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Sibling cannibalism in aphidophagous ladybirds: its impact on sex-dependent development and body weight

Omkar[1], A. Pervez[2] and A. K. Gupta[1]
[1]Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, India; [2]Department of Zoology, Govt. Degree College, Talwari, Chamoli, Uttaranchal, India

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Abstract: The effects of sibling egg cannibalism on sex-dependent development and adult body weight were determined by rearing simultaneously two groups of sibling larvae of ladybirds, viz. *Propylea dissecta* and *Coccinella transversalis* individually. The first group included cannibals (i.e. neonates, which took a sibling egg as the first meal and later fed on aphids, *Aphis craccivora*) and the other included non-cannibals (reared exclusively on aphids). The cannibal larvae developed faster with heavier adults than non-cannibals. This expedited development and nutritional advantage (increased body weight) was greater in first instars indicating maximum benefit of sibling cannibalism to them. Sibling cannibalism was relatively more advantageous to male than to female ladybirds. Laboratory data predict that the larger size of adults in the field could possibly be the result of sibling egg cannibalism at the neonate level.

Key words: *Aphis craccivora*, *Coccinella transversalis*, *Propylea dissecta*, body weight, development, sibling cannibalism

1 Introduction

Sibling cannibalism is of common occurrence in predaceous ladybirds (Col., Coccinellidae). It could be considered as a direct maternal investment in the offspring and a survival tactic at low prey density (Osawa 1992). It is largely held that food scarcity promotes sibling cannibalism, as eggs become food for the developing sibling instars. This is seemingly under maternal control, as it often results in asymmetrical hatching with few instars hatching earlier than the others (Alexander 1974; Polis 1981; Mock and Forbes 1995). As a result of this, mothers sacrifice some offspring to others when they gain more offspring from the increased survival of the cannibals than they lose as victims (Crespi 1992). Thus, when offspring starvation risk is high, it is beneficial to eat a sibling. The other maternal investment in a prey-scarce situation is to produce trophic offspring that serve as a meal (Perry and Roitberg 2005). The trophic offspring or trophic eggs are non-developing ovariole-produced structures that are formed to feed the offspring (Crespi 1992).

The benefits of sibling cannibalism on the life history traits of a multicoloured ladybird, *Harmonia axyridis* (Pallas) was recently reported (Osawa 2002). In a food-scarce situation, the ladybirds could benefit only if the immature stages develop faster, become adults and search for foraging sites elsewhere (Dixon 2000). The optimal foraging theory suggests that sibling cannibalism is one of the important components operational in a declining prey colony (Kindlmann and Dixon 1993). It is advantageous to ladybirds if the developmental period shortens allowing the emerging adults to escape the food-scarce situation. Their body weight is also crucial as it is directly associated with the quantity and quality of the progeny and could explain the fate of offspring in the new habitat. Heavier females are largely favoured by natural selection as they could provide better progeny (Osawa and Nishida 1992; Andersson 1994; Ueno et al. 1998).

Propylea dissecta (Mulsant) and *Coccinella transversalis* Fabricius are aphidophagous having a wide prey range (Omkar and Pervez 2004). In the laboratory, they preferred aphids, *Aphis craccivora* and *Aphis gossypii* (Glover) (Koch) compared with other aphid species, resulting in faster development and greater oviposition (Omkar and James 2004; Pervez and Omkar 2004; Omkar and Mishra 2005). Their neonates preferentially consume conspecific eggs rather than heterospecific ones (Omkar et al. 2004). The two ladybirds exhibit similar patterns of cannibalism (Pervez et al. 2006); however, their spatial distribution varies, as *P. dissecta* is negatively geotactic (Omkar and Mishra 2005) and *C. transversalis* is positively geotactic (Singh 2005).

We hypothesized that sibling cannibalism would be advantageous to immature stages and their fitness would increase because of shortening of the developmental period, resulting in adults of increased body weight. We tested this hypothesis using *P. dissecta* and *C. transversalis* with an aim to address the question

that if sibling cannibalism is advantageous, is it sex-dependent? If so, which sex is more favoured?

