Effect of temperature on life history traits of the predatory thrips, Scolothrips takahashii Priesner (Thysanoptera: Thripidae)

Tetsuo Gotoh, 1,* Koichi Yamaguchi, 1,† Makiko Fukazawa and Katsuhiko Mori 2,‡

¹ Laboratory of Applied Entomology and Zoology, Faculty of Agriculture, Ibaraki University; Ami, Ibaraki 300–0393, Japan

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Abstract

Scolothrips takahashii is an indigenous thrips in Japan that feeds on many spider mite species. To evaluate whether S. takahashii has potential as a biological control agent for spider mites, we investigated the development, survivorship and life-history parameters of S. takahashii on a diet of Tetranychus urticae (red form) eggs at different temperatures. More than 74% of thrips eggs hatched and more than 76% of newly hatched larvae attained maturity at 15–35°C. No females laid eggs at 37.5 or 40°C. The lower threshold temperature for development from egg to oviposition was 11.7°C and the thermal constant was calculated as 204.1 degree-days. Based on these data, the maximum number of generations that could complete development in a year under field conditions in Ibaraki, central Japan would be between seven and ten. Mating was unnecessary to induce oviposition but unmated females produced only male progeny. At 25°C, females laid a mean of 90.5 eggs during a mean oviposition period of 17.8 days. The values for the intrinsic rate of natural increase ($r_{\rm m}$), one important life-history parameter, were 0.113 at 20°C, 0.195 at 25°C, and 0.246 at 30°C. These results suggest S. takahashii has considerable potential as a biological control agent against spider mites.

Key words: Intrinsic rate of natural increase; lower threshold temperature; predatory thrips; *Scolothrips takahashii*; *Tetranychus urticae*

INTRODUCTION

Spider mites are major agricultural pests in Japan that are difficult to control with agricultural chemicals alone. This is because spider mites can develop resistance to new kinds of acaricides within a few years (Cranham and Helle, 1985; Georghiou, 1990). Therefore, there has been an increasing interest in controlling spider mites with biological control agents, such as predatory thrips, acarophagous ladybugs and predatory mites (Chazeau, 1985; McMurtry and Croft, 1997).

Thrips are phytophagous, pollinophagous, mycetophagous, predacious or general feeders. Only three families (Phlaeothripidae, Aeolothripidae and Thripidae) contain acarophagous thrips (Chazeau, 1985) with various degrees of specialization on

mites but all species of *Scolothrips* appear to be specialized predators of spider mites (Priesner, 1950; Lewis, 1973; Gilstrap and Oatman, 1976; Gilstrap, 1995). Among the species of *Scolothrips*, the best known and most studied is the North American six-spotted thrips, *Scolothrips sexmaculatus* (Pergande) (Chazeau, 1985; Gilstrap, 1995). This species is consistently the earliest, most abundant and most significant natural control agent of spider mites on strawberry (Oatman and McMurtry, 1966), rhubarb (Oatman, 1970) and peach (Rice and Jones, 1972).

Scolothrips takahashii Priesner is a native beneficial thrips in Japan and Formosa (Priesner, 1950; Miyazaki and Kudo, 1988). It is common in fields of bean, citrus, pear and tea (Miyazaki and Kudo, 1988), and considered to be an important predator

² Research Institute of Japan Plant Protection Association; Ushiku, Ibaraki 300–1212, Japan

^{*} To whom correspondence should be addressed at: E-mail: gotoh@mx.ibaraki.ac.jp

[†] Present address: Ishihara Sangyo Kaisha, Ltd., 2–3–1 Nishi-Shibukawa, Kusatsu, Shiga 525–0025, Japan

[‡] Present address: Kohchi Experiment Station of Japan Plant Protection Association, Noichi, Kohchi 781–5231, Japan DOI: 10.1303/aez.2004.511

of numerous spider mites (Nakagawa, 1993). *S. takahashii* is the earliest and/or most frequent predator of spider mites on tea (Nakagawa, 1993), hydrangea (Gotoh and Gomi, 2000) and Japanese pear (Kishimoto, 2002). Yamasaki et al. (1983) examined the lower threshold temperature for development of *S. takahashii* and Nakagawa (1993) examined its prey consumption rate, but little else is known about the biology of this species.

