



Diet-mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing?

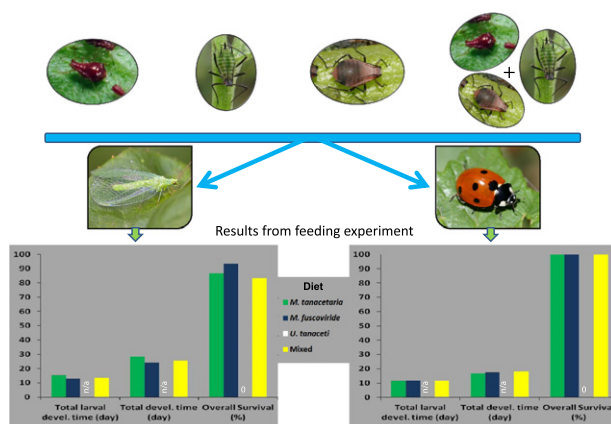
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HIGHLIGHTS

- We investigated the effects of diet mixing on generalist aphid predators.
- The aphids were *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanacetii*.
- The suitability of each aphid species is different and affects the fitness of its predator.
- The mixed diet was worse than the best single-aphid diet for *Coccinella septempunctata* and *Chrysoperla carnea*.
- The dietary mixing is not always beneficial for generalist predators.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 26 September 2012

Accepted 22 December 2012

Available online 3 January 2013

Keywords:

Aphid
Food suitability
Ladybird
Green lacewing
Nutritional ecology
Mixing diets benefits

ABSTRACT

Some predators have a broad prey range, but not all prey are equally suitable for a predator. We tested the suitability of three specialized tansy (*Tanacetum vulgare*) aphids, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanacetii*, on biological parameters of their major predators, *Coccinella septempunctata* and *Chrysoperla carnea*, when aphid species were offered either alone, or as a mixed diet of all the three aphid species. For the lacewing *C. carnea*, a diet consisting only of the generally ant-tended *M. fuscoviride* resulted in the shortest larval and total developmental time, in highest larval survival and pupation success. For the ladybird *C. septempunctata*, a pure diet of the non-tended *M. tanacetaria* was most suitable, resulting in the shortest total developmental time, heaviest fresh and dry weight. Larvae of both predator species had low survival and none of them developed to pupal stage when offered only *U. tanacetii* that has a bright red colour, is not ant-tended and feeds on the underside of lower leaves. The mixed diet of all three aphid species was worse than the best single-aphid diet for both predators, for almost all fitness parameters. Thus, while diet mixing may allow predators to avoid the negative impact of unsuitable prey, diet mixing does not necessarily result in the highest fitness of predators.

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1. Introduction

The fitness of aphid predators varies distinctly according to the prey species that they fed on (Blackman, 1967; Kalushkov and Hodek, 2004; Khuhro et al., 2012; Omkar et al., 2009; Pappas et al., 2007; Phoofolo et al., 2007; Zhang et al., 2012). Certain aphid species can cause increased mortality, a prolonged developmental time or a decrease in larval survival rate in predators (Canard and

Principi, 1984). So far, several aphid species have been reported as being generally less suitable or even toxic for predators, among which are *Aphis sambuci* L. and *Macrosiphum albifrons* Essig for *Coccinella septempunctata* (L.) (Gruppe and Roemer, 1988; Nielsen et al., 2002), *Megoura viciae* Backton and *Aphis fabae* Scopoli for *Chrysopa perla* (L.) and *Adalia bipunctata* (L.) (Canard, 1970; Canard and Principi, 1984; Dixon and Agarwala, 1999), *Aphis nerii* Boyer de Fonscolombe for *Schizocosa* sp. (Toft and Wise, 1999).

The benefits of dietary mixing have been intensively investigated in generalist insect herbivores (Bernays et al., 1994; Unsicker et al., 2008; Waldbauer and Friedman, 1991) while less is known for generalist insect predators (Borg and Toft, 2000; Wallin et al., 1992). Diet mixing theory suggests that a generalist benefits from developing on a diversified diet, because (a) the different food items differ in their nutrient composition, thus satisfying better a varied nutrient demand (Evans et al., 1999; Hauge et al., 1998), or (b) the concentration of toxins in the diet is diluted (toxin dilution hypothesis) (Behmer et al., 2002). For aphid predators, there are some studies that focus on dietary mixing effects (Evans et al., 1999; Hauge et al., 1998; Hauge et al., 2011; Nielsen et al., 2002). The studies provided evidence that dietary mixing is not always beneficial. For example, Hauge et al. (1998) raised larvae of *C. septempunctata* on a mixed diet of three cereal aphid species, *Sitobion avenae* (Fabricius), *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Walker), and showed an intermediate performance for predators that fed on mixed diet in comparison with single-species diets.

