

POPULATION FIELD STUDIES OF THE APHIDOPHAGOUS LADYBIRD
BEETLE *HARMONIA AXYRIDIS* (COLEOPTERA: COCCINELLIDAE):
LIFE TABLES AND KEY FACTOR ANALYSIS

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SUMMARY

1) Life tables of the predatory ladybird beetle *Harmonia axyridis* were analysed by taking samples from twenty or twenty four sites colonized by eight species of aphids for two years.

2) Larval mortality was a key factor in the *H. axyridis* populations. Mortality of all the stages tended to be density-dependent when life cycles were divided into four developmental stages, except in the case of mortality at hatching due to sibling cannibalism.

3) Sibling and non-sibling cannibalism played an important role on population stability and persistence.

KEYWORDS: Cannibalism, density-dependence, *Harmonia axyridis*, key factor analysis, ladybird beetle, life table, polyphagous predator.

INTRODUCTION

Many entomological studies have focused on natural enemies as a regulatory mechanism for insect prey populations (e.g. Varley et al., 1973; Dempstar, 1975). Some authors emphasized parasitism or predation as an important biological factor in the control of prey populations (e.g. Hagen, 1962; Hariston et al., 1960; Varley and Gradwell, 1960; Huffaker, 1970; Southwood and Comins, 1976; Hassell, 1976, 1978; Strong et al., 1984), while others took the opposite views (e.g. Kuno and Hokyo, 1970; Dixon, 1971; Dempstar, 1983). This discrepancy may relate to specific population characteristics of different predators in relation to their prey populations. Furthermore, in many studies the main focus was placed on prey populations and the role of predation was only treated in the context of density-dependence (e.g. Huffaker et al., 1971; Stiling, 1987, 1988). Thus, to clarify the population characters of an insect predator, there is a clear need for detailed population studies of insect predators, particularly polyphagous species which would interact with many prey species.

In some predators including the coccinellid species, egg cannibalism occurs frequently (Hodek, 1973; Osawa, 1989; Stevens, 1992), which inevitably has implica-

tions for predator population dynamics. However, no field study has clarified the role of egg cannibalism on a population in coccinellids. For in other animal taxa, some authors (e.g. Brinkhurst, 1960; Dueli, 1978; Polis, 1980, 1981; Leonardsson, 1991) suggested that cannibalism may play an important role in maintaining population stability and stable age structures, while others indicated that cannibalism may destabilize populations, often causing cycles (e.g. Orr et al., 1990). Thus, further investigation is necessary to clarify the role of cannibalism, particularly in relation to the population characteristics of a predator.

This study attempts to elucidate the population characteristics of the Asian polyphagous ladybird beetle *Harmonia axyridis* and the role of egg cannibalism on the population through life table analyses.

MATERIALS AND METHODS

Field Observations

Ladybird beetle. All the observations were made in the Botanical Garden, Kyoto University (N35°02'W135°47') (Fig 1). The different stands of plants and colonizing

