Dietary self-selection behaviour by the adults of the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae)

ANTÓNIO ONOFRE SOARES*, DANIEL CODERRE† and HENRIQUE SCHANDERL*

Department of Biology, University of the Azores, Rua da Mãe de Deus, Apart. 1422, PT-9501–801 Ponta Delgada, Azores, Portugal; and †Département des Sciences Biologiques, Université du Québec à Montréal, CP 8888 Succ. Centre-ville, Montréal, Canada, H3C 3P8

Summary

1. *Harmonia axyridis* is a generalist predator with a high range of accepted prey. Prey differ in nutritive contents, energetic values and cost associated with their capture and ingestion. As a result of selection pressures, animals will tend to hunt for their prey efficiently. In this paper we evaluated the suitability of *Myzus persicae* and *Aphis fabae* to the adults of the *aulica* phenotype of *H. axyridis*, their feeding preferences and the impact of mixed diets on their fitness. Feeding preference of predators was evaluated through their response to different relative abundance of prey.

2. Under a single diet regime, the adults of the *aulica* phenotype fed on more individuals *M. persicae* than *A. fabae* but consumed less biomass from the former. None of those prey affect relative growth rate and reproductive capacity of the ladybeetles.

3. Males and females present different types of response to three levels of different relative abundance of prey. While males show a constant feeding preference for *M. persicae*, females did not show a feeding preference (i.e. null switching response). Under a mixed diet regime, adults' voracity gradually increased as the proportion of *M. persicae* increased, but biomass consumed and relative growth rate was not affected. On the other hand, fecundity and fertility increased.

4. Our results suggest that *H. axyridis* present self-selection behaviour because they agree with the basic criteria of Waldbauer and Friedman's self-selection, i.e. (i) the animal's choice of food or nutrients is non-random, and (ii) the coccinellid benefits from self-selecting.

Key-words: *Aphis fabae* Scopoli, *Harmonia axyridis* Pallas, *Myzus persicae* Sulzer, prey preference, reproductive capacity, voracity.

Journal of Animal Ecology (2004) **73**, 478–486

Introduction

Animals can eat two or more natural foods in proportions that yield a more favourable balance of nutrients than will any of these foods alone. This behaviour, which has important consequences for optimal foraging theory, is usually called dietary self-selection. Dietary self-selection behaviour is a continuous regulation of food intake that involves frequent shifts between foods. Two basic criteria of self-selection are (i) that the animal's choice of food or nutrients is non-random and (ii) that it benefits from self-selecting (Waldbauer & Friedman 1991).

In spite of their considerable polyphagy as accepted food, coccinellids are very specific as far as essential food is concerned. Thus it is necessary to define the prey–predator relationship in these terms and to assess the possible impact of a coccinellid against any given pest, by testing the range of essential prey of the predator (Hodek 1973; Hodek & Honěk 1996). When harvesting for food, ladybeetles are confronted with many prey species which differ in nutritive value (Blackman 1967a; Olszak 1986, 1988; Schanderl, Ferran & Garcia 1988; Obrycki & Orr 1990;

Hazzard & Ferro 1991) and escape and defensive responses (Brodsky & Barlow 1985; Malcolm 1992; Dixon 1998). Prey choice is regulated by all these conditions (Mills 1981; Houck 1991; Lucas, Coderre & Vincent 1997). Given the fact that prey preferences are correlated with fitness, ladybeetles will choose the prey most suitable from a nutritive viewpoint (Iperti 1978b; Hemptinne *et al.* 1993; Hodek & Honěk 1996). Nutritive prey quality is not, however, the single factor involved in prey choice. Prey choice is constrained by the preferences of adults for certain habitats, associations of prey/hosts, synchronization with life cycles of antagonists and discrimination capacity of adults (Iperti 1965; Way 1966; Brun & Iperti 1978; Iperti 1978a; Hodek 1993; Hodek & Honěk 1996).

Predators, when offered a choice between prey types, will often show a preference for one of them and the predator's response is influenced strongly by the relative abundance of the two prey offered (Murdoch 1969; Cock 1978; Sherratt & Harvey 1993). When tested with different relative abundance, a predator can show four types of response: (i) a constant preference for one prey species; (ii) no preference, when the ratio of consumed prey is equal to the ratio of prey individuals in the environment (i.e. null switching) (Chesson 1984); (iii) a switching behaviour, when the predator eats disproportionately more of the more abundant prey (Murdoch 1969); and (iv) an antiswitching behaviour, when the predator eats disproportionately more of the less abundant prey (Chesson 1984).