Temperature strongly affects the performance of predatory species as biological control agents. Therefore, knowing the temperature requirements of the different stages of a predator life-history can be used to forecast the potential distribution and dynamics of predator populations. Especially the intrinsic rate of natural increase $(r_{\rm m})$ is a key parameter to assess the potential of a predator under laboratory conditions, and temperature is a very important determinant of $r_{\rm m}$ (Sabelis, 1985b; Roy et al., 2003). In this study, we determined the developmental and reproductive traits of indigenous *S. takahashii* at different temperatures, and evaluated its potential as a biological control agent of spider mites.

MATERIALS AND METHODS

To establish a stock culture, S. takahashii were collected from a field population on kudzu vine, Pueraria lobata (Willd.), at Ami (36°01'N-140°11′E), Ibaraki Prefecture, in the central part of Japan in May 1997. Field-collected thrips were added to the stock culture once a year to maintain genetic diversity. Predatory thrips were maintained on leaves of kudzu vine (June-October) or the lima bean, *Phaseolus lunatus* L. (November–May), which became infested with an ample number of spider mites. Each leaf was placed on agar (0.5%, 10 mm thick) including 1% gentian violet in a plastic cup $(80 \text{ mm}\phi \text{ top} \times 55 \text{ mm}\phi \text{ bottom} \times 60 \text{ mm})$ high) with a lid at 25±1°C and a 16L:8D photoperiod. A 30-mm-diameter hole was cut in the lid of each cup and covered with fine nylon mesh to allow ventilation. To provide food for the thrips, the two-spotted spider mite, Tetranychus urticae Koch (red form), was cultured on leaf discs (ca. 12 cm²) of kudzu vine or lima bean placed on a water-saturated polyurethane mat in a Petri dish $(9 \text{ cm}\phi)$. When the mite densities on a leaf disc reached an acceptable level, the leaf disc was

placed in a cup. For the experiments, *S. takahashii* was allowed to feed on only mite eggs. To obtain prey eggs for *S. takahashii*, 20–40 adult females of *T. urticae* from a stock culture were introduced onto a clean leaf disc (ca. 12 cm²) of lima bean and allowed to lay eggs (ca. 300–500 eggs) for 48 h at 25°C and 16L:8D, and then the females were removed. Each lima bean leaf with mite eggs was placed on agar in a plastic cup, referred to as a leaf cup in this paper.

Scolothrips takahashii adults with parallel wings were examined under a stereomicroscope to determine sex after the procedures of Lewis (1973). Males (body length, $1.1\pm0.09\,\mathrm{mm}$ (mean $\pm\mathrm{S.D.}$), N=100) are always smaller than females ($1.4\pm0.11,\,N=100;\,p<0.001,\,Z=-11.838,\,\mathrm{Mann-Whitney}\,U$ -test). The terminal segments in males are bluntly rounded at the tip. Females have a conspicuous brownish ovipositor, which usually lies retracted beneath a gradually tapered abdomen.

To determine the effect of temperature on survival, development and fecundity of S. takahashii, an inseminated adult female was placed in a leaf cup and allowed to lay eggs for 24 h at eleven constant temperatures from 15 to 40°C at 2.5°C intervals under a long-day photoperiod (16L:8D). Females laid their eggs singly in an incision made in the leaf tissue with their ovipositor. Eggs were identified as whitish ellipses floating in a greenish background when viewed with a transmitted light under a stereomicroscope. The eggs on a leaf disc were counted every day to determine the time to hatching and the percent hatched. Newly hatched 1st instar larvae were individually placed in a leaf cup after hatching. The instar stage was recorded daily. The leaf cups were renewed every two days until pupation. When a female adult emerged, one adult male was introduced into the leaf cup for mating. Two days later, the male was removed and females were observed daily to assess the date of first oviposition. At 20, 25 and 30°C, the number of eggs laid by predatory females was counted daily until the females died. The predatory female was transferred to a new leaf cup every two days to ensure she ate only mite eggs and not hatched mite eggs (i.e., mite larvae).

