)g	0.5 (0.0)fg
Protonymph		5.2 (0.3)a	2.4 (0.1)b	1.9 (0.1)c	1.3 (0.1)d	1.0 (0.0)e	0.7 (0.0)h	0.8 (0.0)fg	0.9 (0.0)f	0.8 (0.0)gh	0.8 (0.0)fgh
Deutonymph		4.6 (0.2)a	2.4 (0.1)b	1.7 (0.1)c	1.4 (0.0)d	1.2 (0.0)e	0.9 (0.0)f	0.9 (0.0)f	0.8 (0.0)h	0.8 (0.0)g	0.8 (0.1)fg
Total preadult		20.2 (0.4)a	10.1 (0.1)b	8.0 (0.1)c	6.2 (0.1)d	4.9 (0.1)e	3.6 (0.0)f	3.5 (0.0)f	3.4 (0.0)f	3.3 (0.0)f	3.5 (0.1)f
Adult duration		26.7 (2.1)a	27.6 (1.9)a	27.1 (2.3)a	21.4 (1.9)bc	25.3 (2.5)ab	19.8 (2.2)bc	18.0 (1.6)cd	14.8 (1.1)d	16.2 (2.0)cd	9.5 (1.1)e
N		16	30	29	38	59	35	26	27	16	6
Egg	M	8.8 (0.2)a	4.5 (0.1)b	3.1 (0.1)c	2.7 (0.1)d	2.4 (0.1)e	1.7 (0.0)fi	1.5 (0.0)gi	1.4 (0.0)h	1.4 (0.0)h	1.4 (0.1)hi
Larva		2.7 (0.2)a	1.2 (0.1)b	1.0 (0.0)c	0.8 (0.1)d	0.6 (0.1)e	0.4 (0.0)fg	0.4 (0.0)fg	0.4 (0.0)gh	0.5 (0.0)f	0.3 (0.0)h
Protonymph		5.3 (0.3)a	2.1 (0.1)b	1.4 (0.0)cd	1.3 (0.1)d	1.0 (0.0)f	0.8 (0.1)ghi	0.8 (0.0)ghi	0.8 (0.0)gh	0.7 (0.0)gi	1.3 (0.3)defg
Deutonymph		5.3 (0.5)a	2.2 (0.2)b	1.5 (0.0)c	1.4 (0.1)de	1.1 (0.1)e	0.8 (0.1)ghi	0.8 (0.0)if	0.9 (0.0)f	0.8 (0.0)h	0.9 (0.1)efg
Total preadult		22.1 (0.6)a	10.1 (0.2)b	7.0 (0.3)c	6.1 (0.1)c	5.0 (0.1)d	3.6 (0.0)e	3.5 (0.0)e	3.4 (0.0)e	3.3 (0.0)e	3.8 (0.3)e
Adult duration		37.1 (8.0)ab	32.8 (3.5)a	21.7 (3.4)b	8.5 (1.1)cd	9.3 (0.9)c	7.0 (1.1)cd	10.5 (1.3)c	6.1 (0.9)d	11.4 (2.8)c	5.9 (5.6)cd
N		10	18	17	21	14	16	13	18	13	2

Means in the same row followed by different letters denote significant differences between temperatures (paired bootstrap test,  $P < 0.05$ ).

N: Number of individuals survived to the adult stage.



**Fig. 1.** The developmental rates of *N. womersleyi* (NW) and *N. longispinosus* (NL) at different temperatures fitted to linear model (black solid line and red dash-dot line) and nonlinear model (Stinner et al. 1974; dashed line). Red data points were not included in the regression analysis of black solid line, while all data points (black and red points) were included in the regression of red dash-dot line.

temperate species (Overgaard et al. 2014), climate change has extensive implications for the distribution of insects, mites, and other invertebrates around the globe. Here, we investigated the effects of temperature on the demographic characteristics of two closely related species, *N. womersleyi* and *N. longispinosus*.

Life tables, which contain life expectancy statistics for a population of animals, can reveal the overall effects of temperature, host plants, and photoperiod at the population level. Life tables have been extensively used to assess the sensitivity of a population to variation in environmental factors and the complex relationships between the environment and demography (Wilson and Martin 2012, Régnière et al. 2012). Previous life tables and population parameters of *N. womersleyi* (Lee and Ahn 2000) and *N. longispinosus* (Rahman et al. 2013) were based on female age-specific life tables. However, ignoring factors such as males and life stage could result in limitations and errors. Including both sexes in a life table analysis is needed because both males and females are economically important and affect population dynamics (Huang and Chi 2012).

To take the contribution of male individuals into consideration and to describe the stage differentiation precisely, life tables of *N. womersleyi* and *N. longispinosus* were constructed based on the age-stage, two-sex life table analysis. Here, we created life tables of *N. womersleyi* and *N. longispinosus* in a wide range of temperatures using life stage and both sexes. The results of this study could be used to elucidate population dynamics as a function of temperature and to provide a better understanding of the distribution patterns of *N. womersleyi* and *N. longispinosus* populations.

## Materials and Methods

### Rearing of Predatory and Spider Mites

The *N. womersleyi* strain was collected from *Mallotus japonicus* Muell. Arg. in Taitung, Taiwan (22° 53' N–121° 11' E), on 9 November 2010, and the *N. longispinosus* strain was collected from *Manihot esculenta* Crantz in Tainan, Taiwan (23° 20' N–120° 27' E), on 9 September 2011. The population of each species in Taiwan, where they occur sympatrically was sampled, to minimize any geographical effect on their biological traits. Both phytoseiids were reared separately on excised leaves (16 cm<sup>2</sup>) of common bean, *Phaseolus vulgaris* L., which were infested with mixed stages of

two-spotted spider mites, *Tetranychus urticae* Koch (green form), which were collected from a watermelon, *Citrullus lanatus* (Thunb.), in Takikawa (43° 33' N–141° 54' E), Hokkaido, Japan, on 16 July 2001. Each excised leaf was placed on a water-saturated polyurethane mat in a plastic cup (10 cm diameter at the top and 8 cm diameter at the bottom, 4 cm depth) with a perforated lid at 25 ± 1 °C and 60–70% RH under a photoperiod of 16:8 (L:D) h. The lid of each cup had a 50-mm-diameter hole covered with fine nylon mesh to allow ventilation. The leaves were replaced when they appeared to be dried out or heavily damaged by spider mites. After collection, both species were reared for many generations before the experiment was performed in 2012–2013. Before starting experiments, females were kept on the leaf disc and allowed to lay eggs for 24 h at a specific temperature, but eggs laid during this period were discarded to avoid the effect of 25 °C environment.

### Immature Development Time

Immature development time of *N. womersleyi* and *N. longispinosus* was studied separately in a chamber at 10 constant temperatures from 15 to 37.5 °C at a 2.5 °C intervals under a long-day photoperiod (16:8 [L:D] h) and 60–70% RH. Adult females obtained from mite cultures were individually transferred and reared on a leaf disc (33 mm in diameter) of kidney bean together with all stages of *T. urticae* at each of the 10 temperatures. Females were allowed to lay egg on the leaf disc for 12 h at 15 °C–25 °C, for 8 h at 27.5 °C, and for 6 h at 30 °C–37.5 °C and then the females were removed from the leaf disc. All but one of the eggs produced by a female were destroyed with a needle. Each individual was observed with a stereoscopic microscope (SZ40, Olympus Corporation, Tokyo, Japan) to record the development time and development stages. The individuals were observed at the respective intervals (12 h at 15 °C–25 °C, for 8 h at 27.5 °C, and for 6 h at 30 °C–37.5 °C) until they reached adulthood. The presence of exuviae on the leaf disc was used as a criterion of immature molt (Ullah and Gotoh 2014).

