Possible Influences of Habitat Characteristics on the Evolution of Semelparity and Cannibalism in the Hump Earwig *Anechura harmandi*

Katsuyuki KOHNO

Laboratory of Entomology, Faculty of Agriculture, Kyoto University, Kyoto 606-01, Japan

**Abstract.** The possible influences of life history and habitat characteristics on the evolution of semelparity and cannibalism in the hump earwig *Anechura harmandi* were studied. This species is univoltine and overwinters as an adult. Females laid single egg-batches during winter in nests under stones at a riverside in a valley. They took care of the eggs which hatched in early spring and the offspring ate their mother before dispersing. The valley was sometimes flooded in summer. Nymphs emerged as adults and dispersed to elsewhere before the rainy season arrived. They returned to the riverside after the rainy season. The flooding and/or summer heat seemed to be the selective force for the evolution of dispersal behavior and semelparity in this species. The cannibalism of the female parent by her offspring seemed to have readily evolved after the evolution of semelparity. The unfavorable environmental conditions seemed to have a large effect on the evolution of semelparity and cannibalism in this species.

**Key words:** earwig, *Anechura harmandi*, semelparity, cannibalism against female parent, life history, habitat characteristics.

**Introduction**

Parental care is one of the unique habits observed in earwig species. Adults of earwigs show various unique behaviors. Female parents make nests and take care of their eggs and early instar nymphs (e.g. Lamb 1976; Sasamoto 1978). All the earwig species so far studied lay several batches of eggs in their lifetime (e.g. Bharadwaj 1966; Knabke and Grigarick 1971; Shepard et al. 1973; Lamb and Wellington 1975). Therefore, iteroparity has been regarded as one of the most fundamental life history traits for this group. Iteroparity may assure a higher fitness than semelparity, because a single female can allocate more effort for each egg or offspring by dividing her effort for caring over several times rather than in the case of semelparity. It has been known that first instar nymphs of the hump earwig *Anechura harmandi* kill and eat their mother before dispersing from the nest (Iwata 1979; Kohno 1984), and such a behavior has not been reported for the other earwig species (e.g. Bharadwaj 1966; Knabke and Grigarick 1971; Shepard et al. 1973; Lamb and Wellington 1975). This fact indicates that the female parent of *A. harmandi* can leave only one egg batch in her lifetime. Explaining the selective force that is responsible for this cannibalism may provide an important cue to understand the evolution of iteroparity and semelparity of earwigs.

Studies of life-cycles and population dynamics in relation to habitat characteristics are important in understanding the selective forces of life-history traits in insects. However, most studies of parental care in earwigs have paid attention to the survival of eggs and early instar nymphs or to the significance of sociality (Lamb 1976). No study has examined the significance of parental behavior or cannibalism in association with the life-cycles of earwigs.

*Anechura harmandi* is commonly distributed in mountainous areas in Japan (Terata and Sakai 1989). Female adults make nests for oviposition at the riversides of valleys, whereas the other earwig species studied construct their nests in habitats such as crop fields and gardens (e.g. Lamb and Wellington 1975).
The primary purpose of this report is to document the population dynamics of *A. harmandi* throughout the life-cycle in relation to habitat characteristics. Based on this information and other facts, I propose a hypothesis on the evolution of semelparity and cannibalism of *A. harmandi*.

**Study area**

My study area was a riverside of the Ega-dani valley with a distance of about 300 m away from the junction with the main stream of the Ado-gawa river, about 30 km from the northern suburbs of Kyoto City (35°N, 136°E). Mark and recapture census for immature stages and adults was conducted at subsite A with an area of about 30 m² located in the upper part of the study area (Fig. 1).

