Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey

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Abstract. 1. Egg cannibalism among coccinellids has been reported widely, however reasons why this type of behaviour is observed so frequently have been neglected. This experiment was undertaken to clarify whether cannibalistic behaviour is advantageous to *Coleomegilla maculata lengi* Thimberlake neonates and to understand the reasons for high levels of egg cannibalism.

2. Benefits gained by neonate cannibals were ascertained by comparing survival, developmental time, and second-instar weight of *C. maculata* larvae that were allowed to cannibalise conspecific eggs or not. Preference and behaviour tests were also conducted to assess the reasons for high levels of egg cannibalism.

3. Cannibal neonates grew faster and were heavier than non-cannibals. The developmental time of neonates was influenced more by prey vulnerability than by prey quality.

4. In choice tests, where three different proportions of conspecific eggs and aphids were offered (33–67, 50–50, and 67–33%), *C. maculata* neonates always consumed significantly more eggs. Manly's preference indexes indicated that neonates showed a consistent preference for conspecific eggs.

5. Seventy-five per cent of neonates observed went directly towards eggs and 90% of the first prey consumed by neonates were an egg. When aphids were painted with extract of crushed eggs and eggs with crushed aphids to determine whether neonates found eggs by chemical cues, neonates preferred aphids painted with egg extract to eggs painted with aphid extract.

6. It was concluded that *C. maculata* neonates benefited from cannibalistic behaviour. Moreover, egg cannibalism is not related only to frequency of encounter; chemical cues are also involved in egg searching.

Key words. Aphid presence, cannibalistic behaviour, chemical cues, *Coleomegilla maculata lengi*, food quality, neonates, preference.

Introduction

Several species of aphidophagous coccinellids are highly cannibalistic (Stevens, 1992; Majerus, 1994). The most common form observed in these species is egg cannibalism (Mills, 1982; Osawa, 1989). Osawa (1989) observed that

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more than 60% of *Harmonia axyridis* Pallas eggs were killed by cannibalistic larvae. Many studies have shown that first-instar larvae eat unhatched eggs indiscriminately, whether they are dead or alive (Banks, 1956; Pienkowski, 1965; Brown, 1972; Majerus, 1994). Pienkowski (1965) found that cannibal larvae destroyed more than 21% of the eggs of their cluster and that 60.2% of those eggs were viable.

Cannibals may benefit indirectly by eliminating conspecifics, thereby decreasing the potential for intra-specific competition. Because population size is reduced, more food will be available to each survivor, enhancing chances of further survival and

rapid growth (Fox, 1975; Polis, 1981). In many species, cannibalism could also benefit the cannibal directly through immediate nutritional gains (Fox, 1975; Polis, 1981; Crump, 1983). Eickwort (1973) suggested that the development of a cannibalistic larva is accelerated considerably, especially in the early first instar. Therefore, first-instar survival and successful further foraging should be enhanced by cannibalism (Banks, 1956; Dixon, 1959; Kaddou, 1960; Brown, 1972; Kawai, 1978).

The first instar is a critical period for the larva. Coccinellid egg batches are often laid on leaves that are not infested with aphid prey (Kawai, 1978), and it is therefore difficult for first-instar larvae to obtain their first meal (Banks, 1956; Dixon, 1959; Kaddou, 1960; Brown, 1972; Kawai, 1978). Many authors have reported that first instars are rather inefficient at finding and capturing aphid prey (Dixon, 1959; Brown, 1972; Kawai, 1978). Banks (1956) and Majerus (1994) suggested that egg cannibalism by pre-dispersal larvae is of survival value for this critical period. Banks (1954) found that the consumption of a single egg nearly doubled the time that a larva could survive and concluded that the searching ability of newly hatched larvae was increased by feeding on eggs.

As predators, cannibals are affected by a number of factors such as prey abundance, quality, and vulnerability of prey (Dong & Polis, 1992). There are numerous examples showing that cannibalism increases as the abundance or nutritional quality of alternative food decreases (Fox, 1975; Polis, 1981), however the role of the food source in cannibalism has been studied primarily from the standpoint of scarcity. Generally, a decreasing food supply increases the frequency of cannibalism (Fox, 1975; Agarwala & Dixon, 1992). Agarwala and Dixon (1992) observed cannibalism even if aphids were abundant, and suggested that a lower level of cannibalism reflected the relatively low frequency of encounters.

