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Influence of diet quality on the respiratory metabolism of a wolf spider *Pardosa prativaga*

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ABSTRACT

We measured the respiration rates of female wolf spiders *Pardosa prativaga* after they had been held on restricted, mostly single-prey diets for 1-3 weeks. Respiration rates were significantly lower in spiders fed one of two high quality prey types than in spiders fed one of three low quality prey. No decrease in respiration was seen in starved spiders. Prey quality was indicated by the relative daily weight change during the experiment. With at least two low quality prey, the spiders lost weight to the same degree as starved controls.

INTRODUCTION

The respiratory metabolism of animals expresses their energetic costs of living. Very little is known about how adverse environmental conditions affect these living costs in spiders. Several studies have dealt with the phenomenon that some spiders are able to lower their metabolism during periods of starvation (Anderson 1974; Tanaka & Ito 1982), thus reducing expenditures when income is low. Several common prey types are of low quality to spiders (e.g. Toft 1995). The spiders' consumption rates of these prey are far below what is expected from their food demand as indicated by their potential consumption rate of high quality prey. The reason for this is that spiders develop aversions towards bad prey following experience with them (Toft unpubl.). Thus, spiders being held on low quality prey are starving in the sense that energy intake is far below demands for normal performance. Will they respond metabolically to this situation in the same way as if they are truly starving, i.e. by lowering metabolism? An alternative possibility is that since low quality prey may be toxic in one way or another, consumption of these prey may induce production of detoxication enzymes to handle the toxic compounds; this response is likely to be energy demanding, thus increasing metabolism.

This study attempts to distinguish the two hypotheses by measuring the respiration rate of a wolf spider subjected to various diet treatments, consisting of prey types of which some from previous experience are known as being of low quality, others as being of high quality.

MATERIAL AND METHODS

I. Spiders

The wolf spider *Pardosa prativaga* (L. K.) was selected as the test spider. It is one of the most abundant *Pardosa* species of a variety of open biotopes in Denmark, especially bogs, meadows and agricultural fields. Subadult females were collected in the field at Stjaer in Eastern Jutland in mid-May through early June. Groups of spiders with approximately the same range of variation in size were created and assigned randomly to treatments. The eight treatments were initiated at the end of May using mostly subadult females. During the treatment period most of these moulted into adults. Some treatments, however, had a substantial mortality; therefore, supplementary replicates were added by mid-June, consisting of a mixture of immature and mature females. When respiration was measured the early spiders had been on their treatment diet for 3-4 weeks, the supplementary ones for ca. 1 week. The spiders were weighed when treatment was started and at the time respiration was measured and their relative daily weight change (weight change/start weight/day in treatment) was calculated.

II. Diets

The eight diets used were the following:

1) the aphid *Rhopalosiphum padi* (L.)
2) the aphid *Sitobion avenae* (F.)
3) the aphid *Metopolophium dirhodum* (Walck.)
4) mixture of the above three aphids
5) the collembola *Folsomia candida* Willem
6) the collembola *Isotoma anglicana* Lubbock
7) fruit flies *Drosophila melanogaster* Meig.
8) starvation

The three species of aphids are all pests of cereal crops. Previous experience (Toft unpubl.) indicated that *R. padi* is of much lower value to spiders than any of the other two, but all three should be considered low quality prey. They were all raised in laboratory cultures on seedlings of wheat. The collembola *F. candida* is also a low quality prey with inhibitory effects on food consumption (Toft & Wise unpubl.). The species was kept in laboratory culture and fed baker's yeast.

Two high quality prey (Toft 1995 and unpubl.) were included: Fruit flies raised on commercial fruit fly medium (Carolina Biological Supply Ltd.) and the collembola *I. anglicana*; of the latter spiders were fed mainly specimens collected in agricultural fields, additionally offspring from a newly started culture (raised on a mixture of baker's yeast and fruit fly medium). Finally a starved group was included as a 'control'. As far as possible prey was supplied in constant superabundance; however, the *S. avenae* culture produced insufficiently to fully comply with this.

