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Short communication

The influence of three cereal aphid species and mixed diet on larval survival, development and adult weight of *Coccinella septempunctata*

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Introduction

The developmental time, weight and fecundity of the aphid specialist predator the seven spotted ladybird (*Coccinella septempunctata* L.) vary considerably according to the species of aphid they are raised on (Blackman, 1967a; Ghanim et al., 1984; Malcolm, 1992). The results of these studies showed that prey of low food quality slowed larval development and produced smaller adult animals. The experiments were carried out with single-species diets. So far there seems to be no studies on the possible benefits of diet mixing in coccinellid beetles (Hodek & Honěk 1996). Hodek (1956) and Blackman (1967b) found evidence that *C. septempunctata* is unselective in its choice of prey; it cannot recognise and avoid unsuitable or toxic species of aphids. Şengonca & Liu (1994) noticed that the larvae of *C. septempunctata* revealed no difference in responding to the kairomones from four different species of aphid prey. It is therefore likely that the larvae of *C. septempunctata* just eat the aphids that they meet. This may be an optimal foraging strategy, when the prey is clumped and unpredictable and acceptance of toxic prey is no worse than starvation.

Even if coccinellids are unselective in a choice situation, a mixture of prey species may provide a higher nutritional diversity and thus be beneficial in terms of improved performance i.e. a lower mortality, a faster development and a higher adult body weight. We used three cereal aphid species *Sitobion avenae* (F.), *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Walker) and an equal number mixture of these three species as prey and compared the performance of *C. septempunctata* larvae. The three cereal aphid species all have grasses as their host plants, thus the coccinellid larvae may encounter all three species on the same plant. It is therefore ecologically relevant to examine if there is an advantage of a mixed diet of these three aphid species.

Our hypothesis is that an aphid specialist predator as C. *septempunctata*, may gain advantage from developing on a diversified diet, compared to a single-species aphid diet, because different species of aphids may have a different composition of nutrients, thus satisfying better a varied nutrient demand. This should be revealed by better performance of the larvae, indicating a higher food value of the mixed diet. Such relationships are known for a wide range of generalist consumers (Reichert & Harp, 1987; Waldbauer & Friedman, 1991; Wallin et al., 1992; Bernays et al., 1994).

Materials and methods

Adult *C. septempunctata* were collected in the shrubbery of the Aarhus University campus, at the beginning of August 1997. The animals were kept as a pool population and fed *R. padi ad lib.* three times per week. In order to get rid of parasitoids and have a standardized population for the experiments, one new generation of ladybirds was reared. Newly hatched (±12 h) larvae were randomly divided into four diet groups with $N = 40$ in each.

The three cereal aphid species were reared on wheat seedlings of mixed cultivars. The aphid cultures had been kept in the laboratory for several years. The coccinellid larvae were isolated in individual containers (plastic tubes (h 8.1 cm, ⌀ 3.4 cm) with ca. 1 cm plaster with charcoal on the bottom to maintain con-

Table 1. Mortality, developmental times, dry weight of the dead prepupae and adult weight (Mean ± SE), of *C. septempunctata* larvae on different diets

Aphid diet	No.	Mortality (%)	Developmental time (days)	Prepupal dry weight (mg)	Adult weight (mg)
S. avenae	40	62.5	17.60 ± 0.63^{a}	6.824 ± 1.360^{a}	28.164 ± 4.570^{a}
R. padi	40	77.5	18.11 ± 0.93^{b}	4.561 ± 1.110^{c}	22.032 ± 2.450^{b}
M. dirhodum	40	55.0	17.94 ± 0.73^{a}	7.250 ± 2.130^{a}	31.732 ± 4.624^{a}
Mixed diet	40	67.5	17.92 ± 1.03^{a}	5.527 ± 1.540^{b}	29.537 ± 5.850^{a}

Within columns, the same letters indicate no significant difference between treatments (LSD test).

stant humidity). The tubes were covered with a foam rubber stopper. The larvae were kept at 20 °C and a L16:D8 photoperiod. Aphids removed from their host plants were offered to the larvae *ad lib.* three times per week. The mixed diet consisted of equal numbers of the three aphid species. The larvae were checked daily for deaths and moults and to be sure that there were living aphids available. The pupal stage was said to start when the larva had fixed the abdomen to the wall of the tube i.e. in the beginning of the prepupal stage. The pupae were checked daily to get the exact day of emergence of the adult ladybirds. After ecdysis the ladybirds were weighed (fresh weight) and sexed according to Baungaard (1980).

Many larvae died in the prepupal stage; these were dried in a vacuum oven at 60 °C for 48 h, and weighed.

