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Metabolic consequences of feeding and fasting on nutritionally different diets in the wolf spider *Pardosa prativaga*

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ABSTRACT

We investigated whether spiders fed lipid-rich rather than protein-rich prey elevate metabolism to avoid carrying excessive lipid deposits, or whether they store ingested lipids as a buffer against possible future starvation. We fed wolf spiders (*Pardosa prativaga*) prey of different lipid:protein compositions and measured the metabolic rate of spiders using closed respirometry during feeding and fasting. After a 16-day feeding period, spider lipid:protein composition was significantly affected by the lipid:protein composition of their prey. Feeding caused a large and fast increase in metabolism. The cost of feeding and digestion was estimated to average 21% of the ingested energy irrespective of diet. We found no difference in basal metabolic rate between dietary treatments. During starvation $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ decreased gradually, and the larger lipid stores in spiders fed lipid-rich prey appeared to extend survival of these spiders under starvation compared to spiders fed protein-rich prey. The results show that these spiders do not adjust metabolism in order to maintain a constant body composition when prey nutrient composition varies. Instead, lipids are stored efficiently and help to prepare the spiders for the long periods of food deprivation that may occur as a consequence of their opportunistic feeding strategy.

1. Introduction

All animals must balance energy intake with energy requirements, and must match the intake of protein, carbohydrates and lipid (i.e. the major macronutrients) to the requirements for metabolism, growth and reproduction. Predatory animals, such as spiders, may experience prolonged periods of food deprivation interrupted by sudden encounters with large prey items. Such animals are often endowed with physiological adaptations that enable them to maintain function during fasting and enable them to digest large meals when the opportunity arises (Wang et al., 2006). Although the infrequent encounters with appropriate prey items can limit the ability of predators to control the nutrient composition of their diet, it has been shown that predatory animals, like herbivores and omnivores (Kyriazakis and Emmans, 1991; Kyriazakis et al., 1991; Raubenheimer and Simpson, 1997; Berthoud and Seeley, 2000; Raubenheimer and Jones, 2006; Simpson et al., 2006), can regulate the intake of macronutrients in their diets (Mayntz et al., 2005; Raubenheimer et al., 2007).

If nutrient composition of the prey deviates from the optimal balance, animals may over-consume food to meet minimal requirements of a given macronutrient, even though the overall energy requirement is surpassed (Raubenheimer and Simpson, 1993). For example, herbivores and omnivores fed a protein-deficient diet typically increase their overall intake and, hence, overingest lipids and carbohydrates to meet their protein requirement (Simpson and Raubenheimer, 2005; Sørensen et al., 2008). Unless this surplus energy is voided, the excess energy intake is stored as body fat, which could result in obesity (Simpson and Raubenheimer, 2005; Sørensen et al., 2008). One way of voiding excess ingested energy when feeding on a low-protein diet is to increase metabolic rate to burn off excessive energy by a process known as facultative diet-induced thermogenesis, as is seen in some herbivores and omnivores (Zanotto et al., 1993, 1997; Stock, 1999; Trier and Mattson, 2003). The extent to which facultative diet-induced thermogenesis is employed might be expected to reflect the balance between the costs of fat storage and the longer term benefit of fat stores as energy reserves in times of food shortage (Warbrick-Smith et al., 2006). As for most spiders,

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wolf spiders are frequently exposed to periods of starvation interspersed with periods of plenty (Riechert and Harp, 1987; Wise, 1993). It is interesting, therefore, to study whether these spiders possess regulatory adaptations to handle nutrient imbalance and/or starvation. It has previously been shown that prey low in protein and rich in lipids reduce growth, survival and fecundity in wolf spiders (Mayntz and Toft, 2001). It is unclear, however, whether wolf spiders increase metabolic rate when exposed to protein-poor, lipid-rich diets. Such a response would aid the spiders in achieving a better nutritional balance, but could also potentially render the animals more vulnerable to depletion of energy stores during food deprivation. It has been shown that wolf spiders can reduce metabolism in response to starvation (Tanaka and Itô, 1982; Tanaka et al., 1985; Nakamura, 1987), but the metabolic response to changes in body and prey nutrient composition, as well as its interaction with food deprivation, is unknown. To gain further insight into this question, the present study investigated how prey of variable macronutrient composition (lipids vs. protein) affects body composition, basal metabolic rate (BMR), metabolic response to feeding and digestion (SDA), and metabolism during fasting in the wolf spider *Pardosa prativaga*.

2. Materials and methods

2.1. Experimental diets

Fruit flies (*Drosophila melanogaster*) used as food for the spiders were raised on three different media based on mixtures (g:g) of a basic medium (Carolina Instant Drosophila Medium Formula 4-24, Burlington, NC, USA), casein (Sigma C-5890, Sigma–Aldrich, Steinheim, Germany) and sucrose (Fluka, 84097, Neu-Ulm, Germany). Lipid-rich flies were raised in a medium with a 1:4 ratio of sucrose and basic medium; intermediate flies were raised on a 1:9 ratio of casein and basic medium; and protein-rich flies were raised on a 3:2 ratio of casein and basic medium. All flies were reared in 3.4 cm Ø vials containing 2.5 g dry medium mixed with 15–22 ml water and a few drops of satiated yeast solution covering the surface. Cultures were inoculated with 40–50 adult *D. melanogaster* of mixed sexes for 3 days and the resulting larvae were raised at 24–26 °C until emergence. The different rearing media produce fruit flies with markedly different protein and lipid contents (Fig. 1).

