Effects of temperature on the development and reproduction of *Orius sauteri* (Poppius) (Heteroptera: Anthocoridae), a predator of *Thrips palmi* Karny (Thysanoptera: Thripidae)

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(Received 17 April 1998; Accepted 11 December 1998)

Abstract
The development and reproduction of *Orius sauteri* reared on *Thrips palmi* larvae were studied at four constant temperatures, 15, 20, 25 and 30°C. Thermal constant (K) and developmental zero (T₀) for eggs and nymphs of *O. sauteri* were calculated at 62.1 day-degrees and 11.1°C and 180.8 day-degrees and 10.3°C, respectively. Egg mortality rate was always 7.1% or less. There was no significant difference in survival rate during the nymphal stage among the four temperatures. Longevity of female and male adults was greatest at 15°C and shortest at 30°C. Female lifetime fecundity reached a maximum at 25°C. The intrinsic rate of natural increase (rₘ) was highest at 30°C.

Key words: *Orius sauteri*, *Thrips palmi*, natural enemy, development, reproduction

INTRODUCTION

*Orius* spp. are one of the most well known groups of natural enemies of thrips pests throughout the world (Riudavets, 1995). Some species have already been used for biological control or integrated control of thrips pests on vegetables and ornamental crops in Europe (van Lenteren et al., 1997). In Japan, an exotic thrips species, *Thrips palmi* Karny, is well known as the most serious insect pest of eggplant. Although *T. palmi* is considered to be native to tropical Asia (Hirose, 1990; Hirose et al., 1990), its damage to vegetable crops had not been reported in the region until an invasion of Japan by this pest in 1978. Seven years after the establishment of *T. palmi*, Kajita (1985) reported *Orius sauteri* (Poppius) and *Orius* sp. as its natural enemies in Japan. Suppressive effects of *Orius* spp. on *T. palmi* on eggplants in the field have been found by many authors (Nagai et al., 1988; Kawamoto and Kawai, 1988; Nagai, 1990, 1993; Kawai and Kawamoto, 1994). In addition, Kawai (1995) demonstrated the possibility of using *Orius* spp. for controlling *T. palmi* in greenhouse experiments. However, these *Orius* spp., studied in both the field and in greenhouses in Japan, presented serious problems of identification because the taxonomy of Japanese *Orius* spp. was unclear. Recently, Japanese *Orius* spp. have clearly been identified (Yasunaga, 1993, 1997; Yasunaga and Kashio, 1993), and *O. sauteri*, *O. minutus* (Linnaeus) and *O. nagaii* Yasunaga are known to effectively control *T. palmi* on eggplants in the field (Takemoto and Ohno, 1996; Ohno and Takemoto, 1997). Among these species, *O. sauteri* is dominant on eggplants in fields (Takemoto and Ohno, 1996; Ohno and Takemoto, 1997). On greenhouse eggplants, the release of *O. sauteri* for controlling *T. palmi* is promising.

Development of a simulation model to describe the population interaction between *T. palmi* and *O. sauteri* would be useful for developing an effective means of biological control using *O. sauteri* in greenhouses. To develop the model, temperature dependent life history traits of *O. sauteri* are required for use as input parameters for the model. The purpose of this paper was to estimate parameters of *O. sauteri* related to development, survival, fecundity and adult longevity under different temperature conditions in the laboratory.
MATERIALS AND METHODS

Insects. A laboratory colony of *O. sauteri* was initiated in the summer of 1993, using adults collected from white clover flowers in the fields of Okayama Prefectural Agricultural Experiment Station in San’yo-cho, Okayama Pref. (34°4′N, 134°24′E). In the colony, *O. sauteri* was reared on the mold mite, *Tyrophagus putrescentiae* (Schrank), and broad bean sprouts were used as ovipositional substrates. *O. sauteri* used in experiments were obtained from the colony kept at 25±2°C, 75±10% RH and 16 : 8 L : D.