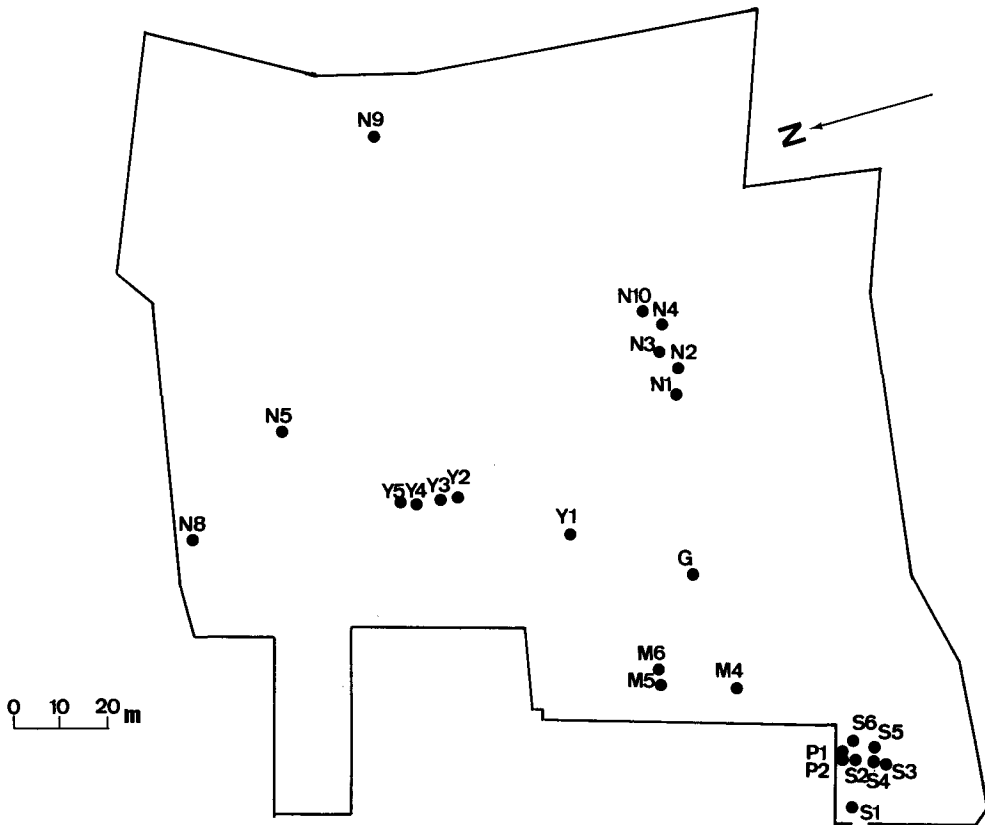
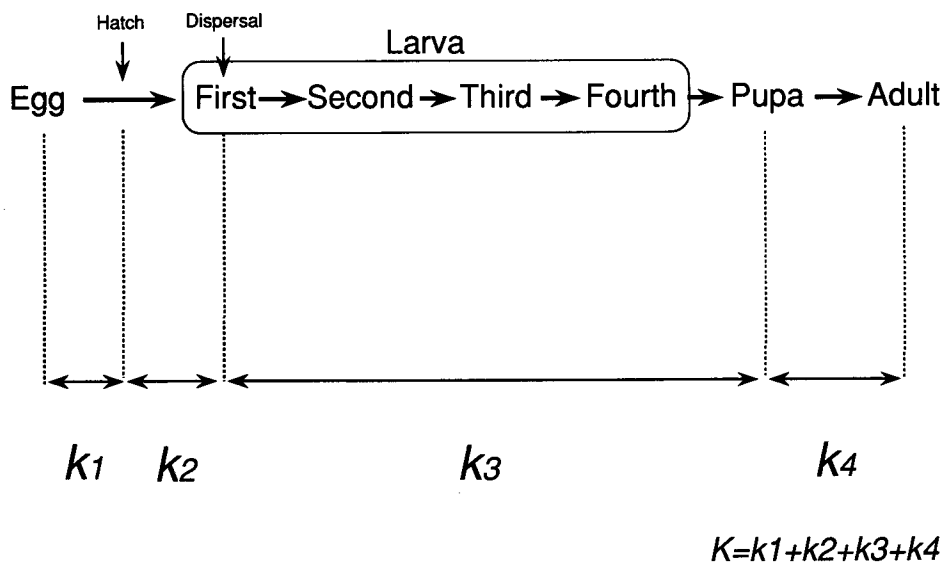


Fig. 1. A map of the Botanical Garden, Kyoto University and the sites of stand plants.

Table 1. Stands of plants and colonizing aphid species in the Botanical Garden.

