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# SIBLING CANNIBALISM IN THE LADYBIRD BEETLE *HARMONIA AXYRIDIS*: FITNESS CONSEQUENCES FOR MOTHER AND OFFSPRING

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## Summary

The adaptive significance of sibling cannibalism was analyzed in the ladybird beetle *Harmonia axyridis* at two prey densities. Possible costs and benefits were considered from three points of view: the mother, the cannibal and the victim. Cannibals ate both infertile and fertile eggs, thereby increasing in body length and survival rate with the intensity of sibling cannibalism. The cannibalistic trait was clearly beneficial to the cannibal when aphid density was low. However, it was not always beneficial when aphid density was high and the victims were full siblings. The altruistic behavior of being a victim was beneficial only when the victim was cannibalized by full siblings at low aphid density. The mother attained almost equal fitness at low aphid density, regardless of the intensity of sibling cannibalism. This suggests that sibling cannibalism is not maladaptive for the mother. At high aphid density, however, mother's fitness decreased with the intensity of sibling cannibalism, indicating that sibling cannibalism is maladaptive for the mother when larval food availability is high.

Keywords: sibling cannibalism, kin selection, fitness, ladybird beetle, *Harmonia axyridis*.

## Introduction

Sibling cannibalism has been reported among many taxonomic groups of animals. This type of predation may act as a delayed regulatory mechanism or it may serve as a nutritional source for young animals (Fox, 1975; Polis, 1980, 1981). In natural populations of arthropods, however, the adaptive significance of sibling cannibalism has been considered mainly in terms of its resultant effects on population stability or persistence (Fox, 1975; Polis, 1980, 1981).

Hamilton (1964a, 1964b) emphasized the evolutionary significance of kinship between a cannibal and its victim. According to Hamilton (1964a, 1964b), the inclusive fitness of an individual will be increased, and the selfish trait selected for if $B/C > 1/r$. In this equation $r$ is the coefficient of relatedness of the two individuals, $B$ is the benefit to the cannibal, and $C$ is the cost to the victim individual. However, empirical field studies on cannibalistic behavior of Arthropods that considered kin relatedness are relatively scarce. Exception is a study on the chrysomelid beetle, *Labidomera clivicollis* (Eickwort, 1973).

Sibling cannibalism may result in three possible beneficiaries: the mother, the cannibal, and the victim (O'Connor, 1978). Additionally it is suggested that the cost and benefit of sibling cannibalism is strongly affected by food stress; sibling cannibalism easily occurs in a scarce food condition, while the reverse is true in a plentiful food condition (Eickwort, 1973; O'Conner, 1978). In order to understand the evolutionary implications of sibling cannibalism, it is essential to examine the consequences of cannibalism from these three different perspectives in different food conditions.

In this study, fitness consequences of sibling cannibalism in the ladybird beetle *Harmonia axyridis* PALLAS (Coleoptera: Coccinellidae) are examined from the viewpoints of the mother, the cannibal, and the victim both in high and low aphid densities, with particular emphasis on the behavior of cannibals.

## MATERIALS AND METHODS

### Laboratory Experiments

*Experiment 1.* Egg fertility and cannibalistic behavior of hatchlings were observed on 9 egg batches laid on 14 April in 1987 by 9 already-mated female ladybird beetle *H. axyridis*. Observations were done at hourly intervals for 8 consecutive hours under laboratory conditions 25°C, 16L-8D on 17 April using a stereomicroscope. A total of 171 first instar larvae emerging from the nine egg batches 24 hours after hatching were killed in 70% alcohol and their body lengths were measured using a stereomicroscope with a micrometer. An egg containing an embryo was regarded as fertile (see Brown 1972). Hatching was defined as the moment when the head of a larva emerged from an egg shell.

