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EFFECT OF NUTRIENT BALANCE ON TOLERANCE TO LOW QUALITY PREY IN A WOLF SPIDER (ARANEAE: LYCOSIDAE)

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Abstract

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The tolerance of the wolf spider *Pardosa prativaga* to two low quality prey types, the aphid *Rhopalosiphum padi* (Aphididae) and the collembolan *Folsomia candida* (Isotomidae), was tested in spiders with different nutrient balance. Good and bad nutrient balance was achieved by feeding the spiders fruit flies raised in cultures of different nutrient content. Spiders with a good balance consumed three times more *R. padi* than spiders with a bad balance, whereas there was no effect of nutrient balance on the tolerance to *F. candida*. The rejection behaviour to *R. padi* and *F. candida* was tested in spiders of good nutrient balance. The spiders ate more *F. candida* than *R. padi* before they refused to attack more prey. Spiders that accepted a fruit fly after the rejection of a low quality prey item were considered to have an aversion against such prey. Of the spiders given *R. padi*, 76% had or acquired an aversion to them. Only 5% of the spiders had or acquired an aversion to *F. candida*.

Introduction

Generalist predators may experience large variation in the quality of prey. Some prey types are of high quality whereas others are so noxious that even a single item may have severe effects on the predator for several days after ingestion (TOFT, WISE, 1999b). Inferior prey types differ in the way they affect predators. They may be nutritionally insufficient, unpalatable or toxic. Examples of toxic prey are the collembolans *Folsomia candida* (WILLEM) and *F. fimetaria* (LINNAEUS). When fed to wolf spiders they produce negative effects, such as increased respiration, increased mortality and reduced fecundity (TOFT, NIELSEN, 1997; MARCUSSEN et al., 1999). The cereal aphid *Rhopalosiphum padi* (LINNAEUS) is a low quality prey for spiders when offered as a single-species diet. As a part of mixed diets with fruit flies, however, *R. padi* may have positive synergistic effects (TOFT, 1995), whereas *F. candida* and *F. fimetaria* retain their negative impact (TOFT, WISE, 1999a; MARCUSSEN et al., 1999).

Previous studies have indicated that spiders can experience nutrient deficiency when fed a monotypic diet of fruit flies or crickets in the laboratory (MIYASHITA, 1968; UETZ et al., 1992). In a field study, GREENSTONE (1979) found that the wolf spider *Pardosa ramulosa* (MCCOOK) consumed three prey species in proportions that optimised the amino acid composition in their diet. Thus, nutrient deficiency in spiders may be possible at least in some habitats.

In this experiment, we studied the relationship between nutrient deficiency and tolerance to the two low quality prey types *R. padi* and *F. candida*. Tolerance indicates the degree to which the spiders can satisfy their food demand on one type of prey. We assume that the low quality of the two prey types is due to noxious chemicals that are costly to handle metabolically (TOFT, NIELSEN, 1997). Despite a possible toxic effect of both prey types, they may still provide essential nutrients to spiders with a bad nutrient balance. Over a short time scale, it may therefore be advantageous for spiders with a skewed nutrient balance to accept more low quality prey than spiders with a better nutrient balance, in order to restore their nutritional state. An alternative hypothesis would be that well-balanced spiders tolerate more defensive chemicals in the prey due to their better nutritional condition. In the latter case, nutrient imbalance would cause the spiders to eat less low quality prey.

We created two groups of wolf spiders with different nutrient balance by feeding them fruit flies raised on media of different nutrient content for several weeks. The tolerance to the two low quality prey was tested with spiders in good and bad nutrient balance. The tolerance of spiders to a specific prey item may depend on whether they develop aversions to the prey or not. The development of aversions to prey, however, is affected by the palatability, toxicity, and behaviour of the prey. Since the two prey types used in this study were quite different, at least in their toxicity and behaviour, we also tested the aversion/rejection behaviour of spiders to the two prey types.

Material and methods

The collembolan (*F. candida*) and the aphid (*R. padi*) used in this study were obtained from laboratory cultures. The collembolan was raised on baker's yeast and the aphid culture was maintained on wheat seedlings. The wolf spider *Pardosa prativaga* (L. KOCH) was chosen as the test species. This is a common wolf spider in Danish agricultural fields and may naturally prey on *R. padi* and *F. fimetaria*. Females with egg sacs were collected in a garden at Skjoldhøj near to Århus, Denmark. They were kept in the laboratory at 20°C until hatching. By rearing the spiders from newly hatched spiderlings we could ensure a controlled feeding history of all spiders. Five days after hatching the spiderlings were transferred individually to small tubes (Ø 20 mm, height 60 mm) with a 1 cm base of plaster-of-Paris and charcoal that was wetted to maintain high humidity. All spiders were raised on wild type *Drosophila melanogaster* (MEIGEN). We cultured fruit flies of two different qualities. Flies of low nutrient quality (called Carolina-flies) were cultured in 4g of Carolina medium (Carolina Biological Supply Drosophila Medium Formula 4-24 Plain®) per culture bottle. Higher quality flies (called dogfood-flies) were produced on a mixture of 1.8g crushed dog food (Techni-Cal® maintenance) and 2.2g Carolina medium per culture bottle. Earlier experiments have shown that *Pardosa* wolf spiders fed these fruit flies will have different growth and survivorship curves, i.e. different nutrient balance (Mayntz, Toft, in prep.).