The intrinsic rate of natural increase, $r_{\rm m}$, was estimated from the life-fecundity table according to the equation given by Birch (1948): $\sum e^{-r_{\rm m}x}l_x m_x = 1$, where x is age in days, l_x is the age-

specific survival rate ((proportion of females alive at age x)×(% egg hatch)), and m_x is oviposition rate at age x ((age-specific oviposition) \times (proportion of females)) (Sabelis, 1985a, 1991; Gotoh, 1986). The Jackknife procedure was used to estimate a standard error for the $r_{\rm m}$ -values (Meyer et al., 1986). For the comparison of the different $r_{\rm m}$ values, analysis of variance (ANOVA) and Tukey's test were used (SPSS, 2002). The net reproductive rate, R_0 , is given by $R_0 = \sum l_x m_x$, the mean generation time, T, in days, is given by $T=\ln R_0/r_{\rm m}$, the finite rate of increase, λ , is given by $\lambda = e^{r_m}$, and the doubling time, D, is given by $D=\ln 2/r_{\rm m}$. To determine hatchability and the proportion of females that appeared in the l_x and m_x formulae, females were placed in leaf cups and allowed to lay eggs for five days after starting oviposition at 20, 25 and 30°C.

Fisher's exact probability test (p < 0.05) was used for all possible pairwise comparisons of eclosion rates of eggs and survival rates at different temperatures. The type-I error was corrected by the Bonferroni method (Sokal and Rohlf, 1995; Nagata and Yoshida, 1997). ANOVA was used to compare the influence of temperature on the number of eggs laid during the first five days of the oviposition period and their hatchability, survival rate and female ratio. ANOVA was also used to compare the influence of temperature on developmental time, oviposition rate, durations of adult female reproductive stages and parameters of population increase. Means were compared among temperatures using the Tukey's test (SPSS, 2002). The logarithmic transferred values or arcsine-root transferred values were used for analysis (Sokal and Rohlf, 1995; Yamamura, 2002). The threshold temperature for the various stages were estimated by linear regression using the values obtained at adequate temperatures and excluding the values at temperatures that resulted in significantly higher mortalities (Lopez-Arroyo et al., 1999; Broufas and Koveos, 2000). The lower threshold temperatures (t_0) were extrapolated from the linear portion of each curve towards the x-axis. The thermal constants (degreedays, K) were calculated as 1/slope of the temperature-developmental rate curve. Standard errors of t_0 and K were computed as in Campbell et al. (1974).

Table 1. Hatchability and survival rate in immature stages of the predatory thrips, *Scolothrips takahashii*, at nine constant temperatures under a 16L:8D photoperiod

Temp.	No. of eggs tested	Eclosion of eggs (%) ^a	No. of larvae introduced	% Maturity ^a
15.0	87	81.6 ab	70	92.9 ab
17.5	371	84.1 ab	65	96.9 a
20.0	110	92.9 a	47	93.6 a
22.5	67	94.0 a	70	92.9 ab
25.0	72	91.7 a	69	97.1 a
27.5	59	94.9 a	100	95.0 a
30.0	42	88.1 ab	55	98.2 a
32.5	76	77.6 ab	59	76.3 b
35.0	121	74.4 b	49	81.6 ab

^a Values followed by the same letters were not significantly different at the 5% level (Fisher's exact probability test with the Bonferroni method).