A χ^2-test was used to see if there were any significant differences in mortality between the diet groups. The developmental time and weight data were tested with 1- or 2-way ANOVAs. Bartlett's test was used to secure equal variances between the groups; a $\sqrt{x}^{-1}$-transformation of the developmental time was tested as necessary before ANOVA (P=0.057) as the only transformation. These tests were followed by a Fisher's LSD test for multiple pairwise comparison of treatments.

Results

Mortality (Table 1) showed no significant overall treatment effects (χ^2-test, $\chi^2 = 4.74$, P=0.192). The two extreme treatments (*M. dirhodum* and *R. padi* single-species diets) tested alone showed an only marginally significant difference (χ^2-test, $\chi^2 = 4.53$, P=0.058). In all diet groups the sex distribution was roughly 1:1. There was no significant difference in the adult weight of males and females (two-way ANOVA, $F = 1.47$, P=0.230 with sex and treatment as the factors) and no significant diet * sex interaction. Accordingly the sexes were combined in the following analyses.

Differences in diet quality could be expressed in the developmental time (one-way ANOVA, $F = 5.77$, P=0.001). Table 1 shows that a single-species diet of *R. padi* gave a significantly longer developmental time than all the three other diet groups (Fisher's LSD test).

There was a significant overall treatment effect in the weights of the fully developed ladybirds (ANOVA, $F = 8.84$, P<0.001). The group given *R. padi* showed the lowest body weight. The animals in the three other groups were significantly heavier than the *R. padi* group (Table 1).

There was also a significant overall treatment effect in the dry weights of the animals that died during pupation (ANOVA, $F = 14.94$, P<0.00001). The single-species diets of *M. dirhodum* and *S. avenae* were the groups with the highest prepupal dry weight, whereas a diet of *R. padi* resulted in the lowest prepupal weight. The mixed aphid diet was intermediate (Table 1).

Discussion

Compared with the results of Blackman (1965) mortality rates in this experiment was high (Table 1), also in the treatments with 'better' prey. The high mortality could be due to sub-optimal rearing conditions, i.e. to high relative humidity or to feeding on dead aphids though live aphids were always available. However, all four replicates suffered in the same way and thus we can make a comparison.

Even though *R. padi* is lower quality food to *C. septempunctata* than *S. avenae* and *M. dirhodum*, it is not poor-quality food since a substantial fraction may complete larval development on this prey alone (25%). Kuznetsov (1975) found *R. padi* less suitable for egg laying of *C. septempunctata*. *R. padi* was also found less suitable essential prey for *Adalia bipunctata* (L.) (Semyanov, 1970) and *Anatis ocellata* (L.) (Kesten, 1969).

The three cereal aphid species vary considerably in food value for the larvae of *C. septempunctata*. The aphid species with the highest food value in this study were *M. dirhodum* and *S. avenae*. Single-species diets of these aphids gave a faster development, higher survival (though not significantly) and bigger adult ladybirds, than the *R. padi* diet. The same ranking of the three cereal aphids was found for the wolf spider *Pardosa prativaga* (L. K.) (Toft & Nielsen, 1997; Toft, 1997). Consumption rates of the carabid beetle *Agonum dorsale* (Pontoppidan) and *Amara similata* (Gyllenhal) also followed this pattern (Bilde & Toft, 1997). The causes of quality differences between these aphid species are uncertain. They may differ in nutrient content or in substances that may act as chemical defences against predators.

The larvae of *C. septempunctata* on the mixed aphid diet did not obtain higher survival, faster development or increased adult weight than those on single-species diets. The food value of the mixed aphid diet was intermediate between the high quality single-species diets of *M. dirhodum* or *S. avenae* and the low quality single-species diets of *R. padi*.

Our result do not confirm the hypothesis that *C. septempunctata* may benefit from a mixed diet. However, it corroborates Blackman's (1967b) findings that *C. septempunctata* larvae cannot select an optimal diet, when given the choice of different species of aphids. The low value of the mixed diet may be due to interference of ingested *R. padi* with the utilization of the higher quality food, or to limitation of the amount of higher quality food that the ladybird can handle and eat.

The lack of a mixing benefit on *C. septempunctata* may be due to lack of nutritional differences among the three aphid species, since they were raised on the same host plant. It is possible that the larvae would gain an advantage of mixing aphids from different plant species. If inhibition by *R. padi* causes the lack of mixing benefit, then a mixture of *M. dirhodum* and *S. avenae* could give an advantage in larval survival, development time and adult weight. Host plants may contain chemical substances that the aphids can sequester. Such substances may influence larval survival, development and adult weight of their predators positively (Martos et al., 1992) or negatively (Hodek, 1956; Rothschild et al., 1970; Malcolm, 1989, 1992).

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