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ENVIRONMENTALLY BASED MATERNAL EFFECT ON REPRODUCTION OF *ADALIA BIPUNCTATA*: IMPACT OF APHID PREY SPECIES

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ABSTRACT

Food quality of ladybirds is known to influence the biological performances of the aphidophagous predators. Development (larval and total durations, mortality) and reproduction of the beetle are modified by changes of both prey species and their relative host plants. Suitablity of many aphid species was already studied and was observed to induce lower consumption until complete rejection of preys by some aphidophagous predators. Even if polyphagous insects are considered, some aphid species provide only low quality food including sometimes toxic compounds.
In response to low nutritional value or food limitation, many insects have evolved developmental plasticity in which larvae mature more rapidly, leading to smaller body size adult. Here we investigate the effect of food quality represented by aphid species on *Adalia bipunctata* reproduction after having relaxed the nutritive selection from adult emergence. Reciprocal crosses between emerging adults fed with *Acyrthosiphon pisum* (optimal diet) or *Aphis fabae* (unappreciated diet) demonstrated that negative effect of the latter aphid species was maternally inherited. Female fecundity (egg laying and egg numbers per female) and egg viability was observed for each cross and compared to a full *A. fabae* nutrition (for both male and female at larval and adult stages) and *A. pisum* references. This environmentally based maternal effect was directly linked to developmental parameters induced by larvae nutrition. Influence of aphid prey constitute an important change of predator environment which was discussed in relation to biological control efficacy.

INTRODUCTION

The ability of insects to counter environmental stresses is an important factor in determining their abundance and distribution. Several works were undertaken to demonstrate the effect of the food quality, as the plant composition, on development and reproduction of phytophagous insects. Indeed, resistance of some crop plant species as wheat or oilseed rape was correlated to their mineral composition: high level of nitrogen in plants were shown to imply higher susceptibility to herbivore pests as aphids (van Emden, 1995). Different kinds of toxic compounds in plants, also called allelochemicals, were detected in several botanical families and were found to modify the biology of the herbivores (Harborne, 1993). Entomophagous insects (parasites and predators) are also influenced by their host or prey quality. Aphid species as *Brevicoryne brassicae* and *Aphis sambuci* are known to be toxic for some aphidophagous ladybirds

(Hodek & Honek, 1996; Francis, 1999). The toxicity of the former one is directly linked to the presence of allelochemicals in Brassicacae plants (Francis, 1999; Francis *et al.*, submitted). Other aphid species as *Aphis fabae*, were also demonstrated to be unsuitable food for some ladybird beetles. In some cases, inadequate preys can be completely rejected by the beneficial insects (Blackman, 1967).

Environmental changes as food limitation determine responses from insects which have evolved developmental plasticity. If plasticity is present, individual phenotypes will be modified by the environment, with results depending on the pattern of environmental variability (Caswell, 1983). Maternal effects have recently become recognized as important in the evolution of natural populations (Mousseau & Dingle, 1991). They may result in large time lags in an evolutionary response to selection, and characters subject to large maternal effects may even respond to selection in a maladaptative direction (Lande & Kirkpatrick, 1990). Is there an environmentally based maternal effect which is linked to the ladybird larval nutrition ? Here we investigate the effect of food quality represented by aphid species on *Adalia bipunctata* reproduction after having relaxed the nutritive selection from adult emergence. Reciprocal crosses between emerging adults fed with optimal or unappreciated diet will be performed to try to demonstrate that the negative effect of the unsuitable aphid species was maternally inherited.

MATERIALS AND METHODS

Plant and insect culture

Broad beans (*Vicia faba* L.) were grown at a 20±2°C temperature and 16 h of light photoperiod in 20×30 cm plastic trays containing a mixture of perlite/vermiculite.

Acyrthosiphon pisum (Harris) and *Aphis fabae* Scopoli were mass reared on bean and were used to feed *Adalia bipunctata* L. Both ladybird and aphid strains had been reared in the laboratory for several years.

Evaluation of ladybird performance parameters

For easier understanding of data mainly with reciprocal crosses, abbreviations will be used for sex and related aphid species of ladybird: beetles fed with *Aphis fabae* and *Acyrthosiphon pisum* will be called A.f. and A.p. respectively.

For each aphid species, 60 newly hatched larvae (twice 30 individuals) of *A. bipunctata* were isolated individually in 5 cm diameter Petri dish to avoid cannibalism. Larvae were collected from different egg clusters of ladybird stock culture fed with *Acyrthosiphon pisum* (Harris).

From hatching, larvae were kept at 20±2°C temperature with 16 h light period and observed individually every day to determine changes of developmental stage. Duration of each nymphal and pupal stages was recorded. After emergence, ladybirds were sexed and at least 10 couples were constituted for each cross. Three kinds of crosses were performed:

EA.f. x Γ A.f., EA.f. x Γ A.p. and EA.p. x Γ A.f.

Egg and egg laying numbers, egg viability were daily observed.

