Intraspecific variation in prey quality: a comparison of nutrient presence in prey and nutrient extraction by predators

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Prey quality can have large impacts on the survival, growth and behavior of predators. A number of studies have examined how different species of prey vary in quality. However, far less is known about intraspecific variation in the quality of prey for predators and even less about what nutrients are extracted from prey by predators. We examined how the sex, feeding level and developmental status of prey affected the quantities of nutrients present in prey bodies and the quantities of nutrients that could be extracted from prey by spiders. Female and well-fed prey were larger and had more nutrients than male and food-limited prey, respectively. After taking into account differences in prey size, spiders extracted relatively more lipid and less protein from female and well-fed prey than from male and food-limited prey, respectively. Mealworms were of higher quality than adult mealworm beetles; spiders were able to extract more lipid, protein and other nutrients from larvae than adults. While lipid present in prey was a good predictor of lipid consumed, protein present in prey was not a reliable predictor of protein consumed. The variation in prey quality that we observed within a single species of prey (i.e. well-fed vs food-limited crickets) was as large as variation in quality among the three species of prey used in these experiments. Intraspecific variation in prey quality may be an important factor affecting predatory arthropods, especially in habitats or at times of year when one species of prey is abundant. Further studies are needed to examine the consequences of intraspecific variation in prey quality on the life history and behavior of predators.

Food quality, the relative concentrations of energy, biochemicals and nutrients in food, can have important implications for the life history, ecology and evolution of predators (Mayntz and Toft 2001, Sterner and Elser 2002, Muller-Navarra 2008). The survival and growth of predators can be dramatically affected by the species of prey upon which they feed (Toft and Wise 1999, Oelbermann and Scheu 2002, Rickers et al. 2006). Even closely related species of prey can result in significant differences in survival and growth of predators (Toft and Wise 1999). Interspecific variation in prey quality is important because many predatory species are polyphagous and consume a wide range of prey species. In addition, there is some evidence that individuals of a single species of prey item can vary in their effects on predator growth rate depending upon the diet on which the prey are raised (Mayntz and Toft 2001, Malzahn et al. 2007). Intraspecific variation in the quality of prey may be important for predators because a single species of prey may be especially abundant in a particular habitat or at a certain time of year. If predators are able to select prey based on inter- and intraspecific variation in quality then they may be at a selective advantage in terms of survival and growth. Rapid growth is important for predators because it increases the size range of prey that can be consumed and decreases the risk of intraguild predation (Polis et al. 1989, Balfour et al. 2003, Rypstra and Samu 2005).

A great deal is known about the consequences of feeding on particular prey species, or a single prey species fed different diets, for the survival and growth of predators (Toft and Wise 1999, Mayntz and Toft 2001, Oelbermann and Scheu 2002, Rickers et al. 2006). Far less is known about why particular prey items differ in quality for predators. Presumably, some variation in the quality of prey is due to the relative abundance of chemical constituents (e.g. nutrients, lipid, protein, fatty acids, vitamins or minerals) in different prey (Mayntz and Toft 2001, Sterner and Elser 2002, Rickers et al. 2006). While the consequences of the nutritional content of food has been well-studied for herbivores (Sterner and Elser 2002), relatively few studies have quantified the nutritional composition of prey items for predators. A better understanding of the nutritional composition of prey and nutrient extraction by predators will advance our understanding of mechanisms responsible for variation in prey quality.

Over three-quarters of terrestrial predatory arthropods consume prey through extraoral digestion (Cohen 1995). In
species with extraoral digestion, enzymes are injected into prey, edible compounds are ingested from the prey body and the inedible components (e.g. chitinous exoskeleton), and possibly some edible components that are difficult to extract, are discarded. This can have important consequences for the measurement of prey quality because predators are selectively extracting certain compounds from the prey and leaving others behind. Hence, simply measuring the content of whole prey items cannot be used as a measure of prey quality without information on what predators are actually extracting from the prey. However, despite the widespread use of extraoral digestion, few studies have addressed how this form of feeding affects the nutritional ecology of predatory arthropods (Cohen 1995, Mayntz et al. 2005, Mayntz and Toft 2006).

