Res. Popul. Ecol. (1989) 31, 153—160.

SIBLING AND NON-SIBLING CANNIBALISM BY LARVAE OF A LADY BEETLE *HARMONIA AXYRIDIS* PALLAS (COLEOPTERA: COCCINELLIDAE) IN THE FIELD

Naoya OSAWA

Entomological Laboratory, Faculty of Agriculture, Kyoto University, Kyoto 606, Japan

INTRODUCTION

Cannibalism has been reported in many groups of animals including several species of lady beetles (FOX, 1975; POLIS, 1981). However, most of these reports were based simply on laboratory observations. Thus cannibalism has often been regarded as an artifact which has hardly any ecological significance in natural populations (COLINVAUX, 1973). Cannibalism has been widely accepted as a widespread and normal phenomenon only recently (FOX, 1975; POLIS, 1981). However, few studies have clarified quantatively the ecological conditions in which cannibalism occurs in a natural population.

Cannibalism has been divided into two different categories depending on kin relationship between cannibals and the cannibalized (HAMILTON, 1964; FOX, 1975). In coccinellid lady beetles, FOX (1975) distinguished egg cannibalism among siblings from cannibalism by older non-sibling individuals, though these two types of cannibalism have usually been confused with each other.

In this paper I examine these two types of egg cannibalism in the lady beetle, *Harmonia axyridis* PALLAS. The first type is that of newly-hatched larvae feeding on fertile and infertile eggs. Such cannibalism is called sibling cannibalism (BROWN, 1972). The other is that of larvae derived from an egg batch feeding on another egg batch before the eggs hatch. Such cannibalism is defined as non-sibling cannibalism. These two types of cannibalism observed in the lady beetle are compared in different ecological conditions such as timings of oviposition and oviposition sites in the field.

MATERIALS AND METHODS

The lady beetle

The lady beetle *H. axyridis* has a wide distribution in north-eastern part of Asia (SASAJI, 1971) and is one of the commonest aphidophagous coccinellids in Japan. The lady beetles which visited a peach tree, *Prunus Persica*, (3.8 m in height) in the Botanical Garden, Kyoto University were counted everyday from April 1 to July 16, 1985. When an egg batch of the lady beetle was found, I recorded the number of eggs per batch and the direct distance between the egg batch and the nearest aphid colony using a tape line. Then the egg batch was marked and the number of eggs and newly-hatched larvae for all marked egg batches were checked daily.

Sibling and non-sibling cannibalism

Newly-hatched larvae aggregated, and stayed near the egg batch from which they hatched for almost 24 h. Thus cannibalism occurring within 24 h after hatching was regarded as sibling cannibalism. If an egg batch was cannibalized by the larvae derived from another egg batch before hatching (non-sibling cannibalism), I recorded the number of eggs consumed by the cannibal larvae.

During the entire census period, 138 egg batches were found. However, since data on 58 egg batches were incomplete, only data from 80 egg batches were analyzed.

The aphid

Only one aphid species, *Myzus varians* DAVIDSON colonized the peach tree. After the aphid formed a colony on a peach leaf, the leaf became cylindrical-shaped. Twenty such cylindrical-shaped leaves were collected and the number of aphids was counted without distinguishing adults and larvae. The total number of aphids per 20 cylindrical-shaped leaves was used as an index of aphid density on the peach tree. During the study season, the aphids were counted 19 times.

RESULTS

Seasonal changes in the number of the lady beetles and the aphids

Both the lady beetle and aphid populations peaked twice, in late May and late June (Fig. 1). The patterns of changes in the number of the lady beetles and the aphids were synchronized.

Mortality due to sibling and non-sibling cannibalism in egg stage

Out of all *H. axyridis* eggs laid ($n=2269$), 39.14% ($n=888$) successfully hatched, 24.76% ($n=562$) were killed by sibling cannibalism and 36.10% ($n=819$) by non-sibling cannibalism (Table 1). Thus more than 60% of all the eggs were killed through these two types of cannibalism.

Table 1. Sibling and non-sibling cannibalism which occurred on *H. axyridis* eggs.