It is generally assumed that eggs are highly nutritious, as they are provisioned by the mother with a yolk to feed the developing embryonic larva. Eggs could therefore be considered as a high quality food source that fits the nutritional requirement of neonates better than alternative prey. It has been reported that for some coccinellids, conspecific eggs constitute a suitable diet (Koide, 1962; Warren & Tardic, 1967; Takahashi, 1987; Hodek & Honek, 1996). In some of these cannibal coccinellids, the energetic and nutritional benefits resulted in higher developmental growth and survival rates, increased size, and higher reproduction compared with non-cannibals (Banks, 1956; Brown, 1972; Dimetry, 1974; Kawai, 1978). Agarwala and Dixon (1992) showed that starved larvae of all instars survived longer when fed on their own eggs than when fed on the aphid *Acyrthosiphun pisum* (Harris) when equal quantities of fresh weight of eggs and aphids were given.

Vulnerability of the prey may also be related strongly to the probability and frequency of cannibalism (Dong & Polis, 1992; Dixon, 2000). Cannibalism is usually restricted to predation of relatively defenceless life stages (Dong & Polis, 1992; Dixon, 2000), such as pupae, newly hatched larvae, and eggs (Hodek & Honek, 1996). Therefore, costs associated with cannibalistic behaviour will decrease as the cannibal spends less time and energy in searching and handling. Many prey species, including aphids, have active defences, which may be efficient, at least against small coccinellid larvae (Majerus, 1994; Hodek & Honek, 1996).

The first objective of the work reported here was to ascertain the advantage of cannibalism for neonates and to understand the importance of vulnerability and prey nutritional value in the cannibalistic behaviour of *C. maculata* neonates. Assuming that eggs are highly nutritious, it was hypothesised that the consumption of conspecific eggs would give first-instar larvae a significant advantage over first-instar larvae fed with aphids. This advantage would be due to higher nutritional quality of eggs compared with aphids, absence of defence behaviour by eggs compared with aphids, or a combination of these factors. If the advantage is only due to egg nutritional quality, better performances would be expected on conspecific eggs with no differences between mobile and defenceless aphids. If the advantage is only due to the absence of defence by eggs, better performances would be expected on conspecific eggs and defenceless aphids than on mobile larvae. Where both factors are involved, larval performance on conspecific eggs should be better than on defenceless aphids, and lowest on mobile aphids.

The second objective was to determine whether cannibalistic behaviour of first-instar larvae is related only to the frequency of encounters, as suggested by Agarwala and Dixon (1992). Considering that larvae gain an advantage by eating conspecific eggs and that performances and preferences are generally closely related (Ohgushi, 1995), it was hypothesised that first-instar larvae would eat conspecific eggs preferentially over aphids when the two prey items were offered simultaneously. If a preference were observed, it would mean that neonates have the ability to discriminate between conspecific eggs and aphids. If the predator has the ability to recognise prey, it was hypothesised that newly hatched larvae would select the more beneficial food available, conspecific eggs.

Material and methods

Insects

The cannibals used throughout this study were first-instar larvae (0–12 h) of *C. maculata*. The neonates, still remaining on their empty shell, were taken using a paintbrush and transferred individually to Petri dishes (9 × 50 mm) so that no cannibalism had occurred before the experiments. All experiments were conducted at 24 °C, 70% RH, and LD 16:8 h photoperiod. Third instars of *Macrosiphum euphorbiae* Thomas, reared on potato plants, were used as prey. Preliminary tests showed that this species of aphid is well accepted by *C. maculata*. Third-instar aphids were used because at this stage they are approximately the same size as *C. maculata* eggs.

Advantages

Developmental time, survival, and weight of newly hatched second-instar *C. maculata* (0–24 h) were evaluated in order to determine whether cannibalism is advantageous for neonate larvae. Twenty-five larvae per treatment were fed *ad libitum* with conspecific eggs (0–24 h), mobile aphids, or defenceless aphids (killed by freezing at $-80\,^{\circ}\mathrm{C}$ for 10 min) for the full duration of the first instar. Each *C. maculata* neonate was kept individually in a 50-mm Petri dish and observed daily for moulting; water was supplied through dental cotton. The developmental time and weight data were analysed using one-way ANOVA, followed, when needed, by a Fisher's Protected Least Significant Difference (LSD) test (Super ANOVA version 1.1; Abacus Concepts, 1989). Chi-squared tests (JMP IN Software; SAS Institute, 1997) were performed for larval survival. To evaluate the dry biomass consumption of each *C. maculata* larva, 50 third-instar aphids and 50 *C. maculata* eggs were dried at $60\,^{\circ}\mathrm{C}$ for 24 h and weighed. The average dry weight obtained for each prey was multiplied by the number of prey consumed by each individual.