The purpose of this study was to test how intraspecific variation in the characteristics of prey, including sex, feeding level and developmental status, affect the nutritional content of prey and nutrient extraction by spiders. We compared how intraspecific variation in prey (sex, developmental stage, feeding condition) affected the nutritional contents of the whole prey items (i.e. lipid, protein and other nutrients) and what was extracted by spiders during feeding. Given that spiders feed using extraoral digestion, there is always a portion of the prey that is discarded after they have fed. By quantifying the nutrition content of intact prey and this discarded portion, we determined if nutrient availability of intact prey is a reasonable predictor of what is actually consumed by the spider.

Methods

Overview

These experiments were conducted using three different species of prey and three different species of wolf spiders (Aranae: Lycosidae). We chose prey that were easy to rear under standard conditions in the laboratory (i.e. Drosophila melanogaster, Acheta domesticus and Tenebrio molitor) and then matched these prey with appropriately-sized wolf spiders. We first tested if sex of the prey affected the nutritional content of the prey by examining consumption of male and female flies, D. melanogaster, by juvenile Pardosa saltans. Given the high lipid content of insect eggs (Kawooya and Law 1988, Giron and Casas 2003), we expected female prey items to have proportionally more lipid and less protein content than males. We then tested if the feeding level of prey items affected nutritional content by examining consumption of well-fed and food-limited crickets, A. domesticus, by adult female Rabidosa rabida. We predicted that well-fed crickets would have proportionally more lipid content than food-limited crickets. Finally, we tested if prey developmental status affected nutritional content by examining consumption of larval and adult mealworm beetles, T. molitor, by Hogna helluo. We predicted that the higher amount of sclerotization in adult beetles would result in proportionally less lipid and protein content than larvae. Finally, we tested if extraoral digestion complicated the measurement of prey nutritional content by examining if the nutritional (i.e. lipid and protein) content of whole prey items was proportional to what was actually extracted by predators.

General methods

We were interested in examining the maximum amount of nutrients that predators could extract from prey and the amount of prey that was discarded following termination of feeding. However, some predatory species may be able to bias their extraction of lipid and protein from prey (Mayntz et al. 2005). For example, if fed a diet high in lipid, some species will consume proportionately more protein from subsequent prey items and vice versa (Mayntz et al. 2005). Presumably, selective extraction of nutrients should occur if spiders have an excess of food and are limited by the relative amount that they can ingest. We assumed that if predators face overall food limitation, they should extract as much of prey biomass as possible. Therefore, in the experiments in this study, we exposed spiders to starvation periods sufficient to ensure that spiders were motivated to extract as much energy and nutrients from prey as possible. In addition, in the first two experiments, all spiders were presented with and consumed a second prey item suggesting that they were still hungry after discarding the remains of the first prey. We were unable to provide spiders in the third experiment with a second prey item to confirm hunger. However, we were confident that the spiders in the third experiment (Hogna helluo) were not satiated by the one prey provided in the experimental trials because this prey item represents approximately 15 percent of the biomass of prey normally consumed by these spiders in a two week period (i.e. the length of the starvation period). In all experimental trials, a single and separate individual spider was paired with a prey item.

Prey sex

Juvenile Pardosa saltans (6–10 mg) were collected from a deciduous forest 35 km north of Aarhus, Denmark and brought to the laboratory at Aarhus University for experiments in June 2007. Individuals were housed in clear plastic vials (2.5 cm ø × 7 cm high) with a foam plug in one end and a substrate of plaster of paris mixed with activated carbon. The substrate of the vials was moistened with water three times each week and vials were stored in a plastic bag at room temperature to avoid desiccation. Individuals experienced a natural light:dark cycle.

Feeding trials were conducted five days after P. saltans were collected from the field and P. saltans were not fed prior to the experimental trials. Prey items were wild-type flies, Drosophila melanogaster (females: 0.7–1.2 mg, males: 0.5–0.7 mg; wet mass), raised on Carolina medium supplemented with 20% sucrose by weight. Fly cultures were started three weeks before the feeding trials and flies used as prey were taken from several different culture tubes. On the day of the trials, male and female D. melanogaster were lightly anesthetized with CO2 and weighed to the nearest 0.001 mg on a microbalance. We determined the sex of flies using the coloration of the end of the abdomen, which is darker in males. Individual male (n = 14) and female
(n = 15) D. melanogaster were then randomly placed in containers with P. saltans and the foam plug was pushed down to restrict the area available in the vial and ensure that the spider captured the fly. We also collected male (n = 13) and female (n = 13) D. melanogaster that were used as controls for the nutritional content of unconsumed flies. Wolf spiders engage in extraoral digestion in which they masticate prey, ingest edible components of the prey and discard a bolus of inedible prey remains. Discarded prey remains were collected once they had been abandoned by spiders. Prey remains were handled as described below in ‘Nutritional analyses’.