	Average eggs/Egg batch Mean ±95% C. L.	Total
Egg batch size	28.36±2.88	2269
No. of eggs successfully hatched	11.06±2.40	888 (39.14%)
No. of eggs killed by cannibalism	17.30±2.70	1381 (60.86%)
by sibling cannibalism	7.04±2.00	562 (24.76%)
by non-sibling cannibalism	10.26±3.10	819 (36.10%)

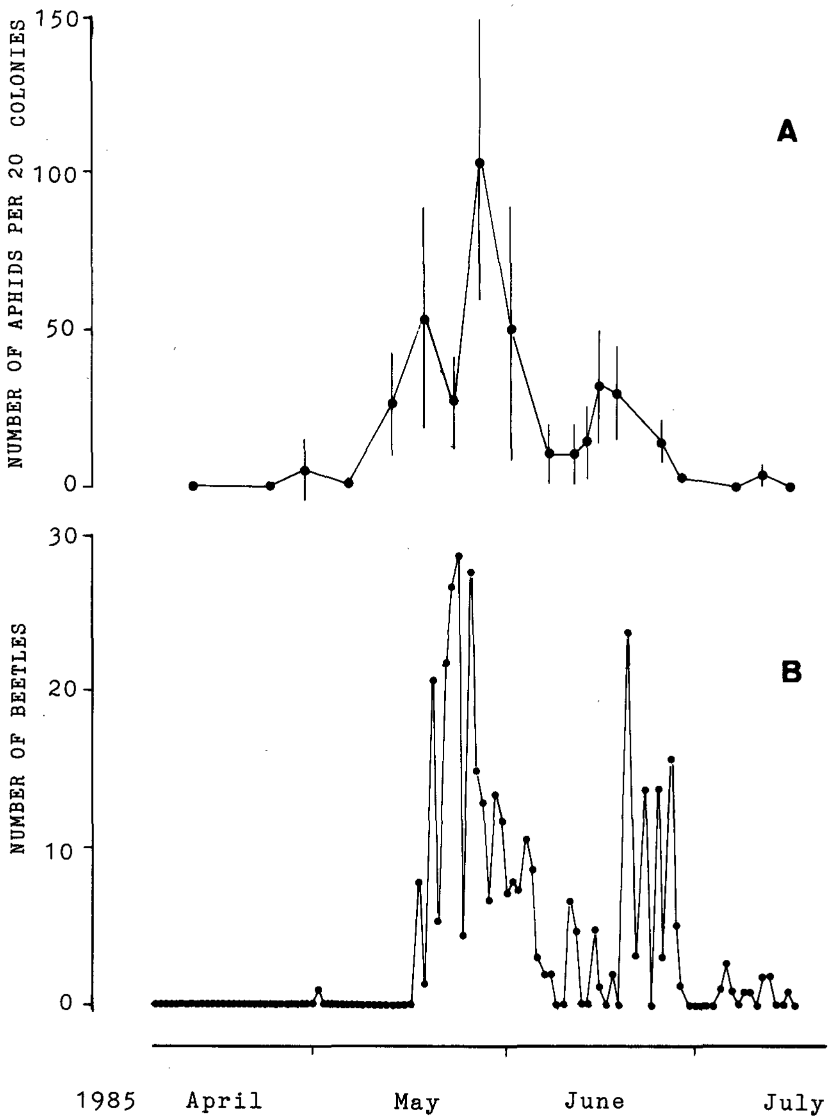

Fig. 1. Seasonal changes in the number of (a) the aphid *M. varians* and (b) the lady beetle *H. axyridis*. Vertical lines indicate 95% C. L.

Effects of ecological conditions on sibling and non-sibling cannibalism

Timing of oviposition. Figure 2 shows seasonal changes in the number of *H. axyridis* eggs found during each census. There were two distinct oviposition periods: in late May (I in Fig. 2) and in late June (II in Fig. 2). However, the number of eggs laid in late June was so small (10.67% of all eggs) that they were excluded from further analysis. To study the effect of timing of oviposition both on sibling and non-sibling cannibalism during oviposition period I, this period (16 days) was divided into 3 sections: the first 5 days (early period: May 17-21), the next 5 days (middle period: May 22-26), and the last 6 days (late period: May 27-June 1) (Fig. 2.).

