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Costs and benefits of prey specialization in a generalist insect predator

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Summary

1. There are very few studies on prey specialization in predatory insects. Of the prey that the larvae of the generalist ladybird beetle *Adalia bipunctata* regularly feed on in the field, some are more suitable as food than others. A laboratory experiment was undertaken to determine whether it is possible to select for improved performance of this insect predator on a 'poor quality' prey, and the cost, if any, of such specialization.
2. The ladybird performed better when reared on the pea aphid *Acyrthosiphon pisum* than on the black bean aphid *Aphis fabae*. Over the course of six generations of selection there was a significant increase in performance on both species of aphid, especially the black bean aphid.
3. Ladybirds previously selected for five generations for better performance on the black bean aphid performed significantly worse when reared on pea aphid compared with those reared continuously for six generations on pea aphids, and vice versa. That is, specialization on one species of aphid resulted in a poorer performance on another.
4. If, as reported here, the specialization on one kind of prey generally entails a trade-off in performance on another, then the interactions between insect predators and their prey are more homologous to those of herbivorous insects and plants than previously thought. The significance of this for prey specialization in ladybird beetles is discussed.

Key-words: *Adalia bipunctata* L., adaptation and trade-off, Coccinellidae, life-history parameters, predator–prey associations, prey specialization.

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Introduction

In contrast to the plethora of studies on feeding specialization in herbivorous insects (Denno & McClure 1983; Strong, Lawton & Southwood 1984; Berenbaum 1990; Jaenike 1990; Schoonhoven, Jermy & Loon 1998), there are few such studies on carnivorous insects and these are mainly on parasitoids (Vinson 1976, 1981, 1984; Arthur 1981; Weseloh 1981; Schultz 1983). This has been attributed to the widely held view that predators tend to be generalists precisely because they eat animals. Plant tissues are mostly poor in nitrogen and are often rich in non-digestible if not toxic materials, whereas animal flesh is thought to provide an excellent balance of nutrients for another animal (Doutt & DeBach 1964; Bristow 1988). That is, plant secondary chemistry is regarded as an important factor in the specialization of herbivores (Ehrlich & Raven 1964) and, by implication, the absence of chemical defences in animals, the markedly less prey specialization of predators.

The one well-studied case of feeding specialization in a predatory insect indicates that the novel defence of the prey in this case is not its biochemical composition but the fact that it is ant attended (Tauber & Tauber 1987; Milbrath, Tauber & Tauber 1993; Albuquerque, Tauber & Tauber 1997). Generally, predator–prey associations are thought to be determined more by characteristics of the habitat and/or the phenology, size or abundance of prey or natural enemies (Evans 1982; Hagen 1987; Hurd 1988; Endler 1991; Nylin & Janz 1993; Sih 1993; Sloggett & Majerus 2000a) than by chemical or other intrinsic characteristics of prey.

It is well known that the aphid prey of several aphidophagous predators vary in suitability as food (Hodek 1962; Blackman 1967; Hodek & Honěk 1996; Kalushkov 1998; Sadeghi & Gilbert 1999, 2000). Of the wide range of aphid species eaten by many generalist ladybirds, those that support larval growth and adult reproduction are referred to as 'essential' (Hodek 1962) or 'nursery' prey (Dixon 2000). These predators

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have sedentary larvae, so one would expect an adult's decision about where to lay her eggs to be related to subsequent offspring performance, that is there would be a preference-performance linkage. However, even relatively unsuitable species of aphid may be common prey of adults and larvae of ladybirds. Blackman (1967) cites the case of the two-spot ladybird *Adalia bipunctata* L., whose larvae are regularly recorded in the field developing in colonies of the black bean aphid *Aphis fabae* Scop. but nevertheless is unable to realize its full reproductive potential feeding on this aphid.

The objectives of this study were to: (i) confirm that not all nursery prey are equally suitable for the growth and reproduction of the ladybird *A. bipunctata*; (ii) improve the performance of this ladybird on a particular aphid by selection; (iii) test the hypothesis that specialization on one aphid entails a trade-off in performance on another; (iv) discuss the significance of the results in relation to the nature and evolution of more specialized predator feeding habits.

Materials and methods

Adults of *A. bipunctata* were collected on the campus of the University of East Anglia, Norwich, UK, in the spring of 2000. These adults were fed *ad libitum* with pea aphids *Acyrthosiphon pisum* Harris. From this culture 10 pairs were selected for use in the following experiments.

