

Oviposition strategy of the green lacewing *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) in response to extraguild prey availability

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Key words. Oviposition strategy, green lacewing, *Chrysoperla rufilabris*, Chrysopidae, sibling cannibalism, hatching synchrony, parental investment, aphid availability

Abstract. The capacity of the green lacewing *Chrysoperla rufilabris* (Burmeister) to modify its oviposition strategy in response to extraguild prey availability in an oviposition site was studied. Gravid females were placed in presence and absence of aphids. Fecundity, fertility, dispersion and hatching synchrony were compared. Results indicate a statistical difference in the hatching synchrony of eggs. However, no statistical differences were observed in the proportion of infertile eggs and in egg dispersion. We suggest that *C. rufilabris* can alter hatching synchrony of eggs in condition of food scarcity in order to favour intra-clutch egg cannibalism by newly hatched larvae and thus increase its overall reproductive success.

INTRODUCTION

In his review on parental investment, Alexander (1974) pointed out that some parental behaviour involve sacrifice of one or many individuals of a parent progeny. Sacrifice of individuals will be selected for as long as it improves the overall reproduction success of the parent. In condition of food scarcity a parent may favour sibling cannibalism (i.e. cannibalism among individuals sharing the same parents), in order to favour survival of a few individuals instead of losing all of its progeny (Alexander, 1974). Eickwort (1973) demonstrated that the selfish trait of sibling cannibalism should be selected for, if it doubles the probability of reaching adult stage.

Sibling cannibalism has often been observed in different insect species (Polis, 1981). Some species have even evolved trophic eggs, i.e. infertile eggs destined to feed progeny (Henry, 1972; Polis, 1981; Crespi, 1992). Even if, to date, trophic eggs are reported only in few insect species, they could be present in many species but not being detected since they are not always different in aspect from normal (fertile) eggs (Crespi, 1992).

Sibling cannibalism and cannibalism of trophic eggs may be considered as a “food caches” strategy and might especially occur in species unable to provide enough nutrients in their fertile eggs, those that cannot feed their developing offspring (Polis, 1981) and those that live in an unpredictable habitat (Crespi, 1992). Sibling cannibalism might however be risky, particularly when resources are abundant, because kin might be cannibalised unnecessarily. Moreover, if trophic eggs are not essential to larval development, a female should avoid producing them in condition of food abundance, since they represent a high energy cost and are unnecessary in those conditions. Hence, it would be advantageous for

parents to evaluate the availability of resources in their environment, and alter their oviposition strategy, in order to enhance or lower the odds of egg cannibalism accordingly.

Dickinson (1992) reported that clutch size, egg dispersion, proportion of infertile eggs within a clutch, hatching synchrony, and egg yolk biomass influence the intra-clutch egg cannibalism, and that many of those factors can be controlled by females that wish to maximise their reproductive success. Crespi (1992) assessed that hatching synchrony adjustment should be favoured in species with facultative cannibalism in which larval survival probability depends upon conditions (for example food availability) that a female can evaluate.

We studied the capacity of the green lacewing *Chrysoperla rufilabris* (Burmeister), a North American species with adults that feed on aphid honeydew, to alter its oviposition strategy in response to extraguild prey availability in an oviposition site, regardless of the general prey availability in the habitat.

Like most aphidophagous species, chrysopids are attracted to aphid presence cues. Laboratory experiments have shown that *Chrysoperla carnea* (Stephens) sensu lato adults can respond positively to aphid honeydew (van Emden & Hagen, 1976) and that *Chrysopa cognata* Wesmael showed the same reaction in response to aphid sex pheromone (Boo et al., 1998). However, unlike other aphidophagous species, many Neuropterans do not seem to seek for a patch with an aphid colony when ovipositing (Miermont & Canard, 1975; New, 1975; Coderre et al., 1987). Coderre et al. (1987) found that even if eggs are laid only during the occurrence of aphids on maize, *Chrysopa oculata* Say do not select oviposition sites in relation to aphid abundance, as most of the eggs were

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found on leaves without aphid colonies. Duelli (1984, 1987) also mentioned the random egg laying of honeydew-feeding adult chrysopid species. This is contrary to the foraging theory developed for invertebrate predators that predicts that females, in order to maximise their fitness, should not oviposit in patches where prey are scarce (Kindlmann & Dixon, 1993). Larvae hatching far from aphid colonies should have less chance of survival than those hatching near them. That arouses questions about the oviposition strategy of lacewings: Can lacewings evaluate the probability of survival of its progeny and alter its oviposition strategy in order to enhance or lower the odds of intra-clutch egg cannibalism accordingly?