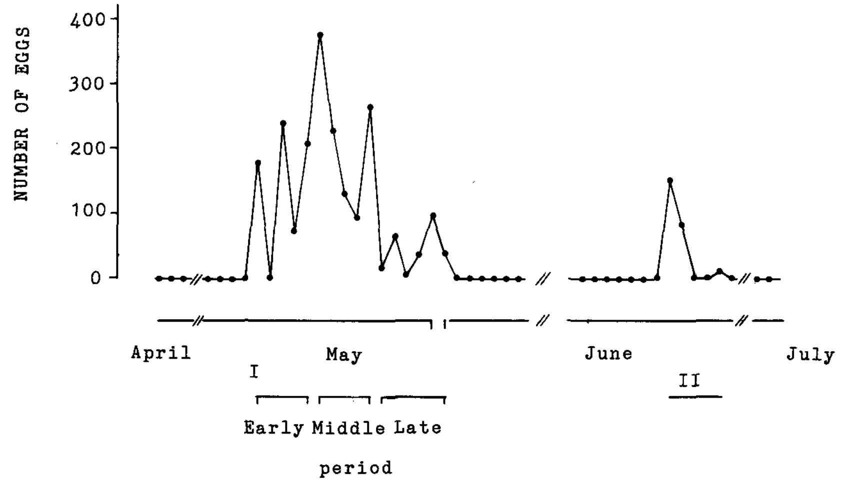

Fig. 2. Seasonal changes in the number of *H. axyridis* eggs. The oviposition period I was divided into 3 categories: the early period (the first 5 days: May 17–21), the middle period (the next 5 days: May 22–26) and the late period (the last 6 days: May 27–June 1).

Table 2 shows the percentage of eggs cannibalized by siblings and that by non-siblings per egg batch during each of the 3 oviposition periods. Intensity of sibling cannibalism in the 3 oviposition period were similar ($P>0.05$). However, non-sibling cannibalism was significantly ($P<0.0001$) more intense in the middle than the early oviposition period and significantly ($P<0.05$) more intense in the middle than the late oviposition period. Thus the later the oviposition period, the more intense was the

Table 2. Comparisons of percentages of eggs cannibalized by siblings and non-siblings per egg batch among the 3 oviposition periods.

Oviposition period	No. of egg batches	% sibling cannibalism Mean±S. E.		No. of egg batches	% non-sibling cannibalism Mean±S. E.		
Early period (May 17–21)	22	38.56±4.14	ns	24	9.09± 5.77	**	**
Middle period (May 22–26)	18	33.67±4.12		37	56.10± 7.78	*	
Late period (May 27–June 1)	1	36.84		10	90.00±10.00		

* *significant at* $P=0.05$, ** significant at $P=0.01$, ^{ns} not significant at $P=0.05$, from *t*-test

Table 3. Frequency of egg batches cannibalized during each of the 3 oviposition periods.

	No. of egg batches	Sibling cannibalism % Occurrence (95% confidence limit)	No. of egg batches	Non-sibling cannibalism % Occurrence (95% confidence limit)
Early period (May 17–21)	22	100.00 (87.35–100.00)	24	12.50 (2.68–31.61)
Middle period (May 22–26)	18	94.44 (73.33– 99.86)	37	64.86 (49.28–79.36)
Late period (May 27–June 1)	1	100.00	10	90.00 (55.50–99.75)

Table 4. Relationships between the direct distance from an egg batch to the nearest aphid colony and percentages of eggs cannibalized by siblings and non-siblings per egg batch.

Distance*	No. of egg batches	% sibling cannibalism Mean±S. E.		No. of egg batches	% non-sibling cannibalism Mean±S. E.	
≤10 cm	11	40.08±5.62	ns	24	56.04±10.04	*
>10 cm	39	35.96±3.01		56	33.02± 6.12	

* significant at $P=0.05$, ^{ns} not significant at $P=0.05$, from t-test

* Direct distance from an egg batch site to the nearest aphid colony

Table 5. Frequency of egg batches cannibalized in relation to the direct distance from an egg batch to the nearest aphid colony.

Distance*	No. of egg batches	Sibling cannibalism % Occurrence (95% confidence limit)	No. of egg batches	Non-sibling cannibalism % Occurrence (95% confidence limit)
≤10 cm	11	100.00 (76.46–100.00)	24	62.50 (42.93–80.79)
>10 cm	39	97.43 (86.75– 99.94)	56	37.50 (24.61–49.75)

* See Table 4.

non-sibling cannibalism.

