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Life-history traits of the acarophagous lady beetle, *Stethorus japonicus* at three constant temperatures

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Abstract. *Stethorus japonicus* Kamiya (Coleoptera: Coccinellidae) is an indigenous ladybird beetle in Japan, which feeds on many spider mite species. We evaluated the development, survivorship and life-history parameters of this lady beetle on a diet of eggs of the two-spotted spider mite, *Tetranychus urticae* Koch (red form) (Acari: Tetranychidae). In addition, the effect of short photoperiod on its reproduction was assessed. Survival rates from egg to adult were more than 71% at temperatures between 17.5 and 30 °C. The highest immature mortality was 100% at 35 °C followed by 76% at 15 °C and 52% at 32.5 °C. The lower threshold temperature for development from egg to egg-laying adult was 13.0 °C and the thermal constant was calculated as 238.7° 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 five and seven. The intrinsic rates of natural increase (r_m) were 0.093 at 20 °C, 0.156 at 25 °C and 0.241 at 30 °C. Reproductive diapause was induced at photoperiods with light phases shorter than 13 h at 18 °C.

Key words: Acari, Coccinellidae, Coleoptera, diapause, intrinsic rate of natural increase, ladybird beetle, lower threshold temperature, predator, spider mite, *Stethorus japonicus*, Tetranychidae, *Tetranychus urticae*

Introduction

Spider mites on crops are typical colonizing species and generally characterized by very high rates of population increase and by extremely high densities. These characteristics, added to the mites' high capacity to quickly develop resistance to acaricides (Dittrich, 1975; Cranham and Helle, 1985; Uesugi et al., 2002), greatly complicate mite management

and suggest the need for alternative control methods. In this context, many studies have been conducted on predators of spider mites to evaluate their potential as biological control agents. These studies resulted in several promising groups of biocontrol agents, e.g. predatory mites, predatory thrips and acarophagous lady beetles (Huffaker et al., 1970; Mowery et al., 1975; Chazeau, 1985; van Lenteren and Woets, 1988; Gerson and Smiley, 1990; McMurtry and Croft, 1997; Obrycki and Kring, 1998).

There are many examples of successful biological control, which include the introduction of exotic agents for control of either alien or indigenous pests (McMurtry, 1982; van Lenteren, 1993). On the other hand, it has been demonstrated that non-indigenous (introduced exotic) biocontrol agents could adversely affect the populations of native non-target species. For example, within 5 years after its introduction in South Dakota (USA) the seven-spotted lady beetle, *Coccinella septempunctata* (L.), had led to a decline of populations of two native species (*Adalia bipunctata* (L.) and *C. transversoguttata richardsoni* Brown) (Elliot et al., 1996; Howarth, 2000). Since all pest control methods have inherent risks (Follett and Duan, 2000; Wajnberg et al., 2001), several authors have recommended to reduce the potential negative impact of biological control by using indigenous rather than exotic agents, because any environmental harm caused by native agents would normally be reversible (Howarth, 2000). However, not every introduced species is a threat for native species (Obrycki et al., 2000). We need to select potential organisms judiciously for safe biological control. Knowing the biology and ecology of both indigenous and introduced exotic predators may broaden our options for the best agents. The present study deals with the acarophagous lady beetle, *Stethorus japonicus* Kamiya, an indigenous spider mite predator in Japan. *S. japonicus* is common in fields of apple, citrus, tea, pear, hydrangea and kudzu vine and it is considered to be an important predator of numerous spider mites such as the two-spotted spider mite, *Tetranychus urticae* Koch, and the Kanzawa spider mite, *Tetranychus kanzawai* Kishida (Shimoda et al., 1993; Ehara and Shinkaji, 1996; Gotoh and Gomi, 2000; Kishimoto, 2002; Kitashima and Gotoh, 2003). However, there is little information on *S. japonicus*' life history, on which to base a better evaluation of its potential use as a biocontrol agent.