SELECTION FOR IMPROVED PERFORMANCE

To determine whether it is possible to improve the performance of a generalist ladybird on a low-quality diet, *A. bipunctata* was reared and selected for improved performance on a diet of *Aphis fabae*. This aphid is known to be a poor quality food for this ladybird. As a control the ladybird was also reared on the pea aphid, which is widely regarded as a suitable prey for this and other species of ladybird (Majerus 1994). The first generation consisted of the offspring of 10 pairs of adults collected from the field. Subsequent generations were the offspring of five pairs, which were the fastest developing and largest of the survivors from the previous generation. The larvae were reared individually and supplied daily with an abundance of aphids. This selection procedure was followed for a further five generations, giving a total of six generations. In each generation the duration of development and mortality of the larval and pupal stages, fresh weight of the male and female adults, pre-oviposition period, fecundity and longevity were recorded. Fewer adults than larvae were monitored because of the technical difficulty of monitoring the fecundity and longevity of large numbers of beetles over long periods of time.

FITNESS

A useful way of summarizing the above data sets is to combine the measurements into a measure of fitness. This has the additional virtue of making the changes that occur in overall performance from generation to generation more obvious. Following Sadeghi & Gilbert (1999, 2000), individual fitness (r) was calculated as a performance measure (McGraw & Caswell 1996) by integrating developmental time (D), survival ($m = 1$ or 0) and potential fecundity (V) via the equation:

$$r = [\mathrm{Ln}(m \cdot V)]/D \qquad \text{eqn 1}$$

where Ln = natural logarithms. In Tables 1 and 2 this is the average performance of the five largest females in each generation. In the results for the trade-off experiment it is based on all the females that survived in each of the treatments.

TRADE-OFF IN PERFORMANCE

To determine whether specialization by a ladybird on a particular prey adversely affected its performance on another, some of the ladybirds in the above experiments were switched from one diet to the other. The offspring of the adults selected at the end of the fifth generation were divided into two groups. One group of offspring was reared on the same species of aphid as the larvae of the previous five generations, and the other group was reared on the other species of aphid. The performance of those groups reared continuously for six generations on the same diet was compared with that of those switched from one diet to the other.

Results

FOOD SUITABILITY

The performance, in terms of the parameters measured, was better when the ladybirds were reared on pea aphid than when they were reared on black bean aphid. Interestingly, even when reared on the pea aphid, which is widely assumed to be a very suitable aphid for rearing aphidophagous ladybirds in general, the performance improved with selection. In addition, in the first three generations the incidence of mortality when reared on black bean aphid was significantly higher than when reared on the pea aphid ($\chi^2_1 = 29$, $P < 0{\cdot}001$; $\chi^2_2 = 12$, $P < 0{\cdot}001$; $\chi^2_3 = 4{\cdot}1$, $P < 0{\cdot}05$; Tables 1 and 2).That is, overall the black bean aphid was less suitable than the pea aphid as prey for *A. bipunctata*.

As the adults reared on black bean aphid were smaller than those reared on pea aphid, it is possible they laid smaller eggs. To check this a sample of 20 eggs laid by adults reared on each of the two diets was weighed in the fourth generation. The adults differed significantly in weight ($t = 23{\cdot}9$, d.f. = 32, $P < 0{\cdot}001$; Tables 1 and 2), with those reared on the pea aphid being 1·2 times heavier than those reared on the black bean aphid. However, the eggs laid by the adults reared on the pea aphid (0·088 ± 0·002 mg) were similar in

Table 1. The life-history parameters of the ladybird beetle *Adalia bipunctata* recorded over a period of six generations when selected for improved performance on a diet of the pea aphid *Acyrthosiphon pisum*