Although adults are glycophagous, lacewing larvae are aggressive generalist predators (Putman, 1937) and cases of egg cannibalism in laboratory have been reported many times (New, 1975). It has been reported that under low food availability condition, larval (Duelli, 1981) and egg (Canard, 1970) cannibalism could have a potential evolutionary advantage for lacewings. However, it has also been assessed that the egg pedicel could reduce the risk of cannibalism, even if it does not prevent it completely (Duelli & Johnson, 1992).

Based on the assumption that egg cannibalism is adaptive and allows newly hatched larvae to survive in condition of food scarcity, three aspects of the oviposition strategy of the lacewing were examined: (1) egg dispersion, (2) proportion of infertile eggs, and (3) hatching synchrony. A greater proportion of infertile eggs, minimal spatial dispersion, and asynchrony of egg hatching should favour intra-clutch egg cannibalism.

MATERIAL AND METHODS

C. rufilabris adults were obtained from Natural Insect Control (Stevensville, Ontario) and were about 10 days old on reception. They were being fed with frozen *Ephestia kuehniella* (Zeller) eggs as larvae. During the transport, adults could feed on the provider's diet. After arrival, adults were only given water. All experiments were done using this generation of adults. The prey used was the potato aphid (*Macrosiphum euphorbiae* Thomas) reared on saplings of potato plants (*Solanum tuberosum* L. Var. Kennebec).

Twenty-five potato saplings infested with aphids (about 50 aphids of all instars) and 25 potato saplings free of aphids were placed individually in cardboard tubes (length: 10.6 cm; diameter: 4 cm). One 10 day-old gravid female of *C. rufilabris* was then added in each experimental unit (aphid treatment: $n = 23$; no aphid treatment: $n = 19$). Units were then put in obscurity at 28°C and 40% RH. After 8hrs, lacewings were removed from tubes. The number of eggs in each tube was counted. Both eggs laid on potato saplings or on tube were considered for this experiment. The Euclidean distance between an egg and all the other eggs, and the Euclidean distance between an egg and its closest neighbour were also noted. Since most eggs were laid on tubes, only those eggs were considered for distance evaluation. All eggs were then collected and put in Petri dishes at 24°C. After two days, the number of non-viable eggs laid by a female was evaluated. Non-viable eggs can easily be differentiated from viable eggs by their colour. Within two days, viable eggs turn from light green to grey, while the colour of non-viable eggs does not change.

C. rufilabris eggs were observed continuously and hatching time was noted. Results were tallied as follows: (1) time interval between hatching of first and last eggs (egg cluster hatching time), (2) time interval between hatching of two eggs, and (3) proportion of time interval between hatching of two eggs that was less than the time taken by larvae to start foraging after hatching.

A Fisher exact test was used to compare the proportion of viable and non-viable eggs of both treatments. The proportions of time intervals of less than 20 min between the hatching of two eggs were compared using a Fisher exact test. Two-way ANOVAs were used to compare Euclidean distances (criteria: distance and number of eggs), and the time between hatching of two eggs (criteria: time and number of eggs). A Wilcoxon test was used to compare egg cluster hatching time because data were not normally distributed according to Shapiro-Wilk test. All statistical tests were executed on JMP ® software (Sall & Lehman, 1996).

RESULTS

Viable vs. non-viable eggs

The proportion of non-viable eggs was very low in both treatments (3% for treatment with aphids, 4% for treatment without aphids). The slight difference observed in favour of the treatment without aphid was not statistically significant (Fisher's Exact Test: $p = 0.7284$) (Table 1).