### Reproduction and Female Longevity

When a female of *N. womersleyi* and *N. longispinosus* reached adult stage, they were paired and kept on an individual leaf disc (33 mm in diameter). A male was kept on the disc for the total experimental period. If a male died before the female, a new male adult was

**Table 3.** Mean and standard errors (in parentheses) of the longevity, fecundity, total preoviposition period (TPOP), adult preoviposition period (APOP), and oviposition days of *N. womersleyi* and *N. longispinosus* at different temperatures

Stage	Sex	Temp (°C)									
		15.0	17.5	20.0	22.5	25.0	27.5	30.0	32.5	35.0	37.5
<i>Neoseiulus womersleyi</i>											
Longevity	F	53.2 (2.0)Aa	47.6 (5.2)Aab	37.1 (2.3)Abc	28.9 (2.7)Ade	33.4 (2.6)Acd	30.6 (3.1)Acde	21.0 (2.2)Afg	24.6 (2.0)Aef	18.4 (1.8)Agh	14.4 (1.0)Ah
Longevity	M	52.7 (5.6)Aa	34.9 (5.5)Ab	31.1 (3.4)Ab	27.7 (3.7)Abc	20.2 (1.8)Acd	18.5 (2.3)Ade	13.5 (1.7)Aef	15.3 (2.6)Adef	20.8 (1.5)Acd	11.7 (1.6)Af
Fecundity	F	14.3 (1.1)Aa	25.3 (1.9)Bb	36.1 (2.1)Ad	37.6 (3.4)Acde	42.2 (2.0)Be	40.0 (1.6)Bde	40.9 (1.9)Bde	41.4 (1.9)Bde	28.9 (2.8)Abc	15.8 (2.8)Aa
TPOP	F	29.7 (0.5)Aa	16.0 (0.2)Ab	11.2 (0.1)Ac	9.5 (0.2)Ad	6.1 (0.1)Ae	5.0 (0.1)Ah	4.9 (0.1)Agi	4.9 (0.1)Aghi	5.0 (0.1)Afg	5.4 (0.2)Af
APOP	F	7.7 (0.3)Aa	3.1 (0.1)Ab	2.8 (0.1)Ac	2.5 (0.2)Ac	1.4 (0.0)Ad	1.2 (0.0)Ae	1.0 (0.0)Af	1.1 (0.0)Ae	0.9 (0.0)Bg	1.4 (0.1)Ad
Oviposition days	F	7.1 (0.5)Ade	12.6 (0.9)Bbc	16.6 (0.9)Aa	14.4 (1.2)Aab	12.3 (0.6)Abc	9.5 (0.4)Acd	8.5 (0.4)Bd	8.4 (0.4)Bd	6.4 (0.6)Ade	3.8 (0.7)Ae
<i>Neoseiulus longispinosus</i>											
Longevity	F	46.9 (2.2)Ba	37.7 (1.9)Ab	35.2 (2.3)Abc	27.6 (1.9)Ade	30.2 (2.5)Acd	23.4 (2.2)Aef	21.6 (1.6)Afg	18.2 (1.1)Bg	19.4 (2.0)Afg	12.9 (1.1)Ah
Longevity	M	59.1 (7.7)Aa	42.8 (3.5)Ab	28.7 (3.3)Ac	14.6 (1.1)Be	14.3 (0.9)Be	10.6 (1.1)Bf	13.9 (1.3)Ae	9.5 (0.9)Bf	14.7 (2.8)Adef	9.6 (5.4)Aef
Fecundity	F	7.4 (1.7)Ba	31.5 (2.2)Ab	39.2 (3.3)Acd	40.6 (2.1)Ad	47.9 (2.0)Ae	49.8 (2.1)Aef	56.2 (2.3)Ag	53.2 (1.6)Afg	32.6 (3.2)Abc	8.8 (3.3)Aa
TPOP	F	28.8 (0.6)Aa	13.2 (0.2)Bb	10.9 (0.2)Ac	8.3 (0.1)Bd	6.4 (0.1)Ae	4.7 (0.1)Bi	4.4 (0.0)Bg	4.3 (0.1)Bhi	4.7 (0.2)Afg	5.0 (0.3)Af
APOP	F	8.6 (0.5)Aa	3.1 (0.1)Ab	2.9 (0.2)Ab	2.1 (0.1)Ac	1.5 (0.1)Ad	1.1 (0.0)Ae	0.9 (0.0)Bf	0.9 (0.0)Bf	1.4 (0.2)Ade	1.6 (0.2)Ad
Oviposition days	F	3.7 (0.9)Bd	15.5 (1.1)Aa	17.3 (1.4)Aa	14.1 (0.7)Aab	13.2 (0.5)Aabc	10.5 (0.4)Abc	10.4 (0.4)Abc	9.5 (0.3)Ac	4.6 (0.4)Bd	2.1 (0.7)Ad

Means in the same column followed by the different uppercase letter denote significant differences between *N. womersleyi* and *N. longispinosus* at the same temperature, while means followed by the different lowercase letter denote significant differences between temperatures in the same species based on the paired bootstrap test at 5% significance level.

recruited from the mass-rearing colony, but it was excluded from life table analysis. The leaf discs were observed at the same times as above (12, 8, or 6 h) to determine the fecundity during each time interval. The number of eggs laid by each female of *N. womersleyi* and *N. longispinosus* was observed and recorded under a stereo-microscope until all mites had died. Because viable eggs are essential for estimating demographic parameters (Mou et al. 2015), eggs laid by individual females were kept until hatch to confirm that they were viable.

### Developmental Rate Model

Developmental rates (calculated as 1/development time) at different temperatures were used in linear and nonlinear models. The lower thermal thresholds and thermal constants of *N. womersleyi* and *N. longispinosus* were determined using the method of Campbell et al. (1974)

$$K = (T - T_0)D \tag{1}$$

where *D*, *T*, *T*<sub>0</sub>, and *K* represent the total preadult duration (d), temperature (°C), lower developmental threshold, and thermal summation, respectively. The thermal summation *K* and lower developmental threshold *T*<sub>0</sub> were estimated by using linear regression from

$$\frac{1}{D} = -\frac{T_0}{K} + \frac{1}{K}T. \tag{2}$$

The total preadult developmental rate was also fitted to the model of Stinner et al. (1974) as

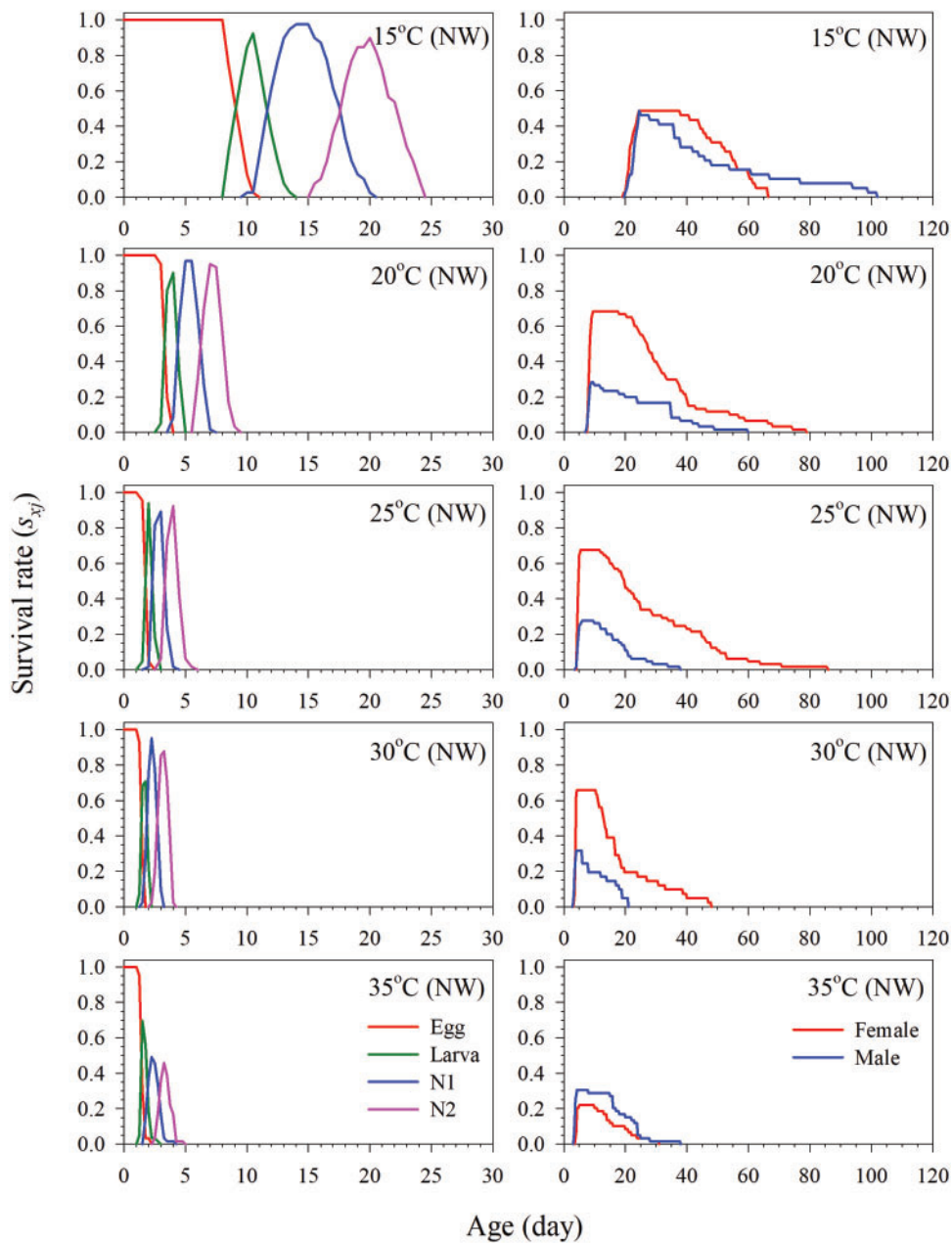
$$R_\tau = \frac{C}{1 + e^{k_1 + k_2\tau'}} \tag{3}$$