	Larval stage		Pupal stage		Adult fresh weight (mg)				Longevity (days)		
Generation	Duration (days)	Mortality (%)	Duration (days)	Mortality (%)	Male	Female	Pre-oviposition period (days)	Fecundity	Male	Female	Individual fitness (*r*)
F_1	11·58 ± 0·08(36)	5·3	6·55 ± 0·09(33)	0·0	9·22 ± 0·11(19)	10·85 ± 0·13(15)	11·40 ± 0·16(10)	927·80 ± 30·20(5)	137·4 ± 4·33(5)	155·44 ± 4·71(9)	0·2293 ± 0·0021(5)
F_2	11·46 ± 0·11(52)	5·5	6·53 ± 0·09(30)	0·0	9·32 ± 0·13(20)	11·13 ± 0·10(14)	11·40 ± 0·16(10)	939·00 ± 25·25(5)	136·4 ± 7·05(5)	157·33 ± 4·60(9)	0·2313 ± 0·0027(5)
F_3	11·08 ± 0·12(36)	2·7	6·67 ± 0·09(30)	0·0	9·49 ± 0·10(19)	11·73 ± 0·28(13)	10·9 ± 0·28(10)	983·80 ± 23·06(5)	137·2 ± 6·11(5)	158·67 ± 4·11(9)	0·2360 ± 0·0017(5)
F_4	10·67 ± 0·13(31)	0·0	6·63 ± 0·09(30)	0·0	9·61 ± 0·09(16)	12·05 ± 0·05(14)	10·8 ± 0·20(10)	987·40 ± 21·89(5)	139·8 ± 6·91(5)	161·55 ± 9·11(9)	0·2429 ± 0·0033(5)
F_5	10·56 ± 0·11(32)	0·0	6·53 ± 0·09(30)	0·0	9·66 ± 0·14(18)	12·12 ± 0·31(13)	10·60 ± 0·22(10)	994·06 ± 13·31(5)	142·4 ± 3·87(5)	160·11 ± 4·16(9)	0·2398 ± 0·0035(5)
F_6	10·41 ± 0·09(32)	0·0	6·55 ± 0·09(31)	0·0	9·63 ± 0·19(18)	12·16 ± 0·25(13)	10·60 ± 0·22(10)				0·2484 ± 0·0048(5)
F	19·82		0·43		1·89	2·24	3·03	1·73	0·18	0·18	5·11
d.f	5,213		5,178		5,104	5,76	5,54	4,20	4,20	4,40	5,24
P	< 0·001		NS		NS	< 0·05	< 0·02	NS	NS	NS	< 0·01

Figures in parentheses are numbers of test animals.

Table 2. The life-history parameters of the ladybird beetle *Adalia bipunctata* recorded over a period of six generations when selected for improved performance on a diet of the black bean aphid *Aphis fabae*

	Larval stage		Pupal stage		Adult fresh weight (mg)				Longevity (days)		
Generation	Duration (days)	Mortality (%)	Duration (days)	Mortality (%)	Male	Female	Pre-oviposition period (days)	Fecundity	Male	Female	Individual fitness (*r*)
F_2	17·18 ± 0·14(30)	58·3	7·34 ± 0·11(32)	6·2	6·70 ± 0·20(23)	8·21 ± 0·07(22)	16·4 ± 0·34(10)	416·00 ± 7·05(5)	117·49 ± 3·75(10)	128·87 ± 4·77(10)	0·1469 ± 0·0025(5)
F_3	14·63 ± 0·25(30)	31·8	6·94 ± 0·10(32)	5·9	8·29 ± 0·06(22)	8·95 ± 0·09(20)	16·00 ± 0·21(10)	553·00 ± 6·832(5)	119·10 ± 4·19(10)	136·40 ± 7·20(10)	0·1728 ± 0·0029(5)
F_4	12·06 ± 0·17(30)	16·7	6·80 ± 0·07(30)	0·0	8·50 ± 0·05(22)	9·80 ± 0·07(20)	15·00 ± 0·21(10)	866·00 ± 6·42(5)	124·40 ± 4·09(10)	138·90 ± 5·07(10)	0·1991 ± 0·0031(5)
F_5	11·80 ± 0·11(30)	9·1	6·80 ± 0·12(30)	0·0	8·61 ± 0·13(22)	10·00 ± 0·06(20)	14·00 ± 0·21(10)	925·00 ± 15·81(5)	128·40 ± 4·75(10)	143·40 ± 3·48(10)	0·2123 ± 0·0034(5)
F_6	11·57 ± 0·10(30)	3·2	6·79 ± 0·08(28)	0·0	9·50 ± 0·10(23)	11·59 ± 0·22(20)	13·40 ± 0·16(10)	949·00 ± 10·53(5)	134·83 ± 4·39(10)	151·10 ± 2·97(10)	0·2143 ± 0·0021(5)
F_7	11·53 ± 0·09(30)	0·0	6·70 ± 0·09(27)	0·0	9·45 ± 0·06(23)	12·08 ± 0·20(20)	12·60 ± 0·16(10)				0·2175 ± 0·0032(5)
F	224·15		5·89		79·46	131·63	44·29	586·15	2·64	2·83	94·16
d.f	5,174		5,173		5,129	5,116	5,54	4,20	4,45	4,45	5,24
P	< 0·001		< 0·001		< 0·001	< 0·001	< 0·001	< 0·001	< 0·05	< 0·05	< 0·001