Several attempts have been made to formalize the diversity of coccinellid foods (Hodek 1973; Mills 1981; Agarwala, Das & Bhaumik 1987; Majerus 1994; Hodek & Honěk 1996). Hodek & Honěk (1996) consider that, from the ecophysiological point of view, types of food can be divided into two main groups: (i) essential foods that ensure the completion of larval development and oviposition; and (ii) alternative foods that serve only as a source of energy and thus prolong survival in comparison with starvation. There are transitions between essential and alternative foods, and essential foods show varying degrees of favourability, enabling different developmental rates, fecundity and survival (Hodek 1993; Hodek & Honek 1996) which are rarely evaluated by researchers. The definition of the limits of essential and alternative prey seems to be a very difficult task. Recently results on costs and benefits of prey specialization revealed that biological performances of *Adalia bipunctata* L. were continuously improved for six generations fed on a single diet of an aphid of poor quality (Rana, Dixon & Jarošík 2002). It seems, however, that generalist predators such as adults of ladybeetles tend to mix both types of prey in order to enhance their ability to capitalize on short-lived and scattered opportunities as they seek out suitable sites in which to reproduce (Evans, Stevenson & Richards 1999), but are dependent on the quality of the constituent species (Nielsen, Hauge & Toft 2002). Despite

that, little research has been conducted in order to evaluate the impact of mixed diets on the development and reproduction on ladybeetles.

Harmonia axyridis Pallas is a Palaearctic species originating in the Far East (Iablokoff-Khnzorian 1982). It is a very polymorphic ladybeetle and some phenotypes differ in their fitness (Soares, Coderre & Schanderl 2001; Soares, Coderre & Schanderl 2003). *H. axyridis* prefer to feed on aphids (Hukusima & Kamei 1970; Hukusima & Ohwaki 1972; Iablokoff-Khnzorian 1982; Osawa 1992), but can feed on psillids (Fye 1981; Michaud 2002), coccids (McClure 1987; Hodek & Honěk 1996), spider mites (Lucas *et al.* 1997) and lepidopteran eggs (Schanderl *et al.* 1988). Despite being euryphagous, and some of their prey occurring in mixed colonies, researchers have not attempted to check the suitability of food combinations. Only single food items have been compared (Hodek & Honěk 1996).

Contrary to *Aphis fabae* Scopoli, *Myzus persicae* Sulzer has been reported as being suitable for many coccinellids species, such as as *A. bipunctata* and *Coccinella septempunctata* L. (Blackman 1967a). In this paper we evaluated the suitability of two essential prey: *A. fabae* and *M. persicae*, under single diets, to the adults of the *aulica* phenotype of *H. axyridis* (Hukusima & Kamei 1970; Iablokoff-Khnzorian 1982; Schanderl, Ferran & Larroque 1985; Schanderl 1987; Schanderl, Garcia & Soares 1995), the feeding preference of the ladybeetles for *M. persicae* and *A. fabae* and the impact of mixed diets on the fitness of the ladybeetles. We hypothesize that (i) ladybeetles present the same biological performance under single diets of the essential prey *M. persicae* and *A. fabae*; (ii) in order to increase fitness, females of *H. axyridis* should present a dietary self-selection behaviour; and (iii) fitness parameters of ladybeetles increase under a mixed diet of *M. persicae* and *A. fabae*.

Materials and methods

H. axyridis individuals were mass reared at $22 \pm 1\ °C$, $75 \pm 5\%$ RH and a photoperiod of 16L : 8D, using fluorescent lamps (Philips ref. TDL 23 W/54 and TDL 18 W/54). The *aulica* phenotype individuals used in our experiments are characterized by the presence of confluent red areas that occupy almost the whole elytra, leaving a narrow black border on proximal and external margins. A recent study has indicated an increase in the performance of ladybeetles reared on a single diet of aphids over six generations (Rana *et al.* 2002). In order to avoid consanguinity and adaptation to food, ladybeetles were fed *ad libitum* on a mixed diet of the aphids *A. fabae* and *M. persicae* and eggs of *Ephestia kuehniella* Zeller, and field-collected ladybeetles were added regularly to the stock culture. The *aulica* phenotype occurs naturally in our stock cultures. Before the experiment, we reared *aulica* phenotype individuals separately in order to increase their numbers.

VORACITY AND RELATIVE CONSUMPTION RATE

In the first experiment, on single diets, we evaluated the number of apterous females of *A. fabae* and *M. persicae*, eaten in 24 h by adults of the *aulica* phenotype of *H. axyridis*. Adults were 15 days old and had been starved for 24 h. All experiments were performed at 20 ± 1 °C, 75% RH, a photoperiod of 16L : 8D under fluorescent lamps (Sanyo FL 40 SS W/37). Individual ladybeetles were provided with 100 aphids on a *V. fabae* plant in a 2-L mesh cage. A minimum of 30 replicates (15 males and 15 females) was conducted per treatment. There were 12 control treatments of 50 aphids without predators where aphid survival was 86·25% and 85% for *A. fabae* and *M. persicae*, respectively, per day.