The lady beetles belonging to the genus *Stethorus* are obligate predators of tetranychid mites (Kapur, 1948; Putman, 1955; McMurtry et al., 1970; Gordon and Chapin, 1983). They have been found on a wide range of crops where tetranychid mites are abundant (Hull et al., 1976; Felland et al., 1995). One of them, *Stethorus punctillum* Weise, is

commercially produced as a mite predator (Copping, 2001). *S. japonicus* is a native lady beetle with a wide distribution in Japan (Sasaji, 1971). In a previous study, we found that female and male immature stages of *S. japonicus* consumed the same number of *T. urticae* eggs, and adult females showed a type II functional response to prey density, regardless of the temperatures tested (Gotoh et al., 2004a). As temperature strongly affects the developmental and reproductive performance of predatory species as biocontrol agents, knowing the temperature requirements of the different stages of a predator's life history can be used to forecast the potential distribution and dynamics of predator populations. Especially the intrinsic rate of natural increase (r_m) is a key parameter to assess the potential of a predator under laboratory conditions, and temperature is a very important determinant of r_m (Sabelis, 1985b; Dixon, 2000; Roy et al., 2003).

In this study, the effect of temperature on development and reproduction of *S. japonicus* was investigated, and the basic thermal requirements for development were determined. These data were also used to estimate the maximum number of generations per year that could potentially complete development in Ibaraki, central Japan. If *S. japonicus* has diapausing ability, then it could affect the number of generations passed in Ibaraki. So, the effect of photoperiod on reproduction was also investigated to examine reproductive diapause.

Materials and methods

The stock culture of *S. japonicus* originated from about 80 adults collected in May–July, 1997, on kudzu vine, *Pueraria lobata* (Willd.), at Ami (36° 01′N–140° 11′E), Ibaraki Prefecture, central Japan. Forty–sixty field-collected beetles were added to the stock culture once a year to maintain genetic diversity. The stock was held at 25 ± 1 °C and 16L:8D photoperiod. Beetles were kept on leaves of kudzu vine (June–October) or lima bean, *Phaseolus lunatus* L. (November–May) that were infested with ample spider mites. Each leaf was placed on a moist filter paper in a plastic cup. Further details regarding the experimental unit are given by Gotoh et al. (2004b). The two-spotted spider mite, *T. urticae* (red form), as prey for the beetles, was cultured on leaf discs (*ca.* 12 cm^2) of kudzu vine or lima bean placed on a water-saturated polyurethane mat in a Petri dish (9 cm in diameter). When the mites reached intended densities on a leaf disc, the disc was put in a cup. For the experiments, *S. japonicus* was allowed to feed only on mite eggs. To obtain prey eggs for *S. japonicus*, 20–40 adult females of *T. urticae* from

a stock culture were introduced onto a clean leaf disc (*ca.* 12 cm^2) of lima bean and allowed to lay eggs for 48 h at 25 °C and 16L:8D, then the females of *T. urticae* were removed. Each lima leaf with mite eggs was placed on a filter paper in a plastic cup, which is referred to in this paper as leaf cup.

The shape of the 8th abdominal plate (8th sternite) was used to sex *S. japonicus* adults as reported for *Stethorus* and *Chilocorus* species (Sasaji, 1971; McMurtry et al., 1974; Hull et al., 1977; Samways and Tate, 1984). The posterior end of the 8th sternite has a small notch in males, while in females it is rounded. By this character, we could easily distinguish sexes in living adults under a stereomicroscope.

The effect of temperature on survival from egg to adult, development and fecundity of *S. japonicus* was determined by placement of individual inseminated adult females (n = 47–99) in leaf cups. The females were allowed to lay eggs for 24 h at nine constant temperatures from 15 to 35 °C at 2.5 °C intervals under a long-day photoperiod (16L:8D). Only one of all the eggs laid was left in each cup and the others were discarded. The leaf cups were checked every day and the beetle instars were recorded. The leaf cups were renewed every 2 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 then adult females were observed daily to assess the date of first oviposition. At 20, 25 and 30 °C, the number of eggs laid by females were recorded every day throughout her life. After counting, the beetle eggs were removed with tweezers. The female was transferred to a new leaf cup every 2 days to ensure that she only ate mite eggs and not larvae.