where *R*<sub>τ</sub> is the developmental rate at temperature τ, *C* is the asymptote, it is calculated as

$C = R_{\max} \times (e^{k_1 + k_2 \times t_{opt}})$ , *t*<sub>opt</sub> is the temperature at which the maximum developmental rate (*R*<sub>max</sub>) occurs, *k*<sub>1</sub>, *k*<sub>2</sub> are empirical constants, τ' = τ, for τ ≤ *t*<sub>opt</sub> and τ' = 2 × *t*<sub>opt</sub> - τ, for τ > *t*<sub>opt</sub>.

### Life Table Analysis

The life history raw data for development, survival rate, longevity, and female daily fecundity of *N. womersleyi* and *N. longispinosus* were analyzed with the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) using the computer program TWOSEX-MSChart (Chi 2016). The following parameters were calculated using methods developed by Chi and Liu (1985): the age-stage-specific survival rate (*s*<sub>*xj*</sub>), age-specific survival rate (*l*<sub>*x*</sub>), age-specific fecundity (*m*<sub>*x*</sub>), age-stage-specific fecundity (*f*<sub>*xj*</sub>), intrinsic rate of natural increase (*r*), finite rate of increase (*λ*), net reproductive rate (*R*<sub>0</sub>), and mean generation time (*T*). The life expectancy (*e*<sub>*xj*</sub>) was calculated according to Chi and Su (2006) and Wang et al. (2016), and the reproductive value (*v*<sub>*xj*</sub>) was calculated using methods from Huang and Chi (2011), Tuan et al. (2016), and Wang et al. (2016). The adult preoviposition period (APOP) is considered to be the time duration from the emergence of the adult female to its initial oviposition, while the total preoviposition period (TPOP) is the total time duration from the beginning of the egg stage to the female's initial oviposition. To take both sexes into consideration, the age-specific survival rate (*l*<sub>*x*</sub>) in the age-stage, two-sex life table was calculated as



**Fig. 2.** Age-stage survival rate ( $s_{xj}$ ) of *N. womersleyi* feeding on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for different adult sexes. The  $s_{xj}$  depicts the probability that a newborn will survive to age  $x$  and stage  $j$ . The variable developmental rates among individuals are depicted as the overlaps between different stages during developmental periods.

$$l_x = \sum_{j=1}^k s_{xj} \tag{4}$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{6}$$

where  $k$  is the number of life stages. The age-specific fecundity ( $m_x$ ) was calculated as

$$m_x = \frac{\sum_{j=1}^k s_{xj} f_{xj}}{\sum_{j=1}^k s_{xj}} \tag{5}$$

The intrinsic rate of natural increase ( $r$ ) was calculated as follows

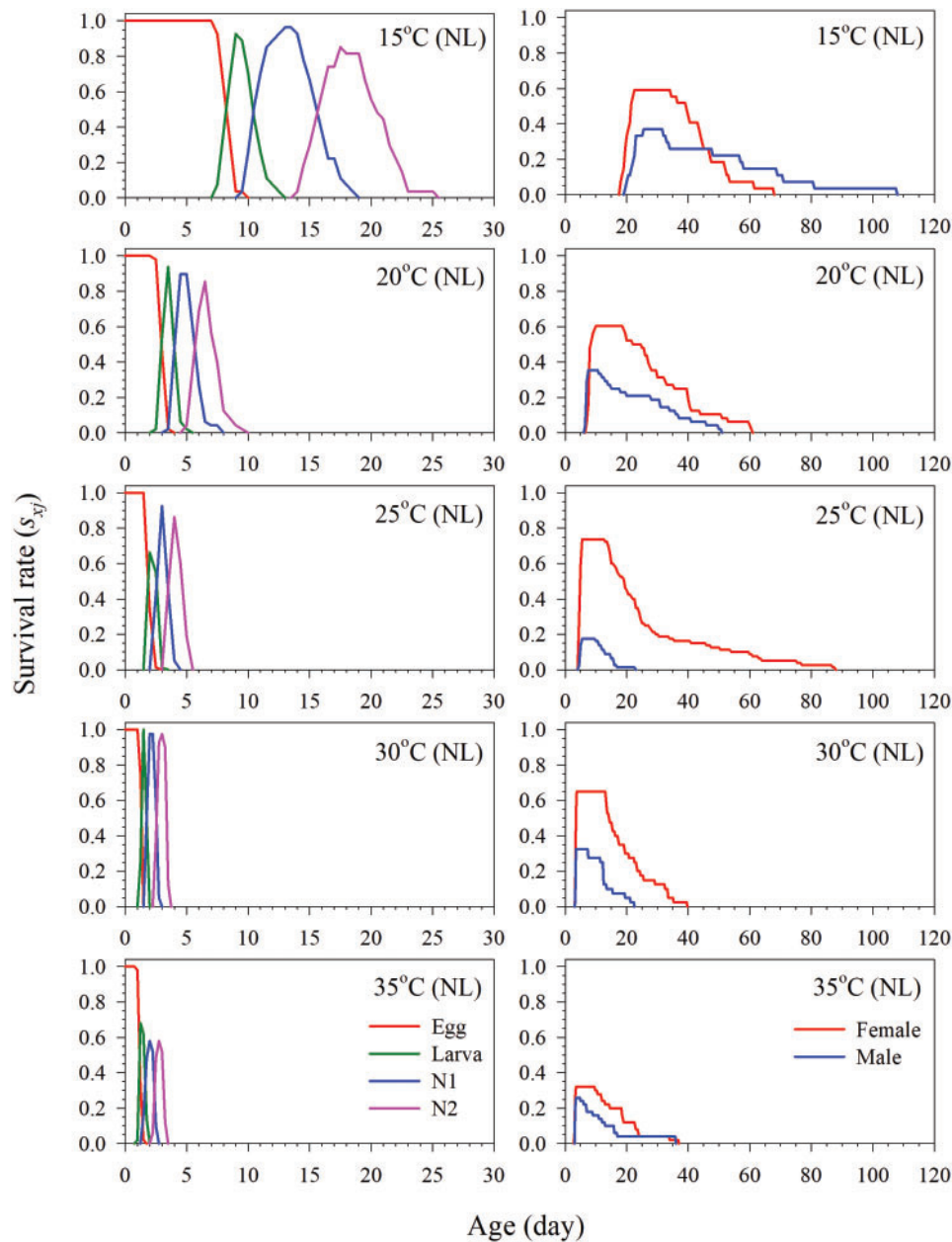
$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{7}$$

with the age indexed from 0 (Goodman 1982). The finite rate ( $\lambda$ ) was calculated as

$$\lambda = e^r \tag{8}$$

The net reproduction rate ( $R_0$ ) is defined as the mean number of offspring that an individual can produce during its life span. It was calculated as

The mean generation time ( $T$ ) is defined as the length of time that is required by a population to increase to  $R_0$ -fold of its size at the stable age-stage distribution, and was calculated as



**Fig. 3.** Age-stage survival rate ( $s_{xj}$ ) of *N. longispinosus* feeding on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for different adult sexes. The  $s_{xj}$  depicts the probability that a newborn will survive to age  $x$  and stage  $j$ . The variable developmental rates among individuals are depicted as the overlaps between different stages during developmental periods.

$$T = \frac{\ln R_0}{r} \tag{9}$$

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

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^k s'_{iy} \tag{10}$$

where  $s'_{iy}$  is the probability that an individual of age  $x$  and stage  $j$  will survive to age  $i$  and stage  $y$  and was calculated by assuming  $s'_{xj} = 1$ , following the procedure described in Chi (1988) and Chi and Su (2006). The intrinsic rate of increases at different temperatures were fitted to linear model and nonlinear model (Lactin et al. 1995).

