Prey preference of ladybird larvae and its impact on larval mortality, some life-history traits of adults and female fitness

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Abstract

Aphids are essential for aphidophagous ladybird beetle reproduction in natural conditions. The different species of aphids vary in quality and abundance from year to year. As a consequence, females may be forced to oviposit in suboptimal colonies of prey. The relationship between the choice of oviposition sites by adults and larval performances is poorly studied in predators.

To determine the performance of larvae reared on optimal and suboptimal prey, two clutches of eggs from each of eight females of the two spot ladybird beetle, *Adalia bipunctata,* were used. The larvae hatching from each clutch of eggs were assigned in equal numbers to one of two groups. The larvae of one group were fed throughout their development on pea aphids (*Acyrthosiphon pisum*), which is a high quality prey, and the other group on cowpea aphids (*Aphis craccivora*), which is considered a suboptimal prey.

Our results confirm that *A. craccivora* is a suboptimal prey for this ladybird as the adults developing from the larvae fed this aphid were lighter and had fewer ovarioles, and overall had a lower fitness than individuals reared on pea aphid.

When offered a choice naïve first instar larvae more frequently attacked cowpea than pea aphids. Fourth instar larvae attacked equally the two species of prey irrespective of the aphids they were previously fed.

This study indicates that larvae do not show a preference for feeding on high quality aphids even though larvae that feed and complete their development on low quality prey are less fit than those that feed on high quality prey.

Key words: Ladybird beetle, prey preference, body weight, ovariole number, fitness.

Introduction

In natural conditions, predatory insects rely on a particular set of prey to support their reproduction. These prey are often described as essential as opposed to alternative prey that just allow predator to survive (Hodek and Honek, 1996). This terminology implies a hierarchy between the two types of prey although they are equally important to the predators. Therefore, Dixon (2000) proposed that all prey supporting to some extend reproduction be named "nursery prey". He coined the term "food prey" to designate the other prey predators eat. In general the range of nursery prey is unlikely to be fixed as it is dependent on several factors, some of which vary in time (Sadeghi and Gilbert, 2000b). One of these factors is the nature and the abundance of prey. In the case of aphidophagous predators the relative abundance of prey species changes dramatically within and between years. Within a season aphid colonies never last for more than 8 weeks (Dixon, 1998). Therefore, ladybirds have to successively attack colonies of different species of prey to realize their fecundity (Hemptinne, 1989). At a larger temporal scale prey that are abundant and highly exploited one year may virtually disappear the next year and remain extremely rare for 5 or 6 years (Majerus and Kearns, 1989; Dixon, 1998). When the preferred prey becomes uncommon predators like herbivores probably include suboptimal prey in their diet (Courtney *et al*., 1989; Fréchette *et al*., 2006).

At first glance it would seem logical to think that generalist species can utilize suboptimal prey because they exploit a large set of nursery prey. However, a generalist species may consist of a collection of specialized populations each specialized on a different food type, or of specialized individuals or an assemblage of truly generalist individuals (Thompson, 1994; Sadeghi and Gilbert, 1999, 2000a; Bolnick *et al*., 2003; Gilbert, 2005). The consequence of including unusual prey in the diet depends on the type of generalist predator. In the first two cases, it will considerably reduce their fitness. This is well documented for *Adalia bipunctata* (L.), a generalist ladybird that feeds and reproduces on more than 20 species of aphids (Hemptinne, 1989; Hodek and Honek, 1996). The pea aphid, *Acyrthosiphon pisum* (Harris), and the black bean aphid, *Aphis fabae* Scopoli, are on the list of its nursery prey, with the former recorded as better quality food than the later (Blackman, 1965, 1967; Kalushkov, 1998). Individuals exclusively reared on pea aphids for more than 20 generations experienced a dramatic decline in fitness when forced to feed on a diet of black bean aphids. This detrimental effect progressively disappears after 7 generations of selection for improved performance on the second prey (Rana *et al*., 2002). The ability of the two spot ladybird to specialize on certain species of aphids and the long time required to become a specialist suggest that this generalist species is made up of specialized populations (the first type) or of specialized individuals (the second type). However, nothing is known about the prey preferences of larvae. When females that have specialized to feed on pea aphids have no choice other than to oviposit in colonies of the suboptimal black bean aphid do the larvae stay with that prey or move in search of better quality food? That is, do larvae presented with a choice prefer to feed on high quality aphids?