*Experiment 2.* To investigate the effects of sibling cannibalism on larval growth, first instar larvae of *H. axyridis* were provided with different number of eggs (0, 1, 2 and 3) in plastic petri dishes (7 cm in diameter) (20 replicates for each food level). Body length of each larva was measured 24 hours after hatching using a stereomicroscope with a micrometer.

### Field Experiments

To examine the effect of sibling cannibalism on larval survival rate, a total of 160 unfed newly-hatched larvae were individually reared under laboratory conditions 25°C, 16L-8D on 20 April 1990. The larvae were provided with different number of conspecific eggs (0, 1, 2 and 3). 24 hours after the beginning of the experiment all larvae were marked by quick drying paint according to the food levels. Eighty larvae

(20 for each food level) were released to the citrus tree, *Citrus unshiu* (50 cm in height), infested by the spirea aphid, *Aphis spiraecola*. It is known that *H. axyridis* females lay eggs about 20 cm-apart from an aphid colony (Osawa, 1991a). Then a 20 cm distance from the nearest aphid colony was kept when the larvae were released. Aphid densities were daily controlled either 300 (low density) or 1200 aphids per tree (high density). From 21 to 25 April and from 6 to 10 May, the number of the first instar exuviae daily collected and its paint colors were checked using a stereomicroscope.

### Definition of Relative Inclusive Fitness

Relative inclusive fitness is here defined as:

$B\text{-}Cr$ for the cannibal;

$Br\text{-}C$ for the victim.

As an approximate measurement of the fitness of the mother, the average survival rates of larvae from the first to second instar were estimated.

$B$ is the increase in survival rate of the cannibal from the first to second instar due to cannibalism and $C$ is the decrease in survival rate of the victim from first to second instar. $r$ is the coefficient of relatedness between the cannibal and the victim.

## RESULTS

### Behavioral Process of Sibling Cannibalism

Figure 1 indicates the positions of infertile and fertile eggs, and foraging tracks of the cannibals during 8 hours observation, in 9 egg batches of *H. axyridis*. Infertile eggs were randomly distributed within an egg batch. Cannibals ate both fertile and infertile eggs but newly-hatched larvae were not eaten. Although cannibals apparently preferred to eat infertile eggs ($\chi^2=60.5$, $d.f.=1$, $p<0.001$), this was probably because of a statistical artifact resulted from the fact that all the unhatched eggs were eaten up.

Figure 2 shows the frequency distribution of larval body length in each egg batch 24 hours after hatching in ascending order of intensity of sibling cannibalism. The frequency distributions of body length were significantly different from normal distribution, and both the average and range of body length increased with the intensity of sibling cannibalism (Table 1).

34.98% ($n=92$) of all eggs ($n=263$) were killed by sibling cannibalism, of which 24.33% ($n=64$) were infertile eggs and 10.65% ($n=28$) were fertile eggs with delayed hatching (Table 2).

### Estimation of Size-Related Survival Rate of Larvae

To investigate whether smaller larvae suffered a higher mortality than larger ones, size-related differences in survival rates were evaluated.

The body length of cannibals was linearly related to the number of eggs consumed in Experiment 2 (Fig. 3).

