Life history of the flea beetle, *Argopistes coccinelliformis* Csiki (Coleoptera: Chrysomelidae)

VI. Overwintering and oviposition abilities of adults which emerged late in the season

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(Received 28 February 1997; Accepted 24 October 1997)

Abstract

Overwintered females of *Argopistes coccinelliformis* usually lay eggs on new leaves of host trees, such as *Osmanthus × fortunei* (Oleaceae) in spring and new adults emerge in early summer. However, when lammas shoots (shoots which are produced after the spring) are produced on host trees during summer and autumn, a small number of eggs are laid again, and a proportion of these can develop into adults. This study aimed to determine whether *A. coccinelliformis* adults which develop on lammas shoots can overwinter and produce offspring the following year. Overwintered or first generation females, introduced on potted host (*O. fragrans* var. *aurantiacus*) trees with lammas shoots laid eggs on new leaves. The offspring (first and second generations) which emerged from mid-summer to autumn could overwinter when supplied with new sprouts of *O. fragrans* var. *aurantiacus*. The overwintering rate of adults was higher with progress of the season at the time of emergence. Most of the overwintered females laid eggs, and these eggs hatched. In recent years, the trimming of ornamental trees is conducted not only in winter, but also in late spring and/or summer. The result of the present experiments suggests that lammas shoot production after trimming conducted from late spring to early autumn promotes oviposition by overwintered and newly-emerged first generation adults, and as a result, trimming may provide *A. coccinelliformis* with an opportunity to increase their population the following year, and to increase the number of generations. It is necessary to consider the timing for trimming the branches of Oleaceae from the viewpoint of population control in *A. coccinelliformis*.

Key words: *Argopistes coccinelliformis*, Chrysomelidae, lammas shoot, trimming, voltinism

INTRODUCTION

*Argopistes coccinelliformis* Csiki is a common pest of Oleaceae. Overwintered females usually mate and lay eggs in tissues of new leaves of host trees in April–May, and new adults emerge in June–July in southern Kanto, central Japan (Inoue and Shinkaji, 1989a) and near Kochi City, southwestern Japan (Inoue, unpublished). This species prefers evergreen Oleaceae, such as *Osmanthus × fortunei* as hosts for feeding and oviposition (Inoue and Shinkaji, 1989b). In the field, when eggs are laid on new leaves of *O. × fortunei* during the normal ovipositional season (April–May), the young larvae develop normally and mature in late spring. However, when the eggs are laid on new leaves of *O. fragrans* var. *aurantiacus* during the same period, the hatchlings usually die (Inoue and Shinkaji, 1989a, b). This is because *O. fragrans* var. *aurantiacus* sprouts before mid-March, thus the new leaves are too old (tough) for the hatchlings to feed on (Inoue and Shinkaji, 1989c).

In the field, most new shoots of Oleaceae, such as *O. × fortunei* and *O. fragrans* var. *aurantiacus* usually appear only once a year, that is in the spring, but they are also produced in other seasons, especially after trimming (Inoue and Shinkaji, 1989a). These shoots have been called “lammas shoots,” and lammas shoot production is thought to be related to a compensatory

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reaction of the plant after defoliation by various factors such as feeding by phytophagous insects and mechanical injury caused by strong winds and human activities (Simbolon and Yukawa, 1993a, b). When lammas shoots were produced by several tree species of Oleaceae, such as O. ×fortunei and O. fragrans var. aurantiacus, a small number of eggs of A. coccinelliformis were laid and some of these developed into adults (Inoue and Shinkaji, 1989a). It is believed that most eggs on lammas shoots were laid by surviving overwintered females (Inoue and Shinkaji, 1990).

If those adults, which had developed on lammas shoots, can overwinter and produce offsprings, it is possible that the presence of lammas shoot affects the population density of this beetle. Moreover, because some newly-emerged females can oviposit when supplied with new leaves soon after emergence (Inoue, 1991), if the eggs laid by first generation females can develop into adults and they can overwinter and produce offsprings, it is possible that this beetle has a bivoltine life-cycle. As mentioned above, the larvae of A. coccinelliformis usually can not develop on the spring shoots of O. fragrans var. aurantiacus, but they can develop into adults on the lammas shoots of the same tree. The purpose of this paper is to investigate the overwintering and oviposition abilities of “lammas adults” of A. coccinelliformis belonging to the first or second generation, which had developed on O. fragrans var. aurantiacus.