Statistical analysis

For the reproductive parameters, daily means were calculated and were used for the statistical treatment.Egg viability (expressed as daily percentages) were analysed by ANOVA after arcsin√x transformation (Dagnelie, 1973) and followed by mean comparisons by the least significant difference method. Other ladybird parameters were analysed directly using ANOVA and mean comparison test. MINITAB (vs 11.2) was used for the statistical analysis.

RESULTS

Effect of aphid species on adult weight

Significant differences of adult weights were observed when both males and females fed with *A. fabae* and *A. pisum* were considered ($F = 14.16$; $P < 0.001$). Emerging adults which were fed with *A. fabae* were significantly lighter ($F = 34.08$; $P < 0.001$) than the ones having had the optimal *A. pisum* aphid species as prey (see Figure 1). Adult weight of the beetle significantly depends on individual sex. Indeed, females of *A. bipunctata* were heavier than the males ($F = 5.19$; $P = 0.026$) whatever was the aphid prey which was used. Considering the duration of the total development, ladybirds significantly needed more time to reach the adult stage when feeding with *A. fabae* ($F = 5.39$; $P = 0.022$).

Maternal effect of aphid species on reproduction

First reproductive parameter we considered was the egg number per female (Figure 2): significant differences ($F = 80.30$; $P < 0.001$) were observed depending of the cross which was studied. Each kind of crosses was significantly different the ones from the others ($t = 5.19$; $t = 11.24$; $t = 6.14$ and $P < 0.001$ for the three comparisons).

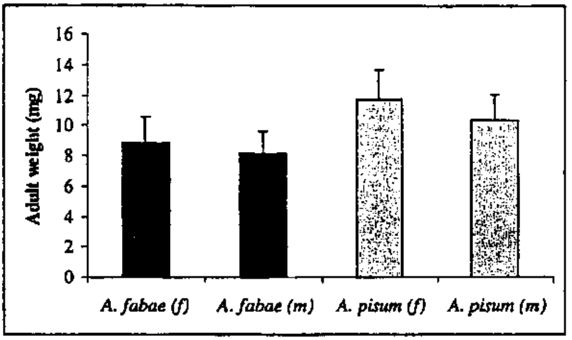

Figure 1: Adult weight of *Adalia bipunctata* fed with *Aphis fabae* or *Acyrthosiphon pisum*. (m) and (f) correspond to male and female ladybird respectively.

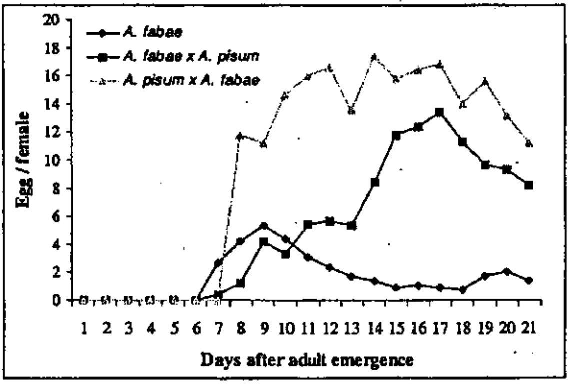

Figure 2: Fecundity (egg number per female) of *Adalia bipunctata* for each cross based on the use of *Aphis fabae* or *Acyrthosiphon pisum* as larval food for the male and female of ladybirds. First aphid food corresponds to the female diet.

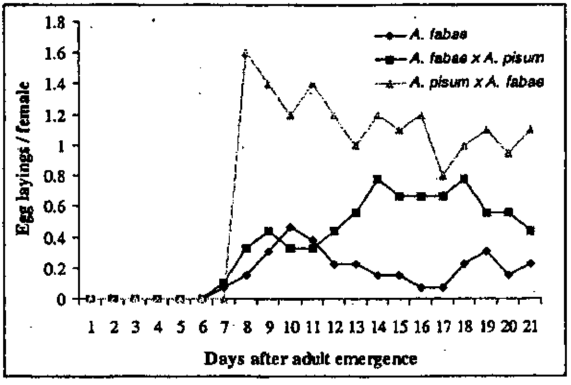

Figure 3: Number of egg laying per female of *Adalia bipunctata* for each cross based on the use of *Aphis fabae* or *Acyrthosiphon pisum* as larval food for the male and female of ladybirds. First aphid food corresponds to the female diet.

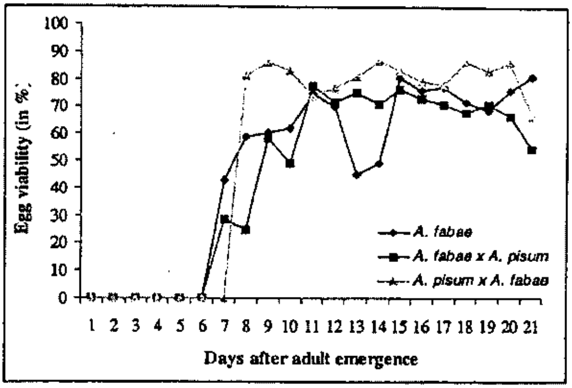

Figure 4: Egg viability of *Adalia bipunctata* for each cross based on the use of *Aphis fabae* or *Acyrthosiphon pisum* as larval food for the male and female of ladybirds. First aphid food corresponds to the female diet.