III. Respiration measurements

During the treatment period the spiders were held at room temperature (ca. 22 °C). They were acclimated for 3-5 days in the temperature controlled room (19 °C) in which the respiration measurements took place. About half an hour prior to measurement each spider was housed in a 10 ml airtight vial with rubber cover. Air samples of 100 μl were taken with a Hamilton syringe from the vial two times with one to three hours between; duplicate or triplicate samples were taken on both occasions. The CO_2 content of the samples was determined using an Infra Red Gas Analyser (ADC Type 225 Mk3, The Analytical Development Co. Ltd.). A conversion factor, allowing translation of the instrument reading into CO_2 volume, was obtained by measuring various volumes of 5 % CO_2 gas mixture. The respiratory rate is calculated as μl CO_2 produced per mg spider per hour.

IV. Statistical analysis

Both data sets presented here were tested with a one-way ANOVA after log-transformation of the original data. Since replicates in most groups had been in treatment for a variable number of days and there was a considerable variation in initial size, the influence of these two factors was tested first. For the relative weight change during the experiment, initial weight but not treatment period had a significant effect, and was included as a covariate in the final analysis. For the respiration rate neither initial weight nor days in treatment had any effect and no adjustments were made. Fisher's Least Significant Difference Test was used for multiple pairwise comparisons.

RESULTS

I. Weight change

The daily change of weight during the treatment period gives a good indication of the relative quality of the prey types (Fig. 1). There are highly significant overall treatment effects (ANOVA, $p = 0.000$). *Drosophila* and *I. anglicana* allowed a high growth rate and thus confirmed that they are high quality food. The three aphids as well as *F. candida* also confirmed their low quality status. The *R. padi* and *F. candida* groups showed a weight loss of the same magnitude as the starved group. *M. dirhodum* allowed some growth. The indicated rank order of the three cereal aphids is the same as found by other measures of diet quality (Toft unpubl.), though in the present study the differences are not statistically significant.