Voracity (V_o) was calculated according to the following model (Soares *et al.* 2003):

$$V_o = (A - a_{24}) r a_{24}$$

where V_o = 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 differ strongly (mean body weight of an *A. fabae* wingless female was 1·09 mg, whereas an *M. persicae* wingless female was 0·48 mg), and thus the beetles' satiation could be achieved with a different number of prey, voracity can be expressed as mg of biomass of prey ingested/unit of time, the so-called relative consumption rate (*RCR*). *RCR* was evaluated according to Schanderl (1987):

$$RCR_{mg} = (W_i/n) V_o\, PUC$$

where RCR_{mg} = relative consumption rate, W_i = total weight of aphids provided, n = number of aphids provided, V_o = number of aphids eaten and PUC = prey utilization coefficient.

*PUC*s of *H. axyridis* 4th instars larvae fed on *M. persicae* and *A. fabae* were estimated previously as 93% (Schanderl 1987). For adults, Schanderl (1987) evaluated *PUC* for adults (96·4%) fed only on *M. persicae* aphids. Because larvae had a similar prey utilization coefficient when fed on *A. fabae*, we expected that for adults it would be near to 96·4%.

RELATIVE GROWTH RATE AND CAPTURE EFFICIENCY

The physiological changes in efficiency can be explored either by relative growth rate or efficiency of conversion of ingested food to biomass (Ferran 1978). Weight gain following predation is a good indicator of energy intake and costs associated with predation (Frazer 1988). We evaluated the *RGR* of *aulica* phenotype individuals following feeding on both aphid species tested

by subtracting the weight of starved predators for 24 h from the weight of predators after 24 h in the presence of the 100 individuals of a given aphid species. Adult body weight was evaluated individually using a 10^{-4} mg Mettler AM 50 analytical balance.

In order to estimate the advantage to ladybeetles, in terms of biomass gain, of preying on a single *A. fabae* or *M. persicae*, capture efficiency (*CE*) was evaluated and compared. *CE* was evaluated as follows:

$$CE = RGR/V_o$$

where CE = capture efficiency, RGR = relative growth rate and V_o = number of aphids eaten.

One-factor ANOVA was used to compare treatments of voracity, relative consumption rate, relative growth rate and capture efficiency between sexes (females vs. males) and diets between sexes [females (*M. persicae* vs. *A. fabae*) and males (*M. persicae* vs. *A. fabae*)] (Abacus Concepts 1991).

FEEDING PREFERENCES

Feeding preference was evaluated in the second experiment. Three different ratios of *M. persicae* and *A. fabae* were offered to adults (30 *M. persicae*/70 *A. fabae*, 50 *M. persicae*/50 *A. fabae* and 70 *M. persicae*/30 *A. fabae*) in an experimental set-up, as described previously. The number of apterous females of *M. persicae* and *A. fabae* eaten in 24 h was recorded. A minimum of 30 replicates (15 males and 15 females) was conducted per treatment.

Feeding preference was estimated using Manly's preference index (Manly, Miller & Cook 1972), which is the only method that took account of the prey density's depletion by predation during experiments (Cock 1978; Chesson 1984; Sherratt & Harvey 1993):

$$\alpha_1 = \ln[(n_1 - r_1)/n_1/(\ln(n_1 - r_1)/n_1) + \ln(n_2 - r_2)/n_2]$$

where n_1 and n_2 = number of *M. persicae* and *A. fabae* offered to predators and r_1 and r_2 = number of apterous females of *M. persicae* and *A. fabae* eaten in 24 h by the predators.

One-factor ANOVA, followed by a multiple comparison tests (Fisher's protected LSD) were used to compare voracity, relative consumption rate and relative growth rate and capture efficiency between treatments (Abacus Concepts 1991).

Wilcoxon's matched-pairs signed rank test (WMPSR) (JMP®; Sall & Lehman 1996) was used to compare the feeding preference of the ladybeetles.