*T. palmi* used in the experiments were derived from naturally occurring individuals on eggplants in greenhouses of Okayama Prefectural Agricultural Experiment Station since its first occurrence in 1984. Only second stadium larvae of *T. palmi* were given to *O. sauteri* in the following experiments.

Development and survival in immature stages. Duration of egg and each nymphal stage of *O. sauteri* were measured at four different temperatures, 15±1°C, 20±1°C, 25±1°C and 30±1°C, under a photoperiod of 16 : 8 L : D.

A pair of *O. sauteri* adults collected from the laboratory colony reared at 25°C was confined in a glass vial (50 ml) for 24 h with an eggplant leaf chip (2 cm × 2 cm) infested with 60 second stadium larvae of *T. palmi* (Fig. 1A). Then, the leaf chip was removed to count the number of eggs laid on its undersurface under a binocular microscope. The reversed leaf chip with eggs was kept on a water surface in a petri dish (Fig. 1B) in a thermostatic incubator. The duration of the egg stage was examined every 24 h at 20, 25 and 30°C and every 48 h at 15°C.

First stadium nymphs of *O. sauteri* within 24 h after hatching were placed individually on a reversed eggplant leaf chip (2 cm × 2 cm) in a petri dish (Fig. 1B) and reared under the same conditions as the eggs. Live second stadium larvae of *T. palmi* were served as food for *O. sauteri* nymphs. The number of supplied prey was increased with the development of *O. sauteri* nymphs; 12, 18, 25, 35 and 50–70 prey items were supplied to first, second, third, fourth and fifth stadium nymphs, respectively, every 24 h at 20, 25 and 30°C and every 48 h at 15°C. Surplus numbers of prey were always given to the nymphs on leaf chips. The developmental stages and the numbers of surviving *O. sauteri* individuals were examined under a binocular microscope every 24 h at 20, 25 and 30°C and every 48 h at 15°C. The presence of nymph exuvia was used as an indication of molting.

Adult longevity and fecundity. All *O. sauteri* adults used in the experiment were reared on second stadium larvae of *T. palmi* during the nymphal stage. A pair of *O. sauteri* adults within 24 h after emergence was reared in a glass vial (Fig. 1A) at the same temperatures as eggs and nymphs. If the male died before oviposition by the coupled female, another newly emerged adult male was supplied. The leaf chip was renewed every 24 h at 20, 25 and 30°C and every

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**Fig. 1.** Rearing containers for adults (A) and nymphs (B) of *O. sauteri.*
48 h at 15°C and then the number of eggs laid on the old chip was counted under a binocular microscope. In the experiment, fecundity and survival of adults were examined until their death. As 60 second stadium larvae of *T. palmi* were supplied to a pair every 24 h at 20, 25 and 30°C and every 48 h at 15°C, surplus numbers of prey were always given to the adults in glass vials.

**Data analysis.** The developmental periods of eggs and nymphs, the longevity of adults and the preoviposition period of females were transformed by Box-Cox transformation to stabilize the variance before analysis of variance (Sokal and Rohlf, 1995). This procedure was followed by a Tukey-Kramer HSD test to compare the measurements under different temperatures (SAS Institute, 1994). Fecundity was analyzed using a Kruskal-Wallis test and differences of means were separated with a Scheffe test (StatSoft Japan, 1996). Mortality rates throughout the duration of the nymphal period were compared using a χ² test of homogeneity of proportions by Marascuilo and McSweeney (1977) after application of the arcsine transformation. The mean generation time and reproductive rate were calculated by the same method described by Matsumura and Yoshida (1988). The intrinsic rate of natural increase (rₚ) was calculated from the survivorship of immature and adult stages (lₙ), and the age specific fertility schedule (mₙ), using an iterative technique after substituting trial values of rₚ in Euler’s equation:

\[
\sum_{x=1}^{\infty} l_n \cdot m_n \cdot \exp(-r_n \cdot x) = 1
\]

where x is age in days. The female sex ratio was assumed to be 0.5. The net reproductive rate (R₀) and the mean generation time (T) were calculated from

\[
R_0 = \sum_{x=1}^{\infty} l_n \cdot m_n \\
T = \log_e R_0 / r_n.
\]