TABLE 1. Mean number and proportion of viable and non-viable eggs laid by *C. rufilabris* females in 8hrs in presence or absence of aphids.

| Treatment | Viable eggs | Non-viable eggs |
|--------------------|--------------------------|-------------------------|
| Presence of aphids | 5 ± 1.50 (97%) | 0.15 ± 0.09 (3%) |
| Absence of aphids | 4.54 ± 0.94 (96%) | 0.17 ± 0.08 (4%) |

Spatial dispersion

No statistical differences were observed in the spatial dispersion of eggs of both treatments, neither in the mean distance between each egg (Two-way ANOVA: $F = 1,6514$; $df = 1, 1262$; $p = 0,1990$) nor in the distance between an egg and its closest neighbour (Two-way ANOVA: $F = 3,0947$; $df = 1, 143$; $p = 0,0807$) (Fig. 1).

Hatching synchrony

Time between hatching of two eggs was statistically shorter for eggs laid in presence of aphids (Two-way

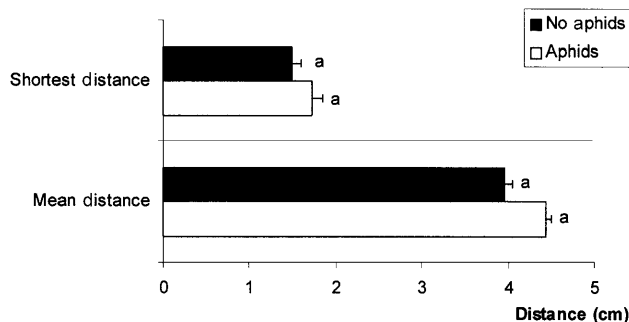


Fig. 1. Spatial dispersion of eggs laid by *C. rufilabris* females in presence and absence of aphids. Different letters indicate a statistical difference ($p < 0.05$).

ANOVA: $F = 6.0765$; $df = 1, 176$; $p = 0.0147$) (Fig. 2). However, total hatching time was not statistically different between the two treatments (Wilcoxon: $\chi^2 = 2,1391$; $df = 1$; $p = 0,1436$) (Fig. 2). Total hatching time was longer than 480 min for 43.75% of egg clusters in presence of aphids and for 73.33% in absence of aphids. Larvae took an average of 19.14 ± 2.30 min to leave their egg after hatching. Less than 20 min intervals between hatching of two consecutive eggs were statistically more frequent in presence of aphids (48%) than in absence of aphids (33%) (Fisher's Exact Test: $p = 0.0256$).

DISCUSSION

Foraging theory predicts that an insect predator should not oviposit in patches where prey are scarce or absent (Kindlmann & Dixon, 1993). However, Coderre et al. (1987) and Duelli (1984, 1987) observed that honeydew-feeding adult chrysopids do not necessarily lay eggs in proximity of aphid colonies. Based on the assumption that sibling cannibalism is a way to enhance chances of survival for a larva that hatches in a low prey density patch, we studied the capacity of the green lacewing to adjust the odds of intra-clutch egg cannibalism by newly hatched larvae in response to prey availability. Three mechanisms of egg cannibalism rate adjustment were proposed: modification of the proportion of viable and non-viable eggs, modification of egg spatial dispersion, and modification of egg hatching synchrony.

Proportion of viable eggs

We found no evidence of the presence of trophic eggs in *C. rufilabris*. The proportion of non-viable eggs was very low in both treatments and no statistical difference was observed. Tassan et al. (1979) have already demonstrated that the quantity and quality of aphid honeydew ingested by adult green lacewings affect the production and fertility of eggs. Based on those results, one can suppose that overall aphid abundance in the habitat or the occurrence of aphids in the immediate area of oviposition could influence egg production and fertility. All individuals were fed with the same diet before our experiments. The fact that no differences were observed in the proportion of viable and non-viable eggs in presence or

absence of aphids indicates that aphid availability in a patch (and consequently quantity of honeydew eventually ingested) does not alter *C. rufilabris* fertility in this very patch.

Egg spatial dispersion

Our experiment also suggests that *C. rufilabris* does not change its spatial dispersion of eggs in response to extra-guild prey availability. This could be explained by the fact that *C. rufilabris* did not evolve to modify egg dispersion in response to prey availability. However, the restricted dispersion allowed by the experimental unit could also have contributed to the non-significant response observed.

