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SPECIES AND AGE EFFECTS IN THE VALUE OF CEREAL APHIDS AS FOOD FOR A SPIDER (ARANEAE)

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Abstract

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All three species of aphids from cereal crops, *Rhopalosiphum padi*, *Sitobion avenae* and *Metopolophium dirhodum* were low quality prey for hatchlings of the wolf spider *Pardosa prativaga,* as revealed by development, growth and survival of the spider when the aphids were given as single-species diets. The species differed in food value, however, with *M. dirhodum* of highest value, *S. avenae* intermediate, and *R. padi* the lowest value. The latter species was no better than starvation. Spiderlings on a mixed diet of all three aphids showed intermediate performance, indicating that they were unable to select optimally among the prey available. Small juvenile instars of *R. padi* were of higher value as food than mature females. This result was predicted from life-history theory on the assumption that low food value is associated with a costly (chemical) defence against predators.

Introduction

Earlier studies (BILDE, TOFT, 1994, 1997a; TOFT, 1995) have demonstrated the poor quality of the cereal aphid *Rhopalosiphum padi* (LINNAEUS) to several species of polyphagous predators from agricultural fields, at least when presented as the only food. BILDE, TOFT (1997b) further found some carabid beetles to have different tolerances to the consumption of three species of cereal aphids, indicating possible differences in food value of the aphid species. This was corroborated for the wolf spider *Pardosa prativaga* (L. KOCH) by TOFT (1997) in a behavioural study demonstrating differential ability of the aphids to induce prey aversions and different duration of the aversions.

Spiders and other generalist predators eat a variety of prey types that they encounter in the field (TURNBULL, 1960) and they are thought to benefit from this, due to the nutritional diversity of the food (UETZ et al., 1992; BERNAYS et al., 1994). However, it is not obvious whether a mixed diet of aphid species developed on the same host plant, will provide the same nutritional benefit.

The present study reports on laboratory experiments that directly aimed at comparing the value of the three common aphids of European cereal fields, *R. padi*, *Sitobion avenae* (FABRICIUS) and *Metopolophium dirhodum* (WALKER) to *P. prativaga*. Development, growth and survival of hatchlings on permanent diets of these aphids were used as indices of food value (cf. TOFT, 1995, 1996). The performance of spiders on single-species aphid diets were compared to that of spiders given a mixed diet of these three aphids. Also, differences between age classes of one of the aphid species, *R. padi*, were analysed. On the grounds that the poor food quality of the aphids is considered to reflect an anti-predator defence mechanism and differences in food quality to reflect different relative investments in this defence, it was *a priori* predicted that early instars of the aphid should be of higher value than mature aphids. The argument is based on life history theory (STEARNS, 1992) according to which young animals, that have a long time to survive before being able to reproduce, should invest relatively more in growth and development than in survival, while a mature animal in the reproductive phase should trade-off investment in reproduction and survival relatively more in favour of survival in order to secure a long reproductive life.

Material and methods

Pardosa prativaga is a common wolf spider of open habitats in Northern Europe, including agricultural fields and meadows. It matures in spring and reproduces throughout summer. Females with egg sacs were collected in the field and the young hatched in the laboratory. After some days on their mother's back they dispersed and became independent. At this stage, and before they had had the opportunity to consume any food, they were isolated in individual containers (plastic tubes (h 6 cm, Ø 2 cm) with a 1 cm block of plaster with charcoal at the base to maintain high humidity). Both experiments were run at a constant temperature of 20°C and a 16L:8D cycle. Prey animals were offered *ad libitum* and were always available in the containers.

Exp. 1. Food value of three aphid species

Cultures of the three aphid species were maintained in the laboratory, raised on wheat seedlings of mixed cultivars. Spiders were offered a mixture of all size classes of aphids. Before starting the experiment, 25 spider hatchlings were randomly assigned to each of the treatments and weighed. Five treatments were used: three composed of single-species diets of one of the aphid species; one given an equal mixture of these three aphids; one group was starved as a control. Fresh aphids and water were supplied every second day; at these inspections deaths and moults were recorded. Weighing was repeated at weekly intervals.

Exp. 2. Relative food value of young and mature aphids

Only *R. padi* was used in this experiment. Spider hatchlings were selected as in exp. 1, and assigned randomly to the three treatments: starvation; fed young aphids of instar 1-2; fed adult apterous females. Each group had 20 replicates. The hatchlings had no problems with subduing a mature aphid. Food supplementation, inspection and data recording were as in exp. 1.

Table 1. Number of spiderlings of *Pardosa prativaga* moulting from the first to second free-living instar when raised on different single-species or mixed aphid diets, compared to a starvation control.

