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SHORT COMMUNICATION

Ovarian dynamics and specialisation in ladybirds

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Abstract. 1. Generalist predatory insects that exploit unpredictable and ephemeral prey should allocate metabolic resources differently to soma and gonads than specialist species. As the former have more opportunities to encounter a wide array of prey than specialists, the expectation is that they will more rapidly resorb oocytes when food is scarce. By doing so, they reallocate resources to the soma to support the search for oviposition sites of a better quality. Similarly, they are expected to resume oogenesis faster than the specialist when good conditions return.

2. This hypothesis was tested by comparing a generalist and a specialist ladybird species belonging to the same genus.

3. A resorption index was calculated for females of both species subjected to several starvation regimes. This index indicated that over a period of fasting of 3 days, the intensity of resorption was greater in the generalist than the specialist. When food was again supplied, oogenesis resumed and within 1 day was faster in the generalist than in the specialist.

4. As predicted, the resorption of oocytes and replenishment occurred faster in the generalist than in the specialist species. This is the first time, to our knowledge, that the speed and intensity of the ovarian dynamics of a predatory insect have been linked to its way of life.

Key words. Ladybird beetles, oocyte resorption, ovarian dynamics, specialisation.

Introduction

Aphidophagous ladybirds feed on unpredictable prey whose abundance fluctuates widely from one year to another (Majerus & Kearns, 1989; Dixon, 1998). Aphid colonies are also ephemeral because they each only last for a short period of time, which is hardly longer than the time taken by ladybirds to develop from egg to adult (Dixon, 1998, 2000). Under such circumstances, not all aphid colonies are suitable for oviposition. Ladybird females will only lay eggs at the beginning of the development of aphid colonies that are not being exploited by other conspecific larvae. Otherwise, the risk of cannibalism may jeopardise their reproductive investment (Kindlmann & Dixon, 1993). When they detect the presence of conspecific larvae, adults refrain from ovipositing, eat some aphids, and leave in search of a more suitable patch (Frechette *et al*., 2004).

Therefore, due to the nature of their prey, females need to balance their energy allocation between oocyte production and fuel in order to search for suitable oviposition sites (Ohgushi & Sawada, 1985; Collier, 1995; Ohgushi, 1996). The rate of patch discovery may increase if females are able to cease oogenesis and resorb oocytes when they continuously encounter poor quality or no adequate oviposition sites at all, and quickly resume egg production when they encounter good conditions again. These two antagonistic processes correspond to Papaj's (2000) 'ovarian dynamics'.

It is known that ladybirds resorb their mature oocytes when prey is scarce (Osawa, 2005). The aim of this paper is to investigate egg resorption in ladybirds in more detail and determine whether the ovarian dynamics of specialist and generalist ladybird beetles differ. *Adalia bipunctata* (L.), the generalist, feeds on more than 50 species of aphids living on herbaceous plants, shrubs, or trees (Hodek & Honek, 1996).

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Table 1. The effect of increasing starvation periods, from 0 to 3 days (0 DS, 1 DS, 2 DS, and 3 DS), on the average (standard deviation) body mass, oocyte length, follicle length, and I_r of *Adalia bipunctata* and *A. decempunctata* females.

	A. bipunctata					*A. decempunctata*				
	Body mass		Oocyte length	Follicle length		Body mass		Oocyte length	Follicle length	
	(mg)	% of 0 DS	(mm)	(mm)	I_r	(mg)	% of 0 DS	(mm)	(mm)	I_r
0 DS	17.30 (1.93)[a]	100.0	0.68 (0.19)	0.68 (0.19)	0.01 (0.07)[l]	12.82 (1.76)[c,d]	100.0	0.58 (0.23)	0.59 (0.23)	0.05 (0.14)[l]
1 DS	15.18 (1.73)[b]	87.7	0.49 (0.22)	0.56 (0.21)	0.32 (0.24)[k]	10.64 (1.29)[e,f]	83.0	0.36 (0.17)	0.45 (0.17)	0.48 (0.19)[j]
2 DS	13.79 (2.74)[b,c]	79.7	0.21 (0.16)	0.46 (0.15)	0.87 (0.44)[i]	10.45 (1.77)[f]	81.5	0.20 (0.13)	0.44 (0.14)	0.89 (0.35)[h,i]
3 DS	12.06 (1.47)[d,e]	69.7	0.08 (0.11)	0.39 (0.12)	1.23 (0.39)[g]	10.36 (0.84)[f]	80.8	0.16 (0.12)	0.41 (0.14)	0.96 (0.33)[h]

The effect of starvation on the oocytes was assessed by the I_r values, which take into account the length of the follicle as a covariate. Body masses and I_r values followed by different letters are significantly different ($P = 0.05$).

