Role of surface chemicals in egg cannibalism and intraguild predation by neonates of two aphidophagous ladybirds, *Propylea dissecta* and *Coccinella transversalis*

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Abstract: The role of surface chemicals in egg cannibalism and intraguild predation by neonates of two aphidophagous ladybirds, *Propylea dissecta* and *Coccinella transversalis* were examined. Neonates of both species prefer to eat non-sibling conspecific eggs than heterospecific eggs, with higher preference in *P. dissecta*. Surface chemicals appear to play a major role for the preference of conspecific eggs, as the ladybird behaviour was reversed when these chemicals were interchanged. The surface chemicals present on the eggs possibly act as feeding stimulants to conspecific neonates but not for heterospecific neonates. Egg clustering enhances the effect of surface chemical and stimulate non-sibling egg cannibalism and appears to reduce intraguild predation. Egg clustering is advantageous to ladybirds, as it can stimulate non-sibling cannibalism by neonates. It appears that aggregation of chemicals present on the conspecific egg surface possibly attracts the hungry conspecific neonate, providing the first meal for its survival, while protecting against heterospecific predators. Neonates of both ladybirds were reluctant to eat heterospecific eggs.

Key words: *Coccinella transversalis*, *Propylea dissecta*, Coccinellidae, egg cannibalism, intraguild predation

1 Introduction

Neonates of aphidophagous ladybirds (Col., Coccinellidae) are under strong selection pressure to find food soon after hatching. They can readily eat unhatched or late hatched eggs of their own batches due to the presence of trophic eggs and asynchronous egg hatching (Osawa, 1992). The unfertile eggs are maternal investments, as they act as nurse or trophic eggs and are first meal providing nutrition to the hatched neonates (Kawai, 1978). Sibling egg cannibalism appears to be beneficial for mother and cannibals resulting in heavier adults and faster development of immature stages. This may be adaptive as large adult size may increase fecundity in females and mating success in males both resulting in the fitness of cannibals (Osawa, 1989, 2002). Although neonates are predisposed to sibling egg cannibalism, it would be interesting to note how they will respond if provided a choice between conspecific (non-sibling cannibalism) and heterospecific (intraguild predation) eggs. The eggs of certain aphidophagous ladybirds, *viz*. *Coccinella septempunctata* Linnaeus may be protected against non-sibling cannibalism and heterospecific predation (Hemptinne et al., 2000). However, eggs of certain species can readily be victimized by hungry ladybirds.

Eggs are generally assumed to be highly nutritious with yolk being a rich protein source for developing embryonic larvae. They are, therefore, a high quality food source meeting the nutritional requirements of the neonates better than alternative prey (Gagne et al., 2002). The same egg can be nutritive to one ladybird species while toxic to the other (Hemptinne et al., 2001; Burgio et al., 2002; Santi et al., 2003; Omkar, A. Pervez, A. K. Gupta, unpublished data). If neonates possess the ability to discriminate amongst their prey (Gagne et al., 2002), it is expected that they would selectively consume the more suitable food: unrelated conspecific or heterospecific eggs. Keeping in view the nutritional benefits of conspecific eggs (Snyder et al., 2000), it is hypothesized that they would be preferred over heterospecific eggs.

Chemicals present on the surface of eggs may also influence the cannibalism and predation by later larval instars and adults (Agarwala and Dixon, 1993; Hemptinne et al., 2000, 2001). They play a major role in attraction/repulsion of predators and have relative costs and benefits on predators' fitness (Hemptinne et al., 2001). We framed a second hypothesis that surface chemicals affect the preference of neonates. If the preference for conspecific eggs is due to surface chemicals, the removal of these chemicals would negate ability to discriminate amongst conspecific and heterospecific eggs result in random predation of eggs. Clustering of eggs is common in aphidophagous ladybirds (Agarwala and Dixon, 1993). Assuming random search, egg clustering might increase an individual's chance of avoiding predatory attacks (Kiltie, 1980). Clustered eggs may have aposematic properties, deterring intraguild predation (Agarwala and Dixon, 1993) and non-sibling cannibalism (Agarwala et al., 1997). Clustering, however, facilitates sibling egg cannibalism (Michaud and Grant, 2004).