Figures in parentheses are number of animals.

weight to those laid by the adults reared on the black bean aphid ($0\cdot086 \pm 0\cdot002$ mg; $t = 1\cdot2$, d.f. = 19, NS). That is, egg size did not appear to be affected by prey quality.

SELECTION FOR IMPROVED PERFORMANCE

Over the course of six generations there was a significant increase in performance, on both the pea and black bean aphids. The increase in performance on the black bean aphid was more marked than on the pea aphid (Tables 1 and 2). The ladybirds reared on the black bean aphid experienced a significant decline in the incidence of mortality with generation ($\chi^2 = 63\cdot9$, $P < 0\cdot001$; Table 2). In the case of those reared on pea aphid there was a decline in the incidence of mortality but it was not significant ($\chi^2 = 5\cdot3$, NS; Table 1). That is, in addition to selection based on performance, those reared on black bean aphid were also subjected to selection via larval and pupal mortality.

The fecundity for the sixth generation was not measured but could be estimated using the relationship between fecundity (F) and female weight (Wt) for generations 1–5.

$$\text{Log}\, F = 0\cdot86 + 2\cdot01\ \text{Log}\, Wt,\ n = 10,\ r = 0\cdot9 \qquad \text{eqn 2}$$

The estimates of the fecundity of the sixth-generation individuals obtained using equation 2, and that measured for the other generations and the other life-history parameters, were used to calculate the individual fitness for the five largest females in each of the generations, using equation 1. The selection for improved performance on both the pea and black bean aphids resulted in a significant improvement in individual fitness over the six generations, especially on the black bean aphid (Tables 1 and 2, and Fig. 1). There is an indication that the improvements in fitness were asymptotic, and that even after an indefinite period of selection for improved performance the two-spot ladybird would still perform less well on the black bean aphid.

TRADE-OFF IN PERFORMANCE

Ladybirds previously selected for five generations for better performance on the black bean aphid performed significantly worse when reared on pea aphids than those reared continuously for six generations on a diet of pea aphid. Similarly, ladybirds reared for five generations on the pea aphid performed significantly worse when fed black bean aphids than those reared continuously for six generations on a diet of black bean aphids (Figs 2 and 3). Not unexpectedly, switching from pea to the black bean aphid had a more marked affect on performance, including a significant increase in mortality during development, than the reverse ($\chi^2 = 5\cdot7$, $P < 0\cdot05$; Fig. 2 and Table 3). Expressed in terms of individual fitness, those switched from a diet of pea aphid to black bean aphid suffered a 31% reduction in fitness, which is more than treble the 8% suffered by those switched from black bean aphid to pea aphid (Table 4). This indicates that specialization on one aphid entails a trade-off in performance on another.

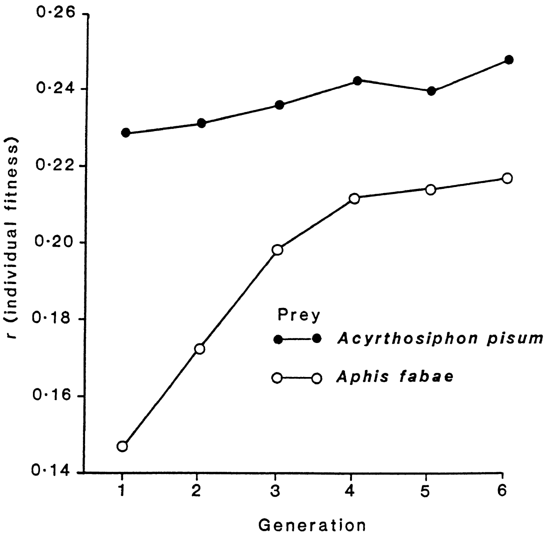

Fig. 1. Trend in the individual fitness (r) with generation when *Adalia bipunctata* was selected for improved performance on diets of pea aphid (*Acyrthosiphon pisum*) and black bean aphid (*Aphis fabae*), respectively, for six generations.