Preferences

To determine whether *C. maculata* neonates prefer conspecific eggs, they were presented with conspecific eggs and third-instar aphids in three different diet combinations: four conspecific eggs – eight aphids, six conspecific eggs – six aphids, and eight conspecific eggs – four aphids. Prey items were arranged alternately in 50-mm Petri dishes. Each treatment was replicated 10 times. Consumed prey (as determined by broken chorion for eggs or sagging of the aphid cuticle) were counted after 24 h. Consumption data were corrected by subtracting the mean number of dead prey observed in the control treatments (same system without the predator). The Manly preference index (M) (Manly *et al.*, 1972) was calculated from the number of prey consumed:

$$M = \ln (r_i/A_i)/\Sigma \ln (r_i/A_i)$$

where r_i is the number of prey of a given species remaining after 24 h and A_i is the number of prey of a given species initially present.

This index was used because it is the only method that takes into account the prey density depletion by predation during experiments (Chesson, 1983; Sherratt & Harvey, 1993). The preference indexes were compared using Wilcoxon's matched-pairs signed rank tests (JMP IN Software; SAS Institute, 1997).

Food discrimination

The discrimination ability of first-instar larvae and the influence of prey defence on their cannibalistic behaviour were evaluated by offering a combination of an equal number of conspecific eggs and aphids arranged alternately in 50-mm Petri dishes. Two different treatments were used: six conspecific eggs – six mobile aphids, and six conspecific eggs – six defenceless aphids. Each larva was observed for 30 min after the first contact with a prey. Each treatment was replicated 10 times. The first prey encounter and first successful attack were recorded. Chi squared tests (JMP IN Software; SAS Institute, 1997) were performed for each data set.

Chemical cues

Conspecific eggs (1 mg) and aphids (1 mg) were crushed in 0.15 ml distilled water. Eggs and aphids were then painted with 0.05 ml supernatant and left to dry for 1 h. An additional treatment of six conspecific eggs painted with aphid extract and six defenceless aphids painted with egg extract was offered to neonates. Two controls, six aphids painted with aphid extract with six conspecific eggs, and six eggs painted with egg extract with six defenceless aphids were also considered. Prey items were arranged alternately in 50-mm Petri dishes. Preference and behaviour tests were then assessed on *C. maculata* neonates. Each treatment was replicated 10 times. Preference indexes were compared by Wilcoxon's matched-pairs signed rank tests. Behaviour data were subjected to χ^2 tests (JMP IN Software; SAS Institute, 1997).

Results

Advantages

The weight of recently hatched second-instar *C. maculata* fed on conspecific eggs was significantly higher than the weight of *C. maculata* fed on both mobile aphids [ANOVA: $F = 13.714$, d.f. $= 2,69$, $P < 0.001$ (Fisher's protected LSD test, $P < 0.001$)] and defenceless aphids (Fisher's protected LSD test, $P < 0.01$). The developmental time of *C. maculata* first instars was similar when fed on conspecific eggs and defenceless aphids [(ANOVA: F $= 9.099$, d.f. $= 2,69$, $P < 0.001$ (Fisher's protected LSD test, $P = $ NS)] but was significantly longer when fed on mobile aphids. *Coleomegilla maculata* cannibals needed significantly less conspecific egg biomass than aphid biomass to reach the second instar (ANOVA: $F = 52.838$, d.f. $= 2,69$, $P < 0.001$). The diets did not affect the survival of the first-instar larvae ($\chi^2 = 3.627$, d.f. $= 2,74$, $P = $ NS) (Table 1).

Preference

For all proportions of aphids offered to *C. maculata* larvae, neonates consumed significantly more conspecific eggs than aphids, independent of prey mobility (Fig. 1). These results demonstrate that *C. maculata* neonates showed a consistent

Table 1. Mortality, development time, dry weight of newly second instar, and biomass needed to reach the second instar of *C. maculata* reared on different prey.