Investigations were designed to test the above-mentioned hypotheses and to answer the following questions: Do neonates prefer conspecific eggs over heterospecific ones? Do surface alkanes affect the probability of cannibalism and/or intraguild predation? Does egg clustering increase the chemical defence/attraction? We selected the neonates of two co-occurring aphidophagous ladybirds for study, *Propylea dissecta* (Mulsant) and *Coccinella transversalis* Fabricius. They are Oriental ladybirds, native to India, and share common prey resources in the agricultural fields of north India. *Propylea dissecta* and *C. transversalis* are ecologically plastic aphidophagous ladybirds, the former having high tolerance to stresses such as starvation and extremes of temperature (Pervez, 2002; Omkar and Pervez, 2003; Pervez and Omkar, 2004), and the latter possessing a wider prey range (Omkar and Pervez, 2004). There are studies on interactions of *C. transversalis* with its prey (Omkar and James, 2004) and other aphidophaga (Agarwala et al., 1998, 2003) but there is no information on its interactions with *P. dissecta*. Their co-occurrence in local aphid habitats indicates likely ecological interactions between them. The present study elaborates one such potential interaction.

2 Materials and Methods

2.1 Stock maintenance

Adults of *P. dissecta* and *C. transversalis* for stock colonies were collected from the bottle gourd (*Lagenaria vulgaris* Seringe) and cultured in a controlled laboratory environment (27 ± 1°C, 65 ± 5% RH and LD 14 : 10). For the stock colony, we kept pairs of conspecific ladybirds in Petri dishes (9.0 × 1.5 cm) containing moist filter paper for oviposition. The ladybirds were fed daily on an *ad libitum* diet of *Aphis gossypii* (Glover) infested on twigs of the above host plant. The eggs were collected daily from the filter paper. The neonates hatched were kept separately in glass tubes (7.5 × 3.0 cm). The eggs used as prey items in the experiments were unrelated to the neonates, coming from different parental lines. This was done to remove any possible effect of kin recognition.

2.2 Experimental design

2.2.1 Do neonates prefer conspecific eggs over heterospecific ones?

To determine the preference for cannibalism over IGP, a 6-h starved neonate larva of *P. dissecta* was introduced into a Petri dish (as above) containing 10 *P. dissecta* eggs and 10 *C. transversalis* eggs arranged singly. The neonate was allowed to feed on the eggs and observations on egg cannibalism and IGP were taken after 4 h, and again after 24 h. The experiment was replicated 10 times ($n = 10$). The remaining eggs were counted to determine the number cannibalized/preyed upon. The experiment was then repeated using neonates of *C. transversalis*. The data on egg cannibalism and IGP were analyzed using non-parametric Kruskal–Wallis test of significance using a statistical software minitab on the personal computer. The Manly preference index (M) was calculated from the number of eggs consumed (Manly et al., 1972).

$$M = \frac{\ln(r_i/A_i)}{\sum \ln(r_i/A_i)},$$

where r_i is the number of eggs of a given species surviving and A_i is the number of eggs initially present. The Manly's preference index was used because it is a method that takes into account prey depletion during predation experiments (Sherratt and Harvey, 1993).

2.2.2 Do surface alkanes affect cannibalism and intraguild predation of eggs?

Conspecific eggs of *P. dissecta* and *C. transversalis* were washed in n-hexane for 2 min to remove the surface alkanes and dried using a filter paper. Hexane was chosen as a solvent because a preliminary study indicated that it does not penetrate eggs during a 2-min extraction period, but only removes chemicals present on the egg surface (Chan, 1995), and does not affect hatching (A. Pervez, unpublished data). These eggs were then painted with the extracts containing surface alkanes of heterospecific eggs prepared by treating eggs of *P. dissecta* (1 mg) and *C. transversalis* (1 mg) separately in 0.15 ml distilled water. Twelve-hour-starved neonates of *P. dissecta* and *C. transversalis* were kept singly in Petri dishes (2.0 × 9.0 cm) containing the above treated 20 eggs (10 eggs of each species painted with heterospecific extract; $n = 10$). The neonate was allowed to feed on the eggs and observations on egg cannibalism and IGP were taken after 4 and 24 h. The experiment was replicated 10 times ($n = 10$). The leftover eggs were counted to determine the number of eggs cannibalized/preyed on. The data on egg cannibalism/IGP were subjected to non-parametric analysis of variance (Kruskal–Wallis test) using the statistical software minitab.