REPRODUCTIVE CAPACITY

In the third experiment, reproductive capacity of ladybeetles was evaluated. We sexed and paired 100 individuals of the *aulica* phenotype of *H. axyridis*. Each couple was isolated in a 60 ml Petri dish (Ø:

5 cm, height: 3 cm). Five different ratios of prey (0 *M. persicae*/100 *A. fabae*, 30 *M. persicae*/70 *A. fabae*, 50 *M. persicae*/50 *A. fabae*, 70 *M. persicae*/30 *A. fabae*, 100 *M. persicae*/0 *A. fabae*) were provided. Ten replicates were conducted per treatment. Abiotic conditions were as described previously. Egg clusters were removed from Petri dishes and observed twice a day. Fecundity, fertility (including sibling cannibalism) and percentage of hatching were compared for the first 15 days of females' lives after sexual maturation. Proportions were arcsin $(\%)^{1/2}$ transformed (Zar 1984). Only the untransformed values are presented. One-factor ANOVA, followed by a multiple comparison tests (Fisher's protected LSD), was used to compare fecundity, fertility (including sibling cannibalism) and percentage of hatching per treatment (Abacus Concepts 1991).

Results

VORACITY AND RELATIVE CONSUMPTION RATE ON SINGLE DIETS

The daily voracity of the adults of the *aulica* phenotype was significantly higher on *M. persicae*. However, adults consumed significantly more biomass of *A. fabae* than *M. persicae* (Table 1). Daily voracity and daily relative consumption rate of females was significantly higher than males (Table 2). There was no significant differ-

ence in females' voracity fed on *M. persicae* and *A. fabae*; however, males' voracity was significantly higher fed on *M. persicae*. Both females and males consumed significantly more biomass of *A. fabae* than *M. persicae* (Table 3).

RELATIVE GROWTH RATE AND CAPTURE EFFICIENCY ON SINGLE DIETS

The daily relative growth rate of the adults of the *aulica* phenotype did not differ significantly when fed on *M. persicae* and *A. fabae*. Capture efficiency was significantly higher when fed on *A. fabae* (Table 1). The daily relative growth rate of females was significantly higher than males, while capture efficiency of males was significantly higher than in females (Table 2). Daily relative growth rate in both females and males did not differ significantly when fed on *M. persicae* and *A. fabae*. There was no significant difference in the capture efficiency of females fed on *M. persicae* and *A. fabae*, but in males it was significantly higher on *A. fabae* (Table 3).

REPRODUCTIVE CAPACITY ON SINGLE DIETS

There was no significant difference in fecundity, fertility and percentage of egg hatching from females fed on *M. persicae* and *A. fabae* (Table 1).

Table 1. Biological characteristics (mean ± SE) of the adults of *H. axyridis aulica* phenotype fed on single diets of *M. persicae* and *A. fabae*

Variable	*M. persicae*	*A. fabae*	
Diet			
Daily voracity (V_o)	45·8 ± 3·5a*	35·4 ± 3·3b	$F = 4·68$, d.f. = 1, 58, $P = 0·034$
Daily relative consumption rate (RCR)	21·2 ± 1·6a	37·2 ± 3·4b	$F = 17·4$, d.f. = 1, 58, $P \leq 0·0001$
Relative growth rate (RGR)	3·9 ± 0·4a	4·1 ± 0·4a	$F = 0·16$, d.f. = 1, 58, $P = 0·691$
Capture efficiency (CE)	0·082 ± 0·007a	0·125 ± 0·01b	$F = 10·44$, d.f. = 1, 58, $P = 0·002$
Reproductive capacity			
Fecundity (Fc)	314·0 ± 42·6a	342·2 ± 32·9a	$F = 0·27$, d.f. = 1, 18, $P = 0·606$
Fertility (Fr)	244·3 ± 41·3a	251·6 ± 29·1a	$F = 0·02$, d.f. = 1, 18, $P = 0·886$
Percentage of hatching (Ph)	63·2 ± 7·5a	63·9 ± 7·0a	$F = 0·12$, d.f. = 1, 18, $P = 0·725$

V_o = mean number of aphids consumed in 24 h ± SE; RCR = mg of biomass ingested in 24 h ± SE; RGR = mg of biomass ± SE; CE = mg used on growth by aphid ingested ± SE; Fc = total number of eggs ± SE; Fr = total number of eggs embrionated ± SE; Ph = mean number of eggs which give larvae in relation to the total of number oviposited ± SE. Different letter indicates significant differences (Fisher's protected LSD test; $P < 0·05$).