Diet	Sample size	No. moulting	% moulting
Metopolophium dirhodum	25	9	36
Sitobion avenae	25	2	8
Rhopalosiphum padi	25	0	0
Mixed aphids	25	3	12
Starvation	25	0	0

Results

Exp. 1. Food value of three aphid species

Development (Table 1) showed significant overall treatment effects (χ^2-test, P=0.0003). In two of the treatments – starvation and *R. padi*-diet – no spiderlings ever moulted. The group given *M. dirhodum* showed the best performance, but still only about one third of the spiders moulted. In the remaining two treatments – *S. avenae* and mixed aphid diets – only a few individuals moulted. No spiderling moulted twice.

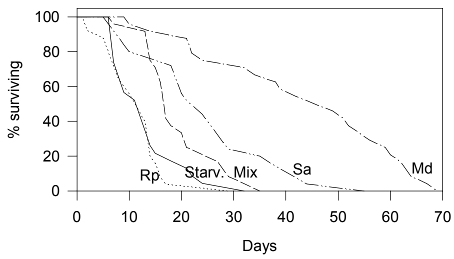

Fig. 1. Survivorship curves for hatchlings of the wolf spider *Pardosa prativaga* maintained on diets of the aphids *Metopolophium dirhodum* (Md), *Sitobion avenae* (Sa), *Rhopalosiphum padi* (Rp), and a mixture of these three (Mix), compared to a starvation control (Starv). Pairwise comparisons of treatments gave the following results: Md > [Sa = Mix] > [Rp = Starv].

Log-transformation of "days survived" created homogeneity of treatment variances (Bartlett's test, P=0.14), therefore ANOVA followed by Fisher's LSD- test was used for comparison of treatments (Fig. 1). A single-species diet of *M. dirhodum* showed the highest survival, whereas *R. padi* was no better than starvation. *S. avenae* and the mixed diet were intermediate.

Fig. 2 shows the weekly weight measurements. A repeated measures ANOVA was performed on the values for weeks 0 to 3 . Since Mauchly's test showed significant violation of the sphericity assumptions (P=0.0004), multivariate tests were used. There were significant diet effects (P=0.018) and a significant treatment*week interaction (Rao R, P=0.020). Thus, diets affected the growth rates of the spiderlings. The *R. padi* treatment followed the starvation treatment closely for the first two weeks; the subsequent "improvement" of the *R. padi* diet is an artefact, being due to death of small individuals. Some real growth took place among the spiders of the other treatments, especially with *M. dirhodum*, while the *S. avenae* and the mixed aphid diets were intermediate. However, even with the best aphid (*M. dirhodum)* no growth took place beyond the fifth week.

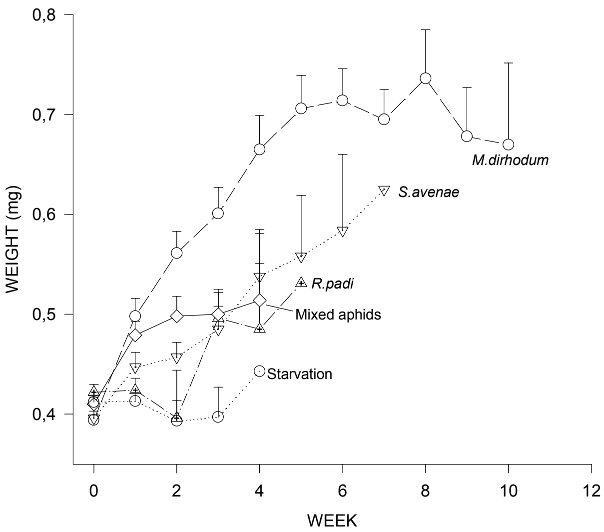

Fig. 2. Body weights (avg. + SE) of hatchlings of the wolf spider *Pardosa prativaga* maintained on diets of the aphids *Metopolophium dirhodum*, *Sitobion avenae*, *Rhopalosiphum padi*, and a mixture of these three, compared to a starvation control.

Exp. 2. Food value of young and mature aphid species

Spiderlings fed mature aphids did not survive significantly longer than the starved group (Fig. 3). Those fed young aphids survived significantly longer, including significantly longer than the mature-aphid group (Mann-Whitney U-test, P=0.046, 1-tailed). A 1-tailed test can be used, since the test hypothesis specified the direction of difference.

Because of heavy mortality before the age of two weeks, only spiders at an age one week had sufficient replicates left to be tested with respect to growth (Fig. 4). Untransformed data showed homogeneity of group variances (Bartlett's test, P=0.18) and were tested with an ANOVA with initial weight as covariate, followed by Fisher's LSD test for pairwise comparisons. There was a significant overall treatment effect (P=0.012). The important comparison here is the young vs. mature aphid treatments, that were also significantly different in the predicted direction (P=0.013, 1-tailed). The weight of spiderlings fed mature aphids was not different from that of starved spiderlings. As in Exp. 1, none of the spiderlings moulted.