2 Materials and Methods

2.1 Stock maintenance

Adults of *P. dissecta* and *C. transversalis* were collected from *Dolichos lablab* fields, where they were feeding on aphid, *Aphis craccivora* Koch, and brought to the laboratory. They were reared on *A. craccivora*-infested leaves of *D. lablab* in Petri dishes in the laboratory [27 ± 1°C; 65 ± 5% relative humidity (RH) and 10 : 14 Light : Dark photoperiod)]. The adults were paired in Petri dishes (9.0 × 2.0 cm) and allowed to mate. The size in length of adult females was significantly greater than that of males [*P. dissecta* male = 4.50 ± 0.33 mm, *P. dissecta* female = 5.55 ± 0.55 mm (t-test: t = 6.03; P < 0.0001; $n = 10$) and *C. transversalis* male = 6.45 ± 0.50 mm , *C. transversalis* female = 7.85 ± 0.47 mm (t-test: t = 6.33; P < 0.0001; $n = 10$)]. The eggs laid were collected and the instars hatched were reared until adult emergence feeding them with aphids *ad libitum*. The females from the F_1 generation were used as mothers to obtain sibling eggs.

2.2 Experimental design

The adult females of *P. dissecta* and *C. transversalis* were paired and allowed to mate and were paired in 9-cm-diameter Petri dishes containing *ad libitum A. craccivora*-infested twigs. The females were allowed to oviposit and the number of eggs in each batch was counted. The egg batches were split into three groups. One group of eggs was refrigerated at 5°C to delay hatching. These were used as victim eggs. The other two groups were incubated at 27 ± 1°C. After hatching, these two groups were marked as cannibal and non-cannibal neonates. A cannibal neonate was first fed on a sibling victim egg and thereafter on *A. craccivora ad libitum*. The non-cannibal neonate was directly fed on *A. craccivora ad libitum*. Data on moulting and pupation were taken to record larval and pupal durations. After 12 h of emergence, the adults were sexed and their body weights were measured to 0.1 mg precision using an electronic balance (Shimadzu AY-120, Shimadzu Corporation, Kyoto, Japan). There were 60 eggs for each treatment. The experiment was conducted under abiotic conditions similar to stock.

The data on the duration of development and each larval instar and body weight were subjected to three-way ANOVA using 'species', 'sex' and 'cannibalism' as independent variables. This was done to determine the effects of species, sex and cannibalism on the above life history traits (SAS 2002).

To address the question, 'which sex is favoured', the following calculations were made:

$$\text{Relative advantage} = \frac{W_c - W_{nc}}{W_{nc}}$$

where W_c is the weight of the cannibal male and W_{nc} the weight of the non-cannibal male. The same calculation was made for female ladybirds of both species. The data on relative advantages were subjected to arcsine square root transformation and then to t-test (SAS 2002).

3 Results

The effect of sibling cannibalism on the developmental time of immature *P. dissecta* and *C. transversalis* in relation to the sex of the individuals is presented in fig. 1. 'Species' has a significant main effect on the duration of second (F = 7.75; P < 0.05), third (F = 9.63; P < 0.05) and fourth instars (F = 18.86; P < 0.001), and pupa (F = 11.59; P < 0.001), which suggests that the developmental duration of these life stages was significantly shorter in *P. dissecta* than those of *C. transversalis*. The interactions between 'cannibalism' × 'sex', 'species' × 'cannibalism', 'species' × 'sex' and 'species' × 'sex' × 'cannibalism' were not significant.