The reproductive value is defined as the contribution of an individual to the future population (Fisher 1993). According to Huang and Chi (2011) and Tuan et al (2016), the reproductive value ( $v_{xj}$ ) in the age-stage, two-sex life table is calculated as

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^k s'_{iy} f_{iy} \tag{11}$$

The variances and standard errors of the population parameters were estimated by the bootstrap technique (Efron and Tibshirani 1993) with 100,000 resampling to obtain stable estimates (Akca et al. 2015). Then, we performed the paired bootstrap test to examine the differences among the temperature treatments.

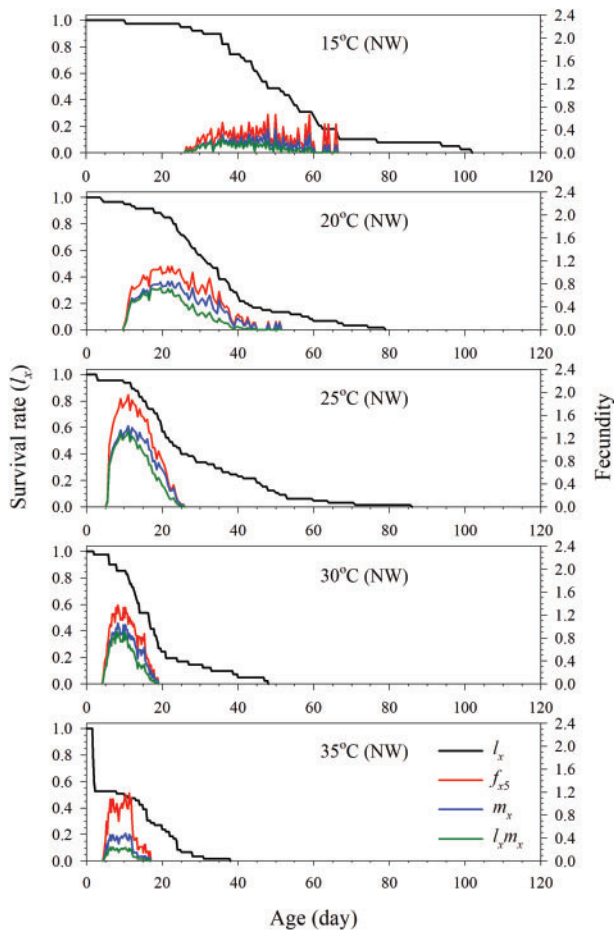


Fig. 4. Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), maternity ( $l_x m_x$ ), and age-stage-specific fecundity ( $f_{xs}$ ) of *N. womersleyi* reared on *T. urticae* at five constant temperatures.

## Results

### Immature Development

The preadult survivorships of *N. womersleyi* (Table 1) and *N. longispinosus* (Table 2) were similar between 15 and 37.5°C, except at 37.5°C where the survival rate of *N. longispinosus* (4.8%) was lower than that of *N. womersleyi* (44.7%). The preadult development time decreased with increasing temperature to 32.5°C and then increased at 35.0 and 37.5°C for *N. womersleyi* (Table 1), whereas it increased at 37.5°C for *N. longispinosus* (Table 2).

### Lower Developmental Threshold and Thermal Summation

When all data points were included in the linear regression analysis (Equation 2), the lower thermal thresholds ( $T_0$ ) for preadult development were 7.67°C and 8.42°C for *N. womersleyi* and *N. longispinosus*, respectively. The thermal constant ( $K$ ) for preadult development were 97.7 DD for *N. womersleyi* and 85.4 DD for *N. longispinosus* (Fig. 1). The coefficients of determination ( $R^2$ ) were 0.8167 and 0.8943 for *N. womersleyi* and *N. longispinosus*, respectively. When only the linear parts were included in the linear regression, the lower thermal thresholds ( $T_0$ ) for preadult development were very similar for *N. womersleyi* (11.61°C) and *N. longispinosus* (11.92°C). The thermal constant ( $K$ ) for preadult development were 69.36 DD for *N. womersleyi* and 61.50 DD for *N. longispinosus*.

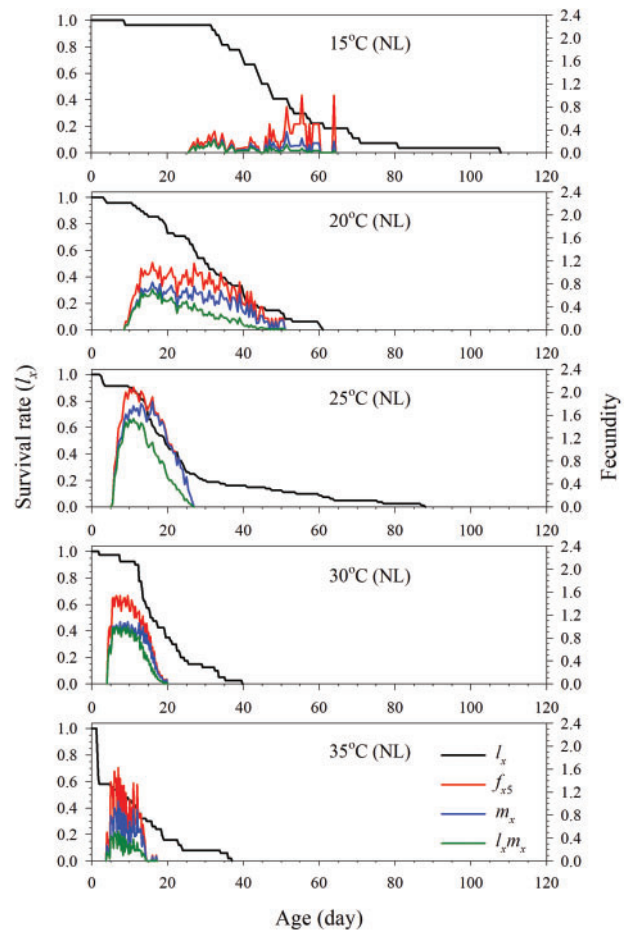


Fig. 5. Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), maternity ( $l_x m_x$ ), and age-stage-specific fecundity ( $f_{xs}$ ) of *N. longispinosus* reared on *T. urticae* at five constant temperatures.

The coefficients of determination ( $R^2$ ) were 0.9577 and 0.9813 for *N. womersleyi* and *N. longispinosus*, respectively. The  $T_{opt}$  and  $R_{max}$  obtained by using the nonlinear model were 32.5°C and 0.2725 d<sup>-1</sup> for *N. womersleyi* and 35°C and 0.3049 d<sup>-1</sup> for *N. longispinosus* (Fig. 1).

### Longevity and Reproduction

In general, the longevity decreased with increasing temperature (Table 3). Longevity was higher for female *N. womersleyi* than for female *N. longispinosus* at 15 and 32.5°C. Total preoviposition period (TPOP) decreased with increasing temperature up to 30°C for *N. womersleyi* and up to 32.5°C for *N. longispinosus*. Total fecundity (eggs/female) varied from 14.3 eggs/female at 15°C to 42.2 eggs/female at 25°C for *N. womersleyi*, while it was 7.4 eggs/female at 15°C and 56.2 eggs/female at 30°C for *N. longispinosus*.

### Age-Stage, Two-Sex Life Table

The stage-specific survivorship curves overlapped, indicating a variation in developmental rates among individuals. The probability that a newly laid egg will survive to age  $x$  and stage  $j$  is given by an age-stage survival rate curve ( $s_{xj}$ ). For *N. womersleyi*, the curves for different stages and different temperatures are shown on the left of Fig. 2 and the curves for male and female adults are shown on the right of Fig. 2. Similar curves for *N. longispinosus* are shown in Fig.