To test this hypothesis *A. bipunctata* larvae from a laboratory culture raised for more than 20 generations on pea aphids were offered a choice of pea and cowpea aphids, *Aphis craccivora* Koch. Cowpea aphids were chosen because they are a poor quality food not listed among this ladybird's nursery prey (Hodek and Honek, 1996). It can even be toxic for this predator (Hemptinne, personal observation). In addition, as the geographical range and habitat of these two species overlap *A. bipunctata* is likely to encounter the cowpea aphid in nature. Although the effect of aphid quality on larval development, growth and female fecundity are well studied it is unknown whether larvae are selective when offered a choice of prey (Blackman, 1965, 1967; Hodek and Honek, 1996). The objectives of this paper were firstly to confirm that cowpea aphid is a suboptimal prey for the larvae of two spot ladybirds and secondly to determine whether they can select the better quality prey when given a choice.

Adult ladybirds are highly mobile and can fly from one patch of prey to another and even between habitats. In contrast, the larvae are rather sedentary and complete their development in one or a few adjacent patches of aphids (Banks, 1968; Ferran and Dixon, 1993). As the time it takes them to complete their development is similar to the duration of an aphid colony leaving a patch in search of a better one is likely to be maladaptive, because of their poor mobility. On the other hand by staying in a patch they are protected from conspecific competitors by the presence of an oviposition deterring pheromone (Hemptinne and Dixon, 2000; Hemptinne *et al.*, 2001; Fréchette *et al.*, 2003). Thus, larvae are likely to remain in a patch and, therefore, their well being is likely to be mainly dependent on their mother's ability to find and select the highest quality patches available (Ferran and Dixon, 1993; Sadeghi and Gilbert, 1999). That is, the expectation is that the larvae will not show a preference and will attack and attempt to eat any aphid they encounter.

Materials and methods

The stock cultures

Separate cultures of the pea aphid, *A. pisum*, and the cowpea aphid, *A. craccivora*, were reared on broad bean (*Vicia faba* L.) at a photoperiod of 16L : 8D and at 19 °C. The beans were grown in compost and watered three times a week.

The culture of *A. bipunctata* had been maintained for more than 20 generations in the laboratory at 18 °C and a photoperiod of 16L : 8D. The ladybirds were reared in 5 l ventilated plastic boxes containing a piece of corrugated filter paper on which the females tended to lay eggs. Three times a week the filter papers and eggs were collected, the ladybirds transferred to clean boxes and fed an excess of pea aphids. Shoots of broad bean were added to each box to improve the survival of the aphids. The eggs on the corrugated filter papers were incubated in 175-cm^3 plastic boxes under the same conditions as the stock culture. Hatchling larvae were reared 10 to 15 per 175-cm^3 plastic box and fed three times a week until

they reached the adult stage. Freshly emerged adults were added to the stock culture. Females from the stock culture laid an average 22 eggs per day, which is the optimal reproductive output of this species (Stewart *et al.*, 1991).

The experiments described below were carried out under the same laboratory conditions as the rearing of the stock culture.

Food preference of larvae

Males and females from the stock culture were isolated in pairs in 9 cm Petri dishes. Each pair received fresh pea aphids every day and any eggs laid in the previous 24 h were removed.

Four egg batches laid by 4 different pairs were randomly selected, isolated and incubated in 5 cm Petri dishes. These eggs were inspected several times per day until they changed in colour from yellow to grey, an indication that they were about to hatch. They were then observed more frequently and when the larvae hatched, those that were still on their egg shell were picked up by means of a fine paintbrush and isolated in 5 cm Petri dishes until a sample of 50 larvae was assembled.

Food preference of naïve 1st instar larvae

Within 24 h of hatching the 50 larvae were individually offered a first meal consisting of a mixture of 30 small pea and 30 small cowpea aphids. Prior to the experiment the aphids were killed by keeping them for 8 min at -18 °C in order to control for the differences in the mobility of the two aphids. Larvae were left for 5 min to acclimatize to the experimental conditions and then the number of aphids they met and the result of these encounters (species encountered, attacked, eaten or avoided) were recorded every minute for 30 min. At the end of the experiment the larvae were transferred to clean Petri dishes and half of them fed pea aphids until the end of the third larval instar. The other half was fed cowpea aphids. The proportions of the two species of aphids attacked were compared using a normal approximation of the binomial test.

Food preference of 4th instar larvae

From the 50 naïve first instar larvae tested for their food preference, 20 were reared to the fourth instar on pea aphids and 17 on cowpea aphids. Twenty-four hours after moulting to the fourth instar these larvae were individually placed in clean Petri dishes and deprived of food for 6 h in order to standardize their hunger. They were then each offered 30 pea and 30 cowpea aphids immobilized as previously by exposing them for 8 minutes to -18 °C. After an acclimatization period of 5 min the number of encounters with aphids and the results of these encounters were recorded for 30 min as in the previous experiment. At the end of this period the larvae were transferred to clean Petri dishes and fed again the aphids they were previously assigned, until they pupated. The proportion of time spent in walking, attacking and eating aphids and the proportion of the two species of aphids attacked were compared using χ^2 tests.