Table 2. Biological characteristics (mean ± SE) of the adults of *H. axyridis aulica* phenotype fed on single diets of *M. persicae* and *A. fabae*, by sex

	Sex		
Variable	Females	Males	
Daily voracity (V_o)	53·7 ± 3·2a*	27·7 ± 1·7b	$F = 49·7$, d.f. = 1, 58, $P \leq 0·0001$
Daily relative consumption rate (RCR)	38·8 ± 3·3a	19·6 ± 1·4b	$F = 28·5$, d.f. = 1, 58, $P \leq 0·0001$
Relative growth rate (RGR)	6·0 ± 0·36a	2·1 ± 0·136	$F = 102·8$, d.f. = 1, 58, $P \leq 0·0001$
Capture efficiency (CE)	0·059 ± 0·005a	0·111 ± 0·009b	$F = 25·5$, d.f. = 1, 58, $P \leq 0·0001$

V_o = mean number of aphids consumed in 24 h ± SE; RCR = mg of biomass ingested in 24 h ± SE; RGR = mg of biomass ± SE; CE = mg used on growth by aphid ingested ± SE. Different letter indicates significant differences (Fisher's protected LSD test; $P < 0·05$).

Table 3. Biological characteristics (mean ± SE) of the adults of *H. axyridis aulica* phenotype by sex, fed on single diets of *M. persicae* and *A. fabae*

Variable	Sex/diet					
	Females			Males		
	M. persicae	*A. fabae*		*M. persicae*	*A. fabae*	
Daily voracity (V_o)	59·6 ± 4·1a*	47·6 ± 4·5a	$F = 3\cdot83$, d.f. $= 1, 28$, $P = 0\cdot06$	32·1 ± 2·5a	23·3 ± 1·9b	$F = 7\cdot6$, d.f. $= 1, 28$, $P = 0\cdot01$
Daily relative consumption rate (*RCR*)	27·5 ± 1·9a	50·0 ± 4·7b	$F = 19\cdot3$, d.f. $= 1, 28$, $P = 0\cdot0001$	14·8 ± 1·1a	24·4 ± 2·1b	$F = 16\cdot2$, d.f. $= 1, 28$, $P = 0\cdot0004$
Relative growth rate (*RGR*)	5·7 ± 0·6a	6·2 ± 0·3a	$F = 0\cdot42$, d.f. $= 1, 28$, $P = 0\cdot521$	2·0 ± 0·16a	2·1 ± 0·2a	$F = 0\cdot016$, d.f. $= 1, 28$, $P = 0\cdot899$
Capture efficiency (*CE*)	0·052 ± 0·007a	0·067 ± 0·007a	$F = 2\cdot26$, d.f. $= 1, 28$, $P = 0\cdot143$	0·091 ± 0·011a	0·13 ± 0·012b	$F = 5\cdot8$, d.f. $= 1, 28$, $P = 0\cdot022$

V_o = mean number of aphids consumed in 24 h ± SE; *RCR* = mg of biomass ingested in 24 h ± SE; *RGR* = mg of biomass ± SE; *CE* = mg used on growth by aphid ingested ± SE. Different letters indicate significant differences (Fisher's protected LSD test; $P < 0\cdot05$).

Fig. 1. Manly's preference index (mean ± SE) of females, males and total of the *aulica* phenotype of *H. axyridis* fed on three different ratios of *M. persicae* and *A. fabae* (30 *M. persicae*/ 70 *A. fabae*, 50 *M. persicae*/50 *A. fabae* and 70 *M. persicae*/ 30 *A. fabae*). Different letters indicate significant differences (Wilcoxon WMPSR test; $P < 0\cdot05$).

Fig. 2. Manly's preference index (mean ± SE) of the adults of the *aulica* phenotype of *H. axyridis* fed on three different ratios of *M. persicae* and *A. fabae* (30 *M. persicae*/70 *A. fabae*, 50 *M. persicae*/50 *A. fabae* and 70 *M. persicae*/30 *A. fabae*). Different letters indicate significant differences (Wilcoxon WMPSR test; $P < 0\cdot05$).