Discussion

Some aphidophagous ladybirds, like *Platynaspis* spp. and *Coccinella magnifica* L. Redtenbacher, appear to feed on a very narrow range of prey. Both specialize in feeding on ant-attended aphids and, as in the case of *Chrysopa slossonae* Banks (Tauber & Tauber 1987; Milbrath *et al.* 1993; Albuquerque *et al.* 1997), the specialization may mainly be a consequence of evolving ways of circumventing the defensive behaviour of the ants. The selective advantage of this would have been considerable when the ant-attended aphids were abundant but unexploited by ladybirds. Thus the need for an additional predisposing factor in the evolution of myrmecophily, such as a seasonal scarcity of prey (Sloggett & Majerus 2000b), would appear to be unnecessary. Some of the coccidophagous ladybirds are also very prey specific, e.g. *Rodolia cardinalis* (Mulsant) (Dixon 2000). Again, this could well be because its coccid prey is very well defended. That is, it is the chemical nature or other intrinsic characteristics of the prey that may have shaped the specialization in this case.

The preferred habitat of the generalist ladybird *A. bipunctata* appears to be trees and shrubs (Honěk 1985). This is associated with a preference for ovipositing on high- as opposed to low-growing vegetation (Blackman 1965, 1967; Iperti 1965) and a better performance on tree-dwelling aphids, such as the lime aphid *Eucallipterus tiliae* (L.) and birch aphid *Euceraphis*

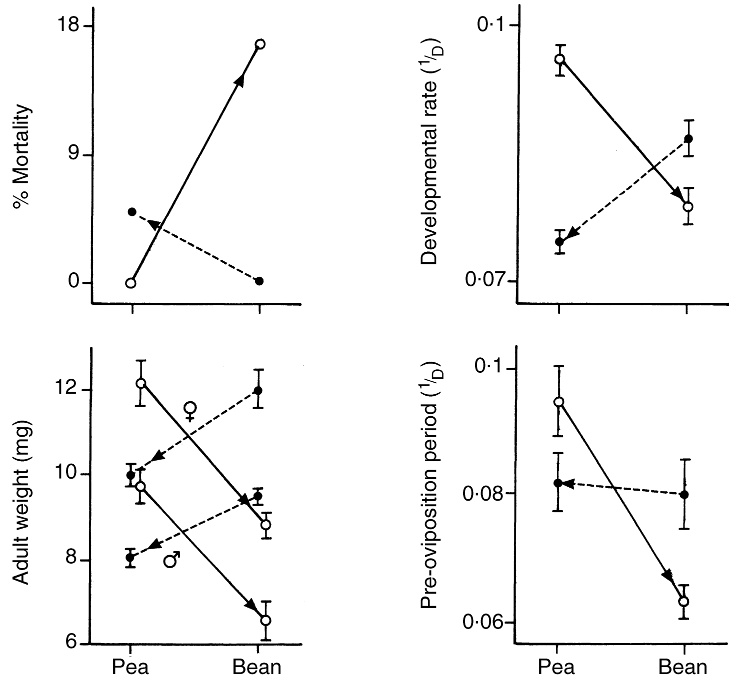

Fig. 2. Plot of mean values in the sixth generation of the life-history parameters of *Adalia bipunctata* selected for improved performance on the pea aphid (PEA) or the black bean aphid (BEAN) and those selected for five generations for improved performance on one of these aphids and then reared in the sixth generation on the other (arrow). The error bars are the 95% confidence limits.

betulae (Zetterstedt), than on other species of aphid (Kalushkov 1998). That is, in this ladybird there appears to be an association between preference and performance. The females prefer to lay their eggs on those aphid-infested trees where their larvae perform best. The lime and birch aphids are very active and more difficult to capture than many of the species of aphids that live on herbaceous plants (cf. Dixon 1958). It is likely that the larvae of *A. bipunctata* are better adapted at capturing and processing these species of aphids than other species, hence their better performance. However, this ladybird is regularly recorded in the field feeding and developing on aphids on herbaceous plants, even species like *Aphis fabae* on which it performs relatively badly (Blackman 1967; Kalushkov 1998). This is surprising because after capturing and eating *Aphis fabae* adults of *A. bipunctata* do not switch to intensive search (Kalushkov 1999). Thus, after feeding on *Aphis fabae* the behaviour of this ladybird is unlikely to result in it staying in the immediate vicinity and laying eggs.