MATERIALS AND METHODS

All experiments were conducted at the experimental fields of the Shikoku Research Center, Forestry and Forest Products Research Institute, located in Kochi City, Kochi Prefecture, southwestern Japan.

Insects. To obtain first generation adults, overwintered adults were collected from fields near Kochi City during May–June (before new adults emerged), 1993, 1994 and 1995. They were individually supplied with host plant leaves in glass cylinders (15 cm in length, 3 cm in dia.), and the cylinders were kept in a wire-mesh cage (22.9 m² × 2.15 m in height) in the field until the start of the experiment. To obtain second generation adults, newly-emerged first generation adults were collected from fields during May–June, 1994. The body color of new adults just after eclosion was lighter than that of overwintered ones, thus they could be distinguished from old adults. A male and female pair was supplied with new sprouts of the host plant and reared in the same manner as described above.

Host plant. Several potted O. fragrans var. aurantiacus trees were prepared. More than 90% of the spring shoots and 50–70% of overwintered leaves were cut off to promote lammas shoot production. The trees were individually covered with a fine-meshed net to prevent escape of insects.

Oviposition by adults on lammas shoots. When lammas shoots were produced on branches of the potted trees, several overwintered or first generation females, which had been laying eggs in glass cylinders, were introduced on the potted tree and kept for 2 to 4 days under field conditions. After that, they were removed from the potted tree. Females laid eggs on new leaves of lammas shoots during this period.

Rearing procedure. Newly-emerged adults were removed from the potted host tree daily and individually reared in a wire-mesh cage in the field. They were supplied with mature leaves or new sprouts of O. fragrans var. aurantiacus, with stems wrapped in water-soaked absorbent cotton. When new sprouts of O. fragrans var. aurantiacus were not available during late autumn and winter, adults were supplied with leaves of Ligustrum japonicum. Food was replenished every five days. At the same time, adult feeding marks were checked and the number of eggs laid was recorded. Adults which lived until late March of the following year were considered to have overwintered. Some of the overwintered females were then coupled with males. The eggs deposited by each female were incubated at room temperature to determine if they had been fertilized. Several adults which died without feeding after emergence were omitted from the analyses. The rearing of adults was terminated at the end of April, 1996.

RESULTS

Overwintering and reproductive abilities of first generation adults

The overwintering and oviposition abilities of
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Table 1. Overwintering ability of first generation males which emerged from early summer to autumn, 1993, 1994 and 1995, under quasi-natural conditions

<table>
<thead>
<tr>
<th>Month of adult emergence</th>
<th>Food supplied</th>
<th>No. of males which were analyzed</th>
<th>lived until the following spring</th>
<th>Survival period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>June</td>
<td>M</td>
<td>25</td>
<td>0</td>
<td>15.9</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>25</td>
<td>8 (32)</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>M</td>
<td>19</td>
<td>0</td>
<td>10.4</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>19</td>
<td>8 (42)</td>
<td>111.9</td>
</tr>
<tr>
<td>September &amp; October</td>
<td>M</td>
<td>5</td>
<td>0</td>
<td>23.4</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>8</td>
<td>7 (88)</td>
<td>264.1</td>
</tr>
<tr>
<td>Total</td>
<td>M</td>
<td>49</td>
<td>0</td>
<td>14.6</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>52</td>
<td>23 (44)</td>
<td>171.1</td>
</tr>
</tbody>
</table>

^a M and N mean mature leaves and new sprouts, respectively.
^b Numerals in parentheses represent percentages.
^c Number of adults which were used for the calculation of the survival period.
^d Not determined.
^e Rearing of adults was terminated at the end of April, 1996. Thus, the adults which emerged in 1995 were omitted from the calculation.