Site	Host plant	Aphid species
S1-S6	<i>Spiraea thunbergii</i>	<i>Aphis spiraeicola</i>
P1-P2	<i>Spiraea blumi</i>	<i>Aphis spiraeicola</i>
M4-M6	<i>Prunus persica</i>	<i>Myzus varians</i> <i>Hyaloperous pruni</i>
G	<i>Typha angustifolia</i>	<i>Schizaphis acori</i>
Y1	<i>Salix sieboldiana</i>	<i>Aphis farinosa yanagikola</i> <i>Tuberolachnus salignus</i>
Y2-Y5	<i>Salix koriyanagi</i>	<i>Chaitophorus horii</i> <i>Tuberolachnus salignus</i>
N1-N10	<i>Sambucus racemosa</i>	<i>Aulacorthum magnolidae</i>

aphid species are listed in Table 1. In spring and summer of 1987 and 1988, all the egg batches found in the all study sites were marked with numbered red vinyl tapes and the number of eggs in each egg batch was counted on a daily basis. The eggs were checked for whether cannibalization by larvae from another egg batch (non-sibling cannibalism) or hatching successfully. When the eggs hatched, newly hatched-larvae usually remained together at the oviposition site for about 24 hours, during which early hatched larvae cannibalized unhatched fertile and/or infertile eggs in the same egg batch (sibling cannibalism). Similarly, all the pupae were marked with numbered red vinyl tapes and checked daily whether they emerged successfully or not. Unsuccessful emergence was caused by either cannibalism by older larvae or parasitism by *Phalacrotophora* sp., the only species of parasitoid fly observed in the study area (see Osawa, 1992a). Cannibalism and parasitism were distinguished by the existence of

Fig. 2. Developmental stages of *H. axyridis* and the relationship between K and K_j .

an emergence hole of the parasitoid (see also Osawa, 1992a).

Aphids. The aphids were counted for the same sites of *H. axyridis* research in 1987 and 1988. Of all the host plants, the number of aphids was counted once or twice a week. In the sites where the colony's borderlines were distinct, the total number in the colony was counted. At the same time, 50 colonies were randomly sampled from the site and the number of aphids in the colony was counted without distinction of adult and larva. Then, the number of aphids from all the site was estimated by the equation:

$$N_A = N_C \times N_{AC}$$

where N_A is number of aphids, N_C number of colonies, and N_{AC} number of aphids per colony.

For the other sites, where colonies were borderless or smaller (usually the density was under 1000), the total number of aphids was directly counted. And the maximum number of aphids per site was used in this analysis.

Key Factor Analysis

To elucidate the mechanisms of *H. axyridis* population change, key factor analysis (Varely and Gradwell, 1960) was performed. This method allows the evaluation of mortalities at different stages of the life cycle, i.e. how much each stage contributes to total mortality. Furthermore, the regression coefficient should be used for the determination of a key factor (Podler and Rogers, 1975). Analysis was done with reference to four developmental stages in *H. axyridis*: k_1 mortality (from egg to hatching), k_2 mortality (from hatching to dispersal of the first instar larva), k_3 mortality (from dispersal of the first instar larva to pupa) and k_4 mortality (from pupa to adult emergence) (Fig. 2). In Varley and Gradwell (1960), k_J (mortality at stage J) was defined as:

$$k_J = \log N_J - \log N_{J+1}$$

However, k_J cannot be calculated when N_J or N_{J+1} is zero. In the *H. axyridis* populations, N_{J+1} often becomes zero, and this is thought to be common among many insect populations. Therefore, in this paper k_J was defined as:

$$k_J = \log (N_J + 1) - \log (N_{J+1} + 1)$$

RESULTS

Life Table

Table 2 shows the life tables of *H. axyridis* on different stands of plants in the Botanical Garden. Sixteen percent of all the eggs (P: P1 and P2 were combined, in 1988) survived to the adult stage on *S. blumei*, while under 2 percent of all the eggs emerged on *P. percica* (M5 and M6) and *S. koriyanagi* (Y2 and Y3), though many eggs

Table 2. Life tables of *H. axyridis* on different plants.