The intrinsic rate of natural increase, r_m (day^{-1}), was estimated from the life-fecundity table according to the equation given by Birch (1948): $\sum e^{-r_m x} l_x m_x = 1$, 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) × (proportion of females)) (Sabelis, 1985a, 1991; Gotoh, 1986). Other parameters were estimated by equations shown in Gotoh (1986). Eclosion rates from eggs and sex ratios were determined by placement of females in leaf cups where they were allowed to lay eggs for 5 days after starting oviposition at 20, 25 and 30 °C.

The eggs and larvae reared at 18 °C and at a series of photoperiods (10L:14D, 12L:12D, 13L:11D, 14L:10D and 16L:8D) were used to investigate reproductive diapause (Hodek and Honek, 1996). After emergence of adults, oviposition of mated females was observed for 60 days under the respective photoperiod condition at 18 °C.

Kruskal–Wallis test was used to compare the influence of temperature on developmental time and various durations and rates for females, and means were compared among temperatures using the Scheffé's test ($p = 0.05$) (SPSS, 2002). χ^2 test ($p = 0.05$) was used for all possible pairwise comparisons of survival percentages at different temperatures. The type-I error was corrected with the Bonferroni method (Sokal and Rohlf, 1995). Percentages of females ovipositing at different photoperiods were also compared by χ^2 test. Mann–Whitney *U*-test was used to compare preoviposition periods between 14L:10D and 16L:8D (SPSS, 2002). The threshold temperatures for the various stages were estimated by linear regression by using the values obtained at adequate temperatures 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 (degree days, *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).

Results

Development

At each of the temperatures between 17.5 °C and 30.0 °C, most individuals (range: 71.2–91.5%; n = 47–69) attained maturity and there was no significant difference in survival among temperatures (χ^2-test with Bonferroni method, $p > 0.05$; data not shown). The survival rate decreased especially at the 1st instar and finally declined to 47.9 and 23.2% at 32.5 (n = 73) and 15.0 °C (n = 99), respectively. Only one egg hatched at 35.0 °C (n = 88), but the individual died as a 1st instar.

Developmental time decreased as the temperature increased from 15.0 to 27.5 °C (Table 1). There were no significant differences in time of development among 27.5, 30.0 and 32.5 °C ($p > 0.05$, Scheffé's test). Total developmental time did not differ significantly between females and males at any of the temperatures examined ($p > 0.05$).

For all developmental stages there was a strong significant relationship between developmental rate and temperature (from 17.5 to 30.0 °C). The regression of the rate of development of the egg-to-adult female to temperature was significant ($y = 0.0055x - 0.0724$, $r^2 = 0.9750$, $F_{1,4} = 154.35$, $p < 0.001$). The lower threshold temperatures (t_0) and corresponding thermal constants (*K*) were 13.2 ± 0.92 °C

Table 1. Developmental duration and preoviposition period of *Stethorus japonicus* at eight constant temperatures under a 16L:8D photoperiod[a]