Table 2. Overwintering and oviposition abilities of first generation females which emerged from early summer to autumn, 1993, 1994 and 1995, under quasi-natural conditions

<table>
<thead>
<tr>
<th>Month of adult emergence</th>
<th>Food supplied</th>
<th>No. of females which were analyzed</th>
<th>oviposited in the year of emergence</th>
<th>lived until the following year</th>
<th>oviposited in the following year</th>
<th>oviposited both in the year of emergence and in the following year</th>
<th>Survival period (days)</th>
<th>No. of eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>S.E.</td>
</tr>
<tr>
<td>June</td>
<td>M</td>
<td>28</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>14.6</td>
<td>3.1</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>29</td>
<td>11 (38)</td>
<td>9 (31)</td>
<td>8</td>
<td>5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>August</td>
<td>M</td>
<td>62</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>16.0</td>
<td>1.6</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>32</td>
<td>8 (25)</td>
<td>18 (56)</td>
<td>15</td>
<td>4</td>
<td>205.1</td>
<td>25.3</td>
</tr>
<tr>
<td>September &amp; October</td>
<td>M</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>40.2</td>
<td>7.2</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>28</td>
<td>0</td>
<td>21 (75)</td>
<td>18</td>
<td>0</td>
<td>189.0</td>
<td>17.3</td>
</tr>
<tr>
<td>Total</td>
<td>M</td>
<td>111</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td></td>
<td>20.2</td>
<td>2.0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>89</td>
<td>19 (21)</td>
<td>48 (54)</td>
<td>41</td>
<td>9</td>
<td>196.1</td>
<td>14.6</td>
</tr>
</tbody>
</table>

^a Same as shown in Table 1.
^b Numerals in parentheses represent percentages.
^c For ovipositing females, the number of eggs laid over their lifetime.
^d Not determined.
^e Number of adults which were used for calculation of the survival period.
^f Number of adults which were used for calculation of the number of eggs laid.
^g Not determined.
^h Rearing of adults was terminated at the end of April, 1996. Thus, the adults which emerged in 1995 were omitted from the calculation.

First generation adults are shown in Tables 1 and 2 for males and females, respectively. Experiments were replicated 3, 5 and 3 times in 1993, 1994 and 1995, respectively. To analyze the effect of the season of emergence, adults which had emerged in the same month were combined...
into one group regardless of the year of emergence. Moreover, adults which had emerged in September and October were treated as the same group because the number of individuals for each of those months was small.

When adults were supplied with mature leaves, the mean survival period was 14.6 (N=49) and 20.2 (N=111) days for males and females, respectively, and none were able to live until the following spring (Tables 1 and 2). Survival periods did not differ significantly between the sexes (p>0.05, by U test), however, when adults were supplied with new sprouts, the mean survival period was 171.1 (N=18) and 196.1 (N=48) days for males and females, respectively, and 44% of males (N=52) and 54% of females (N=89) survived after the winter (Tables 1 and 2). The survival periods and the overwintering rates did not differ significantly between the sexes (p>0.05, by U test and Chi-square test, respectively). The overwintering rate of adults was higher with progress in the season of emergence (Tables 1 and 2), and the rates differed significantly between the emergence seasons (by Chi-square test, p<0.05 and p<0.01 for males and females, respectively). The survival periods (mean±S.E.) of adults (including both sexes) supplied with mature leaves were 15.2±2.2 (N=53), 14.7±1.3 (N=81) and 37.0±6.0 (N=26) days for adults which emerged in June, August and September–October, respectively, differing significantly between the emergence seasons. Adults which emerged in September–October lived the longest (p<0.01, by Kruskal-Wallis test followed by a non-parametric multiple range test). On the other hand, the survival periods (mean±S.E.) of adults (including both sexes) supplied with new sprouts were 173.1±21.5 (N=32) and 204.5±16.6 (N=34) days for adults which emerged in August and September–October, respectively, showing no significant difference between the emergence seasons (p>0.05, by U test).

The females which had emerged in September–October did not lay eggs before winter, but 38% (N=29) and 25% (N=32) of females which had emerged in June and August, respectively, laid eggs within the year of emergence when supplied with new sprouts (Table 2). The number of eggs (mean±S.E.) laid by females which emerged in June and August within the year of emergence were 104.0±44.8 (N=11, range=4–438) and 81.9±40.7 (N=8, range=1–344), respectively, and did not differ significantly between the emergence seasons (p>0.05, by U test). These females finished oviposition by late October. Ten out of 19 females which had oviposited within the year of emergence overwintered and nine of them laid eggs the following spring, as well (Table 2).