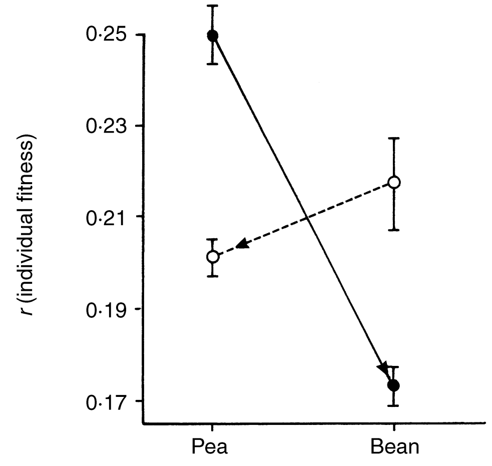

Fig. 3. Plot of the individual fitness in the sixth generation of *Adalia bipunctata* selected for improved performance on the pea aphid (PEA) or the black bean aphid (BEAN) and those selected for five generations for improved performance on one of these aphids and then reared in the sixth generation on the other (arrow). The error bars are the 95% confidence limits.

The results reported here indicate that specialization on one aphid entails a trade-off in performance on another. Thus, a mechanism that could lead to greater specialization is present in *A. bipunctata*. Therefore, it is reasonable to ask: why has *A. bipunctata* not become more of a specialist on tree-dwelling aphids? Each species of aphid is usually abundant for a relatively short period each year. If *A. bipunctata* were to specialize on one or a few of these aphids it would have a relatively short breeding season. As the adults that oviposit on trees in spring live on into summer, then breeding on aphids that thrive then (Pruszynski & Lipa 1970) could add to their fitness. However, this would depend on the cost associated with being able to exploit a wide range of aphid species. In addition, in some years tree-dwelling aphids can be relatively rare in spring (Dixon 1998), and being able to exploit other species of aphids could be important in determining the fitness of this ladybird in those years. In the absence of preferred

Table 3. Comparison of the life-history parameters in the sixth generation for *Adalia bipunctata* reared continuously for six generations on pea aphid *Acyrthosiphon pisum* (A) and those previously reared for five generations on pea aphid and then switched to a diet of black bean aphid *Aphis fabae* in the sixth generation (B), and those similarly reared for six generations on black bean aphid (C) and then switched from black bean to pea aphid in sixth generation (D). (***$P < 0{\cdot}001$, *$P < 0{\cdot}05$, †when transformed to ${}^1/D$ also not significant)

Treatment	Rate of larval development (${}^1/D$)				Mortality (%)			Pupal† duration (days)				Mortality (%)
A Pea	0·096 ± 0·00089 (32)				0·00			6·55 ± 0·09 (31)				0·00
		***	***			NS			NS			
D Bean → pea	0·075 ± 0·0011 (19)				5·00			6·78 ± 0·13 (18)		NS		0·00
		***		***					NS		NS	
C Bean	0·087 ± 0·0007 (30)				0·00		NS	6·70 ± 0·08 (27)				0·00
		***	***			*			NS	NS		
B Pea → bean	0·079 ± 0·0007 (20)				16·71			6·50 ± 0·12 (18)				0·00

Treatment	Adult weight (mg) male				Adult weight (mg) female				Pre-oviposition period (${}^1/_D$)			
A Pea	9·63 ± 0·19 (18)				12·16 ± 0·25 (13)				0·095 ± 0·0019 (10)			
		***	NS			***				***		
D Bean → pea	8·03 ± 0·07 (10)				9·98 ± 0·12 (11)		NS		0·082 ± 0·0025 (12)		***	
		***		***		***		***		*		***
C Bean	9·45 ± 0·06 (23)				12·08 ± 0·20 (20)				0·080 ± 0·0016 (12)			
		***				***	***			***	***	
B Pea → bean	6·52 ± 0·24 (10)				8·83 ± 0·14 (11)				0·063 ± 0·0012 (12)			