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Effect of food quality on fitness components and fitness

The effect of food quality on fitness components and fitness was measured using the results for the larvae isolated for the tests on food preference. However, rather few fourth instar larvae remained at the end of these tests. Therefore, a second sample of 65 larvae was isolated from four clutches of eggs laid by four females, as explained earlier; 33 larvae were fed pea aphids and 32 cowpea aphids throughout their development. Every day at the same time the larvae from the first and the second sample were transferred to clean Petri dishes and given freshly collected aphids *ad libitum*. The previous day's Petri dishes were then carefully searched under a binocular stereomicroscope and any exuviae, indicating that the larva moulted during the previous 24 h, was noted. This was used to estimate the duration of each instar. The resultant adults were weighed to an accuracy of 0.1 μg within 24 h of emergence and before eating any food. They were then fed for 3 to 4 days until their integument hardened. At the end of this period their sex was determined by examining the shape of their 6th abdominal sternite under a binocular stereomicroscope (Hodek, 1973). Females were dissected and their ovarioles counted.

Fitness

Following Sadeghi and Gilbert (1999), individual fitness (r) was calculated as a performance measure (McGraw and Caswell, 1996) by integrating developmental time (D), survival (m = 1 or 0) and potential fecundity (V) using the equation:

$$r = [Ln(m.V)]/D,$$

where Ln = natural logarithms. D, the developmental time, is the duration in days of larval and pupal instars and V, the potential fecundity based on ovariole number; m is 0 for larvae that died before completing their development.

Statistical analysis

Developmental time and adult weight of the beetles reared on pea and cowpea aphids were compared using two-way ANOVAs with sex and aphid species as fixed variables, ovariole number using a t test and individual fitness using a two way ANOVA with pair and aphid species as fixed variables. The influence of the feeding regime on mortality was analysed using a Fisher exact test.

Results

Food preference of larvae
#### Food preference of naïve 1st instar larvae

The naïve larvae were seen feeding on 733 (48.9%) out of 1500 occasions, and were recorded eating cowpea aphids on 422 and pea aphids on 311 occasions, respectively. This ratio is highly significantly different from 0.5 (figure 1; normal approximation of the binomial test: $z_{obs} = 4.0999$; P < 0.001). That is, they appear to prefer cowpea to pea aphids.

Food preference of 4th instar larvae

Fourth instar larvae previously fed pea aphids were more often recorded eating than those previously fed cowpea aphids, which tended to be more active (figure 2; Proportions observed eating: $\chi^2 = 4.86$, 1 d.f., P < 0.05; proportions observed walking: $\chi^2 = 2.73$, 1 d.f., P > 0.05). However, neither group of larvae showed a significant preference for either pea or cowpea aphids (figure 2; $\chi^2 = 0.61$, 1 d.f., P < 0.05).
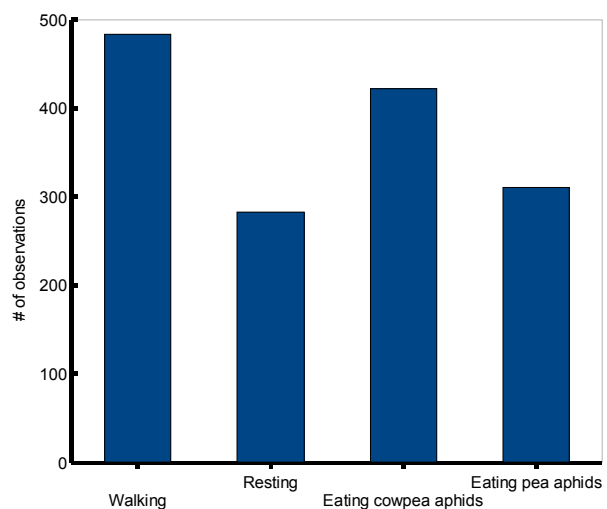
Figure 1. Feeding preference and activity of naïve first instar larvae of *A. bipunctata*: the number of occasions on which they were observed eating pea or cowpea aphids, walking or resting.
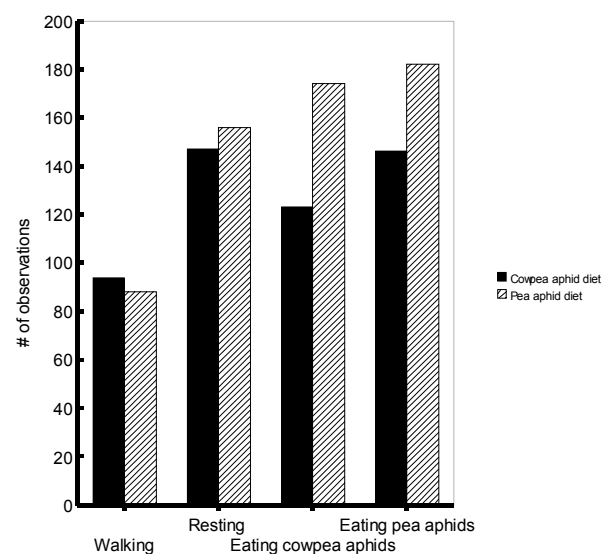
Figure 2. Feeding preference and activity of fourth instar larvae of *A. bipunctata* previously fed pea or cowpea aphids: the number of occasions on which they were observed eating pea or cowpea aphids, walking or resting.