Temp. (°C)	Sex[b]	*N*[c]	Egg	Larval stage				Pupa	Total[d]		Pre-oviposition period[e]	% Ovipositing females (*N*)[f]	
				1st	2nd	3rd	4th						
15.0	F	11	16.6 ± 0.25	8.9 ± 0.49	6.1 ± 0.25	5.8 ± 0.33	11.2 ± 0.44	12.1 ± 0.28	60.6 ± 1.10	a	18.3 ± 1.14 (4)	26.4	'(11)
	M	12	16.2 ± 0.21	9.3 ± 0.70	5.7 ± 0.19	6.2 ± 0.34	10.7 ± 0.31	12.3 ± 0.13	60.3 ± 1.08	a			
17.5	F	16	10.1 ± 0.26	5.0 ± 0.22	3.3 ± 0.18	3.5 ± 0.13	6.5 ± 0.16	8.1 ± 0.11	36.5 ± 0.37	b	10.8 ± 0.43	72.7	(22)
	M	33	10.1 ± 0.15	4.9 ± 0.13	3.2 ± 0.07	3.7 ± 0.08	6.6 ± 0.12	8.1 ± 0.06	36.5 ± 0.19	b			
20.0	F	19	7.3 ± 0.17	4.4 ± 0.33	2.5 ± 0.14	2.7 ± 0.10	5.1 ± 0.13	6.4 ± 0.11	28.4 ± 0.59	c	7.3 ± 0.34	76.0	(25)
	M	20	7.3 ± 0.16	4.1 ± 0.12	2.9 ± 0.16	3.0 ± 0.13	5.1 ± 0.12	6.3 ± 0.12	28.7 ± 0.30	c			
22.5	F	23	5.6 ± 0.12	2.5 ± 0.15	2.0 ± 0.10	2.4 ± 0.12	3.2 ± 0.10	4.6 ± 0.10	20.2 ± 0.21	d	4.9 ± 0.17	82.1	(28)
	M	23	5.6 ± 0.10	2.7 ± 0.16	2.0 ± 0.08	2.3 ± 0.09	3.2 ± 0.08	4.6 ± 0.12	20.3 ± 0.19	d			
25.0	F	19	4.8 ± 0.08	2.0 ± 0.09	1.7 ± 0.10	1.8 ± 0.10	3.3 ± 0.10	3.5 ± 0.12	17.1 ± 0.13	e	4.7 ± 0.34	100.0	(19)
	M	23	4.8 ± 0.10	2.0 ± 0.09	1.7 ± 0.10	1.9 ± 0.06	3.4 ± 0.11	3.6 ± 0.10	17.4 ± 0.18	e			
27.5	F	18	3.2 ± 0.12	1.7 ± 0.12	1.0 ± 0.00	1.1 ± 0.06	2.6 ± 0.12	2.6 ± 0.12	12.0 ± 0.17	f	3.2 ± 0.13	100.0	(18)
	M	20	3.4 ± 0.11	1.5 ± 0.11	1.3 ± 0.10	1.2 ± 0.08	2.6 ± 0.11	2.6 ± 0.11	12.4 ± 0.13	f			
30.0	F	16	2.8 ± 0.11	1.4 ± 0.13	0.9 ± 0.06	1.3 ± 0.12	1.9 ± 0.14	2.4 ± 0.13	10.8 ± 0.14	f	3.3 ± 0.25	84.2	(19)
	M	26	2.8 ± 0.08	1.4 ± 0.10	1.0 ± 0.07	1.2 ± 0.08	2.0 ± 0.10	2.4 ± 0.10	10.9 ± 0.10	f			
32.5	F	16	2.8 ± 0.10	1.6 ± 0.16	1.1 ± 0.06	1.1 ± 0.09	2.4 ± 0.13	2.8 ± 0.10	11.8 ± 0.19	f	3.7 ± 0.18	72.7	(22)
	M	13	2.8 ± 0.12	1.8 ± 0.12	1.0 ± 0.00	1.1 ± 0.08	2.4 ± 0.14	2.9 ± 0.08	11.9 ± 0.18	f			

[a] Mean ± SE (day).
[b] F, females; M, males.
[c] Number of individuals tested. Except for 15 °C, only the females ovipositing were used for calculation of developmental duration.
[d] Means differed significantly at $p < 0.001$ ($\chi^2 = 297.7$, Kruskal–Wallis test). Values followed by the same letter within the column were not significantly different at the 5% level (Scheffé's test).
[e] At 15 °C, four out of 11 females examined were ovipositing, and the pre-oviposition period was calculated based on the data for these four females. Observation for determining the pre-oviposition period was done during 60 days after emergence.
[f] Percentage of females ovipositing was calculated as (ovipositing females/(ovipositing females + non-ovipositing females)), numbers in parentheses indicate total number of females emerged at each temperature except for 15 °C.