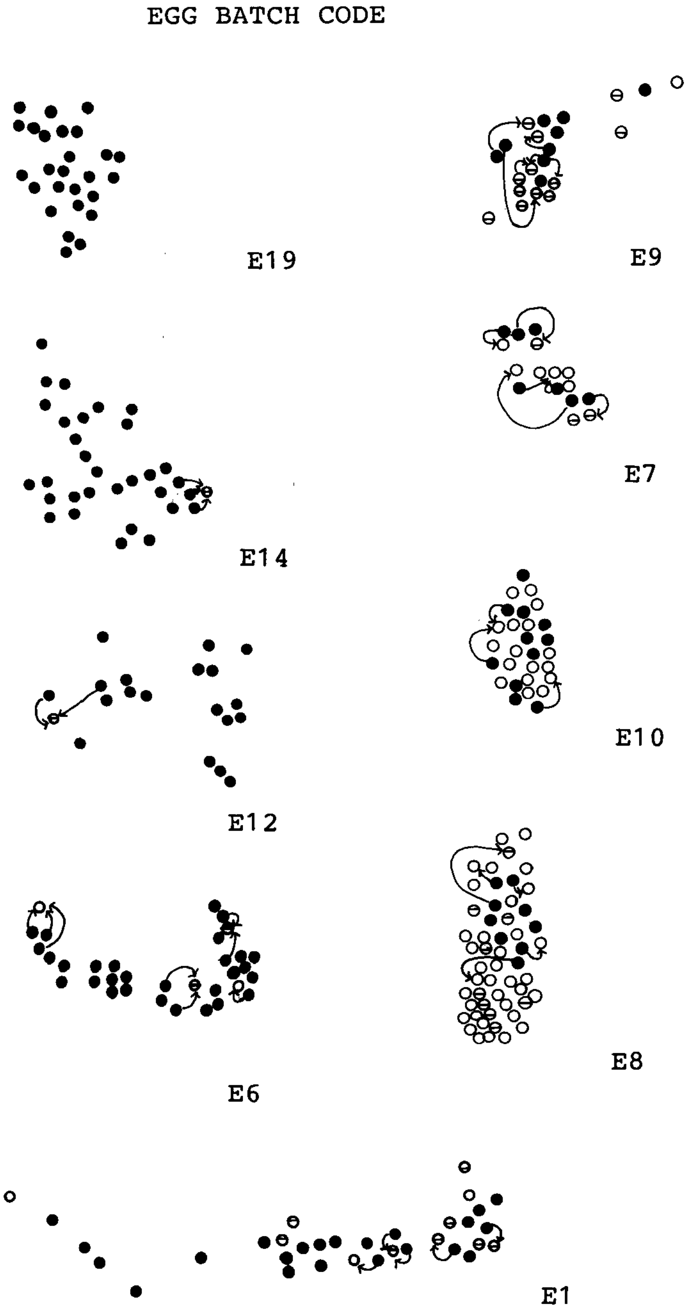

Fig. 1. Diagram showing 9 observed egg batches of *H. axyridis* in which hatching has been observed, 8 hours after hatching. Open circles indicate infertile eggs, closed circles fertile eggs that hatched, and dashed circles fertile eggs with delayed hatching. Arrows indicate feeding routes of cannibalistic larvae.