1987

Stage/ dxF/	Site/ G	M4	M5	M6	N1	N4	S1	S2	S6	Y1	Y2	Y3	Y4	Y5
Egg	100	100	3145	1279	45	56	28	24	25	23	885	134	143	215
Cannibalism by non-sibling	60	68	1503	629	19	14	10	14	7	17	561	73	112	136
by sibling	53	56	465	298	0	0	0	0	0	0	285	23	81	29
Miscellaneous death	7	12	1038	331	19	14	10	14	7	17	276	50	31	107
First instar larva	20	0	5	70	8	0	0	0	0	0	13	0	0	0
Pupa	20	32	1637	580	18	42	18	10	18	6	311	61	31	79
Parasitism	13	0	78	21	0	0	0	0	0	0	5	5	0	0
Cannibalism	0	0	5	0	0	0	0	0	0	0	1	0	0	0
Adult	0	0	11	1	0	0	0	0	0	0	0	0	0	0
% Adult emergence/Total eggs	13.0	0	2.0	1.6	0	0	0	0	0	0	0.5	3.7	0	0

1988

Stage/ dxF/	Site/ G	M4	M5	M6	N1	N3	N5	P	S2	S5	S6	Y1	Y2	Y3	Y5
Egg	30	171	978	414	15	22	191	62	18	18	26	54	515	1106	42
Cannibalism by non-sibling	5	70	519	235	0	6	71	40	9	11	8	17	349	619	27
by sibling	0	0	238	128	0	0	10	25	0	0	0	0	155	329	0
Miscellaneous death	5	70	281	107	0	6	61	15	9	11	8	17	194	290	27
First instar larva	0	3	40	0	15	7	0	1	0	0	0	0	0	0	0
Pupa	25	98	419	179	0	9	120	21	9	7	18	37	166	487	15
Parasitism	5	3	4	5	0	0	0	16	0	0	0	0	10	16	0
Cannibalism	1	1	0	0	0	0	0	4	0	0	0	0	2	3	0
Adult	0	1	0	1	0	0	0	2	0	0	0	0	2	6	0
% Adult emergence/Total eggs	4	1	4	4	0	0	0	10	0	0	0	0	6	7	0
	13.3	0.6	0.4	1.0	0	0	0	16.1	0	0	0	0	1.2	0.6	0

Table 3. Life tables of *H. axyridis* in the Botanical Garden.

Stage	<i>dx_f</i>	<i>lx</i>	<i>dx</i>	100 <i>qx</i>
1987				
Egg		6202		
	Cannibalism		3223	52.0
	by non-sibling		1290	20.8
	by sibling		1933	31.2
	Miscellaneous death		116	1.9
	<u> Total</u>		3339	53.9
First instar larva		2863		
			2741	95.7
Pupa		122		
	Parasitism		6	4.9
	Cannibalism		12	9.8
	<u> Total</u>		18	14.7
Adult		104		
1988				
Egg		3629		
	Cannibalism		1977	54.5
	by non-sibling		876	24.1
	by sibling		1101	30.1
	Miscellaneous death		66	1.8
	<u> Total</u>		2043	56.3
First instar larva		1610		
			1551	97.8
Pupa		59		
	Parasitism		11	18.6
	Cannibalism		12	20.3
	<u> Total</u>		23	38.9
Adult		36		

were laid on these plants. In *S. racemosa* (N1, N3, N4, N5 and N8) and *S. thunbergii* (S1, S2, S5 and S6) no pupa was observed, although eggs were laid (Table 2).

Table 3 shows the life tables of *H. axyridis* in the Botanical Garden as a whole population. The mortality of the larval stage was the highest (96%) in both years. Half of the all eggs were killed by cannibalism, of which about 20 % were by non-sibling cannibalism and about 30 % by sibling cannibalism. Mortality factors in the pupal stage were cannibalism and parasitism: 4.9 % in 1987 and 18.6 % in 1988 were killed by parasitism, while 9.8 % in 1987 and 20.3 % in 1988 were killed by cannibalism.