2.2.3 Does egg clustering increase chemical repulsion/attraction?

Two sets of experiments were designed. In the first set, two clusters of 10 eggs of *P. dissecta* were kept in a Petri dish (as above). The first cluster contained freshly laid conspecific eggs and the second, surface washed eggs. A 12-h-starved first instar larva (neonate) of *P. dissecta* was introduced into the Petri dish to feed on the eggs. After 24 h of exposure, the neonate was removed and the number of eggs cannibalized determined by counting the number of remaining eggs. The experiment was replicated 10 times ($n = 10$). In the second set of experiments, the same experimental set-up was repeated using heterospecific (*C. transversalis*) eggs both washed and unwashed, and with neonates of *P. dissecta* as predators. The entire experiment was then repeated using *C. transversalis* neonates as the predator. The data were analysed by Kruskal–Wallis test of significance using minitab.

3 Results

3.1 Do neonates prefer conspecific eggs over heterospecific ones?

Neonates of *P. dissecta* ($H = 7.00$; $P = 0.008$; d.f. $= 1$) and *C. transversalis* ($H = 3.17$; $P = 0.01$; d.f. $= 1$) significantly preferred consumption of conspecific over heterospecific eggs during a period. After 24 h of exposure, neonates of *P. dissecta* ($H = 14.29$; $P = 0.000$; d.f. = 1) and *C. transversalis* ($H = 10.08$; $P = 0.002$; d.f. = 1) also consumed more conspecific eggs than heterospecific ones (fig. 1). This preference for cannibalism estimated by the Manly preference index was found to be more pronounced in *P. dissecta* than in *C. transversalis* (fig. 2).

3.2 Do surface alkanes affect cannibalism and intraguild predation of eggs?

The neonates of *P. dissecta* significantly preferred eggs of *C. transversalis* coated with surface alkanes of conspecific eggs, when exposed for 4 h ($H = 5.14$; $P = 0.024$; d.f. = 1) and 24 h ($H = 6.22$; $P = 0.013$; d.f. = 1) (fig. 3). Similarly, the neonates of *C. transversalis* consumed more *P. dissecta* eggs coated with the surface alkanes of conspecific eggs, when exposed for 4 h ($H = 3.04$; $P = 0.082$; d.f. = 1) and 24 h ($H = 0.07$; $P = 0.786$; d.f. = 1) (fig. 3). Thus, changes in surface alkanes affected the egg-consumption behaviour of neonates of both species.

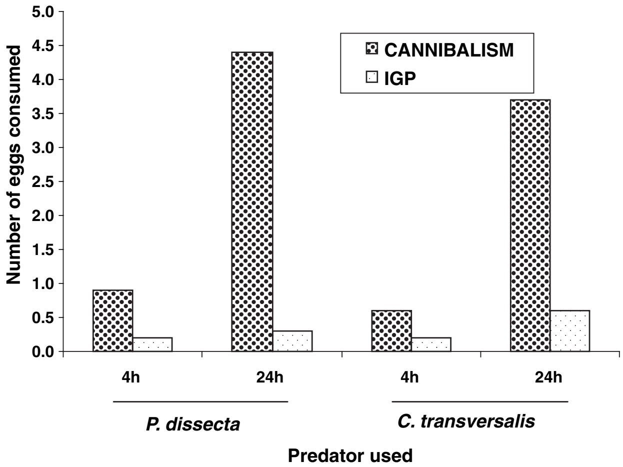

Fig. 1. *Preference for cannibalism over intraguild predation by neonates of* Propylea dissecta *and* Coccinella transversalis