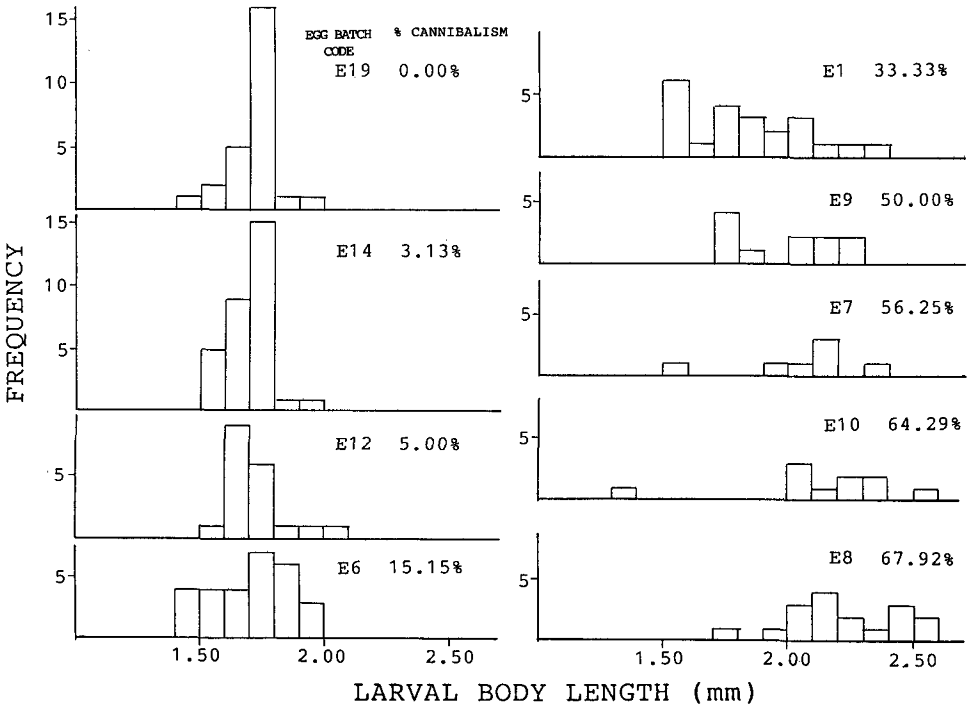

Fig. 2. Frequency distribution of larval body length 24 hours after hatching.

Using this equation the number of eggs cannibalized were calculated for each of the 171 larvae in Experiment 1 because the number of eggs eaten by the larvae could not be directly measured due to group feeding.

In the field experiment, the relationship between the number of eggs cannibalized ($X$) and the survival rate of the larva from first to second instar ($Y$) was,

$Y = -0.031X^2 + 0.311X + 0.124$ ($r^2 = 0.953$, $F = 50.49$, $p < 0.0005$) at low aphid density, (Fig. 4A).

The corresponding relationship at high aphid density was,

$Y = 0.063X^2 - 0.008X + 0.343$ ($r^2 = 0.973$, $F = 91.09$, $p < 0.0001$) (Fig. 4B).

Using these two equations, survival rates from first to second instar of all 171 larvae were calculated at low and high aphid density.

### Fitness Consequences of Sibling Cannibalism for the Cannibal and the Victim

Table 3 shows the costs and benefits of sibling cannibalism to the cannibals. At low aphid density, the benefits of sibling cannibalism for cannibals were larger than the costs at all levels of cannibalism (Table 3). However, at high aphid density, the benefits of the cannibals were only larger than the costs when the cannibals consumed three full sib eggs or two and more half sib eggs (Table 3).

Table 4 indicates the costs and benefits of sibling cannibalism to the victims. The costs of the victims were always larger than the benefits, except in two cases at low

Table 1. Univariate analysis of frequency distribution of larval body length in each egg batch 24 hours after hatching.

| Code of egg batch | % sibling cannibalism | Body length | | W: normal* | $p<W$ |
|---|---|---|---|---|---|
| | | Mean±S.E. ($n$) | Range | | |
| E19 | 0.00 | 1.71±0.02 (26) | 0.49 | 0.92 | 0.07 |
| E14 | 3.13 | 1.68±0.02 (31) | 0.44 | 0.95 | 0.31 |
| E12 | 5.00 | 1.71±0.03 (19) | 0.49 | 0.80 | 0.01 |
| E6 | 15.15 | 1.69±0.03 (28) | 0.56 | 0.96 | 0.42 |
| E1 | 33.33 | 1.81±0.05 (22) | 0.86 | 0.93 | 0.17 |
| E9 | 50.00 | 1.97±0.07 (11) | 0.42 | 0.79 | 0.01 |
| E7 | 56.25 | 2.04±0.09 ( 7) | 0.74 | 0.87 | 0.24 |
| E10 | 64.29 | 2.19±0.10 (10) | 1.14 | 0.77 | 0.01 |
| E8 | 67.92 | 2.21±0.05 (17) | 0.77 | 0.97 | 0.87 |

* Shapiro-Wilk statistic.