Diet	Mortality (%)	Development time (mean ± SD, days)	Dry weight (mean ± SD, mg)	Biomass needed (mean ± SD, mg)
Conspecific eggs	0%	3.56 ± 0.10a†	0.31 ± 0.03a	1.59 ± 0.06a
Defenceless aphids	0.04	3.71 ± 0.09a	0.23 ± 0.02b	3.29 ± 0.21b
Mobile aphids	0.12	4.13 ± 0.09b	0.18 ± 0.03c	3.62 ± 0.15b
	Chi squared $c2 = 3.627$ $P < 0.1631$	ANOVA $F = 9.099$ $P < 0.0003$	ANOVA $F = 13.714$ $P < 0.0001$	ANOVA $F = 52.838$ $P < 0.0001$

†In the same column, different letters indicate significant differences ($P < 0.05$).

preference for conspecific eggs. Manly's indexes did not differ between treatments in which defenceless aphids or mobile aphids were offered with the same proportion of eggs (Wilcoxon's matched-pairs signed rank tests: $Z = 1.3453$, $P = NS$) or a different proportion of eggs (Wilcoxon's matched-pairs signed rank tests: 33% of eggs: $Z = -0.3119$, $P = NS$; 67% of eggs: $Z < 0.000$, $P = NS$) (Fig. 1).

Food discrimination

When *C. maculata* was given an equal choice of conspecific eggs and aphids, the first meal was more frequently a conspecific egg. The defence and mobility of the prey did not influence the choice of *C. maculata's* first meal ($\chi^2 = 2.222$, d.f. = 1, $P = NS$) (Fig. 2b). Neonate first contact with prey was significantly more frequent on conspecific eggs than aphids. Discrimination in favour of conspecific eggs was similar in the presence of defenceless and mobile aphids ($\chi^2 = 0.267$, d.f. = 1, $P = NS$) (Fig. 2a).

Chemical cues

Neonates preferred aphids painted with egg extract to eggs painted with aphid extract (Wilcoxon's MPSR: $Z = -2.59215$, $P < 0.01$) (Fig. 1). Painted eggs with egg extract used as a control showed the neonates' consistent preference for eggs (Wilcoxon's MPSR: $Z = -4.2069$, $P < 0.001$), however in the other control, where aphids were painted with aphid extract, more eggs were eaten but there was no significant preference (Wilcoxon's MPSR: $Z = -1.1255$, $P = NS$). *Coleomegilla maculata* neonates moved significantly more often towards aphids painted with egg extract than towards eggs painted with aphid extract ($\chi^2 = 5.165$, d.f. = 1, $P < 0.05$).

Discussion

Some authors have suggested that the incidence of cannibalism is simply a consequence of frequency of encounters between conspecifics, and their relative vulnerability (Agarwala &
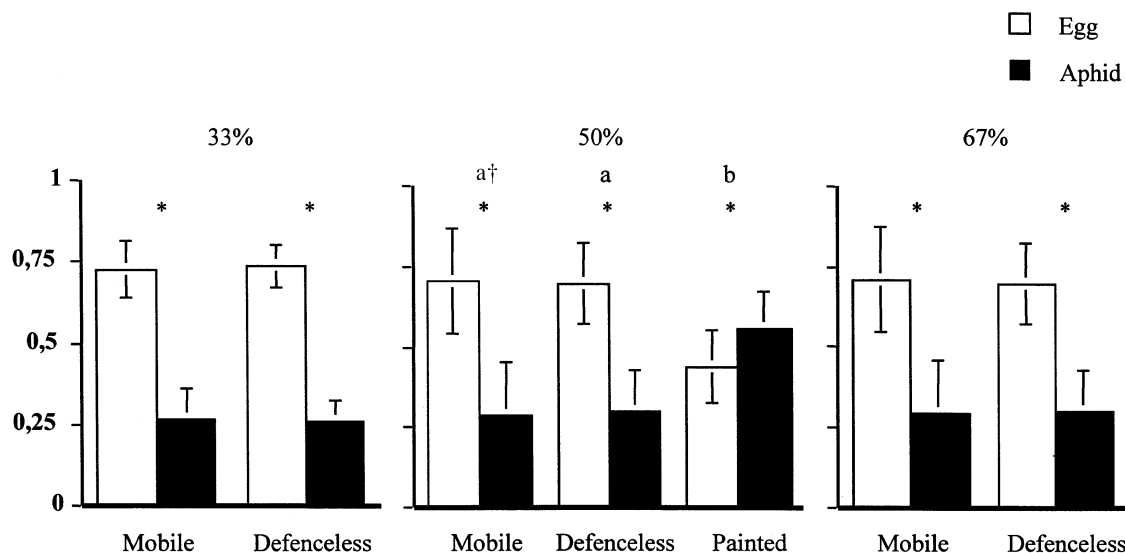