**RESULTS**

**Development and survival in immature stages**

The durations of the egg stage at four constant temperatures are given in Table 1. From 15 to 30°C, the average egg duration was reduced from 13.7 to 3.2 days and the egg developmental rate was accelerated by about 4-fold. The mean developmental time of eggs decreased significantly with increasing temperature (*F* = 701.7; d.f. = 3, 153; *p* < 0.001). Egg mortality rate was always 7.1% or less at all temperatures (Table 2).

The developmental times of nymphs reared at four constant temperatures are also given in Table 1. From 15 to 30°C, the mean developmental time throughout the nymphal period was decreased from 40.9 to 9.5 days, and the nymphal developmental rate was accelerated by about 4-fold. The developmental time of all nymphal stages decreased significantly (*F* = 1797; d.f. = 3, 81; *p* < 0.001) with increases in temperature. The mortality rates throughout the nymphal period were 21.7–24.0% at 20, 25 and 30°C, but 48.6% at 15°C (Table 2). Although the differences in mortality rates throughout the nymphal period between the temperature regimes were significantly different (χ² = 8.600; d.f. = 3; *p* = 0.035), none of these pair-wise contrasts were significantly different.

The regression equations for the developmental velocity of egg and nymphal stages

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Egg (days)</th>
<th>1st stage nymph (days)</th>
<th>2nd stage nymph (days)</th>
<th>3rd stage nymph (days)</th>
<th>4th stage nymph (days)</th>
<th>5th stage nymph (days)</th>
<th>Nymph to adult (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>13.7±0.2 (26) a</td>
<td>6.6±0.3 (29) a</td>
<td>6.1±0.3 (29) a</td>
<td>6.8±0.2 (27) a</td>
<td>7.9±0.2 (25) a</td>
<td>13.5±0.2 (19) a</td>
<td>40.9±0.6 (19) a</td>
</tr>
<tr>
<td>20</td>
<td>7.5±0.2 (35) b</td>
<td>4.3±0.2 (21) b</td>
<td>3.0±0.2 (19) b</td>
<td>2.8±0.2 (19) b</td>
<td>3.2±0.2 (19) b</td>
<td>5.6±0.2 (18) b</td>
<td>18.9±0.3 (18) b</td>
</tr>
<tr>
<td>25</td>
<td>4.5±0.1 (59) c</td>
<td>2.3±0.1 (37) c</td>
<td>1.8±0.1 (37) c</td>
<td>1.7±0.1 (36) c</td>
<td>1.9±0.1 (36) c</td>
<td>4.0±0.1 (35) c</td>
<td>11.5±0.2 (35) c</td>
</tr>
<tr>
<td>30</td>
<td>3.2±0.1 (36) d</td>
<td>2.0±0.0 (19) d</td>
<td>1.5±0.2 (19) d</td>
<td>1.2±0.2 (19) d</td>
<td>1.5±0.2 (19) d</td>
<td>3.0±0.2 (19) d</td>
<td>9.5±0.2 (19) d</td>
</tr>
</tbody>
</table>

*Means followed by the same letter in the same column were not significantly different at *p* = 0.05 (Tukey-Kramer HSD test).

*Number of samples tested at each temperature is denoted in parentheses.
Table 2. Mortality of immature stages of *O. sauteri* at different constant temperatures

