

INFLUENCE OF PREY QUALITY ON THE REPRODUCTIVE CAPACITY OF TWO PHENOTYPES OF *Harmonia axyridis* PALLAS (COLEOPTERA: COCCINELLIDAE).

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SOARES, A.O., D. CODERRE & H. SCHANDERL 2003. Influence of prey quality on the reproductive capacity of two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Pp. 51-54 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

H. axyridis is a highly polymorphic ladybird beetle with a wide geographical distribution in the palearctic region. Genetic polymorphism seems to be the strategy adopted in order to face different habitats at different times. In this paper we suggest that a genotype that confers a specific elytral pattern may also confer a particular reproductive capacity when fed on single diets of essential preys such as *A. fabae* or *M. persicae*. We discuss KOMAI & HOSINO (1951) hypothesis, which predicts that the differences in the relative frequency of elytral pattern phenotypes in relation to the host plants in a same habitat could be related with specific composition of aphid populations. Our results revealed that *A. fabae* significantly increased reproductive capacity of *nigra* phenotype without affecting reproductive capacity of *aulica* phenotype.

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INTRODUCTION

Asian populations of *Harmonia axyridis* Pallas show a highly level of genetically polymorphic, with more than one genotype occurring in a population. To identify precisely selective forces that act to maintain different phenotypes of *H. axyridis* in the same population is a very difficult task. Genetic polymorphism should persist only when different genotypes are selectively favoured in varying parts of the environment or at different times. Thus a single phenotype cannot be equally fit in all environmental conditions. This fact challenges our understanding of adaptation. One of the important issues raised concerns how environmental heterogeneity facilitates the coexistence of more than one genotype within a population (RICKLEFS 1991).

H. axyridis is a euriphagous predator that prefers aphids (HUKUSIMA & KAMEI 1970; HUKUSIMA & OHWAKI 1972; OSAWA 1992; IABLOKOFF-KHNZORIAN 1982; SCHANDERL et al. 1988). It also feeds on psyllids (FYE 1981), coccids (MCLURE 1987; HODEK & HONĚK 1996), spider mites (LUCAS et al. 1997) and lepidopteran eggs (SCHANDERL et al. 1988).

A particular phenotype of *H. axyridis* may confer different specific morphological, physiological and behavioural attributes (TAN 1946, 1949; KOMAI 1956; FUTUYMA 1998). If so, then the differences in nutritive demands of phenotypes, or in nutritive value of different prey, could affect relative fitnesses of different phenotypes, when fed different prey. In Japan, KOMAI & HOSINO (1951) reported differences in the relative frequency of elytral pattern phenotypes between host plants in the same

habitat (so called micro-geographic variation). They suggested that such differences could be correlated somehow with differences in the composition of the aphid populations, and the feeding preferences of the phenotypes. However, the hypothesis was not addressed further until this study.

We have shown recently that the *nigra* and *aulica* phenotypes of *H. axyridis* differ in their fitness fed on the same prey (SOARES et al. 2001, 2003), but we do not know if the differences would remain consistent on other diets. Despite the well-documented polyphagy in *H. axyridis*, we hypothesise that *aulica* and *nigra* phenotypes will display different reproductive capacity fed on *Aphis fabae* Scopoli or *Myzus persicae* (Sulzer). In this study, we evaluate the reproductive capacity of *aulica* and *nigra* fed diets of either *A. fabae* or *M. persicae*.

MATERIAL & METHODS

Biological material

H. axyridis individuals of the *aulica* and *nigra* phenotypes came from mass cultures reared at $22 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). Coccinellids were fed a mixed diet of the aphids, *A. fabae* and *M. persicae*, and eggs of *Ephestia kuehniella* Zeller. Prey were provided on bean plants (*Vicia fabae* L. Major) placed in the rearing cages. Individuals of *M. persicae* and *A. fabae* strongly differed in size. The average weight of a wingless female of *M. persicae* was 0.48 mg and of *A. fabae* 1.09 mg. Field collected ladybirds were added to the mass culture at regular intervals in order to minimize inbreeding. The *aulica* and *nigra* phenotypes occurred naturally in our cultures. The different phenotypes were reared separately.

Measure of reproductive capacity

To evaluate reproductive capacity, we sexed and paired 40 individuals of each phenotype. Each of the twenty pairs was isolated in a 60 ml Petri dish (\varnothing : 5 cm, height: 3 cm). One of two diets was provided to 10 couples of each phenotype. The *A. fabae* and *M. persicae* were supplied daily in excess. Abiotic conditions were $20 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). Egg clusters were removed from Petri dishes twice daily. Fecundity, fertility and percentage hatch were compared over the first fifteen days of a females' reproductive life. Percentages were arcsin $\sqrt{\%}$ transformed (ZAR 1984). One-factor ANOVA was used to compare fecundity, fertility and percentage hatch of the eggs of the phenotypes fed on the different diets. All statistical tests were done using JMP[®] (SALL et al. 2001).