2.2. Experimental animals

Juvenile *P. prativaga* wolf spiders (Lycosidae) were collected in wet meadows around Aarhus (Jutland, Denmark) in February 2008 as they were hibernating under vegetation. They were kept in individual transparent plastic vials (2 cm Ø, 6 cm height) with moist Plaster-of-Paris bottoms and foam rubber stoppers at 5 °C in darkness without food for 1–2 months before experiments started. This mimicked the conditions in nature during winter when the spiders were caught, and experiments started in middle spring. Five days before initiation of feeding, the spiders were transferred to an incubator at 25 °C and a 16:8 h light:dark photoperiod. Each spider ($N = 268$) was weighed to the nearest 1 μg and 16 randomly selected spiders were frozen at −18 °C to determine initial body composition. The remaining spiders were distributed randomly between three dietary treatments: lipid-rich flies, intermediate flies, or protein-rich flies for 16 days. During the feeding period, the spiders were allowed to feed to satiety every second day.

2.3. Experimental protocol

Basal metabolic rate (BMR) of 44 randomly selected spiders from each feeding regime was measured just before the feeding

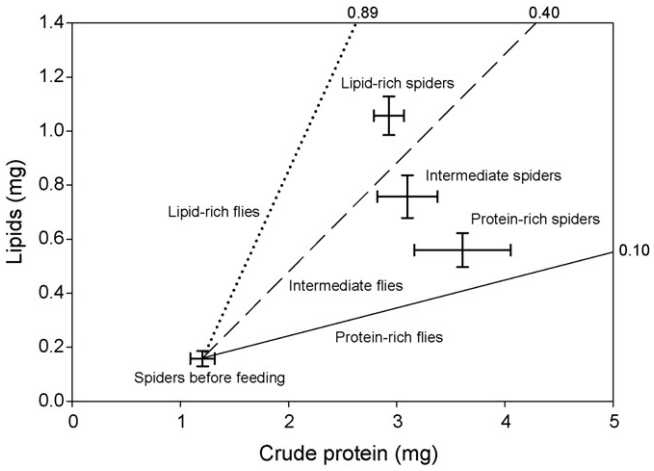

Fig. 1. Lipid vs. crude protein content (mean ± SE) of *Pardosa prativaga* wolf spiders immediately after winter hibernation and after 16 days of *ad libitum* feeding on lipid-rich, intermediate, or protein-rich *Drosophila melanogaster* fruit flies. The slopes of the inserted lines, indicated by the number at the end of each line, represent the lipid: crude protein ratio of the three *D. melanogaster* fly types. Crude protein content is calculated by multiplying the nitrogen content with a constant factor of 6.25 (AOAC, 2000). Data for fly body compositions are from similarly produced *D. melanogaster* (Jensen, 2010).

period, and measurements of mass and BMR were repeated after the 16 days on the respective diets. Ten other spiders from each feeding regime were frozen to assess how the diets had influenced body composition. The remaining spiders were then fasted for 7 days, weighed, and BMR measurements were repeated. To measure the metabolic cost of feeding, often termed the specific dynamic action of a meal (SDA), we fed the spiders a single pre-weighed fly from their respective diet directly in the respiration chamber. This measure therefore includes the metabolic cost of handling, ingesting, digesting, and assimilating a prey item (McCue, 2006). When the fly was taken, the respiration chamber was closed immediately and gas exchange was measured over two consecutive 3-h periods. All spiders completed meal extraction within the first 3-h period. Gas exchange was measured again over the following 14 h after which respiration levels had returned to resting rates. The spiders were then returned to their vials and fed flies *ad libitum* for 24 h to ensure that they were fully fed before exposure to long-term starvation. During the starvation period, mass and BMR were measured after 5, 11, 17, and 35 days.

2.4. Measurements of metabolism

Gas exchange was measured by closed respirometry, in which the spiders were enclosed in individual 10-ml glass syringes sealed with vacuum grease. Except during SDA measurements, enclosure periods were 24 h, after which the decrease in O_2 volume ($\dot{V}_{O_2}$) and increase in CO_2 volume ($\dot{V}_{CO_2}$) were measured. The syringes contained a small drop of water to keep the air saturated, and were submerged in a water bath at 25 °C to stabilize temperature. Measurements of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were performed by injecting 8 ml gas from the respiratory chambers into a CO_2 and O_2 analyser (Applied Electrochemistry, Sunnyvale, CA, USA). This gas sample was then drawn through the analyser at a known and constant rate so that the O_2 decrease and CO_2 increase could be calculated relative to injections of standard gas samples of known O_2 and CO_2 contents. $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were corrected to standard temperature and pressure under dry conditions (STPD), and mass specific metabolic rate was calculated using the latest measure of body mass prior to the measurement. In most cases, CO_2 of the respiratory chamber did not exceed 2% and O_2 did not decline below 18%. For comparison, standard concentrations of CO_2 and O_2 in the air were