Table 2. Eclosion of eggs laid during the first 5 days of oviposition and the proportion of females reaching adulthood in *S. japonicus* at three constant temperatures under a 16L:8D photoperiod

Temperature (°C)	N^a	Eclosion of eggs (%)	Proportion of females (%)
20.0	7	98.2 ± 0.89	53.9 ± 2.31
25.0	7	94.9 ± 1.52	57.0 ± 3.72
30.0	8	97.9 ± 0.80	56.3 ± 2.82
χ^2-value[b]		4.682 ns	0.971 ns

[a] Number of females tested.
[b] Means did not differ significantly at the 5% level (Kruskal–Wallis test). Data are shown as mean ± SE.

(Mean ± SE) and 181.8 ± 14.83 DD, respectively. Likewise the t_0 and K for the egg-to-egg developmental rate were 13.0 ± 0.93 °C and 238.7 ± 19.15 DD, respectively ($y = 0.0042x - 0.0543$, $r^2 = 0.9750$, $F_{1,4} = 155.74$, $p < 0.001$).

The reproductive period for *S. japonicus* was assumed to last from May to November, the period when insect predators had been observed in the field (Kishimoto, 2002; Kitashima and Gotoh, 2003). When degree-days (1284–1830 DD) accumulated above a lower threshold of 13.0 °C (egg-to-egg) for the years 1993–2002 were divided by the total degree–days (238.7 DD) for egg-to-egg, the maximum number of generations that *S. japonicus* could complete in each of these 10 years ranged between five and seven.

Eclosion of eggs ranged from 94.9 to 98.2% and sex ratio (proportion of daughters) ranged from 53.9 to 57.0% at 20, 25 and 30 °C (Table 2). None of these parameters was significantly affected by temperature in this range ($p > 0.05$, Kruskal–Wallis test).

Reproduction

The total number of eggs laid per female was significantly lower at 25 °C than at 30 °C ($p < 0.05$, Scheffé's test), but was intermediate at 20 °C ($p > 0.05$, Table 3). As temperature increased, the daily egg production increased and the pre-oviposition period became shorter. Oviposition period and total adult longevity were longer at 20 °C than at 25 and 30 °C ($p < 0.05$). The post-oviposition period did not differ among the three temperatures tested ($p > 0.05$, Kruskal–Wallis test).

The l_x (age-specific survival rate) declined at earlier ages as the temperature increased from 20–30 °C (Figure 1, dotted lines). The m_x (age-specific fecundity rate) peaked at earlier ages and the width of the peak, i.e., the fecundity period, became narrower as the temperature

Table 3. Oviposition rates and various durations (in days) of female adults of *S. japonicus* at three constant temperatures under a 16L:8D photoperiod[a]

Parameter	Temperature (°C)						Kruskal–Wallis test (χ^2-value)
	20.0 (n = 19)		25.0 (n = 19)		30.0 (n = 16)		
No. of eggs/female (Maximum fecundity)	620.0 ± 61.93 (986)	ab	500.7 ± 50.23 (876)	b	736.2 ± 67.68 (1147)	a	6.887*
No. of eggs/female/day	5.9 ± 0.26	c	9.6 ± 0.44	b	15.0 ± 0.93	a	43.733***
Preoviposition period	7.3 ± 0.34	a	4.7 ± 0.34	b	3.3 ± 0.25	c	33.711***
Oviposition period	104.2 ± 8.94	a	53.5 ± 5.83	b	51.6 ± 4.76	b	17.830***
Postoviposition period	16.6 ± 5.10		11.5 ± 2.52		11.6 ± 3.58		0.445ns
Total adult longevity	128.1 ± 9.70	a	69.6 ± 6.45	b	66.4 ± 7.06	b	19.129***

[a] Data are shown as mean ± SE. Means differed significantly at $p < 0.05$ (*) and $p < 0.001$ (***); ns: not significant at the 5% level. Values in a row followed by the same letters were not significantly different ($p > 0.05$; Scheffé's test).