Effects of nutrient deficiency on the tolerance to R. padi and F. candida.

A 24 hour food consumption experiment was used to test whether the nutrient balance of the spiders affected the tolerance to the two low quality prey types.

Forty-three spiderlings were raised on Carolina-flies for 10 weeks. A pilot experiment had shown that the spiders after this period had a bad nutrient balance, indicated by a reduced growth rate compared to spiders fed dogfood-flies. The spiders were then randomly assigned to one of four treatment groups (between 8 to 10 individuals/group). Two of the groups were subsequently fed dogfood-flies for two weeks and were thereby allowed partly to recover a good nutrient balance. The two other groups continued on Carolina-flies in this period and were thus maintained in a bad nutritional state. To avoid creating a weight difference between spiders with good and bad nutrient balance we limited this treatment period to two weeks. The spiders were weighed at the start and at the end of the treatment period. The live weights of spiders in good and bad nutrient balance were compared and no significant difference was found (t-test, $P=0.83$). Thus, weight differences among treatments would not confound the results.

The ability to tolerate *R. padi* or *F. candida* was tested for spiders of good and bad nutrient balance. To ensure that the spiders would eat a measurable amount of food, they were starved for 7 days before the test. Each spider in the four groups was then offered either 10 *F. candida* or 10 *R. padi* (adults) for a 24-hour period. This amount was sufficient to ensure that live prey would be present throughout the test period. Prior to presentation, the wet weight of the 10 prey items was measured. At the end of the 24-hour test period surviving prey and the remains of those eaten were dried at 60°C for 48 hours in a vacuum oven. Five samples of 100 individuals of both prey types were also weighed and dried to obtain wet-weight-to-dry-weight conversion factors. The specific amount of prey eaten in dry weight was calculated as:

$$\frac{\text{Prey given (FW)} \times \text{Conversion factor - Remains (DW)}}{\text{Spider weight (FW)}}$$

Rejection behaviour of spiders offered R. padi or F. candida.

For this experiment, only spiders with a good nutrient balance were used. They were obtained by raising hatchlings on dogfood-flies for 14 weeks. After one week of starvation the spiders were divided in two groups (with 20 or 21 individuals/group). One group of spiders was used to test the rejection behaviour to *R. padi* and the other group to *F. candida*. Each individual spider was weighed and transferred to a test cup (Ø 100 mm) where the spider was allowed to acclimatise for 60 minutes. One prey item was weighed and dropped from about 100 mm height so that it landed just in front of the spider. When an aphid or a collembolan was presented in this way the spiders were more likely to attack and grab it. Subsequently, the spiders either started consuming the prey, or released it dead or alive. Whenever the spider had finished eating a prey the remains were collected and a new prey item presented. This procedure continued until the spider refused to accept new prey for a period of five minutes during constant presentation. This behaviour was defined as a rejection, and the number of test prey eaten until rejection, was noted. If a spider did not accept any prey at all, the experiment was terminated after five minutes. Immediately after rejection, a fruit fly was presented to the spider. Spiders accepting this fruit fly within a period of five minutes were considered to have an aversion to the test prey. If not accepted, the spiders might have been satiated or poisoned by the test prey. Remains of eaten prey were dried at 60°C for 48 hours and the specific food consumption was calculated in the same way as described for the previous experiment.

Results

Effects of nutrient deficiency on the tolerance to R. padi and F. candida.

Fig. 1 shows the consumption of Collembola and aphids in spiders with good and bad nutrient balance. There was a significant interaction between prey species and nutrient status in the relative prey consumption (Two-way ANOVA, $P<0.007$, log-transformed data). This interaction reflects the fact that well-balanced spiders consumed 3 times as many aphids as did deficient spiders (Fisher's LSD test, $P<0.05$) whereas there was no effect of nutrient balance on the consumption of Collembola (Fisher's LSD test, $P>0.05$). Collembola were in general eaten in larger quantities than aphids although this was not significant for spiders with good nutrient balance (Fisher's LSD test, $P>0.05$).

Rejection behaviour of spiders offered R. padi or F. candida.