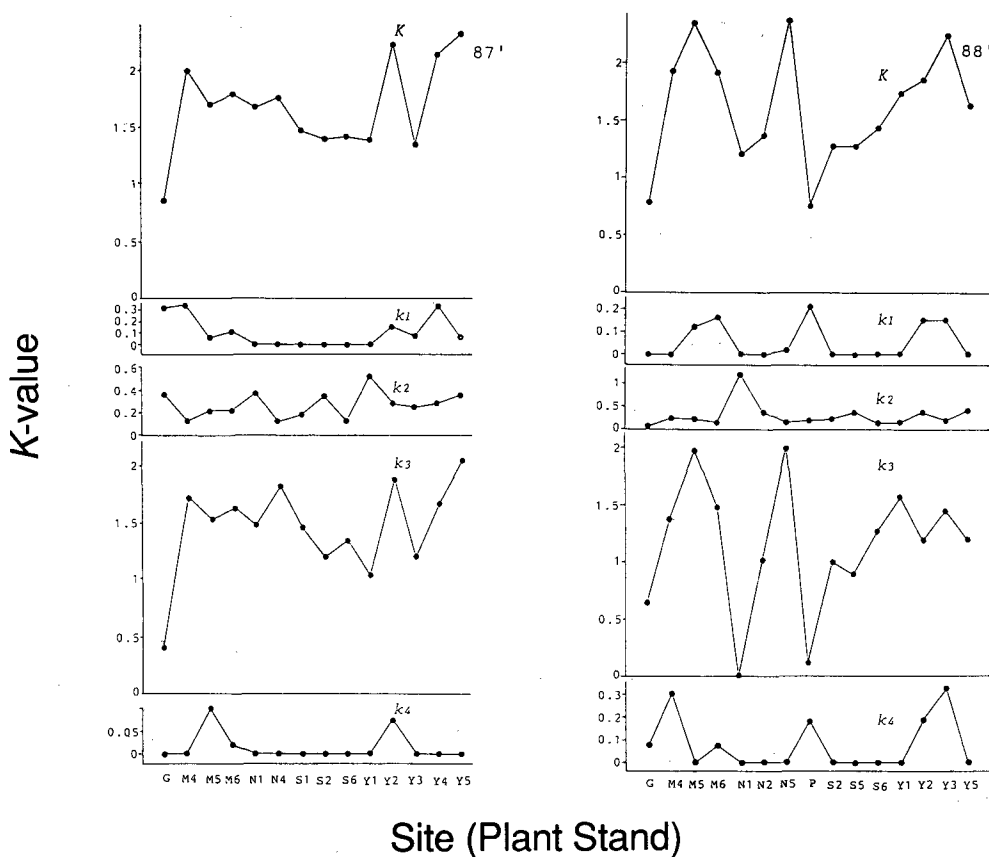


Fig. 3. Relationship between total mortality and mortality at each developmental stage.

Key Factor Analysis and ANOVA of Larval Mortality

Figure 3 shows total mortality rate K and the contributions of each component k_j on different host plants. A positive and strong relationship was observed between K and k_3 ($K=0.86k_3+0.63$, $r^2=0.94$, in 1987; $K=0.99k_3+0.56$, $r^2=0.89$, in 1988), suggesting that the key factor in *H. axyridis* population was the mortality of the larval stage. The species of host plants, the maximum number of aphids per site and their interaction significantly affected the larval mortality (Table 4).

Density-Dependence of Stage Specific Mortality

To clarify the density-dependence of mortality factors at each stage, the relation-

Table 4. ANOVA of the larval mortality.