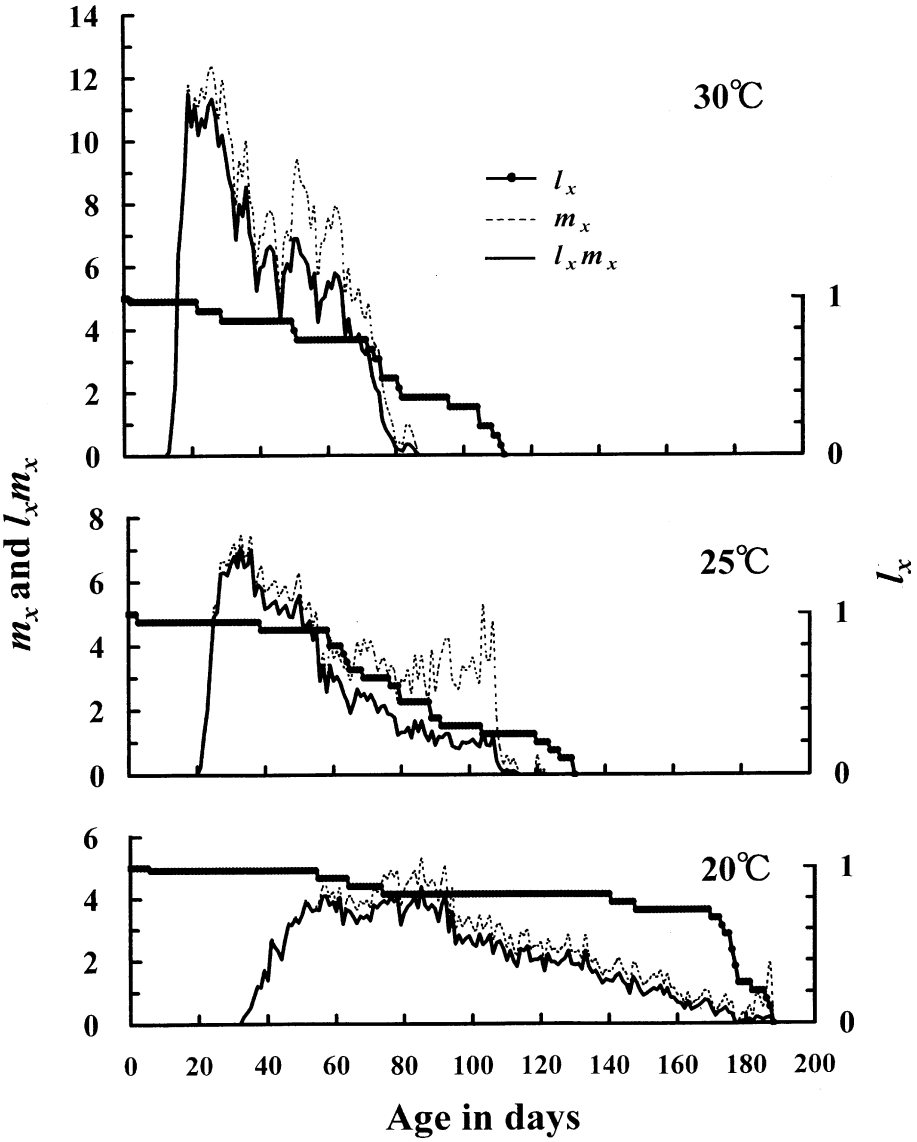

Figure 1. Age-specific survival rate (l_x), age-specific fecundity rate (m_x) and $l_x m_x$ curves in *S. japonicus*. l_x = (eclosion of eggs) × (proportion of females alive at age x). m_x = (proportion of females) × (age-specific oviposition).

increased (dashed lines). At 20, 25 and 30 °C, age at first oviposition was 33, 21 and 13 days, respectively. Daily egg production reached a peak of 9.8 eggs on day 85 at 20 °C, 13.1 eggs on day 33 at 25 °C and 21.9 eggs on day 26 at 30 °C. Female adults started to die on day 55, 39

Table 4. Parameters of population increase in *S. japonicus* at three constant temperatures under a 16L:8D photoperiod

Temp. (°C)	Net reproductive rate (R_0)	Intrinsic rate of natural increase (r_m day^{-1})	Mean generation time in days (T)	Finite rate of increase (λ)	Doubling time (D) in days
20.0	328.805	0.093	62.256	1.098	7.446
25.0	270.494	0.156	51.103	1.169	4.431
30.0	405.770	0.241	39.877	1.272	2.881

and 22 at the respective temperatures. The $l_x m_x$ curve closely resembled the m_x curve (solid lines).