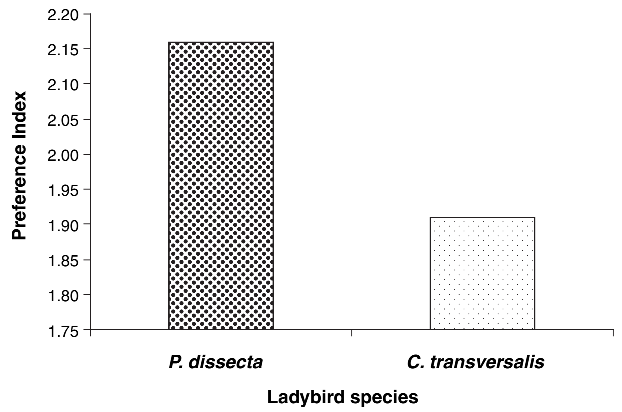

Fig. 2. *Manly preference indicies showing preference of cannibalism by neonates of* Propylea dissecta *and* Coccinella transversalis

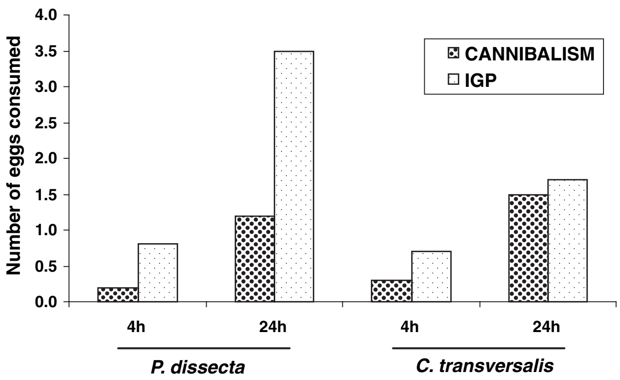

Fig. 3. *Neonates of* Propylea dissecta *and* Coccinella transversalis *indulging in cannibalism and intraguild predation after interchanging egg surface chemicals*

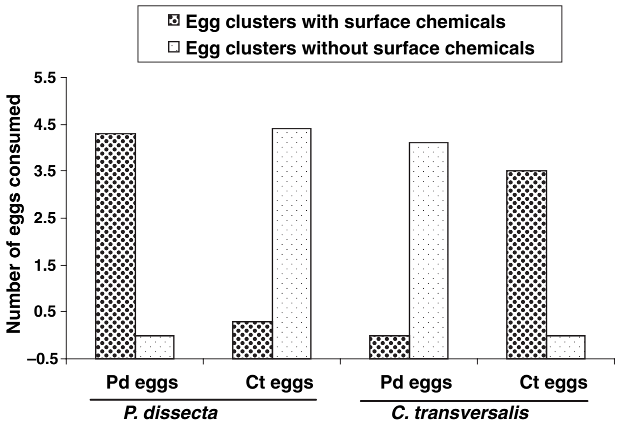

Fig. 4. *Cannibalism and intraguild predation of clustered eggs of* Propylea dissecta *and* Coccinella transversalis*, with and without surface chemicals*

3.3 Does egg clustering increase chemical repulsion/attraction?

Neonates of *P. dissecta* ($H = 16.64$; $P = 0.000$; d.f. = 1) and *C. transversalis* ($H = 16.65$; $P = 0.000$; d.f. = 1) consumed more conspecific eggs containing surface chemicals than those without surface chemicals. Interestingly, no conspecific egg having surface chemicals removed was eaten by neonates of either species in most of the trials (fig. 4). This reveals that chemicals present on the egg surface stimulate egg cannibalism by neonates. In IGP trials, neonates of *P. dissecta* ($H = 15.43$; $P = 0.000$; d.f. = 1) and *C. transversalis* ($H = 16.67$; $P = 0.000$; d.f. = 1) consumed heterospecific eggs without surface chemicals, whereas fewer heterospecific eggs containing surface chemicals were consumed (fig. 4). Thus, chemicals present on the egg surface deter neonates from engaging in IGP.