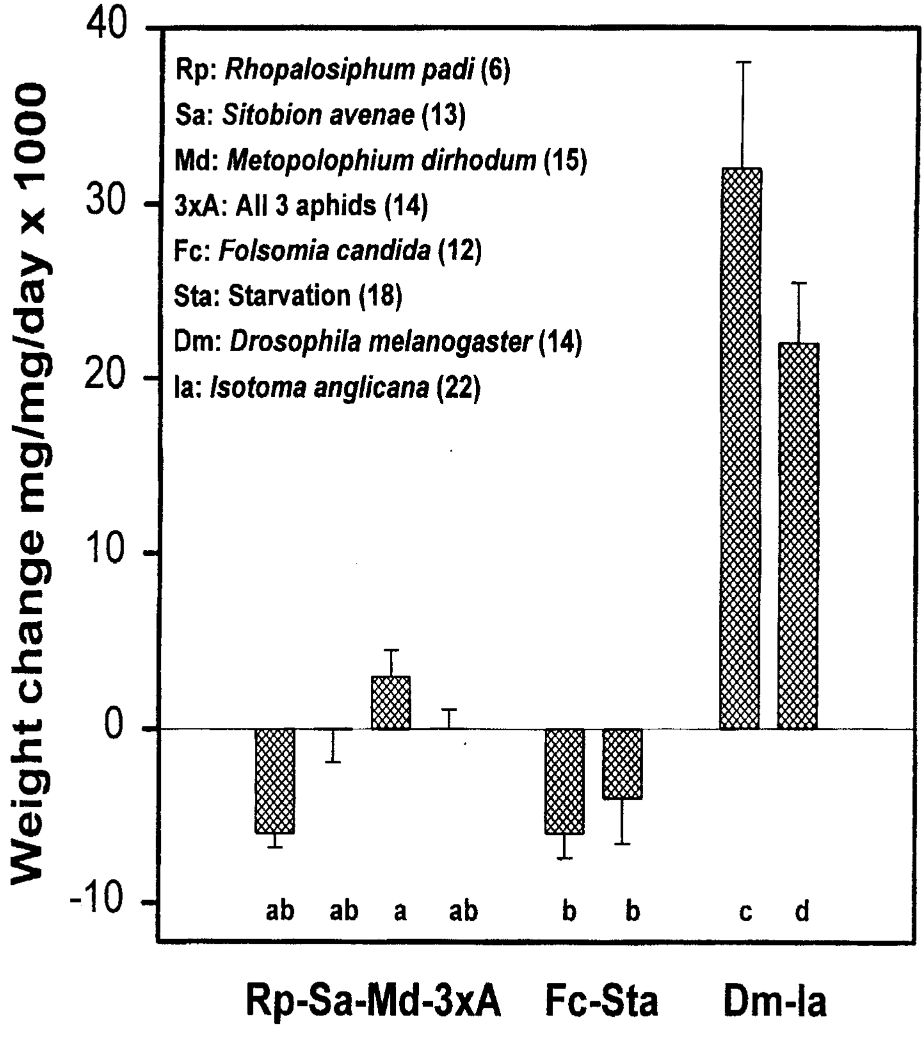

Fig. 1. Relative daily weight change (+SE) of female *Pardosa prativaga* during experimental treatment with different diets. Treatments with the same letter indicated are not significantly different (LSD test). Sample sizes for each treatment are shown in parentheses.