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Effect of food quality on fitness components and fitness

The larvae of the two samples did not differ in terms of mortality (Fisher test $_{pea\ aphid}$: 0.5421; Fisher test $_{cowpea\ aphid}$: 0.7625) and total developmental time (t test $_{pea\ aphid}$: 0.77, 36.27 d.f., P = 0.4480; t test $_{cowpea\ aphid}$: 1.69, 24.79 d.f., P = 0.1040). They gave birth to females of a similar weight at emergence (t test $_{pea\ aphid}$: 1.15, 16.9 d.f., P = 0.2668; t test $_{cowpea\ aphid}$: 2.10, 15.7 d.f., P = 0.05187) or ovariole number (t test $_{pea\ aphid}$: 0.12, 14.0 d.f., P = 0.9067; t test $_{cowpea\ aphid}$: 0.35, 7.3 d.f., P = 0.7359). Thus, the data for the two samples were pooled.

M o r t a l i t y

Mortality occurred mainly in the first larval instar and affected all other instars equally but to a lesser extent in both groups. The final mortality was similar for the larvae fed either pea or cowpea aphids (table 1, Fisher test: 0.2546).

D e v e l o p m e n t a l t i m e

The duration of development was not influenced by an interaction between sex and diet (F = 1.6259, 1 and 73 d.f., P = 0.2063). There was no significant difference in the duration of development of males and females (F = 0.2348, 1 and 73 d.f., P = 0.2348). However, a daily diet of cowpea aphids resulted in a significant lengthening of development [mean dev. time $_{pea\ aphid}$: 24.4 (1.12) days; mean dev. time $_{cowpea\ aphid}$: 25.5 (1.96) days; F = 9.8856, 1 and 73 d.f., P = 0.0024; table 1]. This effect is significant for larval but not pupal development.

A d u l t w e i g h t a t e m e r g e n c e

The weight of recently emerged adults was significantly affected by the interaction between sex and diet (F = 7.6481, 1 and 64 d.f., P = 0.0074. As expected females were generally heavier than males (F = 29.3552, 1 and 64 d.f., P = 0.0001). Both sexes of individuals fed pea aphids were heavier than those fed cowpea aphids (F = 17.8500, 1 and 64 d.f., P = 0.0001; table 1).

O v a r i o l e n u m b e r

Females fed pea aphids had an average of 46.7 ovarioles compared to 42.7 for those fed cowpea aphids. These means are highly significantly different (table 1, t test: 2.97, 31.3 d.f., P = 0.0056).

Fitness estimate

Fitness was not influenced by the interaction between pairs and diet (F = 1.3422, 3, 26 d.f., P = 0.2823). The fitness of some pairs was significantly higher than that of others independent of the aphids the larvae were reared on (F = 9.2948, 3, 26 d.f., P = 0.0002). More importantly, the fitness of ladybirds reared on cowpea aphid was significantly lower than that of those reared on pea aphids (average fitness $_{cowpea\ aphid}$: 0.1809; average fitness $_{pea\ aphid}$: 0.1894, F = 5.3799, 1, 26 d.f., P = 0.0285).