The probability of their encountering suitable concentrations of prey is possibly large, because when aphids become scarce in a particular habitat, they are likely to be more abundant in other habitats and on other host plants. In contrast, *Adalia decempunctata* (L.), the specialist, feeds on a few species of aphids living on trees, all of which show the same seasonal dynamics strongly linked to changes in the concentration of nitrogen in tree sap (Dixon, 2005; Dixon *et al*., 2005). If these preferred habitats do not provide enough prey for reproduction, then there is less likelihood of discovering better oviposition sites elsewhere and rapid egg resorption is less advantageous. Therefore, we predict that generalist ladybirds will have faster ovarian dynamics than specialist ladybirds, both in terms of resorption and maturation of oocytes.

Material and methods

The experiments were carried out on *A. bipunctata* and *A. decempunctata* collected in the field and reared in the laboratory as described in Ferrer *et al*. (2008).

Well fed 15-day-old females of the two species were isolated in 9 cm Petri dishes and subjected for 3 days to one of the following treatments: fed pea aphids in excess (0 DS), fed pea aphids in excess for the first 2 days and starved on the third day (1 DS), fed pea aphids in excess on the first day and then starved for 2 days (2 DS), starved for 3 days (3 DS), starved for 2 days and then fed pea aphids in excess on the third day (1 DR).

There were nine replicates of each treatment for each species.

At the end of the third day the females were weighed to an accuracy of 0.1 μg. They were dissected under a binocular microscope and their ovaries isolated and stained with Brilliant Cresyl Blue. A gap appears between the oocyte membrane and the inner wall of the follicle in case of resorption. The first 20 ovarioles that were isolated per female were examined: the length of the last follicle and of the oocyte it contained were measured. The intensity of the resorption was expressed as:

$$I_r = \arcsin\{\sqrt{[(\text{follicle length} - \text{oocyte length})/(\text{follicle length})]}\}. \quad (1)$$

The effect of starvation (treatments 0 DS, 1 DS, 2 DS, and 3 DS) on body mass was analysed using an ANOVA (species and starvation regime as fixed independent variables) followed by Tukey *post hoc* tests. The I_r values were compared using an ANOVA (females nested within ladybird species crossed with starvation regimes) followed by Tukey *post hoc* tests. The effect of the resumption of feeding was assessed by comparing the body mass and the I_r values of the females of the treatments 3 DS and 1 DR using the same methods.

Results

Oocyte resorption

Regarding female body mass, there was no significant interaction between the species and the length of the starvation period ($F = 2.6$; d.f. $= 3, 64$; $P = 0.062$). At the beginning of the experiment both species differed in body mass, with the generalist species being heavier than the specialist ($F = 71.0$; d.f. $= 1, 64$; $P < 0.001$). The two species significantly lost weight when deprived of food ($F = 15.6$; d.f. $= 3, 64$; $P < 0.001$) (Table 1).

There was a significant effect of the interaction species-starvation regimes on the I_r values ($F = 36.9$; d.f. $= 3, 1368$; $P < 0.001$). The effect of species was not significant ($F = 0.7$; d.f. $= 1, 1368$; $P = 0.386$) but starvation had a highly significant effect on resorption ($F = 1000.0$; d.f. $= 3, 1368$; $P < 0.001$). The generalist species resorbed its oocytes significantly more intensely than the specialist. To illustrate the results: the last oocytes were only 12.2% and 27.8% of their length at the beginning of the experiment after 3 days of starvation in the generalist and the specialist, respectively (Tables 1 and 2).