FEEDING PREFERENCES

Adults of the *aulica* phenotype of *H. axyridis* show a feeding preference for *M. persicae* (WMPSR; $Z = -5\cdot69$, $P \leq 0\cdot0001$). However, contrary to males, which preferred to eat *M. persicae* (WMPSR; $Z = -6\cdot91$, $P \leq 0\cdot0001$), there was no significant difference in the mean of Manly's preference index of females (Manly's preference index ~ 0·5, WMPSR; $Z = -0\cdot04$, $P = 0\cdot964$) (Fig. 1). Independently of the ratio of *M. persicae*/*A. fabae* provided to ladybeetles, in general *M. persicae* was the preferred prey (WMPSR; 30 : 70, $Z = -4\cdot25$, $P \leq 0\cdot0001$; 50 : 50, $Z = -2\cdot91$, $P = 0003$; 70 : 30, $Z = -1\cdot97$, $P = 0\cdot047$) (Fig. 2). However, differences per sex were found, i.e. no significant difference in feeding preference was found in females, and males showed a preference for *M. persicae* (WMPSR; 30 : 70 females, $Z = -1\cdot03$, $P = 0\cdot29$; 30 : 70 males, $Z = -4\cdot52$, $P \leq 0\cdot0001$; 50 : 50 females, $Z = -1\cdot12$, $P = 0\cdot254$; 50 : 50 males, $Z = -4\cdot02$, $P \leq 0\cdot0001$; 70 : 30 females, $Z = -0\cdot373$, $P = 0\cdot694$; 70 : 30 males, $Z = -3\cdot23$, $P = 0\cdot001$) (Fig. 3).
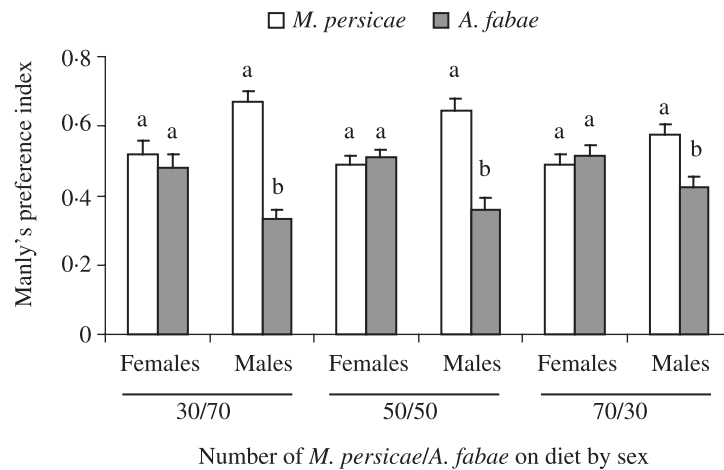
Fig. 3. Manly's preference index (mean ± SE) of the females and males of the *aulica* phenotype of *H. axyridis* fed on three different ratios of *M. persicae* and *A. fabae* (30 *M. persicae*/70 *A. fabae*, 50 *M. persicae*/50 *A. fabae* and 70 *M. persicae*/30 *A. fabae*). Different letters indicate significant differences (Wilcoxon WMPSR test; *P* < 0·05).

VORACITY AND RELATIVE CONSUMPTION RATE ON MIXED DIETS

Daily voracity increased gradually as the proportion of *M. persicae* increased and a significant difference was found for the ratio of 70 *M. persicae*/30 *A. fabae*. No significant difference in daily voracity was found for the ratios, with a lower proportion of *M. persicae* than 50 *M. persicae*/50 *A. fabae* (Table 4). Concerning daily relative consumption rate on mixed diets, there were no significant differences in the amount of the biomass ingested by the adults of ladybeetles (Table 4).

RELATIVE GROWTH RATE AND CAPTURE EFFICIENCY ON MIXED DIETS

No significant difference in the daily growth rate was found (Table 4). Capture efficiency was significantly lower for the ratio of 70 *M. persicae*/30 *A. fabae* (Table 4).

REPRODUCTIVE CAPACITY ON MIXED DIETS

Daily fecundity and daily fertility were significantly higher when adults were reared on mixed diets, mainly for the ratios of 30 *M. persicae*/70 *A. fabae* and 70 *M. persicae*/30 *A. fabae* (Table 4). There were no significant differences in percentage of hatching between all the diets offered to ladybeetle (Table 4).

Discussion

Generalist predators are confronted with a great variety of prey, which differ in nutritive and energetic values and cost associated with their capture and ingestion (Stephens & Krebs 1986; Hodek 1993; Hodek & Honěk 1996; Roger, Coderre & Boivin 2000). Aphid suitability as a food source depends on the physiological status of its host plant and aphid performance, their nutritional requirements, enzyme equipment and nutritional budgets (Klingauf 1988; Srivastava 1988; Dixon 1998). It also

Table 4. Biological characteristics (mean ± SE) of the adult's *aulica* phenotype of *H. axyridis* fed on mixed diets containing different proportion of *M. persicae* and *A. fabae*