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Parameter&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Egg</th>
<th>1st stage nymph</th>
<th>2nd stage nymph</th>
<th>3rd stage nymph</th>
<th>4th stage nymph</th>
<th>5th stage nymph</th>
<th>Nymph to adult&lt;sup&gt;b&lt;/sup&gt;</th>
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<td>24</td>
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<td>37</td>
<td>29</td>
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<td>8</td>
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<td>2</td>
<td>2</td>
<td>2</td>
<td>0</td>
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<td>0.071</td>
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<td>0.000</td>
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<td>0.074</td>
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<td>0.486</td>
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<td>8</td>
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<td>1</td>
<td>0</td>
<td>0</td>
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<td>10</td>
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<td>0.178</td>
<td>0.000</td>
<td>0.027</td>
<td>0.000</td>
<td>0.028</td>
<td>0.222</td>
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<td>25</td>
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<td>19</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
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<tr>
<td></td>
<td>0.000</td>
<td>0.240</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.240</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Parameters are as follows: *n*, number of individuals provided for the test; *d*, number of individuals that died during the stage (s); *q*, the mortality rate during the stage (s).

<sup>b</sup>The mortality rates (*q*,) throughout nymphal period were significantly different at *p*=0.05 (χ² test). All pair-wise contrasts of mortality rate (*q*,) in the same column were not significantly different at *p*=0.05 (χ² test of homogeneity of proportions (Marascuilo and McSweeney, 1977)).

Table 3. Adult longevity and fecundity of *O. sauteri* at different constant temperatures

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Longevity (day)&lt;sup&gt;a,b&lt;/sup&gt;</th>
<th>% ovipositing females&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Preoviposition period (day)&lt;sup&gt;a,b&lt;/sup&gt;</th>
<th>Total No. of eggs laid/female&lt;sup&gt;a,c&lt;/sup&gt;</th>
<th>No. of eggs laid/female/day&lt;sup&gt;a,c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>35.8±12.9 (10) a</td>
<td>50 (10)</td>
<td>15.6±3.4 (5) a</td>
<td>12.2±5.3 (10) a</td>
<td>0.3±0.4 (10) a</td>
</tr>
<tr>
<td>20</td>
<td>19.6±7.1 (19) b</td>
<td>100 (19)</td>
<td>6.3±0.5 (19) b</td>
<td>51.3±7.2 (19) b</td>
<td>2.6±0.2 (19) ab</td>
</tr>
<tr>
<td>25</td>
<td>20.3±1.7 (15) b</td>
<td>100 (15)</td>
<td>4.3±0.5 (15) c</td>
<td>74.5±10.7 (15) b</td>
<td>3.6±0.3 (15) bc</td>
</tr>
<tr>
<td>30</td>
<td>9.0±0.5 (13) c</td>
<td>100 (13)</td>
<td>2.3±0.3 (13) d</td>
<td>52.8±5.4 (13) b</td>
<td>5.7±0.4 (13) c</td>
</tr>
</tbody>
</table>

<sup>a</sup>Number of samples tested at each temperature is denoted in parentheses.

<sup>b</sup>Mean±S.E. Means followed by the same letter in the same column were not significantly different at *p*=0.05 (Tukey-Kramer HSD test).

<sup>c</sup>Mean±S.E. Means followed by the same letter in the same column were not significantly different at *p*=0.05 (Scheffé test).

against temperature were

\[ y = -0.178 + 0.0161x \quad (r^2 = 0.992) \]

and

\[ y = -0.0570 + 0.00553x \quad (r^2 = 0.987) \]

respectively, where *y* is the developmental velocity and *x* is the temperature. From these equations, the thermal constants (*K*) to complete development from oviposition to egg hatch and from egg hatch to adult eclosion were calculated at to be 62.1 and 180.8 day-degrees, respectively. The developmental thresholds (*T₀*) for egg and nymphal stages were estimated at 11.1 and 10.3°C, respectively.