Hatching synchrony

C. rufilabris females responded to extraguild prey availability by adjusting hatching synchrony. Even if the total hatching time was not different in the presence of aphids, time interval between hatching of two consecutive eggs was shorter. This could result in a higher cannibalism rate in the absence of aphids. However, in order to understand how hatching synchrony really influences intra-clutch egg cannibalism probability, we compared the proportion of eggs that hatched more than 20 min apart. Since newly hatched larvae remained immobile for about 20 min before starting search for a prey, egg hatching at more than 20-min intervals should increase the odds of egg cannibalism. Indeed, in such conditions, the first larva to hatch will more likely encounter an egg than an larva, thus increasing the risk of egg cannibalism. In presence of aphids, the fact that 52% of hatching intervals is longer than 20 min invalidates the hypothesis that *C. rufilabris* should try to avoid intra-clutch egg cannibalism when prey are available. This oviposition strategy could be an adaptation to the high instability of aphid colonies. Even if eggs are laid near an important aphid colony, this colony could be extinct by the time eggs hatched. Thus, females should adjust for this possibility by keeping a partial intra-clutch egg cannibalism. However, when aphids were absent a statistically greater proportion of hatching interval were longer than 20 min. Females thus increase intra-clutch egg cannibalism probability in the absence of aphids. This tends to confirm Crespi's (1992) hypothesis that hatching synchrony should be modified in order to favoured intra-clutch egg cannibalism in species where cannibalism is facultative.

Three mechanisms could explain the modification of hatching synchrony by *C. rufilabris*: (1) selection of places with different micro-climates for oviposition (Baur, 1988; Dickinson, 1992), (2) modification of yolk content in order to delay embryo development (Dickinson, 1992), and (3) modification of temporal distribution of oviposition. Since females were not allowed to lay eggs in different environmental conditions in this experiment, the first hypothesis is thus excluded. The two other mechanisms are however possible; a female could slow down or accelerate its oviposition rate in response to extraguild prey availability in a patch, and the fact that many eggs took more time to hatch than the total oviposi-

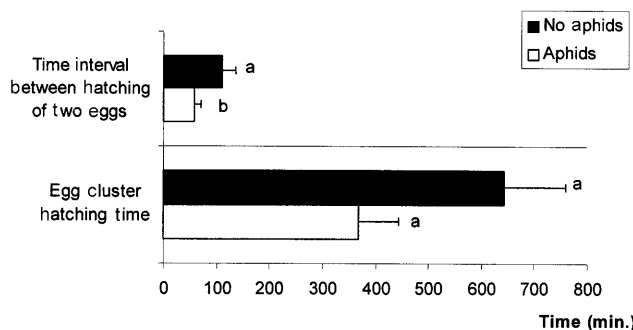


Fig. 2. Egg cluster total hatching time and time interval between hatching of two consecutive eggs laid in presence and absence of aphids by *C. rufilabris*. Different letters indicate a statistical difference ($p < 0.05$).

tion time allowed (i.e. more than 480 min) suggests that modification of yolk content is also possible. However, the importance of each mechanism remains to be tested.

Green lacewings are vulnerable to intraguild predation by ladybirds (Lucas et al., 1998). This could explain the oviposition niche partitioning among aphidophagous species observed by Coderre et al. (1987). Non-predatory chrysopid adults do not seek for high prey density patches to lay eggs (where intraguild predation is high) but rather seem to lay eggs wherever they land (Duelli, 1984, 1987). However, they can adjust intra-clutch egg cannibalism odds in response to prey availability in order to maximise their reproductive success. If oviposition occurs near an aphid colony, the odds of cannibalism will be reduced as females will synchronise hatching of their eggs. On the other hand, if aphids are absent, the females can enhance the odds of cannibalism, in order to maximise the probability of survival of a few individuals.

ACKNOWLEDGEMENTS. This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to D. Coderre, and by a graduate scholarship from Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR) to B. Fréchette. We thank F. Pelletier and F. Courchesne for technical assistance and D. Vincent for English revision of the manuscript.

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Received January 6, 2000; accepted May 4, 2000