There was snowfall from late November to early March. The snow in February 1984 was over 2 m deep, though it was only 20 cm in 1983. The study area was flooded by sudden heavy rainfall due to typhoon No. 10 in 1982. The water level rose to about 2 m above the usual water level. The shape of the stream was greatly modified by the flooding. However, no large flooding occurred during the summers of 1983 and 1984. The vegetation was afforested Japanese cedar *Cryptomeria japonica* in most parts of the study site with some area covered with deciduous temperate trees such as *Quercus crispula* and *Eupeola polyandra*. No other earwig than *A. harmandi* and one individual of the higejiro-ring-legged earwig, *Gonolabis marginalis* were found in the survey site during the present study.

**Methods**

A series of censuses was conducted from May 1982 to December 1984. To estimate population parameters, the mark-release and recapture method was adopted. Most earwigs were found in their nests beneath stones during winter. In other seasons, they were collected by hand or by beating shrubs and herbs with a net. Adults were marked with four dots of color lacquer paints on the forewings, two dots on each forewing. Ten different colors were used to identify each individual. Nymphs were marked with one color at a census and with another color at another census on the thorax or abdomen. As a consequence, individuals captured again before the next molting had more than one dot. Jolly-Seber's stochastic model (Seber 1973) was applied for the estimation of the population parameters in sub-site A (Fig. 1), where a detailed census was carried out in 1982. The total joining numbers of third and fourth instar nympha and adults were represented by sum total of $\hat{B}i$, the estimated joining number on each census day.

Behaviors such as foraging, copulation, flight, etc. were also recorded. When a female adult laid eggs, the date and the number of eggs laid were recorded. The female parent was held in a 10-ml vial while the number of eggs were counted. All the egg batches found were examined at every census. The mortality factors of egg batches were identified as follows: When a predator was found in the nest, the egg batch was judged to be killed by the predator. When eggs darkened, they were judged to be infected by microorganisms. When eggs were soaked in water, they were judged to have been killed by soaking. The censuses were conducted every two to four days from spring to mid-summer, approximately every week from late summer to autumn, and every two weeks in winter. No data were obtained from January to February 1984 because of the heavy snowfall. Some females collected in October 1982 were dissected to determine the degree of ovarian development.

**Results**

**Reproductive period**

By the end of November, most *A. harmandi* adults moved from herbs or shrubs to the ground and were found usually under stones. They overwintered as adults at the riverside. Most of them were found in pairs (Fig. 2). In the study area, 59 out of 82 nests in 1983 and 74 out of 85 in 1984 had been situated at the places flooded in 1982.

In January, females began to lay eggs (Fig. 2). The mean clutch size was $75.7 \pm 3.5$ (mean ± SE, $n=21$, range: 24-96) in 1983 and $69.3 \pm 1.8$ (mean ± SE, $n=53$, range: 36-106) in 1984. Egg hatching occurred from April to May and eggs of the same batch hatched simultaneously (Fig. 2). Eggs laid under stones in exposed places like the
riverside near the junction of the two streams hatched early. On the other hand, those laid in shaded places like the northern side of a building and near a forest hatched later (Table 1).

Male adults left their nests before egg hatching (Fig. 2). Male adults were sometimes found dead outside their nests during this period.

### Maternal care and cannibalism

After oviposition, female parents began to take care of their eggs by licking, turning and piling them up. She appeared to help her nymphs hatching by removing the egg shell with her mouth parts. When nymphs walked out of their nest, the mother put them back in the nest with her mouth parts and legs.

Out of 167 egg batches found in the study area, 75 produced nymphs (Table 2). Some batches were killed by predators such as spiders, centipedes and wireworms, or died off after flooding caused by a melted snow. A few batches were killed by unidentified microorganisms.

In 65 out of 75 egg batches, hatchlings began to eat their mother alive several days after hatching (Table 3). It took them a few days to consume their mother completely. Then, they left the nest as first instar nymphs. Although no ecdysis occurred, they had apparently gained weight. It appeared that the female parent consumed no food after oviposition.