Prey feeding level

Adult female Rabidosa rabida (200–400 mg) were collected from a forest-field edge at the Miami University Ecology Research Center in Oxford, OH, USA and brought to the laboratory at Miami University for experiments in August 2007. Individuals were housed in clear plastic containers (10 cm ø × 12 cm high) with a one cm substrate of peat moss and soil and a small amount of synthetic straw. Mesh screen covered the top of the containers to allow ventilation and the substrate was moistened three times each week to avoid desiccation. Containers were stored in an environmental room at 25°C and a 13:11 L:D cycle.

Feeding trials were conducted 10 days after R. rabida were collected from the field. Individuals were not fed anything prior to the experimental trials to ensure a high hunger level. Prey items were juvenile crickets, Acheta domesticus, (50–130 mg, wet mass) purchased from a local supplier. We placed A. domesticus on either well-fed or food-limited feeding regimes for five days before feeding them to R. rabida. Juvenile A. domesticus were housed in plastic containers with a substrate of sand, a mesh lid and a gel water source. In the well-fed treatment A. domesticus were also provided with ad libitum crushed dog food, while in the food-limited treatment A. domesticus were deprived of food. Well-fed (n = 15) and food-limited (n = 12) A. domesticus were randomly assigned to R. rabida. We also collected well-fed (n = 16) and food-limited (n = 10) A. domesticus as controls for the nutritional content of unconsumed crickets. Discarded prey remains were collected once they had been abandoned by spiders and prey remains were handled as described below in ‘Nutritional analyses’.

Prey developmental status

Female Hogna helluo were raised to the adulthood (300–800 mg) in the laboratory at Miami University. These females were the offspring of females collected from the field at the Miami University Ecology Research Center (Oxford, Butler County, OH, USA) in 2006. Upon hatching and dispersal from the mother, H. helluo were placed in plastic containers (8 cm ø × 5 cm high) with a one cm substrate of peat moss and soil, a slice of potato and an active culture of the collembolan Sinella curviseta (Collembola, Entomobryidae). Spiders were maintained in an environmental chamber at 25°C and a 13:11 light:dark cycle. After three to four weeks, spiderlings were switched to a diet of two appropriately sized juvenile A. domesticus once or twice per week. Individuals were transferred to larger containers (11 cm ø × 8 cm high) upon reaching approximately one cm body length.

Female H. helluo were fed two juvenile A. domesticus and then starved for 17 days prior to the experimental trials. Prey items were larval and adult mealworms, Tenebrio molitor (90–130 mg, wet mass), purchased from a commercial supplier. Tenebrio molitor were maintained on bran flakes and potatoes prior to being fed to H. helluo. Larval (n = 7) and adult (n = 8) T. molitor were randomly assigned to H. helluo. While these sample sizes were relatively small, they were sufficient to detect highly significant treatment effects. We also collected larval (n = 10) and adult (n = 10) T. molitor as controls for the nutritional content of unconsumed mealworms. Discarded prey remains were collected once they had been abandoned by spiders and prey remains were handled as described below in ‘Nutritional analyses’.

Nutritional analyses

We measured two aspects of the nutritional content of prey items and prey remains, the total amount of lipid and protein. All other compounds (e.g. carbohydrates, vitamins, minerals, chitin, etc.) were grouped into the ‘other compounds’ category. Prey remains or whole prey items were placed in 2 ml centrifuge tubes and stored in a freezer at −20°C until they were analyzed. Prior to analysis, samples were dried at 60°C for 48 h and then weighed to the nearest 0.001 mg. Lipid content was calculated gravimetrically using chloroform extraction. Briefly, dried samples were soaked in chloroform for 24 h after which the chloroform was removed. Each sample experienced three soaking periods and then was reweighed to calculate the difference in mass before and after lipids were extracted by the chloroform. We packaged 2–3 mg of each sample in a tin capsule and analyzed these samples in a CHN analyzer (D. melanogaster were analyzed at Aarhus Univ. and A. domesticus and T. molitor were analyzed at Miami Univ.) to measure nitrogen content.