The net reproductive rate (R_0) was lowest at 25 °C followed by 20 °C (Table 4). The intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) increased with temperature and the r_m-value reached a peak of 0.241 day^{-1} at 30 °C. Mean generation time (T) and doubling time (D) decreased with increasing temperature.

Diapause

More than 60% of females reared at 16L:8D and 14L:10D oviposited, but all females exposed to photoperiods with light phases shorter than 12 h did not lay eggs within 60 days after emergence (Figure 2). The mean preoviposition period was 10.8 days (range: 8–15 days) at 16L:8D

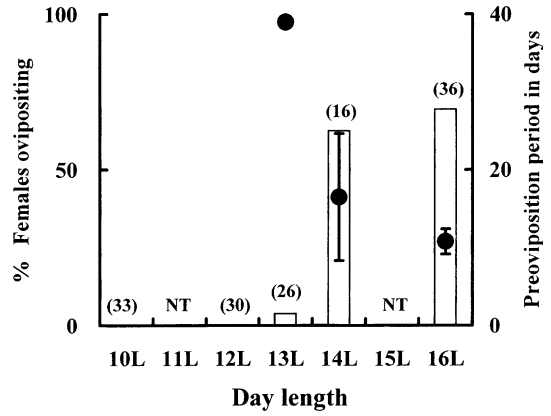

Figure 2. Percentage of females ovipositing (bars) and preoviposition period (dots; mean ± SD) of *S. japonicus* under various constant photoperiod conditions at 18 °C. Numerals in parentheses indicate the number of females tested. Percentages of females ovipositing between 14L:10D and 16L:8D were compared by χ^2-test ($\chi^2 = 0.244$, $p > 0.05$), and the preoviposition periods between the respective photoperiods by Mann–Whitney U-test ($Z = -2.494$, $p = 0.013$). NT: not tested.

and 16.5 days (range: 9–36 days) at 14L:10D. At 13L:11D, one female oviposited on the 39th day after emergence. These results show that the critical daylength, i.e. the daylength at which 50% of a population enters diapause, is between 13 and 14 h, and only a few females may enter diapause at 14L:10D.

Discussion

Stethorus japonicus developed successfully to the adult stage over the range of 17.5–30 °C with a high pre-imaginal mortality at 15 °C (76.8%) and 32.5 °C (52.1%). At 35 °C no larvae survived beyond the first instar. A relatively high death rate in larvae at extreme temperatures has been reported in *S. punctillum* (Roy et al., 2002). *S. punctillum* failed to attain maturity at 12 and 36 °C, and showed higher mortality at 14 and 34 °C. So, *S. japonicus* may have the potential to develop over a similar thermal range of temperatures as *S. punctillum*. However, occasionally the limited development of *S. japonicus* at 32.5 and 35 °C may reduce its presence and thus its potential role as a biocontrol agent during the summer period, although behavioral responses may also play a role, for example the beetle may seek cooler places, thereby limiting the detrimental effect of high ambient temperatures.

Stethorus picipes entered reproductive diapause at 10L–14D and 21–22 °C (McMurtry et al., 1974). Reproductive diapause of *S. japonicus* was induced by a photophase shorter than 13 h at 18 °C. The critical day-length for *S. japonicus* seems to be between 13 and 14 h, and larvae (the sensitive stage) will be exposed to this condition in mid- to late-September in the field of Ibaraki Prefecture, when twilight hours (80 min) are included. However, this photoperiodic reaction of *S. japonicus* is likely to be only one factor influencing the annual generation number. The annual generation number (5–7 generations) of *S. japonicus* was estimated by accumulated temperatures above the lower threshold temperature alone, but effective temperatures in October and November in the field are between 107 and 198 degree-days, allowing the passing of less than one generation during these 2 months.