4. Discussion

The results indicate that neonates of *P. dissecta* and *C. transversalis* prefer to eat unrelated conspecific eggs over heterospecific ones, thus supporting our first hypothesis. However, the preference was stronger in *P. dissecta*. A similar preference for conspecific eggs by later instars and adults was observed in *Adalia bipunctata* (L.), *C. septempunctata* (Agarwala and Dixon, 1991), *Cheilomenes sexmaculata* (Fabr.) and *C. transversalis* (Agarwala et al., 1998). This preference may possibly be due to (i) the presence of surface alkanes, and/or (ii) alkaloids present in the conspecific eggs, which might be palatable or nutritious. Larvae of ladybird, *Harmonia axyridis* (Pallas) and *Cycloneda sanguinea* L. consumed more conspecific eggs than heterospecific ones in no-choice condition (Michaud, 2002). Our finding, although under imposed choice condition, agrees with the findings of other workers (Agarwala and Dixon, 1991; Agarwala et al., 1998; Michaud, 2002). Surface chemistry of conspecific eggs, apparently, acts as feeding stimulant, which might be less effective or lacking in the heterospecific eggs.

Conspecific eggs are known to be highly nutritious to developing larvae (Gagne et al., 2002), who could thus be benefitted by cannibalizing eggs when aphids are rare or of poor quality. The preference for conspecific eggs indicates that neonates can discriminate between different foods. Neonates of *Coleomegilla maculata lengi* DeGeer readily ate conspecific eggs than aphids resulting in faster development, which indicates that they select food having better nutritional value (Gagne et al., 2002). The nutritional value of conspecific and heterospecific eggs in terms of development and reproduction, however, needs to be further studied. Insect eggs are rich in cholesterols (MacDonald et al., 1990) and it appears that the egg cholesterols are species-specific and are more palatable to conspecfics. This could, however, be explained by further detailed chemical analysis of egg contents.

Not much is known about how searching neonates recognize their prey (Gagne et al., 2002). Ladybird larvae, especially the neonates, have poorly developed eyes and do not appear to use visual stimuli in prey recognition (Dixon, 2000; Hemptinne et al., 2001). Therefore, it is likely that surface chemistry of the prey influences recognition by neonates. Surface chemistry of different insects varies (Carlson et al., 1999; Nielsen et al., 1999) and, is thus likely to be more similar within than between species. This might function as species-specific signals (Lahav et al., 1999; Liu et al., 1999). The recognition of species-specific signals by predators is highly supported in the present study, as the cannibalistic behaviour of neonates was greatly altered when exposed to eggs with manipulated surface chemistry. The significant inverse effect of the interchange of surface chemicals of the eggs on the cannibalistic and predatory behaviour of neonates supports our second hypothesis that these chemicals do affect the preference of the neonates resulting in differential consumption of conspecific and heterospecific eggs.

Although lesser heterospecific eggs were consumed by the neonates in the present study, it is likely that these eggs will be readily eaten during immense starvation. In the trade-off between the likely costs and benefits of attacking heterospecific eggs, the behavioural decision of a starving individual might also depend on the critical stage of its life cycle. Neonates preferentially attacked and ate the clusters containing unwashed conspecific eggs, and washed heterospecific eggs. The laying of eggs in clusters may confer an advantage by concentrating surface-defensive chemicals, thus deterring intraguild predators. It is advantageous to hungry conspecific neonates, as the aggregation of chemicals in a cluster stimulates consumption and provides them the first meal. Hungry fourth instars of *C. sexmaculata* avoided clusters made up of large proportions of eggs of *C. transversalis* and fed on them only after encountering the clusters several times (Agarwala and Yasuda, 2001). Larvae of *C. sanguinea*, *H. axyridis* and *Olla-v-nigrum* Mulsant consumed cluster eggs at a higher rate than those laid singly (Michaud and Grant, 2004). It is likely that aggregation of chemicals as a result of egg clustering plays a major role in greater egg consumption by conspecifics. As the surface chemicals are less preferred to heterospecifics, the aggregation of surface chemicals could further decrease this preference and approach. Egg clustering in ladybirds seems to be an adaptive mechanism providing an aggregation of chemical defence against heterospecific predators sharing common food resources.

Thus, it can be concluded that: (i) neonates of ladybirds *P. dissecta* and *C. transversalis* prefer to eat their own eggs than those of other species; (ii) this preference is higher in *P. dissecta*; (iii) surface alkanes present on the eggs act as feeding stimulants to conspecifics, while deterrents to heterospecific neonates; (iv) the cluster-laying of eggs is advantageous to the ladybirds, as it can stimulate non-sibling cannibalism by neonates.

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