**Adult longevity and fecundity**

The adult longevity of *O. sauteri* females and males, the proportion of ovipositing females, the preoviposition period, the total number of eggs laid per female and the number of eggs laid per female per day at four constant temperatures are given in Table 3. The survivorship and oviposition curves at four constant temperatures are shown in Fig. 2. The longevity of females was greater than that of males at every temperature regime. The longevity of both sexes at 20°C was not significantly different from that at 25°C, and the survivorship curves of both sexes were very similar (Fig. 2). However, the
longevity of both sexes was significantly greater at 15°C than at 20, 25 and 30°C, and it was significantly shorter at 30°C than at the other temperature regimes (female, $F=24.10$; d.f. = 3, 53; $p<0.001$; male, $F=14.78$; d.f. = 3, 48; $p<0.001$) (Table 3). The mean preoviposition period decreased significantly with increases in temperature ($F=41.20$; d.f. = 3, 48; $p<0.001$) (Table 3). The survivorship and oviposition curves of females did not differ greatly between 20 and 25°C (Fig. 2). There was a clear high peak in the oviposition curve at 30°C, but no such peak was found for each of the curves at other temperature regimes throughout the oviposition period (Fig. 2). All females oviposited at 20, 25 and 30°C, whereas 50% of females died without ovipositing at 15°C (Table 3). Most of the ovipositing females continued oviposition until the day before their death at all temperatures. The total fecundity per female at 15°C was significantly smaller than that at other temperatures ($\chi^2 = 19.03$; d.f. = 3; $p=0.003$).

**Population growth**

Basic population growth parameters, such as mean generation time ($T$), net reproductive rate ($R_0$) and intrinsic rate of natural increase ($r_m$), at four constant temperatures are presented in Table 4. The value of $r_m$ for *O. sauteri* clearly increased with temperature, calculated at 0.0135 at 15°C, 0.0763 at 20°C, 0.128 at 25°C and 0.166 at 30°C.

**DISCUSSION**

The mortality rates in the immature stages of *O. sauteri* shown in Table 2 were lower than those of the previous study by Nagai (1993). This difference in mortality between the two studies was probably due to differences in rearing methods. In the rearing method shown in Fig. 1B, the eggplant leaf chip could be kept fresh and also provided sufficient water for drinking during the nymphal stages at all temperatures.

The thermal constants ($K$) and the developmental thresholds ($T_0$) estimated for egg and nymphal stages in this study were slightly lower and longer, respectively, than the previous results of Nagai (1993). Nagai (1993) estimated these parameters using the data obtained from rearing experiments at 20 to 30°C. Since *O. sauteri* was reared at 15 to 30°C in this study, the estimated values of $K$ and $T_0$ are more reliable than those of Nagai (1993). Nakata (1995) calculated the thermal constant and developmental threshold of *O. sauteri* which was collected at a potato field in Sapporo (43°0’N, 141°25’E) and reared on *Myzus persicae* (Sulzer). The estimated developmental threshold for eggs in his study is very similar to this study, but the other parameters are intermediate between Nagai (1993) and

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Mean generation time ($T$) (day)</th>
<th>Net reproductive rate ($R_0$)</th>
<th>Intrinsic rate of natural increase/day ($r_m$) (/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>82.1</td>
<td>3.03</td>
<td>0.0135</td>
</tr>
<tr>
<td>20</td>
<td>40.6</td>
<td>19.9</td>
<td>0.0763</td>
</tr>
<tr>
<td>25</td>
<td>28.1</td>
<td>28.4</td>
<td>0.128</td>
</tr>
<tr>
<td>30</td>
<td>21.9</td>
<td>19.0</td>
<td>0.166</td>
</tr>
</tbody>
</table>
the present study. Thus, these parameters in Nagai (1993), Nakata (1995) and the present study are approximately equal. *O. sauteri* has a lower developmental threshold for nymphs than *Orius insidiosus* (Say) (Isenhour and Yeargan, 1981) and *O. tantillus* (Motschulsky) (Nakashima and Hirose, 1997), and the developmental threshold of *O. sauteri* is almost equal to that of *O. laevigatus* (Fiber) (Alauzet et al., 1994). This property is considered more useful for *O. sauteri* than for *O. insidiosus* and *O. tantillus* in relation to their releases in early spring greenhouses.