### Nymphal stage

First and second instar nymphs were found mainly under stones or fallen leaves. Third instar nymphs began to climb shrubs or herbs. They were often observed eating pollen of various flowers. Fourth instar nymphs usually stayed on plants, and were rarely found on the ground. Especially on flowers of *Deuzia scabra*, many fourth instar nymphs were observed eating the pollen. Thus the nymphs appeared to eat mainly plant materials, though some individuals were seen eating live dipteran adults.

The number of nymphs in the study area decreased gradually from May to June (Fig. 3). The total joining

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**Table 1.** Hatching dates of egg-batches at different sites in 1983 and 1984. The numbers indicate the number of egg batches producing hatchlings on the indicated date.

<table>
<thead>
<tr>
<th>Date of hatch</th>
<th>1983</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riverside near junction</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Island in the stream</td>
<td></td>
<td></td>
</tr>
<tr>
<td>exposed place</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>shaded place</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>Near forest</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Northern side of building</td>
<td>14</td>
<td></td>
</tr>
</tbody>
</table>
number of third instar nymphs in sub-site A estimated by Jolly-Seber's model (Seber 1973) was 3432.7, and that of fourth instar nymphs was 2443.2.

Adult emergence
Adults emerged in June and July, but disappeared during

Disappearance of adults in summer
Only a few adults were observed from early August to early October at riversides (Fig. 4). During this period there were found no eggs or nymphs. The proportion of
Table 4. Condition of the ovaries and fat bodies of *Anechura harmandi* in autumn 1982.

<table>
<thead>
<tr>
<th>Date of dissection</th>
<th>Fat body</th>
<th>No. of oocytes in:</th>
<th>Oocyte length (mm)</th>
<th>Oocyte diameter (mm)</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>right ovary</td>
<td>left ovary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 19</td>
<td>+±</td>
<td>24</td>
<td>26</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>47</td>
<td>49</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>48</td>
<td>49</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>28</td>
<td>26</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>25</td>
<td>29</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>46</td>
<td>50</td>
<td>0.6–0.7</td>
<td>0.6–0.7</td>
</tr>
<tr>
<td>Oct. 29</td>
<td>±</td>
<td>53</td>
<td>52</td>
<td>1.0</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>50</td>
<td>50</td>
<td>1.0</td>
<td>0.7</td>
</tr>
</tbody>
</table>

* ±, developing; +, well-developed.

Recaptured individuals during this period was high (about a half). An adult stayed in a rolled leaf of *Deuzia scabra* on the riverbank for more than one month from July 30 to September 3 in 1982.

**Re-appearance of adults in autumn**

In early October, the number of adults increased suddenly in the study area (Fig. 4). They flew around during the day time of sunny days. Five to 12 adults of both sexes marked before the end of July were recaptured after mid September in each year. The ovaries of females were developing on October 19, 1982 and had been well-developed by October 29 (Table 4). These adults mated on leaves or flowers of herbs such as a thistle *Cirsium* sp. and a mugwort *Artemisia princeps*. They ate the pollen of these flowers. The food items seemed to be similar to those of nymphs, although the plant species and the size of insects they ate were different. Adults preyed also on noctuid pupae and dipteran adults.

Adults stayed on plants until late November when they began to move to the ground. In early December and later, most adults were found in a pair in their nest.

**Parasitoids**

No parasitoids were found on *A. harmandi* during this study.

**Discussion**

The hump earwig *A. harmandi* is univoltine, and overwinters as an adult. The female lays a single egg batch in the nest and takes care of her eggs. Hatchlings appear in early spring and eat their mother before dispersing. In summer they emerge as adults, but soon disappear from their growing habitat at the riverside (Figs. 3 and 4). Adults return to the riverside in autumn (Fig. 4) and pair there. Compared with other earwigs, three peculiar traits were found in *A. harmandi*: (1) semelparity, (2) consumption of the female parent by her offspring, and (3) living at riversides often flooded in summer.