While most studies on nutritional ecology of aphid predators have focused on economically important aphid species, these predators also feed on aphids of little economic importance that may have significant effects on the population dynamics of the predators. For economically relevant aphids, predators often encounter different aphid species only sequentially, often in different fields, e.g. when a single crop is only infested by a single aphid species, or when one species is strongly dominant. In contrast, in many natural systems a number of aphids of potentially different suitability occur on the same host plant or on different plants nearby. In our model system, there are three common aphid species that feed on tansy (*Tanacetum vulgare* L., Asteraceae): the ant-tended *Metopeurum fuscoviride* Stroyan and the untended *Macrosiphoniella tanacetaria* (Kaltenbach) and *Uroleucon tanacetii* (L.) (Aphididae) (Blackman and Eastop, 2006; Holman, 2009). *Macrosiphoniella tanacetaria* and *M. fuscoviride* feed on the apical part of the shoots while the third species, *U. tanacetii*, feeds on the underside of lower leaves of its host plant. These aphids hatch from overwintering eggs in March–April and go through parthenogenetic reproductive generations until late autumn (October). All three species may occur together in the same site or even on the same plant (pers. obs.).

In this study, we addressed two questions: (1) Do tansy aphids differ in their effects on survival and development of the common aphid predators *Chrysoperla carnea* (Stephens) and *C. septempunctata*? (2) Is a mixed diet of three tansy aphid species beneficial for the predators? To answer these questions the performance of two predators were investigated in the laboratory.

2. Materials and methods

2.1. Experimental insects

Predator insects, *Chrysoperla carnea* (Neuroptera: Chrysopidae) and *Coccinella septempunctata* (Coleoptera: Coccinellidae) were obtained as eggs from a commercial supplier (Katz Biotech Services, Welzheim, Germany). Upon arrival, the eggs were maintained in a climate chamber at 20 ± 2 °C, ~75% R.H. and a long day 16:8 h (L:D) photoperiod until emergence of larvae.

Three specialized tansy aphid species, *M. tanacetaria*, *M. fuscoviride* and *U. tanacetii* were collected in July 2010 from tansy plants in the botanical garden of Jena, Germany and were reared in a greenhouse on potted tansy plants. As *M. fuscoviride* is an obligatory myrmecophilous aphid, colonies of black garden ants, *Lasius niger* (L.), were collected in the field and used for rearing of this aphid species. Each ant colony had several hundred workers, many larvae and pupae. The colonies were kept in 10-litre volume buckets, half-filled with humid soil and coated on the inside with Fluon (Fluoropolymer Dispersion, Whitford GmbH, Germany). Access of the ants to plants was regulated by using bamboo (~5 mm. diam.) bridges.

2.2. Experimental design

The experiment was conducted in the climate chamber (see subsection 2.1). There were four different diet treatments: each of the three aphid species alone or a mixed diet of all the three aphid species (30 replicates per treatment). To evaluate larval performance in terms of development and survival, newly hatched predator larvae (± 12 h old) were randomly allocated to the four diet treatments. The larvae were individually placed in plastic petri dishes (5.5 cm in diameter and 1.5 cm in depth) with moist filter paper in the bottom, and were fed with sufficient numbers of third and fourth nymphal instars until the larvae either pupated or died. In the mixed diet treatment, an equal number of individuals of each aphid species were offered to each larva. The larvae were checked daily and their survival, and any changes in the developmental stage (moult or pupation), were noted. At the time of checking, food remains were removed and new live aphids were added to the petri dishes. While the number of aphids eaten was not counted, we noted if in the mixed treatment the predators consumed aphids of all species, i.e. whether there was approximately the same number of each aphid species left. The pupal stage of *C. septempunctata* was considered to begin when the larva fixed its abdomen to the petri dish. The pupal duration time for *C. carnea* was measured from the day when a larva started to spin a cocoon until the day when the adult emerged. Adults were weighed (fresh weight) and dried in an oven at 60 °C for 48 h to determine the dry body weight.

From the raw data, the following variables were derived: larval survival for each larval instar, total survival, i.e. survival from birth to adulthood, pupal survival, developmental time for each larval instar, total larval developmental time, pupal duration time, total developmental time (from egg hatch to adult emergence) and percentage reaching the pupal stage ($\frac{\text{total no. pupae}}{\text{total no. first larval stage}} \times 100$).

2.3. Statistics

The results are presented as mean \pm standard error. To analyse developmental time for each larval instar, total larval developmental time, pupal duration time and total developmental time, survival analysis (Kaplan–Meier) was employed. For pairwise comparison between different diet treatments a separate analysis was performed for each dependent variable using the *log-rank* test (a test for the equality of survival distributions which all time points are weighted equally). A χ^2 -test was used to see if there were significant differences between the numbers of individuals that successfully completed a particular larval instar. Fresh and dry weight of adults were analyzed using Generalized Linear Models. Where necessary, data was transformed as $\log_{10}(x + 1)$. As the larvae of predators which fed on *U. tanacetii* all died, this treatment was excluded for the analysis of adult fresh and dry weight. All analyses were conducted using SPSS version 19 (SPSS Inc, 2010).

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