

Influence of prey quality on the fitness of two phenotypes of *Harmonia axyridis* adults

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Abstract

The performance of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) adults of the *aulica* and *nigra* phenotypes fed on *Aphis fabae* Scopoli and *Myzus persicae* (Sulzer) was compared by measuring their voracity, daily biomass consumption, daily weight gain, efficiency of food utilisation, and reproductive capacity. Our results demonstrated differences in the suitability of *A. fabae* and *M. persicae* for the two phenotypes of the predator. This suggests that either differences occur in the nutritive requirements of the predators, or in the nutritive value of the two prey species. Both *A. fabae* and *M. persicae* supported the growth and oviposition of the *aulica* and *nigra* phenotypes. Although *nigra* females consumed fewer *M. persicae*, they achieved the same daily weight gain as *aulica* females. The predator phenotypes consumed the same amount of *A. fabae*, but the daily weight gain of *aulica* females was higher than that of *nigra*. The two predator phenotypes had the same feeding efficiency when consuming *M. persicae* or *A. fabae*. The reproductive capacity of *nigra* females was higher, when this phenotype consumed *A. fabae* rather than *M. persicae*.

Introduction

Asian populations of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) show a high level of genetic polymorphism, that is, multiple genotypes occur within a population. Genetic polymorphism is expressed not only by intraspecific variation in body size and shape (Soares et al., 2001; Soares et al., 2003), but also by striking intraspecific variation in colour morphs (Komai, 1956). Phenotypes are classified into two groups, the *succinea* group, which is characterized by a light reddish or brownish ground colour, and the melanic group, which includes the *conspicua*, *spectabilis*, and *aulica* subgroups, characterized by melanic elytral patterns (Komai, 1956). Rare phenotypes, such as the pure black *nigra* form, can be found in natural habitats (Tan, 1946). The frequency of colour morphs varies according to geographical location of the

populations, as well as over time. Macrogeographical variations in Asian populations of *H. axyridis* are related mainly to climatic factors, because light and melanic phenotypes have different physiological responses to them (Komai, 1956). The relative frequency of elytral pattern phenotypes also varies with the host plants (microgeographical variation) that support aphid prey (Komai & Hosino, 1951). A seasonal variation in the proportion of dark and light forms in Japanese populations was observed by Osawa & Nishida (1992), who reported a significant increase in light phenotypes during the spring and early summer. It seems that non-random mating may influence the morph proportions observed under natural conditions. Long-term changes in the relative frequency of elytral pattern phenotypes were observed in the Suwa population in Japan. Komai (1956), suggested that these changes were due to natural selection, probably in response to the mild climatic conditions of Suwa.

H. axyridis is a polyphagous predator that prefers aphids (Hukusima & Kamei, 1970; Hukusima & Ohwaki, 1972; Osawa, 1992), but also feeds on psyllids (Fye,

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1981; Michaud, 2002), coccids (McLure, 1987; Hodek & Honěk, 1996), spider mites (Lucas et al., 1997), lepidopteran eggs (Schanderl et al., 1988) as well as on other insect prey. If a particular genotype of *H. axyridis* possesses particular morphological, physiological, and behavioural attributes, then differences in nutritional requirements and/or the nutritive value of prey species could affect the fitness of the phenotype in specific ways. Indeed, Komai & Hosino (1951) reported different frequencies of phenotypes among host plants in the same habitat, and suggested that they could be correlated with the different aphid populations found on these plants.

In spite of their considerable polyphagy, coccinellids are very specific as far as essential food is concerned (Soares et al., 2004). It is therefore necessary to define the prey–predator relationship in terms of essential prey, and to assess the possible impact of a coccinellid species against any given pest by testing the range of essential preys (Hodek & Honěk, 1996). We have recently shown that the *nigra* and *aulica* phenotypes differ in their fitness for a given diet and temperature (Soares et al., 2001; Serpa et al., 2003), and that fitness varies with the shape and size of the coccinellids (Soares et al., 2003). We hypothesize that the phenotypes will differ in their biological performance (i) when feeding on the same prey, and also (ii) when feeding on different prey species. Therefore in this study we evaluated voracity, daily biomass consumption, daily weight gain, efficiency of food utilization, and the reproductive performances of the *aulica* and *nigra* phenotypes, fed on two species of aphid prey, viz., *Aphis fabae* Scopoli and *Myzus persicae* (Sulzer).