RESULTS

Development

At each temperature between 15° C and 32.5° C, hatchability was more than 77% (range: 77.6-94.9%) and there was no significant difference among temperatures (Table 1; Fisher's exact probability test with the Bonferroni method, p>0.05). At 35° C, hatchability was slightly lower than at $20-27.5^{\circ}$ C. Survival rate from larva to adult was more than 76% at all temperatures. For eggs that were obtained at 25° C and incubated at 37.5° C, about half (53.2%, N=218) hatched and about half of the resulting larvae (57.1%, N=42) attained maturity. However, at 40° C, no hatching (N=107) was observed, even in eggs that were laid at 25° C.

Developmental time in females and males decreased as the temperature increased from 15 to 30° C (Table 2; p < 0.05, Tukey's test). The total developmental time from egg to adult was 49.5 days for females and 48.2 days for males at 15° C, and 10.3 days and 9.9 days, respectively, at 30.0° C. Developmental time at 32.5 and 35° C were not significantly different in both sexes (p > 0.05, Tukey's test). At all temperatures between 15 and 35° C, all emerged females laid eggs within 0.5-8 days (p < 0.05, Tukey's test).

Developmental rate was significantly related to temperature between 15 and 35°C for all developmental stages. The prepupal stage had the lowest temperature threshold, 10.4°C, while the preoviposition period had the highest temperature threshold,

Table 2. Developmental duration and preoviposition period for *S. takahashii* at nine constant temperatures under a 16L:8D photoperiod

			Development	al duration in day	vs (Mean±S.E.)			
Temp. (°C)	N^a	Egg	1st instar larva	2nd instar larva	Prepupa	Pupa	Total ^b	Preoviposition period ^b
Females								
15.0	33	23.8 ± 0.26	6.2 ± 0.26	9.4 ± 0.43	3.2 ± 0.12	6.9 ± 0.14	$49.5 \pm 0.45 \text{ h}$	$7.8 \pm 0.54 \text{ f}$
17.5	62	15.5 ± 0.18	4.0 ± 0.09	4.9 ± 0.11	2.0 ± 0.04	4.0 ± 0.06	30.4±0.19 g	3.7 ± 0.14 e
20.0	41	12.4 ± 0.10	2.3 ± 0.08	4.9 ± 0.20	1.8 ± 0.07	3.0 ± 0.08	24.4±0.23 f	3.8±0.33 e
22.5	19	8.6 ± 0.11	2.3 ± 0.11	2.5 ± 0.12	1.2 ± 0.10	2.2 ± 0.09	$16.8\pm0.14 e$	$2.1\pm0.11 d$
25.0	32	6.7 ± 0.11	1.8 ± 0.07	2.2 ± 0.08	1.0 ± 0.03	1.7 ± 0.09	$13.3 \pm 0.10 d$	1.7±0.10 d
27.5	28	5.9 ± 0.12	1.4 ± 0.10	1.8 ± 0.12	0.8 ± 0.08	1.5 ± 0.10	11.4±0.14 c	1.6±0.13 cd
30.0	18	5.4 ± 0.14	1.3 ± 0.11	1.6 ± 0.12	0.7 ± 0.11	1.4 ± 0.12	$10.3 \pm 0.14 b$	1.1 ± 0.06 bc
32.5	23	4.6 ± 0.10	1.2 ± 0.09	1.3 ± 0.10	0.5 ± 0.11	1.0 ± 0.00	8.6 ± 0.10 a	$1.0\pm0.04 b$
35.0	14	4.3 ± 0.16	1.0 ± 0.00	0.8 ± 0.11	0.8 ± 0.11	1.0 ± 0.00	8.2 ± 0.24 a	0.6 ± 0.13 a
F							3,265.947	86.927
df							8, 261	8, 261
p							< 0.0001	< 0.0001
Males								
15.0	28	23.9 ± 0.47	7.4 ± 0.24	7.1 ± 0.34	3.4 ± 0.13	6.4 ± 0.16	$48.2 \pm 0.49 \text{ h}$	
17.5	47	15.6 ± 0.19	4.1 ± 0.16	4.6 ± 0.18	2.1 ± 0.09	3.8 ± 0.10	$30.2 \pm 0.30 \text{ g}$	
20.0	35	12.3 ± 0.15	3.5 ± 0.18	3.7 ± 0.18	1.6 ± 0.09	2.9 ± 0.12	$23.9 \pm 0.26 \text{ f}$	
22.5	25	8.8 ± 0.18	2.5 ± 0.10	2.2 ± 0.08	1.1 ± 0.06	2.0 ± 0.04	16.6±0.17 e	
25.0	21	6.6 ± 0.13	1.8 ± 0.13	2.2 ± 0.12	0.9 ± 0.07	1.6 ± 0.11	$13.1\pm0.17 d$	
27.5	24	5.7 ± 0.09	1.5 ± 0.10	1.6 ± 0.10	0.8 ± 0.08	1.3 ± 0.10	11.0 ± 0.12 c	
30.0	16	5.4 ± 0.13	1.3 ± 0.12	1.4 ± 0.13	0.7 ± 0.12	1.1 ± 0.09	$9.9\pm0.17 \text{ b}$	
32.5	22	4.5 ± 0.11	1.2 ± 0.08	1.1 ± 0.10	0.5 ± 0.11	1.0 ± 0.00	$8.5 \pm 0.11 a$	
35.0	16	4.3 ± 0.11	1.1 ± 0.09	0.6 ± 0.13	0.6 ± 0.13	1.1 ± 0.06	$8.3\pm0.24 a$	
F							2,253.486	
df							8, 225	
p							< 0.0001	