Although relatively little information is available about the life history of earwigs, all the earwig species so far studied are iteroparous, live in habitats where the risk of disturbance by natural phenomena is low, and non-cannibalistic. For example, *Forficula auricularia* lays two batches of eggs (Behura 1950; Lamb and Wellington 1975). *Euborellia annulipes* (Bharadwa 1966), *E. cincticollis* (Knabe and Grigarick 1971), *Labidura riparia* (Shepard et al. 1973) and *Gonolabis marginalis* (Kohn 1984) lay several batches of eggs. Their offspring do not eat their mother, and they make their nests in places such as gardens and crop fields. *Forficula mikado*, which is distributed in the northern part of Japan, is often observed at the riversides of valleys (Kohn unpublished). Unfortunately, we know too little about the life history traits of this species to compare it to *A. harmandi*.

Habitat characteristics may be very important factors contributing to the evolution of life-history traits in insects (Southwood 1977). Compared with the other earwigs so far studied, only *A. harmandi* occurs in riversides with an exception of *F. mikado* mentioned above. However, the evolution of life-history traits may also be affected by the phylogenetical constraints (Harvey and Pagel 1991). Among the other earwigs, only *F. auricularia*, which belongs to the family Forficulidae, shares some common life history traits with *A. harmandi*. Both species are univoltine, overwinter as adults, reproduce during early spring and live on shrubs or trees in summer (Worthington 1926; Lamb and Wellington 1975). On the other hand, the other species mentioned above, which belong to other families, have more than one brood per year, reproduce during warm seasons and overwinter as various stages including adults and nymphs. Therefore, the life history traits of *A. harmandi* including univoltinism, overwintering as adults, reproducing during early spring and living
on shrubs or trees in summer may be its phylogenetical constraints. On the other hand, semelparity and cannibalism of *A. harmandi* may have evolved by different environmental factors.

Flooding could be one of the probable selective forces for the evolution of the dispersal behavior of *A. harmandi* from the riverside to elsewhere before the rainy season comes. The primary habitat of this species are riversides in mountainous valleys, which are sometimes flooded during summer after a heavy rainfall or typhoon. Although the flooding does not occur every summer, once it occurs, most living organisms would be killed or severely damaged. Therefore it would be highly adaptive for *A. harmandi* to have evolved a mechanism to avoid flooding in summer. This seems to be a special requirement of this species that other earwigs do not normally encounter. In *A. harmandi*, flooding seems to be avoided by initiating immature development early and leaving the riverside before the rainy season comes. This, together with the fact that the nymphs of a second brood, if ever produced by *A. harmandi*, are not likely to attain adulthood before the rainy season arrives, might have favored the evolution of semelparity in this earwig.

Another possible selective force that might be involved in the evolution of dispersal behavior and semelparity in this species is summer heat at the riversides. Because *Anechura* species, most of which are distributed in the temperate zone of the Palaearctic region (Sakai 1982), appear to have a poor ability to tolerate hot conditions as mentioned above, they usually stay on shrubs or trees in summer. Therefore, it is possible that summer heat at riversides has played an important role in the evolution of dispersal behavior before the rainy season and semelparity of *A. harmandi* as for the same reasons as mentioned for flooding.

In such conditions as discussed above, producing another brood outside the riverside in mountainous valleys could be an alternative strategy that raises fitness. However, the fact that the major portion of egg batches were laid at the riverside in spring may indicate that some unfavorable environmental conditions exist outside the riverside.

Killing a female parent by her offspring may evolve more easily in semelparous species like *A. harmandi* than in iteroparous species. In the former, production of the first brood marks the end of the reproductive activity of the female and little or no contribution would be expected once her offspring become ready for dispersing. On the other hand, the body of the female parent would become the most reliable food resource for her offspring, because hunting of prey always accompanies a risk of failure or of predation by others. Though this possibility should be tested experimentally, cannibalism may play an important role in ensuring early adult emergence in nymphs of *A. harmandi* because they can start development early in the spring when the food resource may still be scarce.

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References


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