Variable	Proportion *M. persicae*/*A. fabae*					
	0	0·3	0·5	0·7	1	
Daily voracity (V_o)	35·4 ± 3·3a*	37·3 ± 2·6ab	41·1 ± 2·6ab	52·6 ± 3·7c	45·8 ± 3·5bc	$F = 4·69$, d.f. = 4, 145, $P = 0·001$
Daily relative consumption rate (*RCR*)	37·2 ± 3·4c	24·3 ± 2·8ab	24·1 ± 2·4ab	30·3 ± 3·1bc	21·2 ± 1·6a	$F = 5·43$, d.f. = 4, 145, $P = 0·0004$
Relative growth rate (*RGR*)	4·1 ± 0·4a	3·5 ± 0·4a	4·1 ± 0·4a	3·7 ± 0·4a	3·9 ± 0·4a	$F = 0·45$, d.f. = 4, 145, $P = 0·768$
Capture efficiency (*CE*)	0·125 ± 0·01c	0·096 ± 0·009ab	0·099 ± 0·009b	0·072 ± 0·007a	0·082 ± 0·007ab	$F = 5·19$, d.f. = 4, 145, $P = 0·0006$
Reproductive capacity						
Fecundity (Fc)	29·2 ± 1·3ab	33·2 ± 1·2c	29·4 ± 0·9b	32·6 ± 1·1c	26·2 ± 1·1a	$F = 6·03$, d.f. = 4, 620, $P ≤ 0·0001$
Fertility (Fr)	21·5 ± 1·1a	25·6 ± 1·1b	22·8 ± 0·9ab	25·5 ± 1·1b	20·3 ± 1·1a	$F = 3·85$, d.f. = 4, 620, $P = 0·004$
Percentage of hatching (Ph)	63·9 ± 2·6a	63·7 ± 2·3a	61·4 ± 2·3a	67·9 ± 2·5a	63·9 ± 2·6a	$F = 0·72$, d.f. = 4, 620, $P = 0·575$

V_o = mean number of aphids consumed in 24 h ± SE; *RCR* = mg of biomass ingested in 24 h ± SE; *RGR* = mg of biomass ± SE; *CE* = mg used on growth by aphid ingested ± SE;, Fc = mean number of eggs ± SE; Fr = mean number of eggs embrionates ± SE; Ph = mean number of eggs which give larvae in relation to the total of number oviposited ± SE. Different letters indicate significant differences (Fisher's protected LSD test; *P* < 0·05).

depends on morphological and physiological traits and the nutritive requirements of predators, as well as the number of prey eaten and the amount of biomass ingested (Ferran 1978; Eubanks & Denno 2000). According to our results, *M. persicae* and *A. fabae* were accepted and suitable for the *aulica* phenotype adults of *H. axyridis* because they ensured both growth and oviposition. From the ecophysiological viewpoint, both prey can be considered essential foods. These results confirmed previous results in which completion of larval development and oviposition was observed in *H. axyridis* (Hukusima & Kamei 1970; Iablokoff-Khnzorian 1982; Schanderl *et al*. 1985; Schanderl 1987). The essential foods, however, show varying degrees of favourability, enabling different developmental rates, fecundity and survival (Hodek 1993; Majerus 1994; Hodek & Honěk 1996). *M. persicae* and *A. fabae* represented a similar source of food, because significant difference in fitness, i.e. in relative growth rate and reproductive capacity, were not observed.

As predicted by optimal foraging theory, animals will tend to hunt for their food efficiently. Generalist predators will feed on different prey types available so as to maximize their energetic gain (Stephens & Krebs 1986; Crawley & Krebs 1992) or to maximize nutrient ingestion (Waldbauer, Cohen & Friedman 1984). Body size may well be a key feature in understanding the dynamics of arthropod predator–prey systems (Sabelis 1992). According to Charnov (1976) larger prey should be preferred to small prey because they provide a higher energetic value and encounter rate is a function of prey size. However, recent results suggest that prey consumption rate is higher on prey of intermediate size leading to a convex prey consumption curve (Roger *et al*. 2000). However, the profitability of prey can be decreased by its defence response or escape ability. On the other hand, mobility of the predator and rapidity of its response following prey contact are constraints that may also strongly influence the capture success rate of predators (Malcolm 1992). In our experiments we offered two prey types of differing size. Mean body weight of a wingless female of *A. fabae* was 1·09 mg, whereas in *M. persicae* it was 0·48 mg. If size were the only factor involved in prey choice, *A. fabae* were the prey preferred independently of the ratio *M. persicae*/*A. fabae* offered.

Our results suggest differences in *M. persicae* and *A. fabae* profitability. Given the fact that relative growth rate and reproduction did not differ significantly when ladybeetles fed on *M. persicae* and *A. fabae*, our results suggest the existence of a trade-off between the nutritive prey content and the costs associated with feeding bout; i.e. searching, prey capture and consumption (Nakamuta 1983). The dispersion of small prey in the environment increases the predator's searching time and its voracity because of the large number of prey needed to compensate for energy spent. While feeding on *A. fabae*, which has a higher energetic content, adults of *H. axyridis* will decrease feeding bouts and increase energetic intake; feeding on *M. persicae* will increase feeding bouts and decrease energetic intake. However, the disadvantage of exploiting *M. persicae* could be compensated for by its higher nutritive content. Indeed, our results demonstrated that ladybeetles fed on *M. persicae* achieved the same biological performance (relative growth rate and reproductive capacity) with approximately 50% less biomass than ladybeetles fed on *A. fabae*.