The same observation was made for the number of egg layings per female (F = 63.22; P <0.001): the three combination were significantly different the ones from the others (t = 4.74; t = 12.61;t = 7.91 and P < 0.001 for the three comparisons). Considering the egg viability, significant differences were determined between the crosses which were realised (F = 8.06; P = 0.001). While the egg viability corresponding to the EA.p. x Γ A.f. cross was significantly higher than the two other kinds of crosses (t = 3.26 and P = 0.003; t = 3.73 and P < 0.001), no significant difference was observed between the EA.f. x Γ A.f. and the EA.f. x Γ A.p. crosses (t = 0.54; P = 0.34).

DISCUSSION

Both organism's genes and its environment together determine its phenotype, not as a structure frozen in time, but as a life cycle which unfolds dynamically over the whole lifespan of the individual (Bonner, 1974). Insects have evolved plasticity to cope with important changes of their environment. Plasticity has been demonstrated in most life-history traits: survival, fecundity (Kahn & Bradshaw, 1976), offspring size (Weinstein & Hass, 1977). Spatial variation generates differences between individuals, based on their location during ontogeny. Growth rates may be plastic, so that plasticity in development may lead to individuals of the same age being in different instars or developmental stages (Birley, 1979).
During its life cycle, ladybirds moved from one environment to others, depending on the abundance of their preys. When new host plants are investigated by the aphidophagous predators, other aphid species are present and will constitute the future preys. After having consumed the local aphid populations, the ladybirds will search a new food source. Here we observed that ladybirds developed plasticity by reached the adult stage at lighter weight when inadequate food was used, even if higher development duration were required. Maternal size was already shown to

affect egg size in animals and this variation often has a large effects on offspring fitness in both insects and vertebrates (Fleming & Gross, 1990). Female body size of *Callosobruchus maculatus* (Coleoptera: Bruchidae) is positively correlated (phenotypically) with the size of her eggs and thus with her resource contribution to hatchlings. Subsequently, this initial disadvantage to larvae results in extended larval development time but not necessarily in an effect on adult size (Fox, 1993). In the gypsy moth, *Lymantria dispar*, maternal diet affects progeny growth rate even after accounting for the effects of egg size, indicating that the latter is not necessarily an adequate measure of parental investment or egg quality (Rossiter, 1991).

Furthermore, we demonstrated that the female food characteristics mainly affect the fecundity and the emergence of their offspring. Indeed, when the female of *A. bipunctata* was fed with the optimal *A. pisum*, daily egg number and egg laying numbers increased significantly. The influence of the male quality food at the larval stage was less important even if there was an effect on the couple reproduction. The more important maternal effect we observed was the impact of the female larval food on the egg viability: higher larval emergence was induced only when *A. pisum* was used to feed the female. The use of male fed with the optimal diet in the crosses had no influence on the egg viability which was as low as the *A. fabae* negative reference for both sexes. Maternally induced changes of the reproductive parameters will influence the future density and distribution of the predator populations. Maternal effect of unsuitable food was observed. Change of ladybird female location, related to the consumption of lower quality prey, can induce large variation in the next generations of beneficial insects. In *Drosophilia*, environmental effects as associated with acclimatation that are passed to the next generation are known for resistance to cold and heat. Other possible sources of environmental influences include disease and nutritional factors passed on from mothers to progeny which may also influence the insect development and reproduction (Jenkins & Hoffman, 1994). Fox *et al.* (1999) demonstrated that females of *Stator pruininus* (Coleoptera: Bruchidae) emerging from high density seeds laid smaller eggs than females reared at low density. Egg size was not affected by male line. Indeed, experimental crosses showed that the differences among lines in development time was maternally inherited; only maternal lineage explained some of the variance in development time.

Utilisation of beneficial insects as predatory ladybird beetles is a way to biologically control aphid pests in several crop plant species. Assays were carried out mainly in perennial cultures as apple fruit trees (Brown & Glenn, 1999). The results of this study showed that even if a generalist predator was used, efficacy of the biological treatment will depend on the target pest species. Indeed, both development and reproduction of the entomophagous insects will change regarding to the aphid prey species. Thus, a short period of negative food consumption corresponding to a plant shift, can imply huge decreases of biological control efficacy. In this work, fecundity and egg viability were demonstrated to be mainly maternally inherited and maternal variation are known to be transmitted across multiple generation (Falconer, 1965). The genotype of the mother can influence the environment experienced by her offspring before and after egg laying, such that environmental and genetic differences in one generation are manifested as phenotypic differences in the next generation (Mousseau & Dingle, 1991). Maternal environment stresses are generally found to have a large influence on progeny body size and growth immediately after hatching or birth (Mousseau & Dingle, 1991). In conclusion, successful biological program must integrate ecological knowledge of both beneficial and pest species keeping in mind that organisms evolve in time in response not only to their environment but also to the life history of their parents.

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