In April, 41 out of 48 females initiated oviposition (Table 2). The other seven females died before late April without laying eggs. The eggs laid by females hatched when they were coupled with males. All adults died by mid-November. The numbers of eggs (mean±S.E.) laid by females which emerged in August and September–October over their lifetime were 107.7±28.8 (N=15, range=1–358) and 235.2±74.4 (N=17, range=6–1,139), respectively (Table 2), and did not differ significantly between the emergence seasons (p>0.05, by U test).

**Overwintering and reproductive abilities of second generation adults**

The overwintering and oviposition abilities of second generation adults are shown in Tables 3 and 4 for males and females, respectively. Experiments were replicated 5 times in 1994. However, adults which emerged in the same month were combined into one group because of insufficient sample size.

The mean survival period of adults supplied with mature leaves was 27.7 (N=9) and 16.1 (N=7) days for males and females, respectively, and none were able to survive until the following spring (Tables 3 and 4). The survival periods did not differ significantly between the sexes (p>0.05, by U test). However, the mean survival period of adults supplied with new sprouts was 175.9 (N=9) and 128.9 (N=7) days for males and females, respectively, and 56% (N=9) of males and 57% (N=7) of females survived until after the winter (Tables 3 and 4). The survival periods and the overwintering rates did not differ significantly between the sexes (p>0.05, by U test and Chi-square test, respectively). The overwintering rate of adults (in-
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Table 3. Overwintering ability of second generation males which emerged in 1994, under quasi-natural conditions

<table>
<thead>
<tr>
<th>Month of adult emergence</th>
<th>Food supplied</th>
<th>No. of males which were analyzed</th>
<th>lived until the following spring</th>
<th>Survival period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td>M</td>
<td>5</td>
<td>0</td>
<td>40.4 ± 16.1</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>5</td>
<td>4</td>
<td>234.4 ± 59.7</td>
</tr>
<tr>
<td>September &amp; October</td>
<td>M</td>
<td>4</td>
<td>0</td>
<td>11.8 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>4</td>
<td>1</td>
<td>102.8 ± 69.8</td>
</tr>
<tr>
<td>Total</td>
<td>M</td>
<td>9</td>
<td>0</td>
<td>27.7 ± 9.9</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>9</td>
<td>5</td>
<td>175.9 ± 48.3</td>
</tr>
</tbody>
</table>

*Same as shown in Table 1.

Table 4. Overwintering and oviposition abilities of second generation females which emerged in 1994, under quasi-natural conditions

<table>
<thead>
<tr>
<th>Month of adult emergence</th>
<th>Food supplied</th>
<th>No. of females which were analyzed</th>
<th>oviposited in the year of emergence</th>
<th>lived until the following spring</th>
<th>oviposited both in the year of emergence and in the following year</th>
<th>Survival period (days)</th>
<th>No. of eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td>M</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>24.7 ± 4.8</td>
<td>302</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>128.0 ± 127.0</td>
<td>9</td>
</tr>
<tr>
<td>September &amp; October</td>
<td>M</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>9.8 ± 5.5</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>129.2 ± 48.0</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>M</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>16.1 ± 4.6</td>
<td>156</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>128.9 ± 43.2</td>
<td>147</td>
</tr>
</tbody>
</table>

*Same as shown in Table 1.
*Same as shown in Table 2.

including both sexes) did not differ significantly between the emergence seasons (p > 0.05, by Chi-square test). The survival periods (mean ± S.E.) of adults (including both sexes) supplied with mature leaves were 34.5 ± 10.2 (N=8) and 10.8 ± 2.8 (N=8) days for adults which had emerged in August and September-October, respectively, and did not differ significantly between the emergence seasons (p > 0.05, by U test). Also, the survival periods (mean ± S.E.) of adults which had been supplied with new sprouts were 204.0 ± 53.4 (N=7) and 117.4 ± 38.4 (N=9) days for adults which had emerged in August and September-October, respectively, and did not differ significantly between the emergence seasons (p > 0.05, by U test).

One out of 7 second generation females laid eggs before the winter. This female laid 210 eggs within the year of emergence, then also laid eggs the following spring. In April, two out of 4 overwintered females including this female started to lay eggs (Table 4). The other two females died in early April without laying eggs. Eggs laid by one female, which had been coupled with a male of the same generation, hatched. All adults died by mid-July. The numbers of eggs laid by these two females over their lifetime were 302 and 9, respectively.