Fig. 1. Manly preference indexes for three different proportions (33–67, 50–50, and 67–33%) of eggs and aphids. †Indicates significant differences in preference; different letters indicate significant differences between treatments for the same proportion.
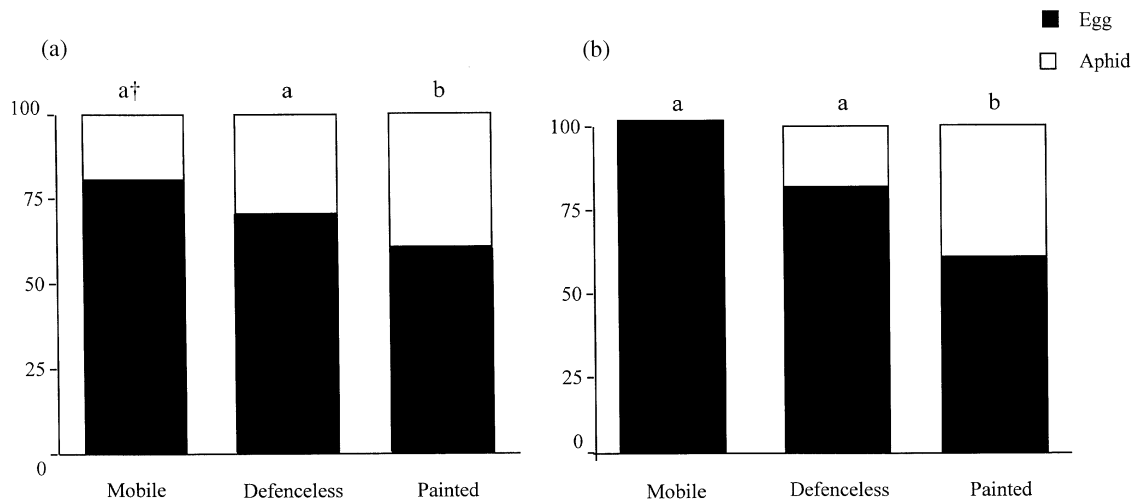
Fig. 2. (a) First prey contact and (b) first prey eaten by *C. maculata* neonates in the presence of conspecific eggs and *M. euphorbiae* aphids. †Different letters indicate significant differences between treatments.

Dixon, 1992; Stevens, 1992), i.e. cannibalistic attack rates are determined by the probability of encountering vulnerable individuals. Results from this study, however, showed that neonate cannibalism was frequent and that prey vulnerability did not influence neonate cannibalism. Moreover, neonates were attracted to conspecific eggs, implying the possible involvement of chemical cues.

The consumption of conspecific eggs gave cannibal neonates an advantage in terms of growth compared with larvae reared on aphids. The relative contributions of prey vulnerability and food quality to the success of cannibalistic behaviour for neonates remain unclear. The data suggest that the cannibal's responses were affected by a combination of both factors. Developmental time of *C. maculata* neonates was affected more by prey vulnerability whereas the advantage of higher weight was enhanced by both prey vulnerability and quality.

In terms of dry biomass needed to reach the second instar, significantly less conspecific egg biomass than aphid biomass was needed for *C. maculata*. This result corroborates those of Agarwala and Dixon (1992), where less dry weight of eggs than aphids was needed to achieve similar larval growth. Therefore, it can be concluded that conspecific eggs fit the nutritional requirement of *C. maculata* first-instar larvae better than do aphids. The higher nutritional value of eggs could be due to several factors. One plausible contribution is egg cholesterol quality because cholesterol content is high in insect eggs (Keiser & Yazlovetskii, 1988; MacDonald *et al.*, 1990). Moreover, the sterol composition of predatory coccinellids is mainly cholesterol (Svoboda & Robbins, 1979) while aphid sterol composition is high in phytosterols (Campbell & Nes, 1983; Keiser & Yazlovetskii, 1988). Therefore, the cholesterol contained in eggs matched more closely the nutritional requirements of the predator.