^a Number of individuals tested.

14.9°C (Table 3). The thermal constant from egg to adult was 188.7 DD for both females and males (Table 3).

The reproductive period for *S. takahashii* was assumed to last from May to November, the period when insect predators had been observed in the field of Ibaraki (T. G., personal observation). When the total degree-days (1,538–2,114 DD) accumulated above a lower threshold temperature of 11.7°C (egg-to-egg) for the past ten years (1993–2002) were divided by a thermal constant of 204.1 DD for egg-to-egg, the maximum number of generations that *S. takahashii* could complete in each of these 10 years ranged between seven and ten generations.

The number of eggs laid during the first five

days of the oviposition period increased significantly as temperature increased (Table 4, p<0.05, Tukey's test). Eclosion of eggs, survival rate in immature stages and sex ratio (proportion of daughters) were not significantly affected by temperature in this range (p>0.05, ANOVA).

Virgin females of *S. takahashii* produced only male progeny: the number of eggs laid per female during the first five days of the oviposition period, the number of larvae hatched and the number of males emerged (N=13) were 26.2 ± 1.29 (mean \pm S.E.), 23.6 ± 0.28 and 21.7 ± 1.24 , respectively. On the other hand, as shown in Table 4 fertilized females produced mostly females with some males from non-inseminated eggs. This shows that this species is arrhenotokous, i.e., females are

^b Values within the same column and/or sex followed by the same letter were not significantly different at the 5% level (Tukey's test).

Stage	Regression equation ^a	r^2	Lower threshold $(t_0, {}^{\circ}\mathrm{C})^{\mathrm{c}}$	Thermal constant (<i>K</i>) (degree-days)
Female				
Egg	y = -0.1075 + 0.0099x	0.9925*** ^b	10.9 ± 0.51	101.0 ± 3.33
1st instar larva	y = -0.4522 + 0.0409x	0.9831***	11.1 ± 0.76	24.5 ± 1.21
2nd instar larva	y = -0.5142 + 0.0394x	0.9805***	13.1 ± 0.72	25.4 ± 1.36
Prepupa	y = -0.7210 + 0.0694x	0.8014**	10.4 ± 3.01	14.4 ± 2.71
Pupa	y = -0.5349 + 0.0443x	0.9776***	12.1 ± 0.83	22.6 ± 1.29
Egg-adult	y = -0.0605 + 0.0053x	0.9935***	11.4 ± 0.46	188.7 ± 5.73
Preoviposition	y = -0.9721 + 0.0653x	0.8809***	14.9 ± 1.67	15.3 ± 2.13
Egg-adult oviposition	y = -0.0573 + 0.0049x	0.9968***	11.7 ± 0.31	204.1 ± 4.36
Male	•			
Egg	y = -0.1103 + 0.0100x	0.9883***	11.0 ± 0.63	100.0 ± 4.08
1st instar larva	y = -0.4831 + 0.0407x	0.9891***	11.9 ± 0.58	24.6 ± 0.97
2nd instar larva	y = -0.4351 + 0.0376x	0.9377***	11.6 ± 1.45	26.6 ± 2.59
Prepupa	y = -0.9171 + 0.0801x	0.9389***	11.3 ± 1.45	12.9 ± 1.20
Pupa	y = -0.4948 + 0.0441x	0.9545***	11.2 ± 1.26	22.7 ± 1.87
Egg-adult	y = -0.0598 + 0.0053x	0.9914***	11.3 ± 0.48	188.7 ± 6.20