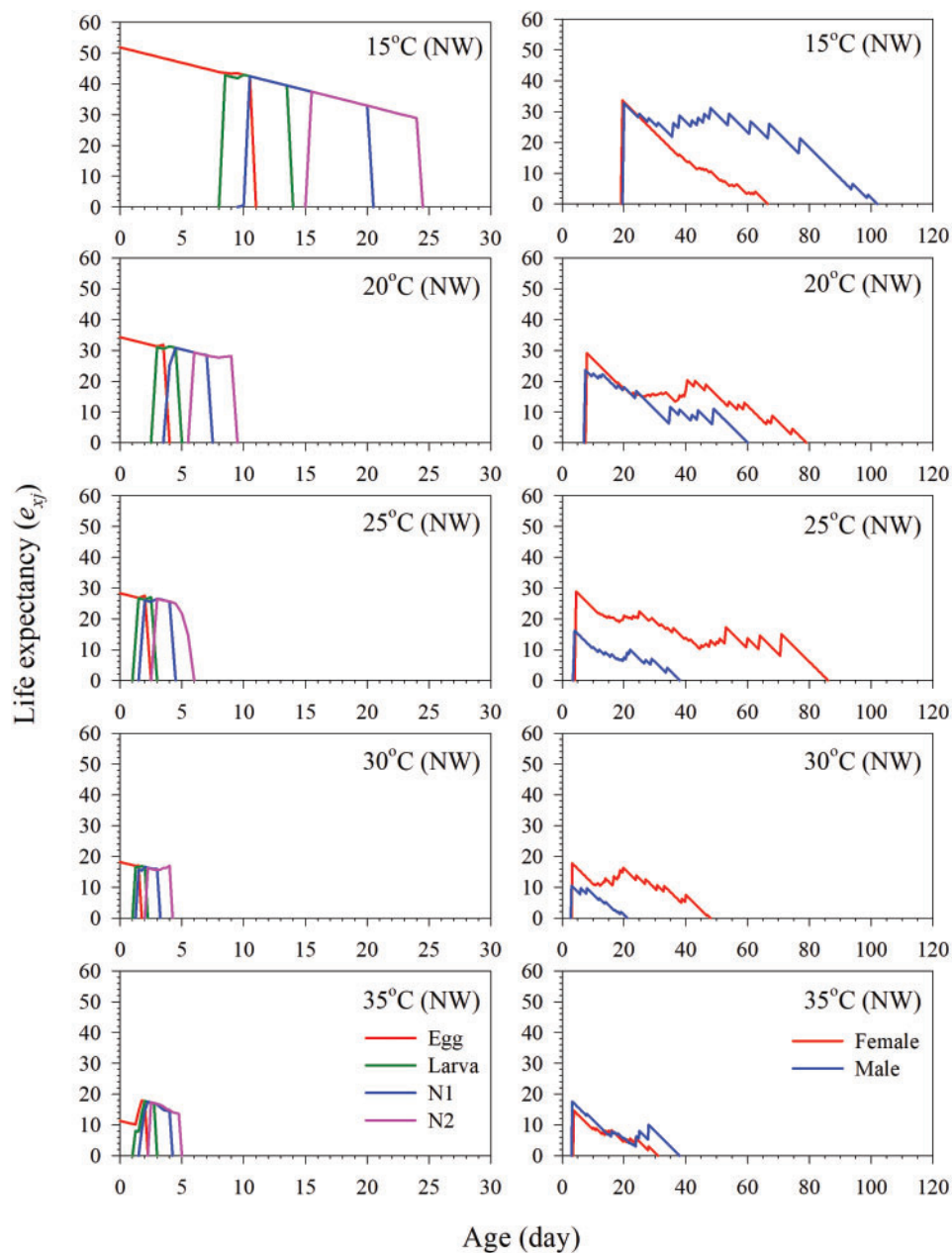


Fig. 6. Age-stage-specific life expectancies ( $e_{xj}$ ) of *N. womersleyi* reared on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for different adult sexes.

3. In general, the age-stage survival rates of *N. womersleyi* and *N. longispinosus* were different.

The age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), age-specific maternity ( $l_x m_x$ ), and age-stage-specific fecundity ( $f_{xj}$ ) for each temperature treatment are presented in Figs. 4 and 5. The oviposition period decreased with increasing temperature for both species. *Neoseiulus womersleyi* took longer time to reach its peak age-specific fecundity ( $m_x$ ) as the temperature decreased (Fig. 4). Similar response was observed in *N. longispinosus* (Fig. 5). Net maternity value ( $l_x m_x$ ) was low at higher temperatures owing to the low survival rate in both species.

#### Life Expectancy

The life expectancy ( $e_{xj}$ ) of each age-stage group of *N. womersleyi* (Fig. 6, left panels) and *N. longispinosus* (Fig. 7, left panels) showed

the time length that individuals of age  $x$  and stage  $j$  were expected to live after age  $x$  at different temperature conditions. Life expectancy for both males and females of *N. womersleyi* tended to decrease with increasing temperature (Fig. 6, right panels). Similar responses were observed for both males and females of *N. longispinosus* (Fig. 7, right panels).

#### Reproductive Values

Reproductive value is defined as the contribution of an individual to the future population (Fisher 1930). The reproductive values ( $v_{xj}$ ) of *N. womersleyi* and *N. longispinosus* individuals at age  $x$  and stage  $j$  are presented in Figs. 8 and 9. The  $v_{xj}$  of a newborn egg is exactly the finite rate. The peak of  $v_{xj}$  of *N. womersleyi* female tended to be higher with increasing temperature (Fig. 8, right panels). A