Materials and methods

Individuals from the *aulica* and *nigra* phenotypes of *H. axyridis* came from the mass rearing laboratory of University of the Azores and were maintained at 22 ± 1 °C, $75 \pm 5\%$ r.h., and a photoperiod of L16:D8, using fluorescent lamps (Philips: TDL 23 W/54 and TDL 18 W/54). *Aulica* and *nigra* phenotypes occur naturally in our cultures. The original individuals came from Asian populations. The coccinellids were fed on a mixed diet of *A. fabae* and *M. persicae* aphids and eggs of *Ephestia (Anagasta) kuehniella* Zeller. Aphids were provided on *Vicia fabae* L. plants placed in rearing cages. To avoid coccinellid consanguinity, an average of 200 field collected individuals of several Canadian populations has been added to the stock culture at least once a year. Before the experiments, the *nigra* and *aulica* phenotypes were reared separately to increase their numbers. Adults were used because (i) the hypothesis of Komai & Hosino (1951) was supported by field surveys of adults, and (ii) adults display

a higher dispersal capacity than larvae, enabling them to search for suitable food on a specific host plant.

Voracity and daily biomass consumption

We evaluated the number of apterous females of *A. fabae* and *M. persicae* eaten in 24 h by 15-day-old adults of the *aulica* and *nigra* phenotypes of *H. axyridis* (15 males and 15 females). One hundred *A. fabae* or *M. persicae* were offered to predators on a *V. fabae* plant in a 2 l mesh cage. Each set of 100 aphids was weighed before exposure to the predators. One beetle adult, which had previously been starved for 24 h, was added to the experimental set-up. The remaining live aphids were counted after 24 h. The experiments were done at 20 ± 1 °C, $75 \pm 5\%$ r.h., and a photoperiod of L16:D8 under fluorescent lamps (Sanyo FL 40 SS W/37). The natural mortality of the aphids was evaluated in a control treatment: 30 replicates of 50 per aphid species were monitored for survival without predators. Control treatments were performed in a similar experimental set-up. Survival in the control treatments was 86.25% and 85% for *A. fabae* and *M. persicae*, respectively.

Voracity (V_0) was calculated according to the following formula (Soares et al., 2003):

$$V_0 = (A - a_{24})ra_{24}$$

where: V_0 = number of aphids eaten, A = number of aphids available, a_{24} = number of aphids alive after 24 h, and ra_{24} = ratio of aphids found alive after 24 h in the control treatment.

Considering that *A. fabae* and *M. persicae* body weights are very different (the mean body weight of an *A. fabae* wingless female is 1.09 mg, whereas a *M. persicae* wingless female weighs 0.48 mg) coccinellid satiation could be reached on varying numbers of prey. Daily biomass consumption (DBC) was evaluated according to Schanderl (1987), based on the following formula:

$$DBC_{(mg)} = (W_i/N)V_0PUC$$

where: $DBC_{(mg)}$ = daily biomass consumption, W_i = total weight of aphids provided, N = number of aphids provided, V_0 = number of aphids eaten, and PUC = prey utilisation coefficient.

The prey utilization coefficient (PUC) is the proportion of the prey consumed. Schanderl (1987) reported that the PUC of *H. axyridis* 4th instars fed on *M. persicae* and *A. fabae* was 93%. However, Schanderl (1987) determined a PUC for adults fed only on *M. persicae* aphids as 96.4%. We assumed that adults fed on *A. fabae* had a similar PUC (96.4%) to this latter result when fed on *M. persicae*.

Daily weight gain and feeding efficiency

Weight increase following predation is a good indicator of energy intake and associated costs (Frazer, 1988). We evaluated the daily weight gain (DWG) of 15-day-old adults of the *aulica* and *nigra* phenotypes (15 males and 15 females), after being fed on *A. fabae* and *M. persicae*. The body weight of the adults after feeding, minus the body weight of starved adults corresponds to the DWG. Adult body weight was evaluated individually using a Mettler AM 50 analytical balance with a precision of 10⁻⁴ mg.

Feeding efficiency (FE) was evaluated as follows:

$$FE = (DWG/DBC_{(mg)}) \times 100\%$$

As females are usually different from males (Soares et al., 2001), a two-factor ANOVA was used separately for each sex to compare treatments of voracity, daily biomass consumption, daily weight gain, and feeding efficiency between the factors phenotypes and diets (SPSS, 2003).