Discussion

All the life cycle parameters (development, survival, growth) used in this study for comparing the value of the three cereal aphid species to the wolf spider gave similar results: *M. dirhodum* was of best quality, *S. avenae* was intermediate, and *R. padi* of lowest quality. Toft (1997) found a similar ranking when he compared the number of aphids needed to induce a prey aversion in the same wolf spider; *R. padi* needed few, *M. dirhodum* the most. Weight changes of large juveniles of *P. prativaga* on the same diets as here also showed the same ranking (Toft, Nielsen, 1997). Thus, it seems that all performance measures reveal the same result with this species. Consumption rates of carabid beetles in general followed the same pattern (Bilde, Toft, 1997b). The evidence so far indicates that a wide range of polyphagous insectivores rank these aphids in the same order. Since these predators all have aphids as just one among a long list of prey types, they are equally unlikely to have evolved specific adaptations to cope with anti-predator defences of aphids. From a management point of view it would be very fortunate if prey values obtained from a few selected predator types can be generalised to hold for the guild of polyphagous predators. Further comparative information on a wider range of taxa should be obtained to confirm this.

All parameters used also resulted in placing the value of the mixed aphid diet intermediate among the single species. This result was unexpected from two points of view. First, mixing of prey species is generally thought to be beneficial to generalist consumers (Uetz et al., 1992; Bernays et al.,1994). Second, even if no mixing benefit exists, spiders were expected to be able to select among the prey available so as to avoid the lowest value prey. Thus, it was expected that the spiders would perform at least as well on the mixed diet as on the best of the single-species diets, possibly better. The results can most easily be interpreted as if the spiders were unselective towards aphids and they composed a suboptimal diet under the conditions given. Similar results have been obtained with wolf spiders presented a mixture of low-quality Collembola and sciarid midges (Toft, Wise, 1999). It is so far unknown to what extent this may be true also when both high and low quality prey are available.

Toft (1997) studied the behavioural aspects of prey selection with respect to the three cereal aphids in more detail. These results corroborate the present findings and provide an explanation for them. Thus, it was shown that the strength of an aversion depended on which aphid induced it, and was independent of which aphid species was facing the spider. Therefore, aphids were accepted in proportion to availability. As shown here, this leads to a food value of the composite diet which is intermediate between that of the single constituents.

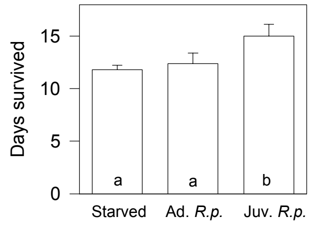

Fig. 3. Days survived (avg. + SE) by hatchlings of the wolf spider *Pardosa prativaga* maintained on diets of mature females (Ad. *R.p.*) or instar 1-2 juveniles (Juv. *R.p.*) of the aphid *Rhopalosiphum padi*, compared to a starvation control. Treatments with different letters indicated are significantly different.

Fig. 4. Weights (avg. + SE) of hatchlings of the wolf spider *Pardosa prativaga* at the age of one week (adjusted for initial weight) when maintained on diets of mature females (Ad. *R.p.*) or instar 1-2 juveniles (Juv. *R.p.*) of the aphid *Rhopalosiphum padi*, compared to a starvation control. Treatments with different letters indicated are significantly different.

Experiment 2 confirmed the prediction that young aphids were of higher value as food for the spider than mature aphids. As with the different species, this may be mainly due to different consumption rates of the spiders, as indicated by the different weight gains of the two groups. A consequence of this should be that spiders in the field should prey preferably on young instars of the aphids. Numerically this would increase aphid predation, not only because more aphid individuals can be consumed within the tolerance limit of the predator, but also because the tolerance limit towards young aphids is likely to be higher than towards mature aphids. Given that there is no selectivity with respect to aphid species, it is doubtful if the spiders can show selectivity with respect to instars of one species. In the field, however, the circumstances will usually be different in the two cases since instars will usually be mixed among each other in an aphid colony, while different species are more likely to be spatially separated. It is therefore not possible to conclude from one situation to the other.

The parameters used here to assess food value are sensitive to the nutritional value of the ingested prey biomass as well as to the quantity of food consumed. Quality and quantity were not distinguished in these experiments. The most likely interpretation of the results is that different quantities were consumed due to different concentrations of unpalatable (or toxic) substances. That some (unknown) chemical defence is involved is indicated by the sometimes extremely low consumption rates relative to the predator's food demand (cf. Toft, 1995), that can hardly result from nutritional deficiency alone. Another argument is a doubling of the resting metabolism of spiders on aphid (and other low value) diets (Toft, Nielsen, 1997) indicating extra costs of processing ingested low value prey.

The reason that no benefit emerged from mixing of prey species may be that the three species of this study were similar in nutritional composition as a result of being raised on the same host plants. The experimental setup, however, mimics the situation in a monocultural cereal field. In more diversified fields (mixed crops or weedy fields) predators may encounter aphids developed on a variety of plants and therefore be more diverse nutritionally. It will be interesting to see if the predators behave differently under those conditions.

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