Defensive response and escape ability are two important traits of prey profitability (Pastorok 1981; Houck 1991; Hazzard & Ferro 1991; Malcolm 1992; Hodek 1993; Lucas *et al*. 1997; Eubanks & Denno 2000; Roger *et al*. 2000). In our experiments the aphids were provided with an experimental set-up containing a *V. fabae* plant, which permitted stimulated predators' searching behaviour and escape of prey. *A. fabae* and *M. persicae* distribution differed in the experimental set-up. While *A. fabae* females preferred the stems, the terminal bud and the central and the secondary main vein beneath the leaf, *M. persicae* females preferred to exploit the blade beneath the leaf. Defensive strategies also differ. When stressed in the experimental set-up, *A. fabae* females run (Murdoch & Marks 1973) while *M. persicae* females drop down. According to our observations, the differences in distribution and defensive strategies did not provide an advantage to any of the aphid species, because ladybeetles searched and fed everywhere in the experimental set-up.

Ladybeetles species are euryphagous predators but when offered a choice between prey types, they will often show a preference for one of them (Mills 1981; Houck 1991; Lucas *et al*. 1997). *H. axyridis* respond to olfactory and visual cues, and can thus search more effectively (Obata 1986). Our results demonstrate that the males and the females showed different types of preferences under the three ratios of *M. persicae*/*A. fabae*. While males show a constant feeding preference for *M. persicae*, females did not show a feeding preference for any prey (i.e. null switching). Murdoch & Marks (1973) demonstrated that *C. septempunctata* displayed null switching when fed on a mixed diet of *A. fabae* and *Acyrthosiphon pisum* (Harris). Rather than maximizing the intake rate of calories or single nutrients, the exploitation of more than one natural prey permits insects to maximize nutrient intake in terms of quality and balance (Waldbauer *et al*. 1984; Waldbauer & Friedman 1991). Evans, Stevenson & Richards (1999) demonstrated that a mixed diet of essential and alternative prey increased fitness of *C. septempunctata* and *C. transversoguttata* Brown. Our results demonstrate that feeding on a mixed diet increased the reproductive capacity of *aulica* females. It might also be suggested that the increase in fitness could be related to females' null switching behaviour. We suggest two possible explanations for the feeding behaviour of females: (i) the maximization of intake rate of calories and decrease of cost associated to handling time, as predicted by optimal foraging theory (Stephens & Krebs 1986); and/or (ii) achieving a more favourable balance of nutrients (Waldbauer & Friedman 1991). Having in

mind the fact that our results agree with the basic criteria of Waldbauer and Friedman's self-selection, i.e. (i) *H. axyridis* females' choice of food is non-random; and (ii) they benefit from self-selecting because reproductive capacity increases feeding on mixed diets (Waldbauer & Friedman 1991), we beleive these results confirm our previous hypothesis about the existence of self-selection behaviour in *aulica* females of *H. axyridis*. We think that a more favourable balance of nutrients could be the main factor involved in this behaviour. Contrary to females, males show a feeding preference for *M. persicae*. Difference in body size of aphids could explain males' feeding preference. Generally, predators' size is positively correlated to mean prey size and capture success decreases with increasing prey size (Pastorok 1981; Malcolm 1992; Sabelis 1992; Roger *et al.* 2000). On the other hand, due to their small size males are probably more prone to eat small prey and to become satiated (Dixon 2000). Apterous females of *M. persicae* are approximately 50% smaller than apterous females of *A. fabae*. The smaller size of *M. persicae* could determine, in part, feeding preferences of males. Our results suggest that instantaneous rate of energy gain, calculated from relative growth rate and capture efficiency, is not the main factor in feeding preferences of males. We found that relative growth rate did not differ between ladybeetles fed on *A. fabae* and *M. persicae* and, on the other hand, the gain of weight per aphid was higher on *A. fabae*.

Geographic and environmental factors (Honěk 1982, 1983, 1985a,b) and trophic composition (Ferran & Dixon 1993; Hodek 1993) determine the habitat preference of predators. Our results suggest that differences in composition of aphid populations, especially if they were complementary from a nutritive point of view, could also determine the habitat preference of ladybeetles. Dietary self-selection by insects is a newly discovered dimension of insect feeding behaviour. Because integrated pest management is essentially applied ecology, knowledge of self-selection will enhance our ability to design IPM programmes for the control of damage to plants by pests (Waldbauer & Friedman 1991).

Acknowledgements

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