Table 2. Frequency of sibling cannibalism.

| | Mean±S.E./egg batch | Total |
|---|---|---|
| No. of eggs | 29.22±3.59 | 263 |
| fertile eggs | 22.11±2.76 | 199 (75.67%) |
| infertile eggs | 7.11±3.92 | 64 (24.33%) |
| No. of eggs successfully hathced | 19.00±2.83 | 171 (65.02%) |
| No. of eggs cannibalized | 10.22±3.78 | 92 (34.98%) (100.00%) |
| infertile eggs | 7.11±3.92 | 64 (24.33%) ( 69.57%) |
| fertile eggs with delayed hatching | 3.11±1.10 | 28 (10.65%) ( 30.43%) |

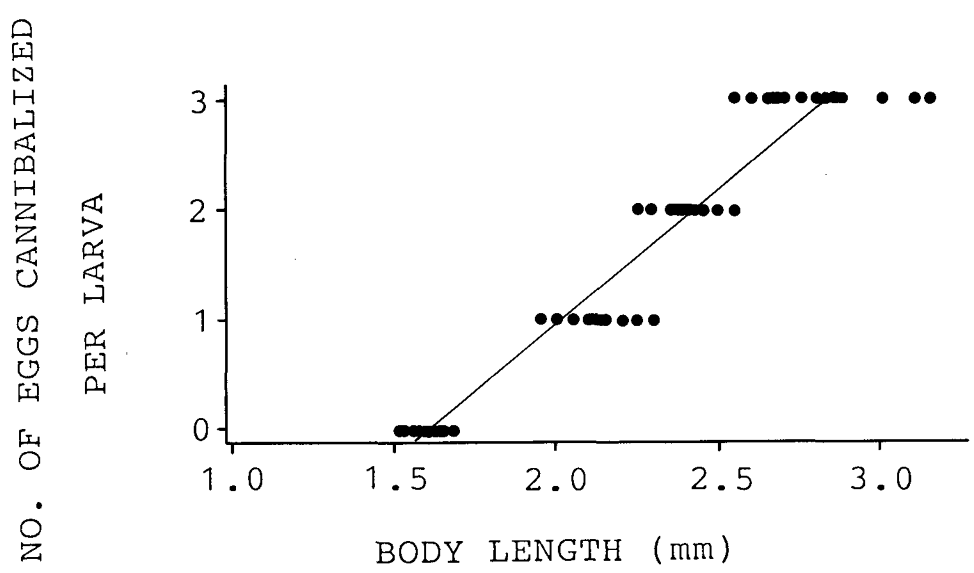

Fig. 3. The relation between number of eggs cannibalized per larva ($Y$) and larval body length ($X$). $Y=2.427X-3.892$ ($r^2=0.926$, $F=976.8$, $p<0.0001$).