Source	d.f.	SS	F	P
Species of host plants (S)	5	0.056	23.28	0.0001
Maximum number of aphids (M)	1	0.062	129.38	0.0001
S*M	5	0.101	42.03	0.0001

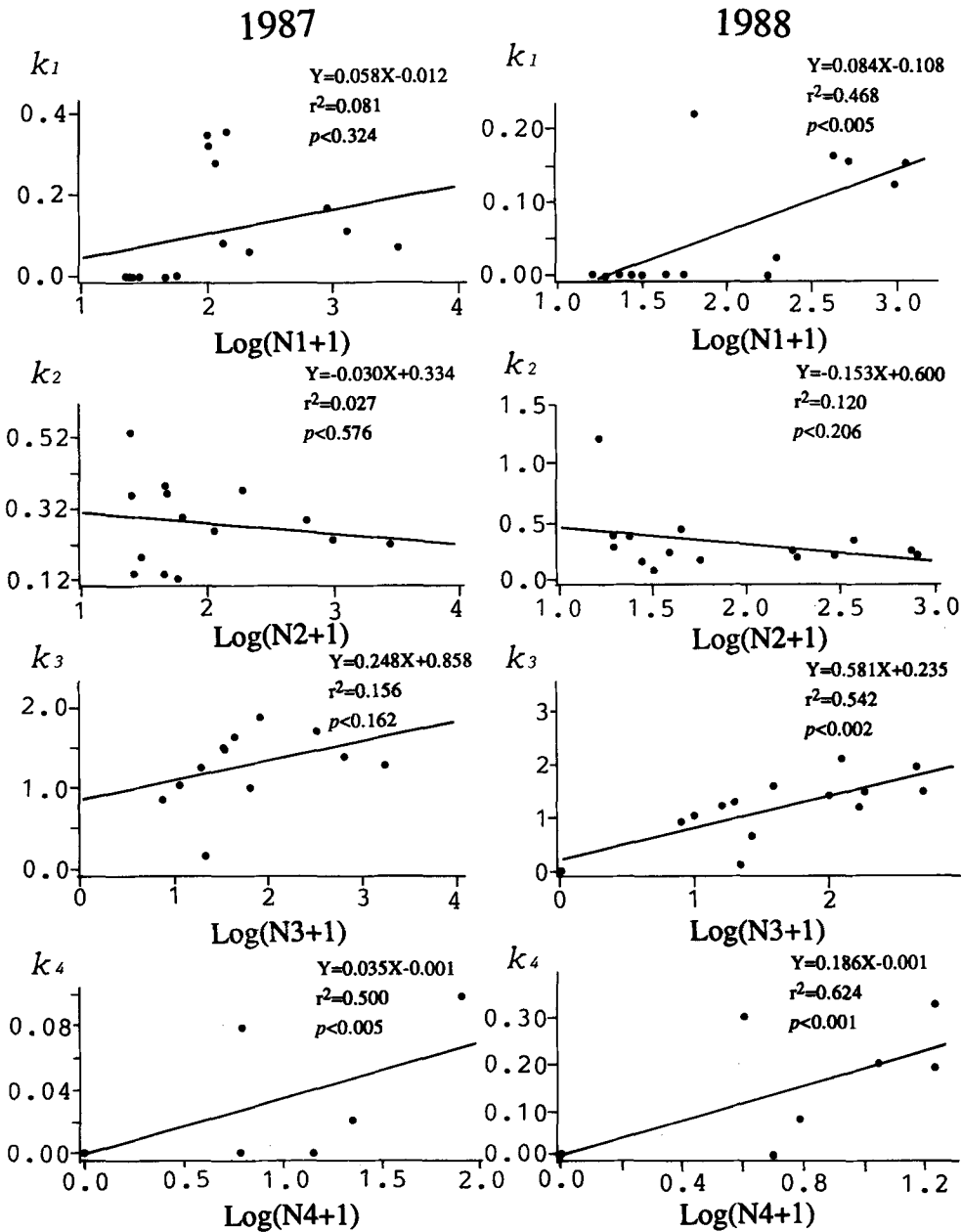


Fig. 4. Relationship between number of individuals (N_j) and mortality rate (K_j) at different stages ($J=1$ to 4).

ship between mortality and the number of individuals in each stage was analysed (Fig. 4). Significant density-dependence was found in pupal mortality in 1987 and egg, larval and pupal mortalities in 1988, suggesting the operation of self-regulatory mechanisms in *H. axyridis* populations. On the other hand, it is notable that mortality due to sibling cannibalism was density-independent in both years.