Fig. 2 shows the specific food intake of *R. padi* and *F. candida* before the spiders rejected them. The spiders accepted significantly more *F. candida* than *R. padi* (t-test, $P<0.022$). *F. candida* was also eaten in larger numbers than *R. padi* before rejection occurred (Kruskal-Wallis Rank Sums, $P<0.0001$, Fig. 3). Of the spiders tested with *R. padi*, 86% did not eat any prey during the first five minutes of presentation whereas only 20% of the spiders in the other group completely refused *F. candida* (Fig. 3). Of the spiders fed *R. padi*, 76% accepted the fruit fly that was presented after the cessation of feeding. Those spiders had an aversion to the aphids or had developed one during the test. Among the spiders offered *F. candida*, however, 95% rejected the following fruit fly. Those spiders must have been either satiated or poisoned by the Collembola. Thus, aversions were much more frequently acquired to the aphids (76%) than to the Collembola (5%).

Discussion

The results of this study show that the nutrient balance of a spider influences its tolerance to the aphid *R. padi*. An earlier study with the same spider species found no influence of hunger level on the tolerance of *R. padi* (Toft, 1995). Thus, nutrient imbalance and hunger are two quite different types of stress factors to the spiders.

Changes in the spiders' physical condition as a result of nutrient deficiency may explain the reduced consumption of aphids. If aphids are chemically protected, negative post-digestive effects will be more serious in spiders suffering from nutrient deficiency and this may reduce consumption. Alternatively, if the threshold for developing an aversion is lowered by nutrient deficiency, spiders with a bad nutrient balance would develop an aversion earlier, and thus consume less aphids.

From other studies it appears that *F. candida* is potentially more harmful to spiders than is *R. padi* (Toft, Wise, 1999b). It was therefore surprising that the spiders had a higher con-

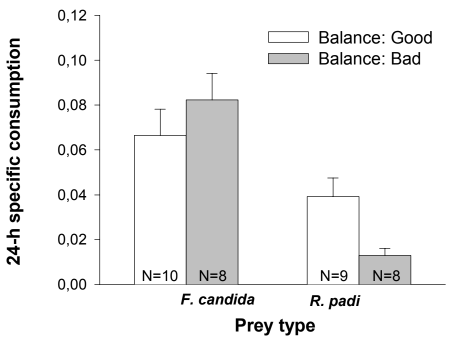

Fig. 1. Specific consumption [mg prey eaten (DW)/ mg spider (FW)] of *F. candida* and *R. padi* by wolf spiders *Pardosa prativaga* with good and bad nutrient balance.

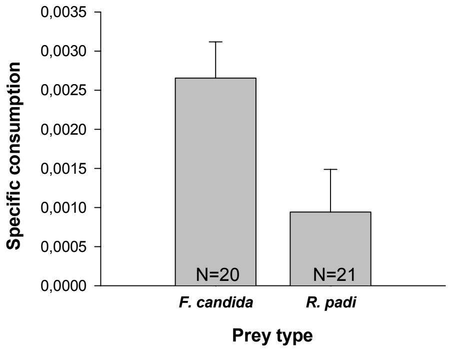

Fig. 2. Specific consumption [mg prey eaten (DW)/ mg spider (FW)] of *F. candida* or *R. padi* before rejection by the spiders. A rejection was realised when the spiders refused to attack and consume the prey for five minutes during constant presentation.

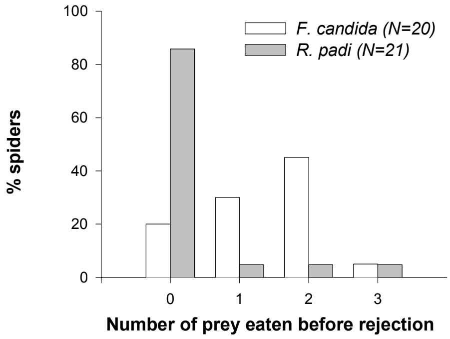

Fig. 3. Number of *F. candida* or *R. padi* eaten by the spiders before rejection. A rejection was realised when the spiders refused to attack and consume prey for five minutes during constant presentation.

sumption of *F. candida* than *R. padi*. One explanation could be that *R. padi* contains feeding deterrents (Bilde, Toft, 1994) but *F. candida* does not. This would make *F. candida* more palatable to the spiders despite its increased harmfulness. It is still unclear, though, why so many spiders developed an aversion to *R. padi* but not to *F. candida*. The reason may be that slow-acting toxins cause the toxicity of *F. candida*. It would then be difficult for the spider to associate delayed post-digestive effects with the prey. Another possibility is that the spiders may be unable to develop aversions to palatable food items (Lee, Bernays 1990).

An earlier study has shown that spiders recently caught in the field, on average eat 2.6 *R. padi* before an aversion develops (Toft, 1997). In the present study, however, most of the spiders completely avoided the aphids at the first encounter (cf. Fig. 3). This neophobia may be an effect of raising the spiders on a monotypic diet of highly palatable fruit flies. However, the spiders did feed on the aphids during the 24-hour food consumption study. The neophobia was therefore quickly overcome.

In conclusion, nutrient deficiency influences not only survival and growth of spiders (Mayntz, Toft, in prep.) but also the acceptance of some low quality prey types.

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