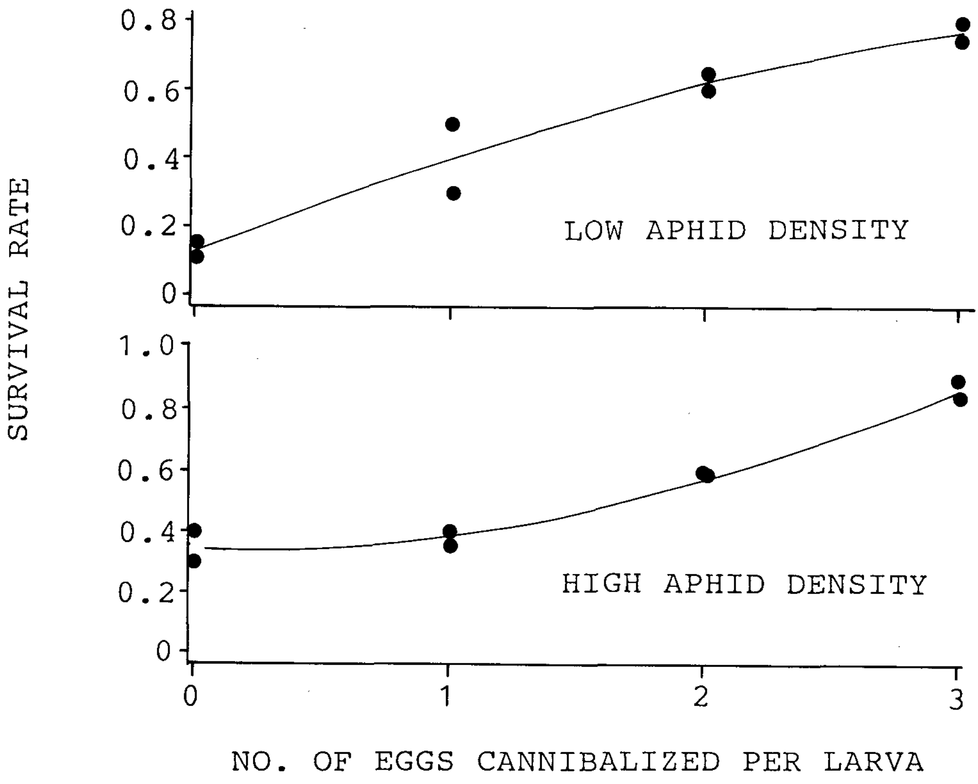

Fig. 4. The relation between number of eggs cannibalized per larva and larval survival rate in low and high aphid density.

aphid density, in which the victim was consumed by full siblings (Table 4). Therefore, full sibling cannibalism may be adaptive both for the cannibal and the victim when the aphid availability for the larvae was low, suggesting that cannibalistic and altruistic behavior can be mutually favorable under severe food stress.

## Fitness Consequences of Sibling Cannibalism for the Mother

Figure 5 shows the relationships between the mother's fitness and the percentage

Table 3. Cost and benefit of sibling cannibalism to the cannibal.

| Food level/Sibling | No. of eggs cannibalized | Survival rate of the cannibal | Benefit (*B*) | Cost (*Cr*) | | Benefit-Cost (*B-Cr*) | | Cannibalism favored? | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Full* | Half** | Full* | Half** | Full* | Half** |
| Low aphid density | 0 | 0.124 | — | — | — | — | — | — | — |
| (300 aphids/tree) | 1 | 0.404 | 0.280 | 0.062 | 0.031 | 0.218 | 0.249 | Yes | Yes |
| | 2 | 0.622 | 0.498 | 0.124 | 0.062 | 0.374 | 0.436 | Yes | Yes |
| | 3 | 0.778 | 0.654 | 0.186 | 0.093 | 0.468 | 0.561 | Yes | Yes |
| High aphid density | 0 | 0.343 | — | — | — | — | — | — | — |
| (1200 aphids/tree) | 1 | 0.398 | 0.055 | 0.172 | 0.086 | −0.117 | −0.031 | No | No |
| | 2 | 0.579 | 0.236 | 0.343 | 0.172 | −0.107 | 0.064 | No | Yes |
| | 3 | 0.886 | 0.543 | 0.515 | 0.257 | 0.028 | 0.286 | Yes | Yes |

*: $r=0.5$ in full sibling, **: $r=0.25$ in half sibling.

Table 4. Cost and benefit of sibling cannibalism to the victim.

| Food level/Sibling | No. of eggs cannibalized | Benefit ($Br$) | | Cost ($C$) | Benefit-Cost ($Br$-$C$) | | Cannibalism favored? | |
|---|---|---|---|---|---|---|---|---|
| | | Full* | Half** | | Full* | Half** | Full* | Half** |
| Low aphid density | 1 | 0.140 | 0.070 | 0.124 | 0.016 | −0.054 | Yes | No |
| (300 aphids/tree) | 2 | 0.249 | 0.125 | 0.248 | 0.001 | −0.123 | Yes | No |
| | 3 | 0.327 | 0.164 | 0.372 | −0.045 | −0.208 | No | No |
| High aphid density | 1 | 0.028 | 0.014 | 0.343 | −0.315 | −0.329 | No | No |
| (1200 aphids/tree) | 2 | 0.118 | 0.059 | 0.686 | −0.568 | −0.627 | No | No |
| | 3 | 0.272 | 0.136 | 1.029 | −0.757 | −0.893 | No | No |