Table 3 shows percentage of egg batches in which the two types of cannibalism occurred at the 3 oviposition periods. Percentage of egg batches in which sibling canniblism occurred was not significantly ($P>0.05$) different between the early and middle oviposition periods. On the other hand, percentage of egg batches in which non-sibling cannibalism occurred significantly ($P<0.05$) increased from the early to the middle oviposition period. Thus sibling cannibalism occurred constantly throughout the entire oviposition period nearly on all the egg batches, whereas non-sibling cannibalism was rare during the early oviposition period but it became more intense at the middle and late oviposition periods.

Effects of distance from egg batch to aphid colony on cannibalism. Percentage of eggs cannibalized in each egg batch was compared in relation to the distance between the egg batch site and the nearest aphid colony. The distance was divided into 2 classes at the point of 10 cm. No significant ($P>0.05$) difference was found in the average percentage of eggs cannibalized by siblings between those egg batches which were shorter and those longer than 10 cm from the aphid colony. However, non-sibling cannibalism was significantly ($P<0.05$) more intense for egg batches which were closer to the aphid colony (Table 4).

The percentage of egg batches in which sibling cannibalism occurred did not differ significantly ($P>0.05$) between the egg batches which were shorter and longer than 10 cm from the aphid colony (Table 5). But the percentage of non-sibling cannibalism was nearly twice higher in the egg batches which were closer to the aphid colony, although the difference was not significant ($P>0.05$) (Table 5).

Thus, although, sibling cannibalism occurred regardless of the distance from an egg batch to the nearest aphid colony, non-sibling cannibalism tended to occur more intensely in the egg batches which were close to the aphid colony.

DISCUSSION

Although a number of studies have reported both sibling cannibalism (DIXON, 1959; PIENKOWSKI, 1965; BROWN, 1972; KAWAI, 1978; KAWAUCHI, 1985) and non-sibling cannibalism (BANKS, 1955; MILLS, 1982) in coccinellids, the ecological conditions under which these two type of cannibalism occurred have hardly been examined (FOX, 1975; POLIS, 1981)

This study showed that sibling cannibalism occurred almost constantly in most egg batches throughout the entire oviposition period, regardless of the site of an egg batch. Sibling cannibalism seems to occur mainly due to two reasons; asynchronization of hatching time among eggs and existence of infertile eggs in an egg batch. These are supported by the laboratory study of KAWAI (1978) which showed that 27.3% of *H. axyridis* eggs were killed by early-hatched larvae of siblings, of which 12.1% were fertile eggs and the rest were infertile eggs. Sibling cannibalism will enhance the successful development of first instar larvae of cannibals to their next stage. The same conclusion was drawn by KAWAI (1978).

No previous study has clarified why non-sibling cannibalism occurs in coccinellids. I showed that non-sibling cannibalism occurs more intensely in the egg batch which was laid in the middle and late oviposition periods, and those which were close to an aphid colony. This seems to be due to the higher density of coccinellid larvae relative to aphid density in the middle and late oviposition periods. The first instar larvae, after feeding an aphid, tend to stay continuing intensive searching nearby (KAWAI, 1976) while not discriminating between aphids and coccinellid eggs (KAWAI, 1978), and my observation shows that 51.4% of non-sibling cannibalism was by the first instar larvae. Thus the occurrence of non-sibling cannibalism is greatly affected by these ecological conditions, which, however, is not the case in sibling cannibalism.

The present study shows that a female *H. axyridis* lays an egg batch apart from an aphid colony, but this will make the searching by newly-hatched larvae more difficult. However, this strange oviposition habit by coccinellids can be understood, if there is an intense non-sibling cannibalism near an aphid colony.

SUMMARY

Sibling (cannibalism among siblings) and non-sibling cannibalism (cannibalism among non-siblings) were studied in a natural population of a lady beetle, *Harmonia axyridis* PALLAS.

Of all the eggs laid ($n=2269$), 24.76% ($n=562$) were killed by sibling cannibalism

and 36.10% (n=819) were killed by non-sibling cannibalism. Sibling cannibalism occurred constantly and intensively in most egg batches throughout the entire oviposition period. On the other hand, non-sibling cannibalism was more intense in the middle and late oviposition periods, and when the egg batches were close to an aphid colony. This may be due to the high density of *H. axyridis* larvae relative to aphid density in the middle and late oviposition periods and also the larvae searching intensively near an aphid colony.