Reproductive capacity

To evaluate the reproductive capacity of the *aulica* and *nigra* phenotypes, we sexed and paired 40 individuals of each. Each couple was isolated in a 60 ml Petri dish (diameter: 5 cm, height: 3 cm). We provided single diets of *A. fabae* or *M. persicae* to 10 pairs of each phenotype. The number of *A. fabae* and *M. persicae* provided exceeded the daily consumption values. Abiotic conditions were the same as previously described. Egg clusters were removed from Petri dishes twice a day. Fecundity, fertility (including sibling cannibalism), and percentage of hatching of egg masses were compared for the first 15 days of a female's life, after sexual maturation, and after laying the first egg mass. Proportions were arcsin(%)^{1/2} transformed (Zar, 1996), but only the raw data is presented here. A single-factor ANOVA was used to compare treatments of fecundity, fertility (including sibling cannibalism), and percentage of hatching between the two phenotypes (SPSS, 2003).

Table 1 Two-factor ANOVA of female and male voracity (number of prey eaten per day) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae* (P<0.05)

Source	Females			Males		
	d.f.	F	P	d.f.	F	P
Phenotype	1	11.695	0.001	1	0.434	0.523
Prey	1	2.670	0.108	1	8.960	0.004
Phenotype × prey	1	2.447	0.123	1	0.645	0.425

Table 2 Female and male voracity (number of prey eaten per day ± SE) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae*

	<i>aulica</i>	<i>nigra</i>	Total
<i>M. persicae</i>			
Females	59.6 ± 4.1	40.4 ± 3.8	50.0 ± 3.3
Males	32.1 ± 2.5	31.7 ± 3.1	31.9 ± 1.9
Total	45.8 ± 3.5	36.1 ± 2.5	
<i>A. fabae</i>			
Females	47.6 ± 4.5	40.4 ± 2.6	43.8 ± 2.6
Males	23.3 ± 1.9	26.7 ± 1.6	24.9 ± 1.3
Total	35.4 ± 3.3	33.6 ± 1.9	

Results

Voracity and daily biomass consumption of the *aulica* and *nigra* phenotypes fed on *Myzus persicae* and *Aphis fabae*

Female voracity was significantly affected by phenotype but not by prey species (Table 1). Voracity was the highest for *aulica* (Table 2). In contrast, male voracity was significantly affected by prey species, but not by phenotype (Table 1). Male voracity was highest towards *M. persicae* (Table 2). Female daily biomass consumption was significantly affected by both prey species and phenotype (Table 3). *Aulica* females had significantly higher daily biomass consumption than *nigra*, and ingested more biomass of *A. fabae* (Table 4). Male daily biomass consumption was significantly affected by prey species but not by phenotype (Table 3). Males ingested significantly more biomass of *A. fabae* than *M. persicae* (Table 4).

Daily weight gain of the *aulica* and *nigra* phenotypes fed on *Myzus persicae* and *Aphis fabae*

Female daily weight gain was significantly affected by phenotype but not by prey species (Table 5). Daily weight gain was highest for *aulica* (Table 6). Male daily weight gain was not affected by prey species or phenotype (Tables 5 and 6).

Table 3 Two-factor ANOVA of female and male daily biomass consumption (mg of biomass ingested per day) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae* (P<0.05)

Source	Females			Males		
	d.f.	F	P	d.f.	F	P
Phenotype	1	7.293	0.009	1	1.135	0.291
Prey	1	56.825	≤0.0001	1	48.843	≤0.0001
Phenotype × prey	1	0.051	0.822	1	1.351	0.250

Table 4 Female and male daily biomass consumption (mg of biomass ingested per day \pm SE) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae*

	<i>aulica</i>	<i>nigra</i>	Total
<i>M. persicae</i>			
Females	27.5 \pm 1.9	18.7 \pm 1.6	23.2 \pm 1.5
Males	14.8 \pm 1.1	14.7 \pm 1.4	14.8 \pm 0.9
Total	21.2 \pm 1.6	16.7 \pm 1.1	
<i>A. fabae</i>			
Females	50.0 \pm 4.7	42.4 \pm 2.8	45.9 \pm 2.8
Males	24.4 \pm 2.1	28.1 \pm 1.7	26.2 \pm 1.4
Total	37.2 \pm 3.4	35.3 \pm 2.0	

Feeding efficiency of the *aulica* and *nigra* phenotypes fed on *Myzus persicae* and *Aphis fabae*

Neither female nor male feeding efficiency were affected by phenotype, but they were significantly affected by prey species (Table 7). No significant differences in the feeding efficiency of the phenotypes were found, but ladybeetles fed on *M. persicae* had a significantly higher feeding efficiency than individuals fed on *A. fabae* (Table 8).