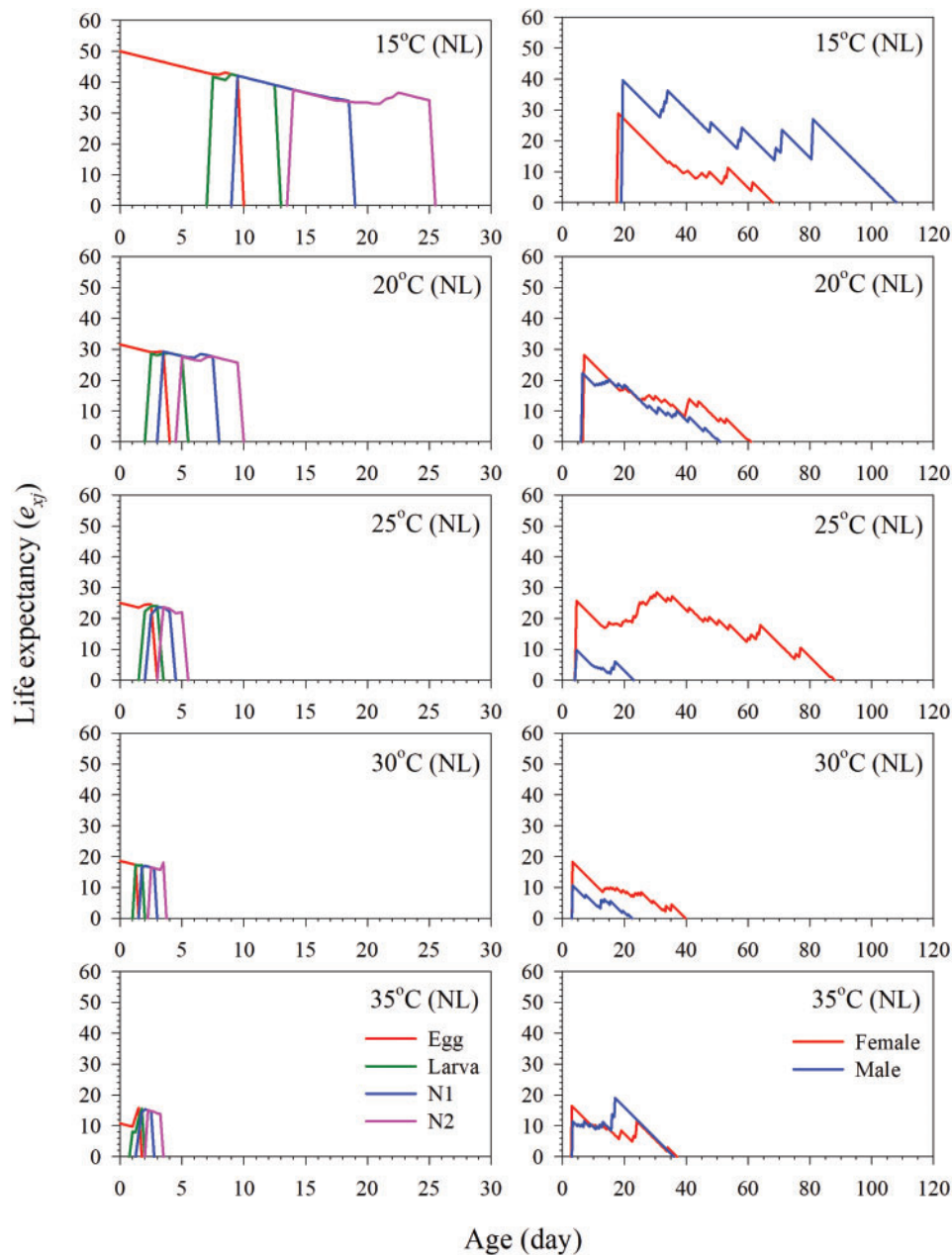


Fig. 7. Age-stage-specific life expectancies ( $e_{xj}$ ) of *N. longispinosus* reared on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for different adult sexes.

similar response was observed in females of *N. longispinosus* (Fig. 9, right panels).

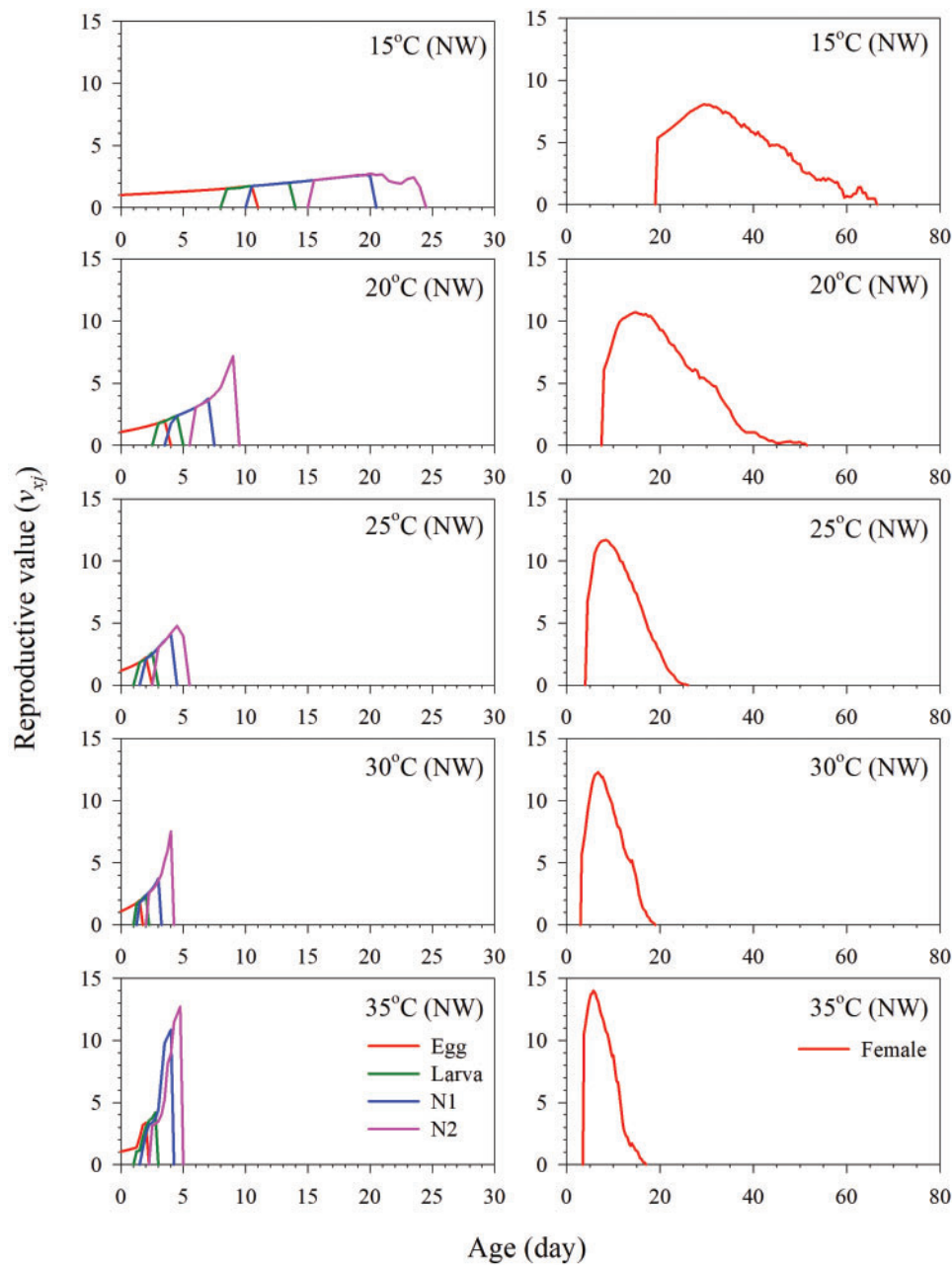
### Population Parameters

The intrinsic rate of natural increase ( $r$ ) increased significantly with temperature from 15 to 32.5°C for *N. womersleyi* and 15 to 30°C for *N. longispinosus*, and then it decreased for both species at high temperatures (Table 4, Fig. 10). Finite rate of increase ( $\lambda$ ) also showed the similar pattern to the intrinsic rate of increase for both species. The greatest  $R_0$ -value was observed for *N. womersleyi* at 25°C, whereas it was 30°C for *N. longispinosus*. The mean generation time ( $T$ ) significantly decreased with increasing temperature up to 32.5°C for *N. womersleyi*, whereas it decreased up to 35°C for *N. longispinosus* (Table 4).

### Discussion

This study describes and compares the developmental rate and demographic characteristics of *N. womersleyi* and *N. longispinosus* under a wide range of temperatures. As expected with most insects and mites, the survival and fecundity of both species were greatly affected by temperature, showing temperature-dependent patterns. Both *N. womersleyi* and *N. longispinosus* individuals were capable of producing offspring across a range of temperatures from 15 to 37.5°C. The age-stage, two sex life table analysis showed that both species are sensitive to temperatures as well.

The population parameters for the intrinsic rate of natural increase and finite rate of increase significantly increased at high temperatures up to 32.5°C for *N. womersleyi* and up to 30°C for *N. longispinosus*, but mean generation time showed a significant