We estimated protein content by measuring nitrogen content and converting to protein using the standard conversion factor of 6.25 (Horowitz 2002, Mayntz et al. 2005). All calculations were done using nitrogen content and were then converted to protein content directly before statistical analysis. Hence, all p-values for protein also correspond to nitrogen analyses and all measures of protein can be converted to measures of nitrogen by dividing by the conversion factor of 6.25 (Horowitz 2002). The use of protein content as a measure instead of nitrogen allows our data to be compared to other published studies and allowed us to more directly estimate our ‘other nutrient’ category.

Since measuring lipids and proteins is destructive, we were not able to measure lipid and protein content before and after a spider fed on a prey item. Instead, we used control data from the whole prey items to calculate a calibration curve relating the wet mass of prey to the dry mass or lean mass (i.e. lipid-free dry mass) of prey (Table 1). We could then use the live mass of a prey item with the calibration equations (calculated from
Table 1. Calibration equations derived from linear regression relating the wet biomass of prey items to the dry biomass and lean biomass (i.e., lipid-free dry mass) of prey items. R^2-values are presented in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>n</th>
<th>Regression lines relating wet mass (×) of prey (g) to:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry mass of prey (mg)</td>
<td>Lean mass of prey (mg)</td>
<td></td>
</tr>
<tr>
<td><em>Drosophila melanogaster</em></td>
<td>Male 13</td>
<td>359.6 × +0.0415 (R^2 = 0.87)</td>
<td>268.9 × +0.0096 (R^2 = 0.85)</td>
</tr>
<tr>
<td></td>
<td>Female 13</td>
<td>405.6 × +0.0687 (R^2 = 0.91)</td>
<td>244.5 × +0.0003 (R^2 = 0.80)</td>
</tr>
<tr>
<td><em>Acheta domesticus</em></td>
<td>Food-limited 9</td>
<td>231.7 × −1.8942 (R^2 = 0.91)</td>
<td>190.6 × −0.6704 (R^2 = 0.82)</td>
</tr>
<tr>
<td></td>
<td>Well-fed 13</td>
<td>345.7 × −5.2483 (R^2 = 0.90)</td>
<td>218.9 × −1.3548 (R^2 = 0.96)</td>
</tr>
<tr>
<td><em>Tenebrio molitor</em></td>
<td>Larval 10</td>
<td>463.6 × −14.109 (R^2 = 0.84)</td>
<td>263.6 × −2.6765 (R^2 = 0.91)</td>
</tr>
<tr>
<td></td>
<td>Adult 10</td>
<td>291.5 × +8.9174 (R^2 = 0.49)</td>
<td>258.9 × +6.1752 (R^2 = 0.74)</td>
</tr>
</tbody>
</table>

measurements of the content of whole prey) to estimate the content of lipids and protein in prey before it was consumed by a spider. The sample size for each calibration curve was the number of control prey for each treatment of each experiment. We calculated the amount of lipid, protein and other nutrients extracted from prey items as the difference between the estimated content of the prey before consumption (using the calibration equation) and the actual measurement of the content of the prey remains. The other nutrients category was defined as the consumed part of the prey that was not lipid or protein and may include a variety of vitamins and minerals. The unconsumed category was the mass of prey item remaining after a female spider terminated feeding.

Statistical analysis

Each of the experiments included two treatment groups. For each of the experiments, we compared the mass of lipids, protein and other components of unconsumed prey items between the treatments to test if they prey differed in overall nutritional content. However, since spiders engage in extraoral digestion and discard an unconsumed portion of the prey, the nutritional composition of control prey may not necessarily reflect what can actually be consumed by spiders. To take this into account, we also calculated the mass of nutrients that were actually extracted from the prey (calculated as described above) between treatment groups. Some of our treatments resulted in significant differences in the overall live mass of prey items. Hence, we also calculated the relative concentration (mg of nutritional component per 100 mg dry mass of prey) of consumed lipids, consumed protein, consumed other nutrients and unconsumed parts of the prey items (i.e., these four numbers add up to 100 mg). Given that the content of lipid, protein, other nutrients and unconsumed parts of prey items may be interdependent, we first analyzed the data using multivariate analyses of variance MANOVA. For any test that showed a significant multivariate difference, we then conducted unequal variance t-tests to examine which of the nutritional measures (i.e., lipid, protein, other nutrients or unconsumed parts) differed between treatment groups.