Reproductive capacity of the *aulica* and *nigra* phenotypes fed on *Myzus persicae* and *Aphis fabae*

Independent of the prey provided, fecundity, fertility, and percentage egg hatching of *aulica* females were significantly higher than *nigra* females. No significant differences were found in the fecundity, fertility, and percentage of hatching of the *aulica* phenotype fed on *M. persicae* or *A. fabae* (Table 9). However, the reproductive capacity of the *nigra* phenotypes was significantly higher when the females were fed *A. fabae* (Table 9).

Discussion

The results of this study suggest differences in the degree of suitability of *M. persicae* and *A. fabae* as prey, because the predators had a higher feeding efficiency when fed on *M. persicae* compared to *A. fabae*. Different voracities and

Table 5 Two-factor ANOVA of female and male daily weight gain (mg of biomass gained per day) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae* ($P < 0.05$)

Source	Females			Males		
	d.f.	F	P	d.f.	F	P
Phenotype	1	7.131	0.010	1	3.221	0.078
Prey	1	0.860	0.358	1	0.023	0.879
Phenotype \times prey	1	0.001	0.971	1	0.073	0.788

Table 6 Female and male daily weight gain (mg of biomass gained per day \pm SE) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae*

	<i>aulica</i>	<i>nigra</i>	Total
<i>M. persicae</i>			
Females	5.7 \pm 0.6	4.3 \pm 0.6	5.0 \pm 0.5
Males	2.0 \pm 0.2	2.6 \pm 0.3	2.4 \pm 0.2
Total	3.9 \pm 0.4	3.4 \pm 0.3	
<i>A. fabae</i>			
Females	6.2 \pm 0.3	4.8 \pm 0.5	5.5 \pm 0.3
Males	2.1 \pm 0.2	2.3 \pm 0.3	2.3 \pm 0.2
Total	4.1 \pm 0.4	3.6 \pm 0.3	

daily biomass consumption were also associated with the diets of *M. persicae* and *A. fabae*, mainly for the *aulica* females. It is noteworthy that: (i) significant differences occurred in the reproductive capacity of *nigra* and *aulica* females, and (ii) the reproductive capacity of *nigra* females (but not *aulica* females) was significantly superior when fed *A. fabae* rather than *M. persicae*. All these results suggest that differences occur in the degree of suitability of *A. fabae* and *M. persicae*, in terms of nutritive requirements or physiological traits of the females from the two *H. axyridis* phenotypes. These results support our predictions that dissimilar phenotypes fed on the same prey species should show different biological performances, and that different prey species should have distinct effects on the biological performance of a given predator phenotype.

Both *M. persicae* and *A. fabae* were acceptable and suitable prey for *H. axyridis*, ensuring the predator's growth and oviposition (so-called essential foods). Previous studies have demonstrated that *M. persicae* and *A. fabae* enabled the completion of larval development and oviposition (Hukusima & Kamei, 1970; Schanderl et al., 1985). Thus, from an ecophysiological point of view, both prey species can be considered as essential foods. Essential foods, however, show varying degrees of favourability, enabling different developmental rates, fecundity, and

Table 7 Two-factor ANOVA of female and male feeding efficiency (% weight gain over biomass consumption per day) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae* ($P < 0.05$)

Source	Females			Males		
	d.f.	F	P	d.f.	F	P
Phenotype	1	0.474	0.494	1	0.003	0.957
Prey	1	7.551	0.008	1	13.323	0.001
Phenotype \times prey	1	1.268	0.265	1	0.27	0.606

Table 8 Female and male feeding efficiency (% weight gain over biomass consumption per day \pm SE) of two phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae*

	<i>aulica</i>	<i>nigra</i>	Total
<i>M. persicae</i>			
Females	20.2 \pm 2.1	22.4 \pm 2.5	21.3 \pm 1.6
Males	15.3 \pm 1.8	17.8 \pm 2.1	16.6 \pm 1.4
Total	17.7 \pm 1.4	20.1 \pm 1.6	
<i>A. fabae</i>			
Females	13.9 \pm 1.2	11.3 \pm 1.2	12.7 \pm 0.9
Males	9.8 \pm 1.6	8.5 \pm 1.0	9.6 \pm 1.0
Total	11.8 \pm 1.1	9.9 \pm 0.8	

survival (Hodek, 1993; Hodek & Honěk, 1996). Recent results have demonstrated that a mixed diet of both prey types enhances the fitness of *H. axyridis* (Soares et al., 2004) relative to a single species diet.