Stevens (1992) proposed that cannibalism occurs when predators do not distinguish between conspecifics and other prey, suggesting that cannibalism should only rely on frequency of encounter. Agarwala and Dixon (1992) also suggested that the low level of cannibalism when aphids are abundant results from the low level of encounter with conspecific eggs. Therefore, if cannibalism by neonates were simply the consequence of absence of discrimination between different types of prey, no preference would have resulted when equal numbers of eggs and aphids were offered. Moreover, *C. maculata* neonates should have consumed more aphids than eggs when aphids were given in a higher proportion. The results obtained in this study, however, suggest that cannibalism occurred at a high rate, even when aphids were the more common prey, showing a consistent preference for conspecific eggs. Agarwala *et al.* (1997) obtained similar results. Their data suggested that aphid presence did not influence the basic rate of cannibalism of first-instar coccinellid *Menochilus sexmaculatus* (Fabricius). Neonates might be expected to prefer eggs because they are defenceless, however the results of the present study showed that even when aphids are defenceless, larvae still prefer conspecific eggs.

The results suggest that *C. maculata* neonates attack and eat conspecific eggs preferentially over aphids. In contrast, Kalushkov (1994) showed that fourth instars of the coccinellid *Propylaea quatuordecimpunctata* (Linnaeus) preferred feeding on aphids when given a choice of aphids and conspecific eggs. This contrast could be due to neonate ability to discriminate high quality food. A preference for conspecific eggs indicates that larvae can discriminate between prey and select those with the highest nutritional value. Neonates moved significantly more often directly towards conspecific eggs, showing that neonate cannibalistic behaviour is not due only to frequency of encounter, as was suggested for older larvae and adults. Few studies have described this ability in Coccinellidae. Roger *et al.* (2001) demonstrated that *C. maculata* larvae can discriminate between two types of food (parasitised and non-parasitised lepidoterans).

Agarwala and Dixon (1993) showed that *A. bipunctata* has the ability to recognise conspecific eggs and larvae. Recently, Joseph *et al.* (1999) suggested that *H. axyridis* has a well developed kin discrimination system.

Very little is known about the mechanisms underlying prey discrimination by coccinellids. Carter and Dixon (1982) showed that prey recognition in some coccinellid species occurs mainly on physical contact while other authors have suggested that adults and older coccinellid larvae use sensory information for kin recognition (Grafen, 1990; Agarwala & Dixon, 1993). Harmon *et al.* (1998) showed that *C. maculata* do not use colour or visual cues in proximity foraging behaviour. Results obtained in this study suggest that neonate egg recognition is mainly chemical. In preliminary tests, in which aphids were painted with extract of eggs, neonates were also observed probing liquid extract around the aphid with their maxillary palps.

Current studies on cannibalism and intraguild predation in ladybirds indicate that the most important sensory cue for foraging larvae is the chemical nature of the cuticular waxes (alkanes) of insects that they encounter. All development stages of ladybirds would also be coated similarly with species-specific alkanes (Dixon, 2000). Majerus (1994) suggested that recognition of sibling eggs is chemically imprinted on larvae immediately after hatching. Therefore, it is possible that these chemical cues could be used by coccinellid neonates to find a first valuable meal. It is also possible that the defensive alkaloid content in eggs (Pasteels *et al.*, 1973) serves as an attractant for neonates because they could enhance its defence efficacy by accumulating such alkaloids.

Cannibalistic behaviour of neonates evolved from selection pressure on individuals, not on populations. As suggested by Majerus (1994), an inherited characteristic that provides its bearer with some advantage in the survival stakes will increase in frequency in a population through time. Its bearer will be more likely to survive than those lacking the trait. Therefore, neonate egg recognition could result from adaptive pressure in favour of a high quality food source. Considering the low mobility of neonates and their difficulty in getting a first meal, cannibalism ensures that some of the offspring will survive. From these results, it can also be concluded that neonates' egg recognition ability is innate because neonates used in this study were taken before they could encounter any food type and were considered to be naive. The results could also explain further why egg cannibalism is found at such a high level in *C. maculata* neonates. Differences between neonate preference and the adults and older larvae could be explained by the ability of neonates to discriminate eggs.

Acknowledgements

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