*: $r=0.5$ in full sibling, **: $r=0.25$ in half sibling.

of sibling cannibalism, the percentage of infertile eggs, and the percentage of fertile eggs with delayed hatching at low (A) and high (B) aphid density. The results obtained here indicate that at low aphid density the mother's fitness did not change significantly regardless of the intensity of sibling cannibalism. Likewise different percentages of infertile eggs and fertile eggs with delayed hatching did not affect the

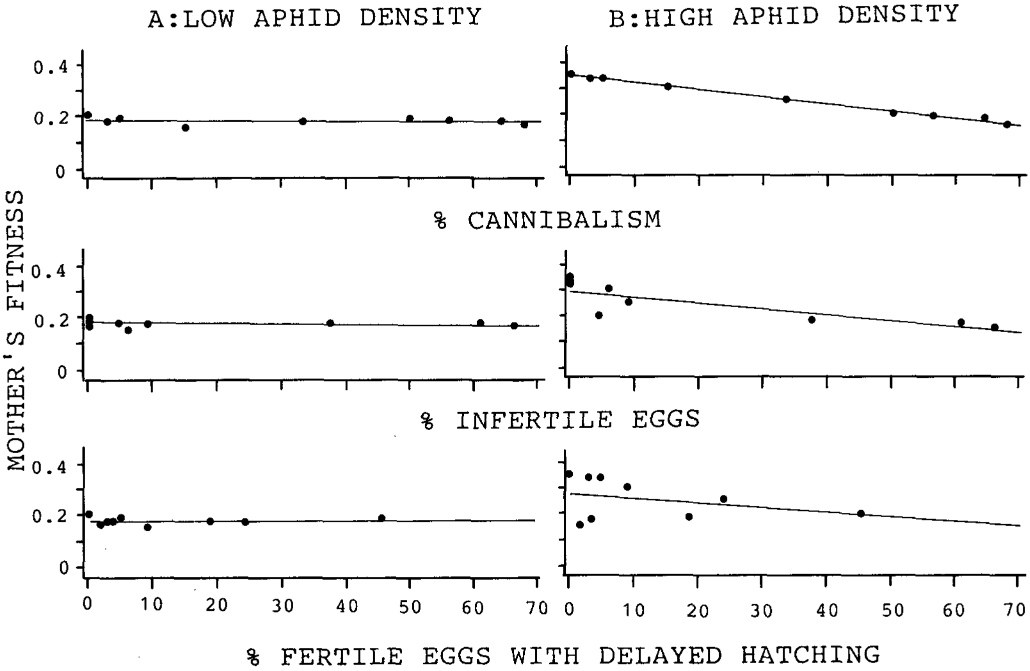

Fig. 5. Relationships between mother's fitness and the percentage of sibling cannibalism (A: $Y=-0.0002X+0.1851$, $r^2=0.1798$, $F=1.534$, $p<0.2554$, B: $Y=-0.0028X+0.3450$, $r^2=0.9955$, $F=1549.025$, $p<0.0001$), the percentage of infertile eggs per egg batch (A: $Y=-0.0002X+0.1829$, $r^2=0.2127$, $F=1.891$, $p<0.2115$, B: $Y=-0.0024X+0.3020$, $r^2=0.6857$, $F=15.269$, $p<0.0058$), and the percentage of fertile eggs with delayed hatching per egg batch, (A: $Y=0.00005X+0.1773$, $r^2=0.0024$, $F=0.017$, $p<0.8996$, B: $Y=-0.0018X+0.2761$, $r^2=0.1232$, $F=0.984$, $p<0.3543$) at low (A) and high (B) aphid density.

mother's fitness. By contrast, at high aphid density, the mother's fitness decreased with regard to the intensity of sibling cannibalism and the percentage of infertile eggs. Thus, sibling cannibalism appears to be not maladaptive for a mother when larval food conditions are unfavorable.