From a strictly physiological point of view, increased feeding efficiency per se may not seem to offer a large advantage, because an insect with a low efficiency may compensate by simply eating more. From an ecological point of view, however, an increased efficiency may be advantageous, because on the one hand, it enhances an insect's ability to compete for scarce food and, on the other hand, it may enable the insect to spend less time foraging, thereby reducing its exposure to predators (Waldbauer & Friedman, 1991).

Feeding efficiency did not differ significantly between phenotypes for each of the two prey species. Nevertheless, differences in daily biomass consumption were dependent on the prey offered, and *nigra* females ate less biomass of *M. persicae* than *aulica* females. These results suggest that it may be more advantageous for *nigra* females to pursue and capture *M. persicae*, and that it may be more advantageous for *aulica* females to pursue and capture *A. fabae*. This suggestion is supported by the fact that, on the one hand, *nigra* females were able to achieve the same daily weight gain as *aulica* females on a diet of *M. persicae*, even when they consumed less of this prey and, on the other hand, for the same

number of *A. fabae* consumed and the same amount of biomass ingested, daily weight gain for *aulica* females was significantly higher than for *nigra* females. This means that for the same amount of *A. fabae* biomass consumed, an *aulica* female grew more than a *nigra* female. However, when preying on *M. persicae*, *aulica* females needed to consume more biomass to achieve the same increase in body weight. These results suggest that differences occur in the nutritive requirements for *aulica* and *nigra* females' growth and/or in the nutritive and energetic values of the preys.

As in other aphidophagous ladybird beetles, the distribution and behaviour patterns of *H. axyridis* around aphid colonies are sex-related (Obata & Johki, 1990). The absence of significant differences in male voracity, daily biomass consumption, and body-weight increase of the *aulica* and *nigra* phenotypes, suggests that in contrast to females, the two prey species did not differ in their suitability for the males. Thus males, contrary to females, may prefer prey species with low costs associated with their capture and ingestion. Generally, predators' size is positively correlated with mean prey size, and capture success decreases with increasing prey size (Roger et al., 2000). Consequently, in this study, males may have preferred *M. persicae* because it is smaller than *A. fabae*.

Our results support the hypothesis of Komai & Hosino (1951), that microgeographical variation in *H. axyridis* (that is, differences in the relative frequency of elytral pattern phenotypes between host plants in the same habitat) could be somehow correlated with differences in the composition of aphid populations. The key point may be that the suitability of different prey species differs for both males and females of different phenotypes. Differences in the composition of aphid populations between host plants could also determine the habitat preference of ladybird beetles, especially if different species of aphids complement each other in their nutritional value for the predators. In general, it is accepted that 'each species has its own ecological niche'. However, because food is one of the most important dimensions that define an ecological niche, our results suggest that each genotype of *H. axyridis* may have its own ecological niche.

Table 9 Fecundity (average number of eggs/female/day \pm SE), fertility (average number of embryonated eggs/female/day \pm SE), and hatching (percentage of hatching \pm SE) of the *aulica* and *nigra* phenotypes of *Harmonia axyridis*, fed on *Myzus persicae* or *Aphis fabae*

	<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	$F_{1,298} = 0.74, P = 0.3902$	17.2 \pm 1.1a	12.6 \pm 0.9b	$F_{1,297} = 9.78, P = 0.0019$
Fertility	20.6 \pm 1.5a	19.3 \pm 1.4a	$F_{1,298} = 0.42, P = 0.5155$	6.2 \pm 0.7a	2.6 \pm 0.6b	$F_{1,297} = 13.27, P = 0.0003$
Percentage of hatching	63.8 \pm 2.7a	63.2 \pm 2.7a	$F_{1,298} = 0.17, P = 0.6799$	25.1 \pm 2.8a	13.7 \pm 2.8b	$F_{1,234} = 19.19, P \leq 0.0001$

*Different letters indicate significant differences (Fisher's Protected LSD test; $P < 0.05$).

Therefore, and as demonstrated by our laboratory results, the *aulica* and *nigra* phenotypes of *H. axyridis* may thrive on different prey species in nature. This may provide a selective basis for the maintenance of genetic polymorphism in this species.

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