To test if nutrient extraction through extraoral digestion was proportional to nutrient availability in whole prey items, we calculated the estimated amount of lipid and protein in prey prior to consumption and the amount of lipid and protein extracted from prey during feeding. We then used a two-factor analysis of variance ANOVA with experimental treatment (either sex: male vs female, feeding level: well-fed vs food-limited, or developmental status: larva vs adult) and nutritional content (predicted in whole prey vs extracted from prey by a spider) as main factors. Separate analyses were run for each nutrient (i.e., lipid and protein) and for each experiment. The interaction factor of this two-factor ANOVA allowed us to evaluate if nutrient extraction was proportional to nutrient availability among the treatments.

Results

Prey sex

In intact prey items, female flies were 53% larger than male flies (t_{14} = 5.70, p < 0.001; Table 2A) and had significantly higher quantities of protein (t_{13} = 6.11, p < 0.001), protein (t_{20} = 2.20, p = 0.04) and other compounds (t_{13} = 3.45, p = 0.004) in their bodies (MANOVA: F_{3,21} = 15.63, p < 0.001; Table 2A). In feeding trials, spiders extracted significantly more lipid (t_{27} = 11.26, p < 0.001), protein (t_{27} = 3.96, p < 0.001) and other nutrients (t_{27} = 8.22, p < 0.001) from female flies than from male flies (MANOVA: F_{4,23} = 50.42, p < 0.001; Table 2B). There were also significantly more unconsumed components discarded by spiders after feeding on female flies than on males (t_{15} = 2.71, p = 0.02).

Because male and female flies differed in total size, we wanted to determine if the treatment differences were due to differences in size or differences in nutritional concentration between male and female prey. So, we calculated the concentration (i.e., mg of nutritional component per 100 mg of dry prey mass) of consumed lipid, protein, other nutrients and unconsumed parts in prey. After controlling for prey size, spiders consumed 27 mg of lipid per 100 mg dry weight of female flies but only 15 mg of lipid per 100 mg dry mass of male flies (t_{27} = 10.58, p < 0.001; Fig. 1). However, spiders were able to extract a higher concentration of protein from male flies compared to female flies (t_{27} = 7.45, p < 0.001; Fig. 1). There was no difference in the concentration of other nutrients extracted (t_{27} = 1.24, p = 0.23) or of unconsumed parts remaining following feeding (t_{27} = 0.26, p = 0.80).

Prey feeding level

In intact prey items, well-fed crickets were almost three times heavier than food-limited crickets (t_{16} = 8.27, p < 0.001). As expected from this difference in body
mass, well-fed crickets had significantly higher quantities of all nutritional measures in intact (i.e. whole) prey and in the parts of prey consumed by spiders (all \( t_{15} > 3.50, \) all \( p < 0.005 \); intact prey MANOVA: \( F_{3,21} = 13.33, \) \( p < 0.001 \); edible components MANOVA: \( F_{4,22} = 73.01, \) \( p < 0.001 \); Table 2).

Since prey differed in size, we also examined the relative concentration of consumed lipid, protein, other nutrients and unconsumed parts in prey. Spiders extracted a higher concentration of lipid from the bodies of well-fed crickets (ca 25 mg lipid per 100 mg dry mass) than from food-limited crickets (ca 10 mg lipid per 100 mg dry mass; \( t_{25} = 19.04, \) \( p < 0.001 \); Fig. 2). However, spiders extracted a higher concentration of protein from food-limited cri.cri.ckets than from well-fed crickets (\( t_{25} = 8.06, \) \( p < 0.001 \); Fig. 2). There were no effects of feeding level on the concentration of other nutrients extracted (\( t_{25} = 0.53, \) \( p = 0.60 \)) and of unconsumed parts (\( t_{25} = 1.30, \) \( p = 0.21 \)) of the cricket body.