Table 3. Regression equation, lower threshold temperatures of development and thermal constants for *S. takahashii*

Table 4. Number of eggs laid during the first five days of the oviposition period, eclosion of eggs, survival rate of immature stages and the proportion of females reaching adulthood in *S. takahashii* at three constant temperatures under a 16L:8D photoperiod

Temp. (°C)	N^{a}	No. of eggs/female ^b	Eclosion of eggs (%) ^b	Survival rate in immatures (%) ^b	Proportion of females (%) ^b
20.0	11	10.9±1.04 a	90.8±2.12 a	90.2±2.16 a	78.0±1.98 a
25.0	12	$26.5\pm2.32 \text{ b}$	91.1 ± 2.06 a	93.3 ± 1.19 a	$75.8 \pm 1.74 a$
30.0	12	$36.0 \pm 1.85 c$	90.4±2.38 a	94.5 ± 1.78 a	80.3 ± 2.13 a
F		54.750	0.024	1.627	1.349
df		2, 32	2, 32	2, 32	2, 32
p		< 0.0001	0.976	0.212	0.274

^a Number of females tested.

diploid but males develop from unfertilized haploid eggs.

Reproduction

The total number of eggs laid per female was not significantly different at 20, 25 and 30°C (Table 5; p=0.056, ANOVA). As the temperature increased, the daily egg production increased, but the preoviposition period, oviposition period and total adult longevity became shorter (Table 5,

p<0.0001, ANOVA). The total adult longevity was shortest at 30°C.

The l_x (age-specific survival rate) started to drop at earlier ages as the temperature increased from 20 to 30°C (Fig. 1, dotted lines). The m_x (age-specific fecundity rate) peaked at earlier ages and the width of the peak, i.e., the oviposition period, became narrower as the temperature increased (dashed lines). At 20, 25 and 30°C, age at the first oviposition was 24, 15 and 12 days, respectively. Daily

^a Regression equations were calculated based on the values obtained from 15.0 to 35.0°C.

^b Regression analysis. **: p < 0.01; ***: p < 0.001.

^c Mean±S.E. Standard errors were calculated according to the equations given by Campbell et al. (1974).

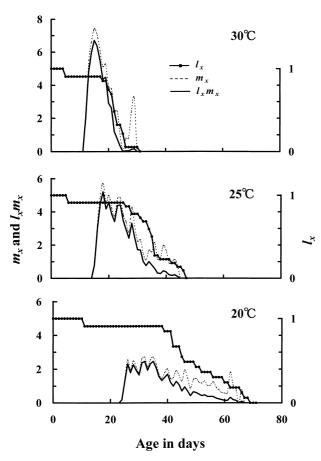
^b Data were analysed using ANOVA and are shown as mean±S.E. Values within columns followed by the same letters were not significantly different at the 5% level (Tukey's test).