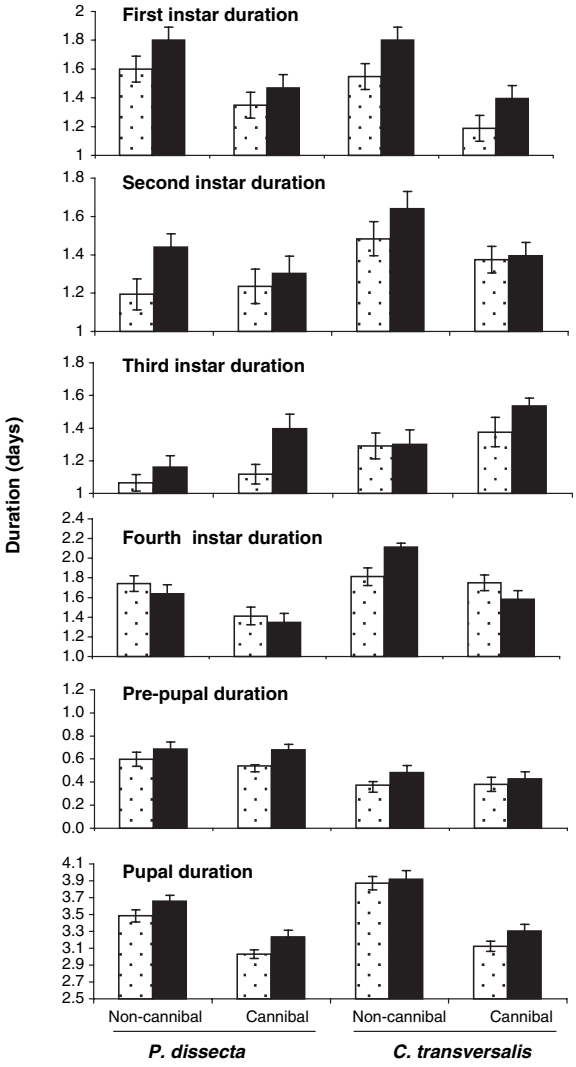

Fig. 1. *Effect of sibling egg cannibalism on the larval and pupal durations of* P. dissecta *and* C. transversalis *(white bar indicates males, black bold bar indicates females; and error bars show SD values)*

There was a significant main effect of 'cannibalism' on duration of first (F = 27.06; P < 0.001), third (F = 6.12; P < 0.05) and fourth instars (F = 22.44; P < 0.001), pre-pupa (F = 5.65; P < 0.05) and pupa (F = 88.51; P < 0.001), which suggests that cannibals of these immature stages developed faster than those of non-cannibals. Three-way ANOVA revealed a significant main effect of 'sex' on the duration of first (F = 8.99; P < 0.05), second (F = 3.56; P < 0.05) and third instars (F = 4.88; P < 0.05), pre-pupa (F = 66.42; P < 0.001) and pupa (F = 6.44; P < 0.05), which

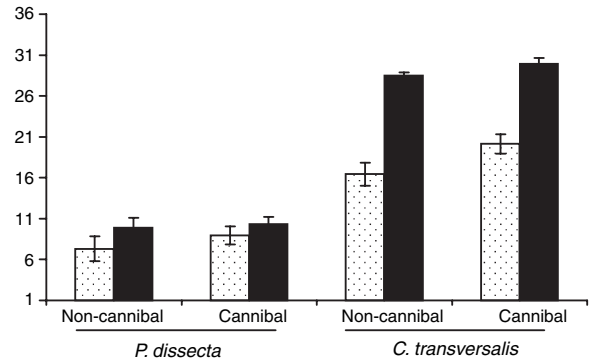

Fig. 2. *Effect of sibling egg cannibalism on body weight (in mg) of* P. dissecta *and* C. transversalis *(white bar indicates males, black bold bar indicates females and error bars show SD values)*

suggests that except fourth instar *P. dissecta* cannibals, all immature stages that developed into adult males took lesser time than those of females.

The body weight of emerging adult male and female cannibals was greater than those of non-cannibals in both the ladybird species (fig. 2). The females of two ladybird species at both combinations (cannibal/non-cannibal) were heavier than the males. The cannibal males and females were heavier than non-cannibal ones. The results reveal that neonates that fed on eggs develop faster resulting in heavier adults than those fed on aphid prey as their first meal. There was a significant main effect of 'species' ($F = 80.86$; $P < 0.001$), 'cannibalism' ($F = 121$; $P < 0.001$) and 'sex' ($F = 1567$; $P < 0.001$) on body weight. The interactions between 'cannibalism' × 'sex' ($F = 27.86$; $P < 0.001$), 'species' × 'cannibalism' ($F = 22.68$; $P < 0.001$), 'species' × 'sex' ($F = 754$; $P < 0.001$) and 'species' × 'cannibalism' × 'sex' ($F = 7.52$; $P < 0.05$) were statistically significant.