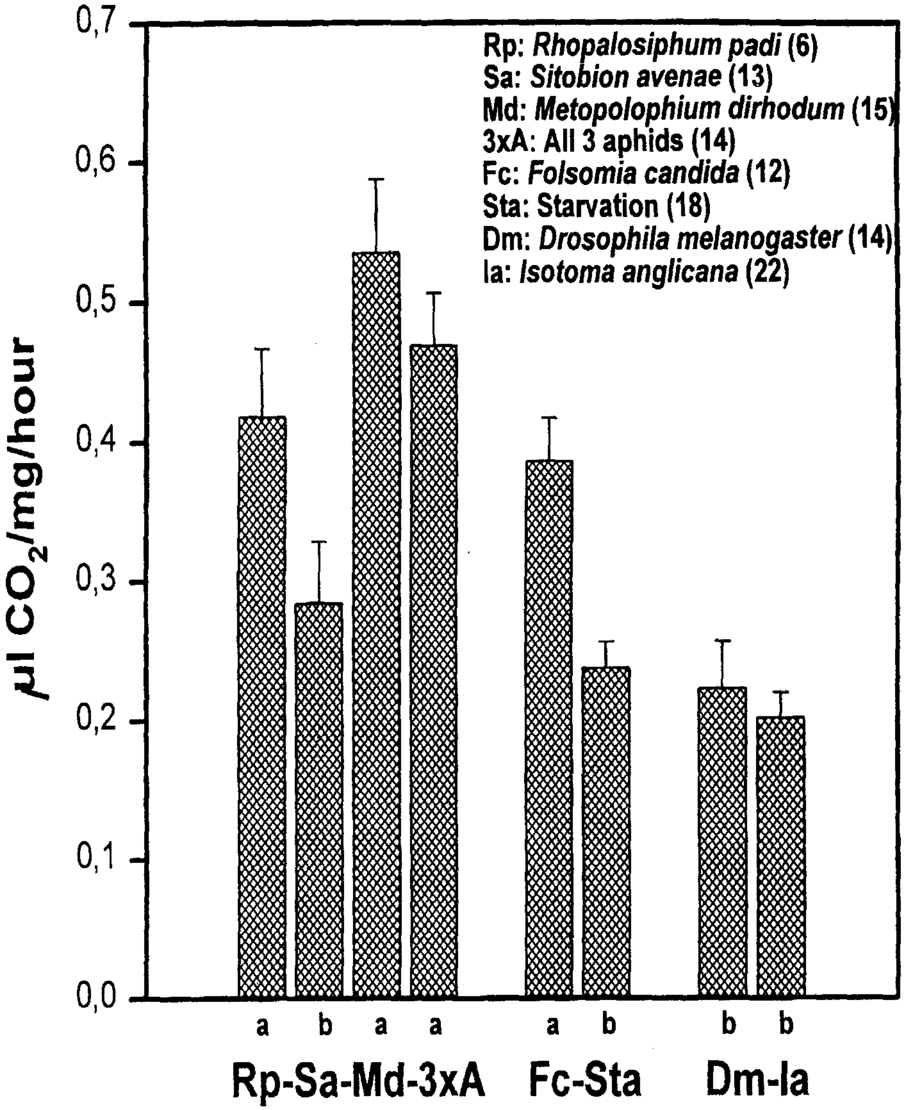

Fig. 2. Respiratory rates (+SE) of female *Pardosa prativaga* during experimental treatment with different diets. Treatments with the same letter indicated are not significantly different (LSD test). Sample sizes for each treatment are shown in parentheses.

II. Respiration

The respiratory rates of the eight treatments are shown in Fig. 2. Statistically there are highly significant treatment effects (ANOVA, $p = 0.001$). The post-hoc tests revealed the pairwise differences and similarities also depicted in Fig. 2. With one exception (*S. avenae*) all the low quality prey types gave high respiration rates, while the two high quality prey gave comparatively low respiration rates. Surprisingly, the starvation group was similar to the high quality prey groups, i.e. there is no indication of a reduced metabolism connected with starvation. The reason for the *S. avenae*-group deviating from the general pattern is not clear; as already noted prey was in short supply, and the actual treatment may have been somewhere between a full aphid treatment and starvation.

The negative relationship between respiration rate and diet quality can be expressed by a correlation between CO_2 production and weight change. Using log-log transformed treatment means there is a marginally significant correlation ($r = 0.682$, $p = 0.062$ two-tailed) in spite of the low number of data points ($n = 8$).

DISCUSSION

The results gave a clear-cut answer to the question posed: Low quality prey that do not allow the spiders to consume food according to their food demand, do not have an effect akin to starvation, but imposes significant energy costs on the animals. The reasons for the raised metabolism are not clear, since the mechanisms behind the low food value of these prey are unknown. Mobilisation of detoxication enzymes to cope with prey toxins, as hypothesised in the Introduction, is but one possibility. The magnitude of the response for the set of prey types analysed here amounts to approximately a doubling of the metabolic rate. Miyashita (1969) measured the respiration rate of another lycosid spider both in a resting state and during forced walking at nearly the same temperature (20 °C) and with methods comparable to ours. His results for resting metabolism (avg. 0.209 µl CO_2/mg/h) is only slightly lower than our result for high quality prey, which may be because he worked with a slightly larger species. He also found a 5-fold increase during walking, i.e. a much larger effect than seen here. Though the extra energy costs of eating bad prey are thus moderate, they are inescapable for a certain time period. Still, they are not of such a magnitude that weight loss is significantly increased compared to starvation, but such an effect cannot be ruled out for other prey types. At least two prey types were no better than starvation. Only in one prey classified as low quality (*M. dirhodum*), feeding more than compensated for the costs. From the results presented here it is not clear why the spiders should accept the bad prey types at all. However, Toft (1995) presented evidence that adding

R. padi to a diet of only *Drosophila* improved the reproductive success of a linyphiid spider *Erigone atra* (Bl.). Thus, it is possible that the overall beneficial effect of a nutritionally diverse mixed diet more than outweighs the energetic costs of handling low quality prey included in the mixture. It would be of interest to test also the effects of various mixed diets, especially mixtures composed of both high and low quality prey, to see if inclusion of low quality prey is similarly costly under normal circumstances of diverse prey availability.

We found no decreased respiration rate in the starved group of spiders, though this has been shown for another *Pardosa* species (Tanaka & Ito 1982). It remains to be established whether the phenomenon is ubiquitous among spiders. Greenstone and Bennett (1980) concluded that there was no general relationship between resting metabolism and foraging strategy, when a wide range of spider families are compared. The present study demonstrates that the prey itself may influence the metabolic costs of living. In this sense low quality prey should be considered natural stress factors.

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