 $30.2\pm2.70 a$

Parameter	Temperature (°C)			- F	df	
rarameter	20.0 (N=15) ^a	25.0 (N=20) ^a	30.0 (N=17) ^a	- <i>F</i>	aı	p
No. of eggs/female	62.2±6.71	90.5±9.36	66.4±4.44	3.054	2, 49	0.056
(Maximum fecundity)	$(104)^{a}$	$(164)^{a}$	$(114)^{a}$			
No. of eggs/female/day	2.7 ± 0.13 c	5.1 ± 0.43 b	6.5 ± 0.37 a	36.990	2, 49	< 0.0001
Preoviposition period	2.9 ± 0.19 a	$1.9\pm0.16 b$	1.1 ± 0.06 c	39.757	2, 49	< 0.0001
Oviposition period	23.4 ± 2.44 a	17.8±1.31 a	10.4±0.61 b	24.303	2, 49	< 0.0001
Postoviposition period	$3.9\pm0.82 a$	$2.8\pm0.52 \text{ a}$	$0.7 \pm 0.32 b$	10.721	2, 49	< 0.0001

Table 5. Oviposition rates and various durations (in days) of female adults of *S. takahashii* at three constant temperatures under a 16L:8D photoperiod

 $22.4 \pm 1.48 b$



Total adult longevity

Fig. 1. Age-specific survival rate (l_x) , age-specific fecundity rate (m_x) and $l_x m_x$ curves in *S. takahashii.* l_x =(eclosion of eggs)×(proportion of females alive at age x). m_x =(proportion of females)×(age-specific oviposition).

egg production reached a peak of 3.5 eggs on day 32 at 20°C, 7.6 eggs on day 18 at 25°C and 9.2 eggs on day 15 at 30°C. Female adults started to die on day 39, 26 and 18 at the respective temperatures. The $l_x m_x$ curve, which is the product of l_x and m_x , was the same as the m_x curve except with slightly lower values (solid lines).

36.102

 12.1 ± 0.76 c

2, 49

< 0.0001

The net reproductive rate (R_0) was highest at 25°C followed by 30°C (Table 6). The intrinsic rate of natural increase $(r_{\rm m}, {\rm day}^{-1})$ and finite rate of increase (λ) increased with temperature, and the $r_{\rm m}$ -value reached a peak of 0.246 day⁻¹ at 30°C. Mean generation time $(T, {\rm in \ days})$ and doubling time (D) decreased with increasing temperature.

DISCUSSION

The predatory thrips, S. takahashii, developed successfully over a range of 15 to 35°C with a low mortality from 1.8% (30°C) to 23.7% (32.5°C), but at 37.5°C no females oviposited. In a study of S. sexmaculatus (Gilstrap and Oatman, 1976), no eggs hatched at 18.3°C but most larvae (90.6%) were able to reach maturity at this temperature, and larval survivorship did not decrease even at 40°C. Developmental time (13.3 days) of S. takahashii at 25°C was shorter than that of S. sexmaculatus (16.1 days, Gilstrap and Oatman, 1976; 15.7 days, Coville and Allen, 1977). The lower threshold temperature (11.4°C) of S. takahashii is slightly lower than the previously reported value for S. takahashii (15.2°C, Yamasaki et al., 1983) and that for S. sexmaculatus (14.0°C, Gilstrap and Oatman, 1976; 13.1°C, Coville and Allen, 1977). The thermal

^a Number of females tested. Data were analysed using ANOVA and are shown as mean±S.E. Values in rows followed by the same letters were not significantly different at the 5% level (Tukey's test).

Temp. (°C)	N^{a}	Net reproductive rate (R_0)	Intrinsic rate of natural increase $(r_{\rm m}, {\rm day}^{-1})$	Mean generation time in days (<i>T</i>)	Finite rate of increase (λ)	Doubling time (D)
20	15	44.053	0.113±0.0016 a	33.650	1.119	6.161
25	20	62.425	0.195 ± 0.0045 b	21.174	1.216	3.550
30	17	45.861	0.246 ± 0.0052 c	15.510	1.279	2.813
F			197.88			
df			2, 49			
p			< 0.0001			

Table 6. Parameters of population increase in S. takahashii at three constant temperatures under a 16L:8D photoperiod

constant (188.7 DD) of *S. takahashii* is higher than the previously reported value for *S. takahashii* (144.7 DD, Yamasaki et al., 1983), but is slightly lower than that of *S. sexmaculatus* (209.9 DD, Gilstrap and Oatman, 1976; 192.6 DD, Coville and Allen, 1977). These results suggest that *S. takahashii* as well as *S. sexmaculatus* has potential to develop over a relatively wide range of temperatures.