The adult longevity of *O. sauteri* observed in the present study is greater than that in the studies of Nagai (1993) and Nakashima et al. (1996). The fecundity is also greater in the present study than in the studies of Nagai (1993) and Nakashima et al. (1996). There are three possible explanations for the differences between the present study and Nagai (1993). First, other *Orius* species may have contaminated the colony of *O. sauteri* in the study of Nagai (1993), because female adults could not be identified to species at that time. Second, field-collected individuals were used by Nagai (1993), whereas individuals from a laboratory colony maintained for more than two years were used in this study; a strain showing a higher reproductive rate may have been selected in the laboratory colony. Third, since adults were fed sufficient numbers of live *T. palmi* throughout the nymphal period in this study, their nutritional condition was better than that of *O. sauteri* in Nagai's (1993) study in which nymphs were not always provided with surplus prey.

All of the tested females oviposited at 20, 25 and 30°C, whereas 50% of the females failed to oviposit at 15°C. Similar results have been reported for *O. laevigatus* (Alauzet et al., 1994) and *O. insidiosus* (van den Meiracker, 1994). The decrease in the rate of ovipositing females at 15°C may be due to induction of reproductive diapause (van den Meiracker, 1994) or a decrease of mating activity under the low temperature. Thus, low temperature also influences the reproductive capacity of *O. sauteri*.

The fecundity of *O. sauteri* fed corn pollen, living nymphs of *Aphis gossypii* Glover, or in combination (Funao and Yoshiyasu, 1995) and freeze-dried larval powder of the melon fly *Bactrocera cucurbitae* Coquillett (FPM) (Nakashima et al., 1996) is lower than that obtained in this study. *A. gossypii* nymphs, corn pollens and FPM appear to be less suitable diets than *T. palmi* larvae.

The fecundity has been examined for several *Orius* spp. As prey species affect the fecundity of *Orius* spp. (Salas-Aguilar and Ehler, 1977; Kiman and Yeargan, 1985), the fecundity was compared among *Orius* spp. fed thrips species. The fecundity of *O. sauteri* fed *T. palmi* in this study is greater than that of *Orius niger* (Wolff), *O. laevigatus* and *O. majusculus* fed *F. occidentalis* (Tommasini and Nicoli, 1993), almost equal to that of *O. insidiosus* fed *F. occidentalis* (Tommasini and Nicoli, 1993) and *O. tristicolor* fed *F. occidentalis* (Salas-Aguilar and Ehler, 1977), and smaller than that of *Orius albipennis* (Reuter) fed *Thrips tabaci* Lindeman (Chyzik et al., 1995). Thus, the fecundity of *O. sauteri* fed *T. palmi* is intermediate among *Orius* spp. fed thrips species. However, the fecundity of *O. sauteri* fed *T. palmi* by Nakashima et al. (1996) is smallest among these *Orius* spp. except *O. niger*.

The values of $r_m$ of *T. palmi* on cucumber were estimated to be 0.035 at 15°C, 0.080 at 20°C, 0.134 at 25°C and 0.144 at 30°C (Kawai, 1985). In the comparison of $r_m$ between *O. sauteri* and *T. palmi* at each temperature, $r_m$ of *O. sauteri* was higher at 30°C, lower at 15°C than $r_m$ of *T. palmi* and nearly equal at 20 and 25°C. Based on these results, we suggest that maintenance of higher temperatures in greenhouses is suitable for biological control of *T. palmi* with *O. sauteri*.

The life history parameters in this study will be used for designing a simulation model for evaluating biological control factors in greenhouses, such as the time and density of *O. sauteri* releases and cropping period. Parameters of functional responses of *O. sauteri* nymphs and adults to density of different stages of *T. palmi* should be estimated as other important components of the model.

**ACKNOWLEDGEMENTS**

We sincerely thank Dr. T. Yasunaga, Hokkaido University of Education, who conducted the taxonomic identification of our laboratory colony. We also thank Dr. K.
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Yamamura, National Institute of Agro-Environmental Sciences, for his useful comments. We appreciate anonymous referees' comments that improved this paper immensely.

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