Discussion

Aphids are the general nursery prey of aphidophagous ladybirds in natural conditions. The occurrence of this resource is very variable in space and time: colonies of aphids have a life span of 6 to 8 weeks and species that form large colonies one year may be extremely rare the following year and vice versa (Majerus and Kearns, 1989; Dixon, 1998). In addition, species of aphids as prey differ widely in quality (Hodek and Honek, 1996). Therefore, female predators may feed on and oviposit in colonies of suboptimal prey. The reaction of larvae hatching near such resources is largely unknown. The link between adult selection of oviposition sites and subsequent larval performance has been frequently studied in phytophagous insects (see for example Thompson, 1988; Berdegué *et al.*, 1998; Harris *et al.*, 2001; Craigh and Ohgushi, 2002; Forrister, 2004). However, there are very few studies on the same theme for predators. The preference for some aphid species over others and its association with larval performance is recorded for a few aphidophagous syrphids (Sadeghi and Gilbert, 1999; Sadeghi, 2002) and chrysopids (Petersen and Hunter, 2002) but not for aphidophagous ladybirds. The little experimental evidence is counterbalanced by two commonly held views on food preference of adults and larvae: firstly, highly seasonal prey are thought to favour selection for a positive relationship between oviposition preferences and larval performance (Nylin and Janz, 1999). Secondly, it is believed that insect predators are less associated with particular prey than herbivores with their host plants. That is, habitat characteristics, prey size and abundance as well as the risk of encountering natural enemies are seen as more important than chemical or intrinsic properties of prey (Albuquerque *et al.*, 1997).

Table 1. The mortality, sex ratio, developmental time, adult weight and ovariole number of two groups of *A. bipunctata* reared from the first larval instar (L1) to adulthood on either pea or cowpea aphids. Results are expressed as means (SEM).

	Pea		Cowpea	
# of individuals	58		57	
Mortality (%)	31.03		36.84	
	Male	Female	Male	Female
# of individuals	20	20	16	20
Dev time (days)	24.45 (0.90)	24.43 (1.29)	25.90 (1.73)	25.20 (2.14)
Adult weight (mg)	9.98 (1.46)	12.93 (1.56)	8.94 (1.95)	10.08 (2.11)
Ovariole number	-	46.7 (3.8)	-	42.7 (3.9)

To investigate the reaction of larvae hatching near a colony of low quality aphids, larvae of the two spot ladybird were reared from the very beginning of the first instar to adulthood on one of two different species of aphids. The first group was fed pea aphids, the prey consumed by their mother and their ancestors for more than 20 generations; the second group cowpea aphids. This prey was selected because it is not on the list of the nursery prey of *A. bipunctata* (Hodek and Honek, 1996) and is therefore likely to be a suboptimal prey for this ladybird.

The results presented confirm that *A. craccivora* is a lower quality food than *A. pisum* for *A. bipunctata*. The larvae fed the former took significantly longer to develop into adults. These adults were also lighter and had fewer ovarioles. These differences translated into a significantly lower fitness index. These observations are in agreement with the observation that *A. craccivora* may even be toxic for *A. bipunctata* (Hemptinne, pers. observation).

When high quality aphids are rare females of the two spot ladybird may have to lay eggs in colonies of poor quality aphids and therefore it is relevant to investigate the behaviour of the larvae. In particular, to address the question "will they eat this prey or leave the patch in search of a better food source?" Our results indicate that when given a choice naïve first instar larvae more frequently attacked cowpea than pea aphids. This may be because the small larvae found it easier to handle the smaller cowpea aphids than the larger and long-legged pea aphids. The presence of small aphids is indeed crucial for the survival of newborn ladybird larvae (Dixon, 1959). The fourth instar larvae showed no preference whatever the aphid they were fed previously. The only difference was in the level of activity: larvae previously fed pea aphids were less mobile and ate more than those previously fed cowpea aphid. Thus, the results support the prediction that they should show no preference and that they are "meet and eat" predators: providing the item encountered is not too different from their image of familiar prey it is attacked (Dixon, 2000). The greater activity of the larvae fed cowpea aphids may be due to their greater "hunger" because they had to handle small prey.

Our laboratory experiments suggest that in the field ladybird larvae will stay in the patch selected by their mother. That is, a positive correlation between female choice and larval performance is unlikely. This strategy is adaptive. As ladybird beetles have a developmental time that is longer than that of their prey, females must lay one batch of eggs early in the development of aphid colonies to maximise the survival of their offspring (Kindlmann and Dixon, 1993; Dixon, 1997). This means that they have to search for aphid colonies that are not already being exploited by conspecific larvae (Hemptinne and Dixon, 2000; Hemptinne *et al.*, 2001). Therefore, larvae staying in their original patch are less likely to be eaten by conspecific larvae. On the other hand, should they leave the colony then they face either the risk of encountering enemies or not finding another suitable aphid colony. This reasoning is compatible with observations made by Banks (1968) and those mentioned in the review of Ferran and Dixon (1993) that larvae are rather sedentary and spend their life in the patch in which they were born or in an adjacent patch of prey.

Acknowledgements

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