ACKNOWLEDGMENTS: I am deeply indebted to Drs. T. NISHIDA and A. TAKAFUJI and Mr. P.-M. SO of Kyoto University for their helpful comments to improve this manuscript and correct the English. I am also indebted to Prof. E. KUNO of Kyoto University for his valuable suggestions and continuous encouragement during this study. I am grateful to Drs. T. INOUE and N. OHSAKI of Kyoto University and Dr. F. NAKASUJI of Okayama University for their valuable suggestions. Thanks also to Dr. H. TAKADA, Kyoto prefectural University, for his indentification of aphid species, Prof. S. KUROIWA, Kyoto University for permitting me to conduct this study in the Botanical Garden of Kyoto University, and Mr. T. KAKUTANI of Kyoto University for his help in statistical analysis by the computer, FACOM-M780/30 at the Data Processing Center, Kyoto University.

REFERENCES

BANKS, C. J. (1955) An ecological study of Coccinellidae (Col.) associated with *Aphis fabae* SCOP. on *Vicia faba*. *Bull. Ent. Res.* **46**: 561–587.

BROWN, H. D. (1972) The behavior of newly hatched coccinellid larvae. *J. Ent. Soc. So. Afr.* **35**: 149–157.

COLINVAUX, P. A. (1973) *Introduction to ecology*. Wiley, New York.

DIXON, A. F. G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* **28**: 259–281.

FOX, L. R. (1975) Cannibalism in natural populations. *Ann. Rev. Ecol. Syst.* **6**: 87–106.

HAMILTON, W. D. (1964) The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**: 1–16.

KAWAI, A. (1976) Analysis of the aggregation behaviour in the larvae of *Harmonia axyridis* PALLAS (Coleoptera: Coccinellidae) to prey colony. *Res. Popul. Ecol.* **18**: 123–134.

KAWAI, A. (1978) Sibling cannibalism in the first instar larvae of *Harmonia axyridis* PALLAS (Coleoptera; Coccinellidae). *Kontyû* **46**: 14–19.

KAWAUCHI, S. (1985) Comparative studies on the fecundity of three aphidphagous coccinellids (Coleoptera; Coccinellidae). *Jpn. J. Appl. Ent. Zool.* **29**: 203–209. (in Japanese with English summary)

MILLS, N. J. (1982) Voracity, cannibalism and coccinellid predation. *Ann. Appl. Biol.* **101**: 144–148.

PIENKOWSKI, R. L. (1965) The incidence and effect of egg cannibalism in first-instar *Coleomegilla maculata lengi* (Coleoptera; Coccinellidae). *Ann. Ent. Soc. Amer.* **58**: 150–153.

POLIS, G. A. (1981) The evolution and dynamics of interspecific predation. *Ann. Rev. Ecol. Syst.* **12**: 225–251.

SASAJI, H. (1971) *Fauna japonica coccinellidae* (Insects; Coleoptera). Academic Press of Japan, Tokyo.

ナミテントウ自然個体群における同胞の幼虫による共食いと他卵塊由来の幼虫による共食い

大沢直哉

ナミテントウ幼虫の卵の共食い（egg cannibalism）を，同胞の幼虫による共食い（sibling cannibalism）と，他卵塊由来の幼虫による共食い（non-sibling cannibalism）に区別し，それぞれの生じる頻度を野外個体群で調査した．全産卵数（$n=2269$）の内，24.76%（$n=562$）が，同胞による共食いによって，36.10%（$n=819$）が，他卵塊由来の幼虫による共食いによって死亡した．

2種類の共食いの頻度をそれぞれ産卵時期別，及び産卵場所からアブラムシのコロニーまでの距離別に比較した．同胞による共食いの頻度は，産卵期間を通して，又アブラムシのコロニーまでの距離にかかわりなく一定であった．一方他卵塊由来の幼虫による共食いの頻度は，産卵期間前期には低く，中期・後期には高かった．また産卵場所がアブラムシのコロニーから10 cm以下の場合の方が10 cmより大きい場合より高かった．この現象は，産卵期間の中・後期に餌密度に比べてテントウムシ幼虫の密度が高いことと，幼虫がアブラムシのコロニー近傍で餌を探索することの2つの理由によるものと思われる．