Effect of the resumption of feeding

The resumption of feeding provoked a significant increase in weight for the generalist and specialist females. However, the gain was more important in the generalist than the specialist (starvation regime × species: $F = 23.3$; d.f. $= 1, 32$; $P < 0.001$; starvation regime: $F = 36.7$; d.f. $= 1, 32$; $P < 0.001$; Table 2). When the females resume eating, oogenesis restarted and as a consequence, oocytes refilled in both species. However, this was significantly more pronounced in the generalist

Table 2. The comparison of the resumption of feeding for 1 day (treatment 1 DR) to a fasting period of 3 days (treatment 3 DS): effect on the average (standard deviation) body mass, oocyte length, follicle length, and I_r of *Adalia bipunctata* and *A. decempunctata*.

	A. bipunctata					*A. decempunctata*				
	Body mass	Oocyte length		Follicle length		Body mass	Oocyte length		Follicle length	
	(mg)	(mm)	% of 0 DS	(mm)	I_r	(mg)	(mm)	% of 0 DS	(mm)	I_r
3 DS	12.06 (1.47)	0.08 (0.11)	12.2	0.39 (0.12)	1.23 (0.39)	10.36 (0.84)	0.16 (0.12)	27.8	0.41 (0.14)	0.96 (0.33)
1 DR	19.76 (3.83)	0.57 (0.20)	84.7	0.64 (0.20)	0.28 (0.22)	11.23 (0.66)	0.42 (0.22)	72.7	0.54 (0.18)	0.44 (0.35)

The effect of the resumption of feeding on the oocytes was assessed by the I_r values, which take into account the length of the follicle as a covariate.

than the specialist females (starvation regime × species: $F = 85.1$; d.f. = 1, 684; $P < 0.001$; starvation regime: $F = 963.1$; d.f. = 1, 684; $P < 0.001$). The percentages of the variation in the length of the last oocytes gave a rough idea of the effect of the resumption of feeding in the two species. Resumption of feeding provoked a 72.5% and 44.9% increase in the length of the last oocyte for *A. bipunctata* and *A. decempunctata*, respectively (Table 2).

Discussion

Adaptation to different habitats is known to lead to the diversification of life-history strategies (Futuyma, 2001; Reznick & Travis, 2001) and more particularly, to affect traits such as the allocation of metabolic resources to the soma and gonads (Van Noordwijk & Dejong, 1986; Stearns, 1992).

We predicted that a habitat generalist, *A. bipunctata*, would react more quickly to the lack of food by initiating egg resorption than a habitat specialist, *A. decempunctata.* We also predicted that the former would resume oocyte maturation more rapidly on encountering a rich food supply. That is, *A. bipunctata* should show faster ovarian dynamics than *A. decempunctata*. These expectations rest on the greater probability of *A. bipunctata* finding areas where aphids are abundant, and over a longer period of time than *A. decempunctata*, whose breeding success is dependent on the spring peak in abundance of a few species of tree-dwelling aphids (Hodek & Honek, 1996).

The experimental results show that starvation had a similar effect on the body mass of both *A. decempunctata* and *A. bipunctata*. After 1 day without food, females started to resorb the most advanced oocytes in their gonads and at the end of the third day of starvation, the average length of the terminal oocytes was 12% of the initial size in the generalist and 28% in the specialist species. In terms of volume, these reductions in size approximately corresponded to two-thirds and to one-third of the initial volume of the oocyte. That is, the generalist resorbed nutrients from its gonads at twice the rate of the specialist. In addition, if it is adaptive for a generalist to more quickly retrieve resource from its gonads, then it should also be advantageous for it to immediately restart maturing oocytes as soon as a good food source is located. Fast ovarian dynamics is adaptive for generalist species, because in addition to being a method of quickly obtaining additional resources for foraging when prey is scarce (Papaj, 2000), it also enables them to quickly mature oocytes when they locate an abundance of prey. Once again the results match the expectation. The generalist *A. bipunctata* resumed oogenesis more quickly than *A. decempunctata* when fed *ad libitum* after 2 days of starvation, achieving nearly 85% of the initial oocyte size.

To our knowledge this is the first record of differences in ovarian dynamics linked to the degree of dietary specialisation in predatory insects.

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