## Discussion

The occurrence of sibling cannibalism has mainly been considered as a result of two proximate factors: asynchrony of hatching among eggs (Kawai, 1978; Baur and Baur, 1986) and the existence of infertile eggs in an egg batch (Kawai, 1978). Osawa (1989) demonstrated that sibling cannibalism occurred with little sensitivity to several ecological conditions, such as timing of oviposition or aphid availability, though these conditions are critical for the occurrence of non-sibling cannibalism. Sibling cannibalism seems to be fortuitous since only a few hours' difference in hatching time offers opportunity for the behavior (Banks, 1956; Kawai, 1978). However, this behavior may have some selective advantage because sibling cannibalism is adaptive both for the cannibal and victim at low aphid density as indicated by this study.

This conclusion supports empirical and theoretical studies on sibling cannibalism (Eickwort, 1973; O'Conner, 1978), which stated that sibling cannibalism occurs easily under severe food stress. Considering the intense larval competition for food that results in rapid decrease of larval survival rate due to food shortage observed in fourth instar (Osawa, 1991b), rapid growth of first instar larvae may well have additional selective advantage for later life stages.

Since infertile eggs will not develop and thus have no reproductive value, their adaptive significance has been regarded as nurse or trophic eggs in other groups of animals (Polis, 1981). This study clearly shows that infertile eggs prepared by a mother enhance the survivorship of cannibals between first and second instar, therefore attaining an equal mother fitness at low aphid density regardless of the percentage of infertile eggs per egg batch. However, the mother's fitness changed in relation to the fluctuation of aphid density in the field. Therefore intense sibling cannibalism is maladaptive when aphid availability is high.

In contrast, when aphids are not nearby, both the reluctance of coccinellids to oviposit and the increased activity of females enhance the ability of these predators to oviposit at particularly favorable sites (Evans and Dixon, 1986). However, aphidophagous ladybird beetles often oviposit during or after the peak of aphid population, and their offspring are often obliged to develop under severe food limitation (Banks, 1955; Dixon, 1970, 1971; Wratten, 1973). In addition, it is also difficult for newly-hatched larvae to capture an aphid (Dixon, 1959; Brown, 1972; Kawai, 1978). Furthermore, beetles tend to lay eggs slightly apart from an aphid colony (Banks, 1954, 1957; Dixon, 1959; Osawa, 1989) and more eggs are eaten in non-sibling cannibalism when an egg batch is laid near an aphid colony (Osawa, 1989). In view of these various factors, the timing and selection of optimal oviposition sites with a high aphid density where food availability for offspring will be ensured, will be quite difficult. Accordingly, food conditions for newly-hatched larvae will usually be severe and unpredictable. In such circumstances, a fluctuating percentage of infertile eggs in an egg batch may be a bet hedge (Stearns, 1977) or a mixed strategy (Maynard Smith, 1982) which prevent annihilation of all the early instars.

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## ナミテントウの同胞による共食い—母と子にとっての適応度

大澤直哉

ナミテントウにおける同胞による共食いの適応的な意義を2つの餌密度で調べ，共食いの利益と損失を，食う者，食われる者，母親の3者の立場から考察した．食う者は同一卵塊内の未受精卵及び受精卵を食べ，共食いの程度に比例して体長を増加させ生存率を高めた．低密度の餌条件では共食いは明らかに食う者にとって適応的であったが，高密度の餌条件で食われる者が全同胞 (full sibling) の場合には適応的ではなかった．食われるという自己犠牲的な行為は，低密度の餌条件で，全同胞に食われる場合のみ適応的であった．一方，低密度の餌条件では，母親は共食いの率に無関係にほぼ同じ適応度を実現しており，同胞による共食いは母親にとって不適応ではなかった．しかし，高密度の餌条件では，同胞による共食いの率が高くなるにしたがって母親の適応度は低下し，同胞による共食いは母親にとって非適応的であった．