In *P. dissecta*, the relative advantage in weights of male and female was 0.46 ± 0.18 and 0.22 ± 0.11, respectively, which suggests that males were significantly ($t = 17.29$; $P < 0.0001$; d.f. = 1, 27) more benefited than females. Similarly, in *C. transversalis* the relative advantage in weights of male and female was 0.48 ± 0.05 and 0.22 ± 0.04, respectively, suggesting significantly ($t = 55.50$; $P < 0.0001$; d.f. = 1, 22) more benefits to male ladybirds.

4 Discussion

Sibling cannibalism by the neonates of *P. dissecta* and *C. transversalis* resulted in significantly faster development and increased body weight of adults. The shortening of developmental periods was largely due to reduction of first instar duration, which indicates that first instars were nutritionally benefited after feeding conspecific eggs as their first meal. The neonates of ladybirds, *Coleomegilla maculata lengi* (Timberlake) (Gagne et al. 2002), *Coelophora saucia* (Mulsant), *C. transversalis* and *P. dissecta* (Omkar et al. 2006) fed on conspecific eggs developed faster with lesser prey biomass requirement than those fed on aphids.

Sibling egg cannibalism seems to be beneficial for the first instars in field conditions because they are less efficient in capturing prey (Brown 1972; Kawai 1978). The probability of survival of the neonates of *H. axyridis* increased five times when they ate a sibling egg in aphid-scarce conditions compared with individuals at high aphid density (Osawa 1992). Furthermore, the first instars of the ladybirds preferred to eat sibling eggs than aphids and moulted to the next instar after consuming only three eggs (Kawai 1978). This suggests that sibling eggs provide additional and better nutrients during larval development akin to trophic eggs in ladybirds (Perry and Roitberg 2005) and social insects (Holldobler and Wilson 1990; Crespi 1992). However, the conspecific eggs were not equally nutritive to later instars, as it resulted in a decrease in their relative weight gain and instar durations than those provided exclusively with aphid diets. Egg consumption by later instars of *P. dissecta* and *C. transversalis* resulted in delayed development and low-weight adults (Pervez et al. 2006).

Regardless of species, first instar cannibals that developed into males had shorter developmental period than females. However, it was higher in *C. transversalis* than *P. dissecta*. These results indicate that effects of sibling cannibalism on life history traits are sex-differentiated and are greater in males. Sex-dependent effect of sibling cannibalism on body weight of adult male and female was significant in both species, however weaker in *P. dissecta*. The males were more advantageous in terms of body weight gain as the percent increase in the weight in response to sibling cannibalism at the neonate level was more pronounced.

The emerged females following sibling cannibalism were also benefited in terms of increased body size than non-cannibal females, although this increase was not as high as that of cannibal males. Females are usually considered to be more cannibalistic than males in many animal species (Polis 1981). It was also suggested that greater incidence of sibling cannibalism in females of many species is related to their high energy requirements, particularly for egg maturation and oviposition. In addition, the increased body size of females is positively associated with the number of offspring in many insect species (Thornhill and Alcock 1983; Birkhead et al. 1998). This is supported by the fecundity advantage hypothesis (Fairbairn 1990). The present study reveals significant effect of sibling cannibalism on the body size in terms of body weights of female ladybirds. The heavy females are likely to be favoured by natural selection.

Regardless of neonates being cannibals or not, the males were smaller and developed faster than the females in all the treatments. Mostly, there were significant effects of 'sex' and 'cannibalism' in different larval duration treatments revealing that both these variables affected larval durations. The effect of 'species' was also significant in most cases which might be due to the disparity in size of the two species, as *C. transversalis* is much heavier than *P. dissecta*. Thus, it could be concluded that first instars cannibalizing sibling eggs developed faster than the non-cannibals

and also resulted in heavier adults. Both adult males and females are benefited from sibling cannibalism, however these benefits are relatively greater in males. Sibling cannibalism appears to be adaptive, as it may result in faster development for resource tracking and larger adults for increased fecundity in females.

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Author's address: Omkar (corresponding author), Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow – 226 007, Uttar Pradesh, India. E-mail: omkaar55@hotmail.com