Table 4. Individual fitness (r) of *Adalia bipunctata* in the sixth generation when reared from the first generation on either *Acyrthosiphon pisum* (A) or *Aphis fabae* (C), or switched at the end of the fifth generation from a diet of *Acyrthosiphon pisum* to that of *Aphis fabae* (B) or from *Aphis fabae* to *Acyrthosiphon pisum* (D). In addition to the critical comparisons (A/D + B/C), all the other comparisons are also significantly different at $P > 0{\cdot}001$

Treatment	r		
A Pea	0·250 ± 0·0028 (10)	***	
B Pea → bean	0·173 ± 0·0019 (11)		***
C Bean	0·218 ± 0·0033 (5)		
D Bean → pea	0·201 ± 0·0017 (11)		

aphids, the ladybird is likely to become less reluctant to eat and lay its eggs close to low-quality prey. That is, the level of reluctance is likely to be time and density dependent. The results presented here indicate that the preferences and subsequent performance of generalist ladybirds like *A. bipunctata* could be in a state of flux, shifting as species within this predator's prey set change in abundance from year to year. In addition, in the field *A. bipunctata* is unlikely to complete more than two generations each year. Therefore, the cost of selection for improved performance on their summer prey on their ability to exploit prey the following spring is likely to be slight compared with the potential increase in overall fitness. In addition, the selection in spring will again favour those that do best on those prey. That is, the nutritional suitability of aphids is likely to have been an important factor shaping the breeding strategies of predatory ladybirds. However, only when the adaptation to feed on one aphid incurs a serious cost in terms of performance on other species of aphid is selection likely to result in the evolution of prey specificity.

Interestingly, the prey on which *A. bipunctata* are currently known to perform best are the host-specific lime and birch aphids (Kalushkov 1998). That is, the results presented here and those of Kalushkov (1998) do not support the 'tasty generalists and nasty specialists' hypothesis (cf. Dyer 1995). The unpalatable nature of *Aphis fabae*, as that of *Aphis nerii*, is also partly dependent on the species of plant they feed on (Pasteels 1978; Kalushkov 1998). However, the relationship between host specificity and palatability of aphids for generalist predators needs to be more widely studied before rejecting this hypothesis.

Although *A. bipunctata* is clearly a generalist predator, the closely related *A. decempunctata* (L.) is a specialist on tree and shrub aphids. Sloggett & Majerus (2000a) attribute this to a trade-off between the benefits of remaining in one habitat, and the costs of moving between habitats and switching from one prey to another. *Adalia decempunctata*, by remaining in one habitat, does not incur high dispersal costs, whereas *A. bipunctata* does, in addition to the costs associated with prey switching. This idea follows from another study (Sloggett & Majerus 2000b), which purports to show that non-ant-attended aphids are a scarce resource for ladybirds from late July onwards in temperate regions, and this has resulted in the prey specialization of ladybirds like *A. decempunctata* and *Coccinella magnifica*. Although often the case for non-attended colonies of mymecophilous species of aphids, it does not appear to be the case for the many species of non-myrmecophilous aphids (cf. Pruszynski & Lipa 1970). Thus, as conceded by Sloggett & Majerus (2000a), the existence of the above trade-off is speculative and much more work is required to confirm or refute its existence, and if present to establish its importance in prey specialization in ladybirds.

This study indicates that insect predators can become better adapted to exploit unpalatable prey. If this is a general phenomenon in insect predators, then palatability is a dynamic state and diet breadth and content are subject to evolutionary change. That is, these results support the claims of Rank, Smiley & Köpf (1996) and Sadeghi & Gilbert (1999) that the interaction between insect predators and their prey are more homologous to those of herbivorous insects than previously thought. In particular, the defensive chemicals in some prey could have been a very important factor determining prey specialization. Diet breadth in insect predators is therefore likely to be a consequence of the relative and seasonal changes in the abundance of potential prey, efficacy of their defences (behavioural, chemical and morphological) and the level of threat to their survival posed by competitors and natural enemies. In addition, even generalist insect predators are likely to have preferred prey on which they perform best, and this preference will be subject to evolutionary change, especially if the relative abundance of the various species of prey within their habitat changes. That is, a generalist strategy may be advantageous for the those ladybirds that exploit an uncertain food supply

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