**DISCUSSION**

The present experiment showed that the presence of lammas shoots has an important in-
fluence on the life history of *A. coccinelliformis*. In the present experiments, most of the overwintered first generation females could lay eggs. Moreover, eggs laid by coupled females hatched. Thus, it is possible that lammas shoot production after trimming promotes oviposition by overwintered adults and, as a result, the population of *A. coccinelliformis* may increase the following year. Also, the fact that a portion of the second generation adults could overwinter and lay fertilized eggs, demonstrated that *A. coccinelliformis* is a facultative multivoltine. In other words, trimming, a traditional management operation may affect the number of generations of *A. coccinelliformis* if it is conducted frequently.

Adults could not overwinter when supplied with mature leaves of *O. fragrans* var. *aurantiacus* (Tables 1–4), but some adults of *A. coccinelliformis* could overwinter under quasi-natural conditions when supplied with mature leaves of *O. × fortunei* (Inoue, 1991). The larvae of *A. coccinelliformis* are usually unable to develop on the spring shoots of *O. fragrans* var. *aurantiacus*, but they can develop into adults on the lammas shoots of the same tree (Inoue and Shinkaji, 1989a, b). *O. fragrans* var. *aurantiacus* produces many lammas shoots when the tree is trimmed, but *O. × fortunei*, the most favorable host species (Inoue and Shinkaji, 1989b), produces only a few lammas shoots. Many species of ornamental trees are planted in gardens or in parks, and often *O. fragrans* var. *aurantiacus* and *O. × fortunei* are planted in close proximity to each other. Generally speaking, trimming for *Osmanthus* spp. should be conducted in early spring or from late autumn to early winter (e.g. Funakoshi, 1990; Nihonzouen-kumiai-rengoukai, 1996). In recent years, however, trimming is also often conducted in late spring and/or summer in order to cut back overgrown branches. In the present experiments, lammas shoots appeared about 20–30 days after trimming. Also, the prepupal plus pupal period of *A. coccinelliformis* is about 20–30 days during late spring to early summer (Inoue and Shinkaji, 1989a). Newly-emerged females can oviposit when supplied with new leaves soon after emergence (Inoue, 1991). When *O. fragrans* var. *aurantiacus* and *O. × for-
tunei* are planted in close proximity and are heavily trimmed in late spring, it is possible that a second generation of *A. coccinelliformis* is produced.

The overwintering rate of first generation adults supplied with new sprouts was higher with progress in the season of emergence (Tables 1 and 2), and the rates differed significantly between emergence seasons. Also, the survival periods of adults supplied with mature leaves differed significantly between emergence seasons, and the first generation adults which had emerged in September–October lived the longest (Tables 1 and 2). Females of *A. coccinelliformis* terminated oviposition by late September or October under quasi-natural conditions when supplied with new leaves (Inoue and Shinkaji, 1990 and the present experiments). New adults of *A. coccinelliformis* could oviposit under long photoperiod (15L:9D) but could not under short photoperiod (12L:12D) (Inoue and Shinkaji, 1990). Namely, the diapause of new adults was induced by short photoperiod. However, overwintered adults could oviposit even under short photoperiod (Inoue and Shinkaji, 1990). Those overwintered adults continued ovipositing under the long photoperiod, but diapause was again induced under the short photoperiod (Inoue and Shinkaji, 1990). The critical photoperiod for diapause re-induction was not clarified in detail in that report. Because a small portion of second generation females laid eggs immediately after eclosion in the present study (Table 4), a third generation might possibly be produced under field conditions. It is necessary to consider the timing of trimming the branches of Oleaceae from the viewpoint of population control in *A. coccinelliformis*. The present results show that, at least, trimming should not be conducted from late spring to early autumn. Further studies are needed to determine the two critical photoperiods, i.e. the photoperiod for diapause induction and that for diapause re-induction, in order to predict the possible number of generations of *A. coccinelliformis* and to estimate the best season for trimming their host plant.

ACKNOWLEDGEMENTS

I thank Dr. S. A. Lawson (Queensland Forest Research
Institute, Australia) for linguistic improvement of the draft.

REFERENCES