RESULTS

Comparative reproductive capacity of *aulica* and *nigra* phenotypes fed *A. fabae* or *M. persicae*

Independent of the prey offered, fecundity, fertility and percentage hatch of the eggs of *aulica* females of *H. axyridis* were significantly higher than for *nigra* females (Table 1).

Influence of prey quality on the reproductive capacity of aulica and nigra phenotypes

There was no significant difference in the fecundity, fertility and percentage hatch of the eggs in the *aulica* phenotype of *H. axyridis* fed either *M. persicae* or *A. fabae* (Table 2). However, the reproductive capacity of *nigra* females was significantly higher than that of *aulica* females when fed on *A. fabae* (Table 2).

Table 1

Fecundity (average number of eggs / female / day \pm s.e.), fertility (average number of embrionate eggs / female / day \pm s.e.) and hatching (percentage of hatching \pm s.e.) of *aulica* and *nigra* phenotypes of *H. axyridis* fed on *A. fabae* and *M. persicae*. Different letters indicate significant differences at $p < 0.05$

	<i>A. fabae</i>			<i>M. persicae</i>		
	<i>aulica</i>	<i>nigra</i>		<i>aulica</i>	<i>nigra</i>	
Fecundity	22.8 \pm 1.6a*	17.2 \pm 1.1b	F=7.88, df=1, 298, P \leq 0.005	20.9 \pm 1.4a	12.6 \pm 0.9b	F=23.57, df=1, 297, P \leq 0.0001
Fertility	20.6 \pm 1.5a	6.2 \pm 0.7b	F=76.75, df=1, 298, P \leq 0.0001	19.3 \pm 1.4a	2.6 \pm 0.6b	F=124.7 df=1, 298, P \leq 0.0001
Percentage of hatching	63.8 \pm 2.7a	25.1 \pm 2.8b	F=100.8, df=1, 229, P \leq 0.0001	63.2 \pm 2.7a	13.7 \pm 2.8b	F=209.4, df=1, 227, P \leq 0.0001

Table 2

Fecundity (average number of eggs / female / day \pm s.e.), fertility (average number of embrionate eggs / female / day \pm s.e.) and hatching (percentage of hatching \pm s.e.) of *aulica* and *nigra* phenotypes of *H. axyridis* fed on *A. fabae* and *M. persicae*. Different letters indicate significant differences at $p < 0.05$

	<i>aulica</i>			<i>nigra</i>		
	<i>A. fabae</i>	<i>M. persicae</i>		<i>A. fabae</i>	<i>M. persicae</i>	
Fecundity	22.8 \pm 1.6a*	20.9 \pm 1.4a	F=0.74, df=1, 298, P=0.39	17.2 \pm 1.1a	12.6 \pm 0.9b	F=9.78, df=1, 297, P=0.001
Fertility	20.6 \pm 1.5a	19.3 \pm 1.4a	F=0.42, df=1, 298, P=0.515	6.2 \pm 0.7a	2.6 \pm 0.6b	F=13.2 df=1, 297, P=0.0003
Percentage of hatching	63.8 \pm 2.7a	63.2 \pm 2.7a	F=0.171, df=1, 298, P=0.679	25.1 \pm 2.8a	13.7 \pm 2.8b	F=19.1, df=1, 234, P \leq 0.0001

DISCUSSION

Generalist predators attack a variety of prey, which differ in energy content and cost of capture and ingestion (ROGER et al. 2000). Food availability (KAWAUCHI 1981; FERRAN et al. 1984; STEWART et al. 1991; DIXON & GUO 1993; DIXON 2000) and prey quality (BLACKMAN 1967; NIJIMA & TAKAHASHI 1980; NIJIMA et al. 1986) affect the fecundity of ladybird beetles, which is an important determinant of their fitness (HEMPTINNE et al. 1993; EVANS et al. 1999). Significant differences in the reproductive capacity of *nigra* and *aulica* females, and a significant increase in the reproductive capacity of *nigra* females when fed on *A. fabae* versus *M. persicae* suggest the quality of *A. fabae* and *M. persicae* as prey differs for the two phenotypes.

As predicted by optimal foraging theory, predators utilize the different prey types available so as to maximize their rate of gain of energy (STEPHENS & KREBS 1986; CRAWLEY & KREBS 1992) or maximize the ingestion of nutrients (WALDBAUER et al. 1984). Such results support the hypothesis of KOMAI & HOSINO (1951), that micro-geographic variation in the relative frequency of elytral patterns within *H. axyridis* populations could be correlated somehow with differences in the composition of aphid populations. The key may lie in intra-specific differences in the food preferences of phenotypes in order to increase their fitness. Requirements for high-energy resources for metabolism and reproduction could determine prey choice by females of ladybird beetles (HOUCK 1991). As demonstrated in the laboratory by our experimental results, different phenotypes of *H. axyridis* may thrive on different preys species in nature. This may provide some selective basis for maintenance of genetic polymorphism in this species.

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Accepted 31 May 2003.