Although a few studies have examined the lifehistory traits of thrips, we are aware of only two studies that have examined the life-history of predatory thrips (S. sexmaculatus) (Gilstrap and Oatman, 1976; Coville and Allen, 1977). The $r_{\rm m}$ value (0.195 at 25°C) of S. takahashii was higher than the values reported for S. sexmaculatus. At around 25°C, the $r_{\rm m}$ -value of S. sexmaculatus was 0.155 (Gilstrap and Oatman, 1976) and 0.180 (Coville and Allen, 1977). However, the net reproductive rate (R_0 =62.4) of *S. takahashii* was lower than that of S. sexmaculatus (192.1, Gilstrap and Oatman (1976); 93.0, Coville and Allen (1977)). The mean generation time, T (21.2), of S. takahashii was shorter than the values for S. sexmaculatus (33.9, Gilstrap and Oatman (1976); 25.2, Coville and Allen (1977)). Thus, the life history parameters of S. takahashii are slightly higher than or almost equal to those of S. sexmaculatus, suggesting that S. takahashii has similar potential as S. sexmaculatus to control spider mites.

In Central Japan (Kanto plain), *S. takahashii* is well synchronized with spider mites such as *T. urticae* and *T. kanzawai* Kishida in early season emergence (Kishimoto, 2002), suggesting the predatory thrips, *S. takahashii*, can act in environ-

ments where target spider mite densities are low. This is because the prey consumption rate of *S. takahashii* is extremely lower than predators such as acarophagous ladybugs (*Stethorus japonicus* Kamiya) and staphylinids (*Oligota kashimirica benefica* Naomi). For example, the prey consumption rate for *S. takahashii* is 1/9 for immatures and 1/13 for female adults when compared to the respective rates of *S. japonicus* (>120 eggs/day for immatures and >294 eggs/day for female adults) (Gotoh et al., 2004). Thus, suggesting *S. takahashii* in synchrony with the target spider mites at the beginning of the season can have a significant impact on spider mite density and considerable potential as a biological control agent for spider mites.

The present study secondarily shows that *S. takahashii* is arrhenotokous, i.e., unfertilized haploid eggs develop into males, whereas fertilized diploid eggs give rise to females, as has been reported in other predatory thrips (Lewis, 1973). The sex ratio is female-biased, ranging from 0.758 to 0.803 (Table 4). Two other arrhenotokous species are *S. longicornis* Priesner with a female ratio of 0.753 (Sengonca and Weigand, 1988) and *S. sexmaculatus* with a female ratio of 0.89 (Gilstrap and Oatman, 1976) or 0.67 (Coville and Allen, 1977). Thus, the sex ratio of *S. takahashii* is similar to that of other predatory species.

Sengonca and Weigand (1988) reported that *S. longicornis* enters diapause as an adult. The overwintering stage and diapause characteristics of *S. takahashii* are unknown and need to be clarified, because the total effective temperatures above 11.7°C (the lower threshold temperature) in October and November exceeded or were close to the

^a Number of females tested.

^b Data were analysed using ANOVA and are shown as mean ± S.E. Values within columns followed by the different letters were significantly different at the 5% level (Tukey's test).

thermal constant (204.1 DD) during the period from 1993 to 2002 in Ibaraki. If *S. takahashii* enters diapause in response to the short-day length in autumn, the number of generations estimated from the total effective temperature (May–November) would decrease and diapause may reduce the effectiveness of *S. takahashii* as a biocontrol agent for spider mites during the short-day periods even in greenhouses.

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