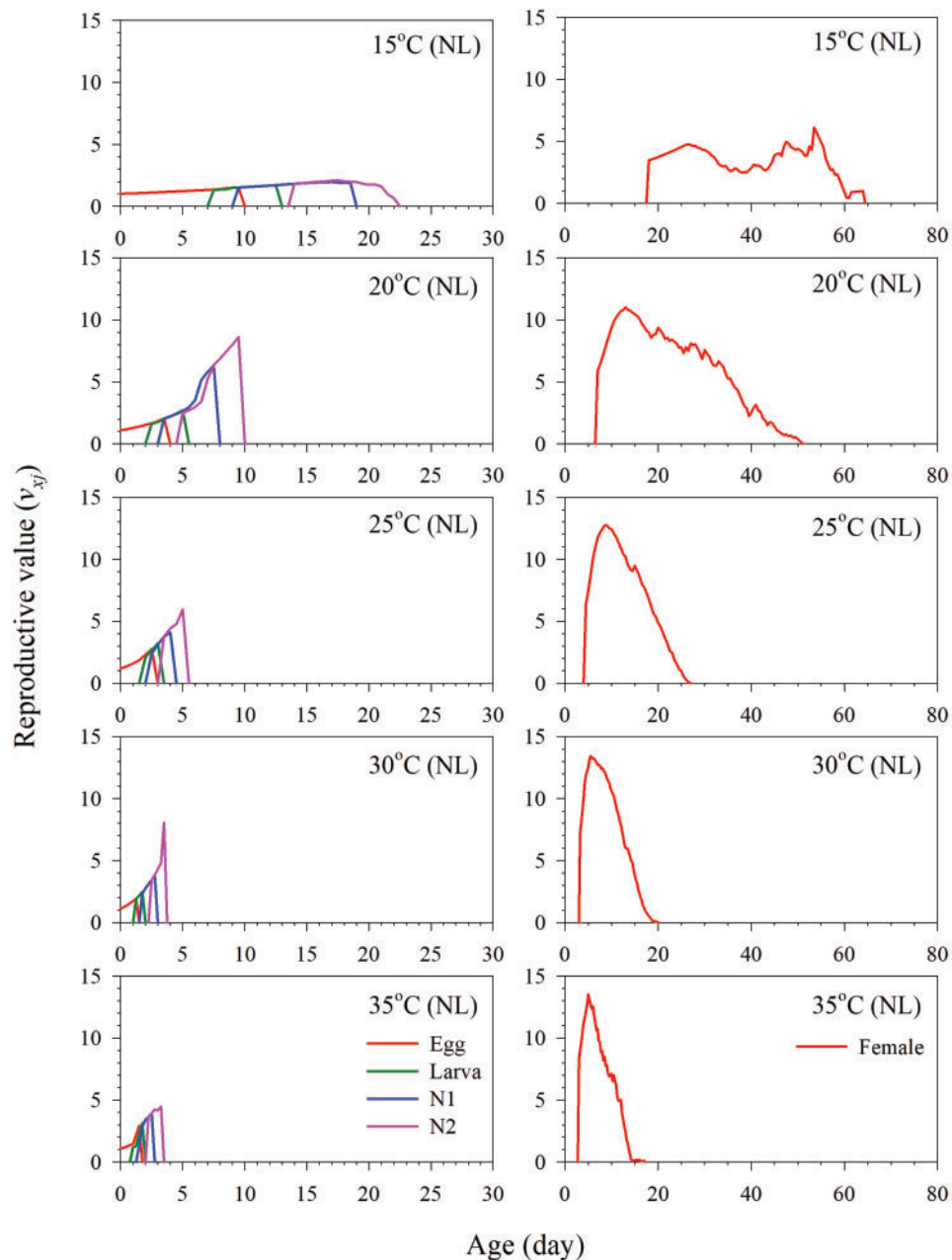


**Fig. 8.** Age-stage-specific reproductive values ( $v_{xj}$ ) of *N. womersleyi* reared on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for female adult.

decrease with increasing temperature for both species. The development time of *N. womersleyi* decreased with increasing temperature up to 32.5°C and then increased at 35°C and more, which was similar with Lee and Ahn (2000). Other studies have shown that the development of predatory mites is affected both by temperature and prey species (Maeda 2006, Nguyen and Shih 2010, Nusartlert et al. 2010, Rahman et al. 2013, Ullah and Gotoh 2014). The present results show that the development time tended to be different for *N. womersleyi* and *N. longispinosus* at similar temperatures.

Campbell et al. (1974) showed the typical relationship between the developmental rate and temperature and pointed out that value for the highest temperature had to be rejected when it did not fit the straight line through the other points. In this study, when all data points were included in linear regression based on Equation 2, data

points of 25~32.5°C were all above the regression line, while data points on both ends (i.e., lower temperatures 15~22.5°C and higher temperatures 35~37.5°C) were all below the regression line. This demonstrates that the predicted developmental rates within 25~32.5°C were underestimated (owing to the overestimation of thermal summation) when all data points were included. Therefore, including all data points in our study will result in inaccurate prediction. Campbell et al. (1974) pointed out that field conditions lie almost exclusively on the straight line section. When the extreme two data points (35 and 37°C) for *N. womersleyi* were excluded, the regression equation  $y = -0.1674 + 0.0144x$  gave more precise estimates of the developmental rates for the range of 15~32.5°C, which is main temperature range of geographic distribution for both mite species. The above discussions are valid for *N. longispinosus* as



**Fig. 9.** Age-stage-specific reproductive values ( $v_{xj}$ ) of *N. longispinosus* reared on *T. urticae* at five constant temperatures. Left panels are for different life stages and right panels are for female adult.

well. We concluded that exclusion of extreme temperatures when they did not fit the straight line through the temperatures of common field conditions is a necessary consideration for applying linear model. Conclusively, our data indicate that both species could be active at low temperature and has a potential to develop over a wide range of temperatures.

The total longevity and oviposition period of *N. womersleyi* and *N. longispinosus* were also affected by temperature and generally decreased with increasing temperature. At 37.5°C, *N. womersleyi* laid more eggs than *N. longispinosus* did. The fecundity of *N. womersleyi* at 15 to 37.5°C was higher than that observed by Lee and Ahn (2000) at 16 to 38°C and the fecundity of *N. longispinosus* at 20 to 30°C was lower than that observed by Rahman et al. (2013). The development and reproductive rates of phytoseiid mites

depend on prey species (McMurtry and Rodriguez 1987, Nguyen and Shih 2010, Ullah and Gotoh 2014) and prey stages (Sabelis 1985, Bruce-Oliver and Hoy 1990, Nusartlert et al. 2010). These findings indicate that the reproductive rates among the examined populations at the same temperature can be attributed differently owing to diverse prey species.

The estimated value of life history parameters of net reproductive rate ( $R_0$ ), intrinsic rate of natural increase ( $r$ ), and generation time ( $T$ ) were affected by temperatures, and there were significant differences between the two species with respect to temperature responses. The highest  $R_0$  and  $r$  values of *N. womersleyi* were observed at 25°C and 32.5°C, respectively. However, the highest  $R_0$  and  $r$  values of *N. longispinosus* were observed at 30°C. The population growth of *N. womersleyi* and *N. longispinosus* varied as

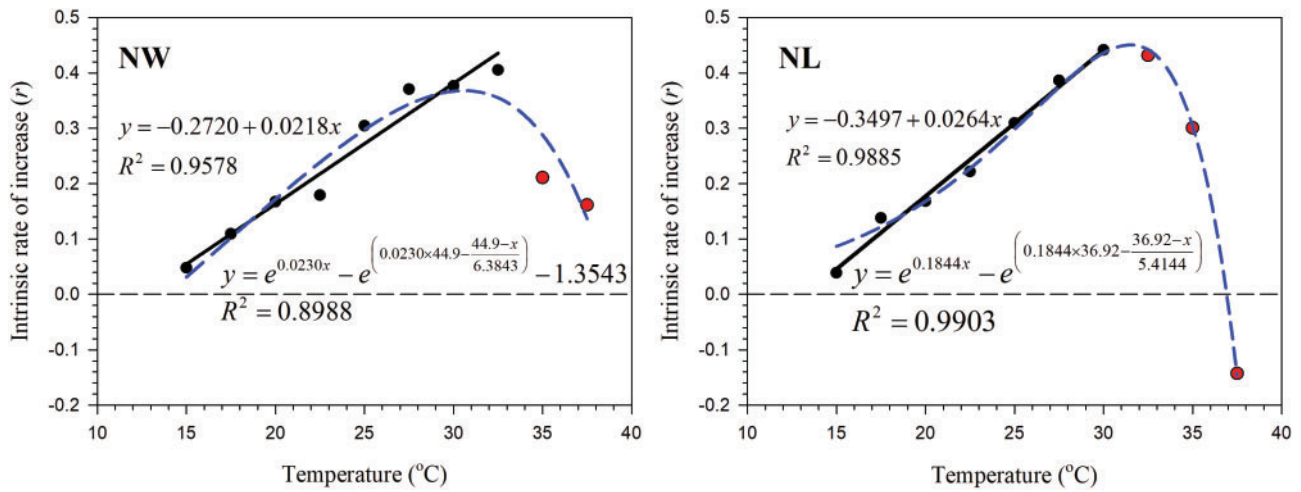


Fig. 10. Intrinsic rate of increases of *N. womersleyi* (NW) and *N. longispinosus* (NL) at different temperatures fitted to linear models (solid lines) and nonlinear models (Lactin et al. 1995; dashed lines). Red data points were not included in the linear models.