DISCUSSION

Key Factor Analysis and Density-Dependent Mortality

The present study revealed that larval mortality was a key factor in the *Harmonia axyridis* populations. Osawa (1989, 1991) suggested that the oviposition of *H. axyridis* was concentrated in the habitat a little before the aphid density peaked. The mortality of younger stage larvae was rather high (Osawa, 1991) because the prey searching and capturing ability of younger larvae was low (Kawai, 1978), even when aphid density in a total habitat was high. Additionally, the distribution pattern of prey aphids was concentrated in the habitat, reflecting that younger larvae cannot easily find their prey. Osawa (1992c) demonstrated that the larval mortality in the fourth instar was the highest due to a rapid decrease of absolute aphid density. Furthermore, neither a strong parasitoid nor predator was known in the larval stage of coccinellids (Hodek, 1973). Therefore, low prey searching and capturing ability in younger instar and absolute food shortage in fourth instar were thought to be important for the occurrence of larval death, resulting in the maximum aphid density significantly affecting larval mortality in this study (Table 4). Moreover, the level of predation upon herbivorous insects may depend upon plant architecture (Carter et al., 1984; Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992), reflecting that species of host plants also affected the larval mortality in this study. Additionally, *H. axyridis* females had depressed ovary development, and the larvae were dead when they were fed *A. magnolidae* (Okamoto, 1978), suggesting that the aphid quality as food influences the mortality.

Mortality in many insects was more likely to perturb densities away from a mean level than to be density-dependent and act to return populations to equilibrium (Stiling, 1988). However, this study showed that most mortality factors were density-dependent, except for mortality due to sibling cannibalism. The density-dependence of larval mortality in *H. axyridis* may have been caused by the following phenomena: (i) Adult arrival and oviposition were concentrated in patchily distributed favourable habitats before the aphid density peaked; (ii) Food requirement of *H. axyridis* larvae increased with developmental stages; (iii) The number of aphids decreased from habitat deterioration by crowding and winged aphid dispersal. These factors may have led to a relative food shortage for the larvae of *H. axyridis*, resulting in density-dependent mortality.

In aphidophagous ladybird beetles, both reluctance in oviposition and increased activity of females enhanced the ability of these predators to oviposit at particularly favourable sites (Evans and Dixon, 1986). Recently, it has also been revealed that gravid females use the presence of conspecific larvae to assess the potential of an aphid colony for supporting the development of their offspring (Hemptinne et al., 1992). A combination of these behaviours may lead to the aggregation of eggs in some favourable habitats and, consequently, intraspecific competition among larvae and density-

dependent mortality. In *H. axyridis*, the fourth instar larvae require more than hundred times as much food as the first instar (Mogi, 1968). This result shows that density-dependent mortality based on relative food shortage may easily occur in the older instars. It is known for aphids that the crowding experienced by nymphs is not only responsible for adult morph determination (= winged morph production) but also for migratory behaviours (Robert, 1987). Accordingly, winged aphids emerged and dispersed to the secondary host just after aphid density peaked. Additionally, growth and development rates rapidly decreased in response to crowding (Chambers et al., 1985). Thus, intraspecific competition for prey aphids caused by an increase in the food requirement of *H. axyridis* larvae, and the crowding and dispersal of aphids may have induced density-dependent processes in the larval stage of *H. axyridis*.