There are few literature reports on life-history traits of acarophagous coccinellids, and they indicate that the r_m-value of *S. japonicus* was almost the same as or slightly higher than the values of the other *Stethorus* species. At around 25 °C the r_m-value is 0.155 in *Stethorus madecassus* Chazeau (Chazeau, 1974), 0.121 in *S. picipes* Casey (Tanigoshi and McMurtry, 1977), 0.152 in *S. loxtoni* Britton and Lee (Richardson, 1977; Roy et al., 2003) and 0.100 in *S. punctillum* (Roy

et al., 2003). The r_m-value is strongly correlated with developmental time and oviposition rate (Sabelis, 1985a; Wrensch, 1985; Dixon, 2000). Developmental time (17.1 days) of *S. japonicus* at 25 °C was similar with that of *S. picipes* (16.9 days (Tanigoshi and McMurtry, 1977)) and of *S. punctillum* (16.5 days (Putman, 1955) or 17.1 days (Roy et al., 2002)). The total fecundity in *S. japonicus* (500.7 eggs) was very much higher than that measured for other *Stethorus* species (184.3 eggs in *S. madecassus* (Chazeau, 1974)); 221.0 in *S. picipes* (Tanigoshi and McMurtry, 1977); 279.5 in *S. punctillum* (Roy et al., 2003)), suggesting that *S. japonicus* is relatively prolific. In fact, net reproductive rate ($R_0 = 270.5$) of *S. japonicus* was almost three times as high as that of two other *Stethorus* species (92.4 in *S. madecassus* (Chazeau, 1974); 103.3 in *S. picipes* (Tanigoshi and McMurtry, 1977)). Hence, the difference of r_m-values among acarophagous lady beetles may be attributed to differences in the ovipositional rate.

Sabelis (1985a, 1991) gives extensive reviews of life-history parameters of tetranychid mites and shows that r_m-values range from 0.160 to 0.293 day^{-1} at around 25 °C, although the r_m-values vary largely among infested plants depending on their capacity to adapt to unsuitable or poor-quality plants even in the same species. For example, the r_m-values of *T. kanzawai* reared on four different plants varied from 0.187 (tea) to 0.283 day^{-1} (mulberry) (Gotoh and Gomi, 2003). On the other hand, the r_m-values of five acarophagous beetles range from 0.100 to 0.156 day^{-1} near 25 °C (Roy et al., 2003, this study). These data suggest that acarophagous beetles are unlikely to provide consistent control of spider mites by their reproductive numerical response to the mites alone. Based on field data, however, Roy et al. (2003) provided an excellent proposal to use a predatory mite (*Amblyseius fallacis* Garman) in synchrony with the target spider mite (*Tetranychus mcdanieli* McGregor) in the beginning of the season, instead of *S. punctillum* which is absent until early summer. In Japan, *S. japonicus* begins to appear on trees and crops from June onwards, when spider mite densities become high (Gotoh and Gomi, 2000; Kishimoto, 2002). But indigenous predatory mites (*Neoseiulus californicus* (McGregor), *A. eharai* Amitai and Swirski and *A. orientalis* Ehara) and acarophagous thrips (*Scolothrips takahashii* Priesner) are well synchronized with spider mites (*T. urticae* and *T. kanzawai*) from early season (Gotoh and Gomi, 2000; Kishimoto, 2002), suggesting that these predators can act in environments where target spider mite densities are still low. This is because their prey consumption rates are lower than that of *S. japonicus*: in *N. californicus* and *Sc. takahashii* the consumption rates are 1/30 and 1/9 for immatures, respectively, and 1/22 and 1/13 for female adults when compared

with the rates for *S. japonicus* (>120 eggs/day for immatures and >294 eggs/day for female adults) (Gotoh et al., 2004a). Thus, co-occurrence of predators with different predatory capacity may have a significant impact on spider mite density, as suggested by Roy et al. (2003). Furthermore, the prolificacy (>500 eggs/female for *S. japonicus*) given here may enhance its potential to become an effective biocontrol agent in Japan in spite of some negative traits such as reproductive diapause and the relatively narrow temperature range of development and reproduction. The clarification of the interactions between predators sharing the same habitat (e.g., intraguild predation) will help in further developing a sound biological control program.

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