Table 4. Means (standard errors) of the intrinsic rate of increase (*r*), finite rate of increase ( $\lambda$ ), net reproductive rate ( $R_0$ ), and mean generation time (*T*) of *N. womersleyi* and *N. longispinosus* at different temperatures

Species	Temp (°C)	<i>r</i> (d <sup>-1</sup> )	$\lambda$ (d <sup>-1</sup> )	$R_0$ (offspring)	<i>T</i> (d)
<i>N. womersleyi</i>	15.0	0.048 (0.005)Ah	1.049 (0.005)Ah	6.9 (1.2)Ac	40.4 (0.9)Aa
	17.5	0.109 (0.005)Bg	1.115 (0.006)Bg	15.7 (2.1)Ab	25.2 (0.4)Abe
	20.0	0.167 (0.006)Af	1.182 (0.007)Af	24.7 (2.6)Aa	19.1 (0.3)Ace
	22.5	0.179 (0.013)Af	1.196 (0.015)Af	18.8 (3.6)Ab	16.4 (0.4)Ad
	25.0	0.305 (0.010)Ae	1.356 (0.013)Ae	28.6 (2.8)Aa	11.0 (0.1)Be
	27.5	0.371 (0.011)Ad	1.449 (0.016)Ad	27.9 (1.3)Aa	9.0 (0.2)Af
	30.0	0.377 (0.015)Bd	1.457 (0.022)Ad	27.0 (3.3)Aa	8.7 (0.1)Ag
	32.5	0.405 (0.016)Ad	1.499 (0.024)Ad	28.2 (3.3)Aa	8.2 (0.1)Af
	35.0	0.211 (0.032)Af	1.235 (0.039)Af	6.4 (1.6)Ac	8.8 (0.2)Af
	37.5	0.162 (0.040)Afg	1.175 (0.046)Afg	3.9 (1.2)Ad	8.4 (0.3)Afg
<i>N. longispinosus</i>	15.0	0.039 (0.007)Ag	1.040 (0.007)Ag	4.4 (1.2)Ad	38.1 (1.7)Aa
	17.5	0.138 (0.007)Af	1.148 (0.008)Af	18.5 (2.5)Ab	21.2 (0.4)Bb
	20.0	0.168 (0.008)Ae	1.183 (0.009)Ae	23.7 (3.3)Ab	18.8 (0.5)Ac
	22.5	0.222 (0.009)Bd	1.248 (0.011)Bd	24.1 (2.9)Ab	14.3 (0.2)Bd
	25.0	0.309 (0.007)Ac	1.363 (0.010)Ac	35.3 (2.8)Aa	11.5 (0.2)Ae
	27.5	0.387 (0.011)Ab	1.472 (0.016)Ab	32.3 (1.8)Aab	9.0 (0.3)Af
	30.0	0.441 (0.018)Aa	1.555 (0.027)Aa	36.6 (4.4)Aa	8.2 (0.1)Bg
	32.5	0.432 (0.019)Aab	1.540 (0.029)Aab	29.9 (3.8)Aab	7.9 (0.1)Bg
	35.0	0.301 (0.035)Ac	1.351 (0.046)Ac	10.4 (2.4)Ac	7.8 (0.4)Bg
	37.5	-0.143 (0.095)Bh	0.867 (0.074)Bh	0.3 (0.2)Be	8.0 (0.5)Ag

Means in the same column followed by the different uppercase letter denote significant differences between *N. womersleyi* and *N. longispinosus* at the same temperature, while means followed by the different lowercase letter denote significant differences between temperatures in the same species based on the paired bootstrap test at 5% significance level.

a result of the variation of life table and population parameters. The populations of *N. womersleyi* and *N. longispinosus* were predicted to reach a population size of ca. 4 and 5 million, respectively, in the absence of disease and with unlimited resources after 50 d at 25 °C. In our results, the *r*-value of *N. womersleyi* were lower than those reported by Lee and Ahn (2000) and the *r*-values of *N. longispinosus* were higher than those reported by Rahman et al. (2013) at around 20, 25, and 30 °C. Similarly, the *r*-values of *N. womersleyi* and *N. longispinosus* that were estimated on different prey mites at 25 °C (Saito and Mori 1975, Shih and Shieh 1979, Kolodochka 1985) are also different from the current study. Each of the above studies estimated *r* values using the traditional female age-specific life table analysis. Additionally, the differences between their results with our results could be owing to different stages of preys used (various

stages) as well as genetic difference between their populations and our populations because they originated from different climatic regions. Therefore, the variation in life table parameters estimated in this study could be owing to several factors. First, a comparison of life-history parameters for different species reared on different prey could produce different parameters as shown in previous studies by Nguyen and Shih (2010) and by Ullah and Gotoh (2014), who reported that the life table parameters of a phytoseiid population can be dramatically affected by prey species and by prey species stages (Nusartler et al. 2010). Although little data are available for comparison in the literature because of differences of thermal conditions among studies, it is well known that temperature strongly influences development and life table parameters (Lee and Ahn 2000, Rahman et al. 2013). The host plants used in the experiments

could directly affect the predator's biology owing to morphological traits and affect indirectly owing to trichome exudates (Sabelis et al. 1999, Koller et al. 2007). However, because there are problems in applying female age-specific life tables to two-sex populations, comparison of life table parameters calculated by using the age-stage, two-sex life table parameters with those obtained by using the traditional female age-specific life table is inappropriate (Huang and Chi 2012, Saska et al. 2016). By using the age-stage, two-sex life table, we could quantitatively simulate the effects of temperature on the population size and stage structure of *N. womersleyi* and *N. longispinosus*, and information obtained from life table studies conducted in a wide range of temperatures might be vital to understanding the population build-up of biological control agent. Considering life table parameters, performance of *N. longispinosus* was low at 15 and 37.5°C than that of *N. womersleyi*. However, the fecundity was higher in *N. longispinosus* than it was in *N. womersleyi* at all temperatures except at 15 and 37.5°C.

The temperature-dependent developmental rate describes, however, only the development and cannot accurately reveal the overall effect of temperature on population fitness. For example, higher developmental rates were observed at 35 and 37.5°C for both species (Fig. 1). However, owing to the low survival rate and low fecundity, the intrinsic rate of increase dropped significantly (Fig. 10). Because the temperature-dependent life tables take the developmental rate, survival rate, fecundity, reproductive age all into consideration, the intrinsic rate of increase and finite rate can give the most comprehensive evaluation on the population fitness than the developmental rate alone.

The population parameters calculated using the life table theories reveal the overall life-long effects of temperature on the developmental rate, survival rate, fecundity, and sex ratio of populations. For example, at 35 and 37.5°C, *N. womersleyi* could complete the preadult development within a short time (3.7~4.2 d) and *N. longispinosus* could also complete its development at similar rate (3.3~3.8 d). However, the preadult survival rate of *N. womersleyi* was 52.5 and 44.7% at 35 and 37.5°C, respectively. For *N. longispinosus*, the preadult survival rate was 58.0 and 4.8% at the respective temperatures. Moreover, the fecundity of *N. womersleyi* was 28.9 and 15.8 eggs at 35 and 37°C, respectively. For *N. longispinosus*, the fecundity was 32.6 and 8.8 eggs at the respective temperatures. Consequently, the net reproductive rates of *N. womersleyi* and *N. longispinosus* were significantly lower at 35 and 37°C than other temperatures. This demonstrates that the data of temperature-dependent developmental rate are actually a subset of the life table data. Temperature-dependent life table reveal much more biological characteristics of a population.

The application of life tables to the study of insect and mite populations for pest management has been underutilized and underemphasized owing to the difficulties involved in data collection and the variability of life tables generated under different environmental conditions and different host plants. The tedious calculations inherent in life table analyses might lead to errors in population parameters and subsequently affect their interpretations (Chi 2015, 2017). Moreover, because the traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) disregard the contribution of the male component of the population and are incapable of correctly differentiating between the different developmental stages, which are unique to insect, mite, and most other arthropod populations, their application causes certain problems (Huang and Chi 2012). Because sex ratio plays an important role in population growth rate and the female life tables do not include male populations, we suggest that the age-stage, two-sex life table should be used in future demographic studies. Finally, both

predators appear better adapted to a wide range of temperatures, and may be a good candidate for biological control agents against spider mites in greenhouse crops in which the temperature is usually maintained high and in the field crops during winter and summer.

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