The Role of Egg Cannibalism in the *H. axyridis* Population

This study showed that egg cannibalism was the second important mortality factor in *H. axyridis* populations; more than 50% of the eggs was killed by cannibalism, among which 30% was caused by sibling and 20% by non-sibling. Cannibalism has been reported for many animal species (Fox, 1975; Polis, 1981; Elgar and Crespi, 1992) and egg cannibalism was often observed in ladybird beetles (Hodek, 1973). However, explanation of the adaptive significance of egg cannibalism has been confused, for two major reasons: i) kin relatedness between a cannibal and a victim was ignored when cannibalism was interpreted on an individual level, and ii) less attention was paid to the level of the interpretation of cannibalism: individuals or populations level. Osawa (1992b) analysed sibling cannibalism in *H. axyridis* with respect to three possible beneficiaries in the kin relationship: the cannibal, the victim and the mother. Sibling cannibalism was adaptive both for a cannibal and a victim, and the mother attained equal fitness regardless of the percentage of sibling cannibalism at low aphid densities (Osawa, 1992b). In the case of non-sibling cannibalism, a cannibal received a one-sided benefit to increase its own survival rate, though females tended to lay eggs away from the aphid colonies to escape non-sibling cannibalism (Osawa, 1989).

The first instar larvae of *H. axyridis* could moult to the second instar in one day after eating three conspecific eggs (Kawai, 1978), c. 2/3 reduction in time compared with a non-cannibal situation. While, the mortality of the fourth instar larvae, which was due to a rapid decrease in aphid density, was the highest in the *H. axyridis* population (Osawa, 1992c). Therefore, fourth instar larvae may shorten the larval period and escape severe food shortage by feeding on conspecific eggs, suggesting that egg cannibalism may help population persistence. Furthermore, sibling cannibalism may play a more important role in a population because i) more eggs were eaten in sibling cannibalism than those in non-sibling cannibalism, and ii) sibling cannibalism occurred in more than 90% of the eggs (Osawa, 1989). Moreover, sibling cannibalism may more effectively increase the cannibal's survival rate because i) all cannibals were just hatched first instar when the prey capturing ability of a larva was

low in sibling cannibalism (Kawai, 1978), while 48.6% of the larvae were second, third, and fourth instar in non-sibling cannibalism (Osawa, 1989), and ii) the cost of a cannibal movement to eat eggs in sibling cannibalism was lower than that in non-sibling cannibalism. This is because as a cannibal larva can safely eat sibling eggs in its own egg batch without a long dispersal, while a cannibal must move to other egg batches in case of non-sibling cannibalism.

Density is a key factor for the frequency of cannibalism in natural populations (Dong and Polis, 1992). Although cannibalism generally increases with density, its effects are not always a clear function of the population density (Dong and Polis, 1992). This study indicated that mortality caused by sibling cannibalism was density-independent, while non-sibling cannibalism was density-dependent. Sibling cannibalism occurs for two reasons; asynchronization of hatching time among eggs and the existence of infertile eggs in an egg batch (Osawa, 1989). Therefore, sibling cannibalism may be caused by internal factors in an egg batch, reflecting density independent mortality. In contrast, there was intense non-sibling cannibalism in the middle and late oviposition periods (Osawa, 1989). This was when the egg batches were close to an aphid colony due to the high density of *H. axyridis* larvae to aphid density and also the larvae were searching intensively near an aphid colony (Osawa, 1989). Therefore, the occurrence of non-sibling cannibalism was influenced by egg and/or larval density (Mills, 1982; Osawa, 1989), resulting in a density-dependent tendency of mortality in this study. This result indicates that non-sibling cannibalism could operate as a population stabilizing mechanism in space. Thus, in *H. axyridis*, sibling and non-sibling cannibalism may cause population persistence and stability.

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アブラムシを捕食するナミテントウの野外個体群に関する研究：
生命表及び変動主要因分析

大澤直哉

- 1) ナミテントウの生命表を、8種のアブラムシの発生した20及び24箇所で2年間作成した。
- 2) 幼虫期の死亡がナミテントウ個体群の変動主要因であった。生活史を4つの段階に分けると、孵化時期の同胞の幼虫による共食いでの死亡以外は、全て密度依存的な傾向が見られた。
- 3) 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は共に、変動する餌条件下で、個体群の安定性や永続性に重要な役割を果たしていた。