### Prey developmental status

For intact prey, there was no difference in the dry mass of larval and adult mealworms (\( t_{11} = 0.33, \) \( p = 0.75 \)). However, larval mealworms had more lipid (\( t_{12} = 3.10, \) \( p = 0.009 \)) and less protein (\( t_{13} = 3.22, \) \( p = 0.007 \)) present in their bodies than adult beetles (MANOVA: \( F_{3,16} = 16.74, \) \( p < 0.001 \); Table 2A). In feeding trials, spiders extracted a higher quantity of lipids from larval mealworms (\( t_{13} = 4.61, \) \( p = 0.005 \)) than from adult mealworms (MANOVA: \( F_{4,10} = 72.52, \) \( p < 0.001 \); Table 2B). Spiders left over three times more unconsumed parts from adult mealworms than from larval mealworms (\( t_{13} = 6.60, \) \( p < 0.001 \)). The unconsumed parts from adult mealworms were easily identifiable as large pieces of the elytra, legs and thorax.

In terms of the concentration of nutritional components, spiders extracted higher concentrations of lipid (\( t_{13} = 10.58, \) \( p < 0.001 \)), protein (\( t_{13} = 2.64, \) \( p = 0.02 \)) and other nutrients (\( t_{13} = 2.73, \) \( p = 0.02 \)) from larval mealworms than from adult mealworms (Fig. 3). Spiders

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#### Figure 1

Effects of prey sex on the extraction of nutrients from flies, *Drosophila melanogaster*, by spiders, *Pardosa saltans*. This analysis controls for differences in prey size between treatments. Asterisks indicate statistically significant differences between treatment groups. *\( p < 0.05 \); **\( p < 0.01 \); ***\( p < 0.001 \).

#### Figure 2

Effects of prey feeding level on the extraction of nutrients from crickets, *Acheta domestica*, by spiders, *Rabidosa rabida*. This analysis controls for differences in prey size between treatments. Asterisks indicate statistically significant differences between treatment groups. *\( p < 0.05 \); **\( p < 0.01 \); ***\( p < 0.001 \).
left a higher mass of unconsumed parts when feeding on adult mealworms than on larval mealworms (t13 = 0.21, p < 0.001).

**Extraoral digestion and the extraction of nutrients**

We also conducted analyses to compare the amount of lipid and protein present in prey items with what was actually extracted by the spiders (Fig. 4, 5). Prey sex (F1,40 = 0.78, p = 0.38), feeding level (F1,36 = 1.84, p = 0.18) and developmental status (F1,19 = 0.10, p = 0.76) did not affect the proportion of available lipid that was extracted by spiders (Fig. 4). There was no effect of prey sex on the proportion of available protein that was extracted (Fig. 5A; F1,40 = 0.28, p = 0.60). However, there was a non-significant tendency for spiders to extract a higher proportion of the available protein from food-limited crickets than from well-fed crickets (Fig. 5B; F1,36 = 3.55, p = 0.068). Spiders also extracted a significantly higher proportion of available protein from larval mealworms than from adult mealworms (Fig. 5C; F1,19 = 30.51, p < 0.001).

**Discussion**

Individuals of a single species of prey can vary in nutritional quality depending upon their sex, feeding level and developmental status. Female flies were larger than male flies (as is the case in many species of insects; Shine 1989) and females had a greater quantity of nutrients in their bodies and a greater quantity of nutrients that could be extracted by spiders. In our experiment, well-fed crickets were larger than food-limited crickets and well-fed crickets had more nutrients in their bodies and more nutrients that could be extracted by spiders. While sex and feeding level are known to affect the size of insects, this is the first evidence that these size differences translate into differences in nutritional content both in whole prey and what is extracted by spiders. In addition, our data demonstrate that the scaling of nutrients is not necessarily proportional to prey size differences. For example, well-fed crickets were three times heavier than food-limited crickets but they had seven times higher lipid content (Table 2A).

While sex and feeding level may affect absolute size of prey, the relative concentration of nutrients in prey from each treatment is also important because spiders need to consume many of these prey items over the course of their lifetime. After controlling for differences in body size, male prey and well-fed prey had a relatively higher proportion of lipid and lower proportion of protein than male and food-limited prey, respectively. In terms of developmental status, larval mealworms were clearly higher quality prey for predators because they contained a higher amount of all nutrients measured (i.e. lipid, protein and other nutrients) and a lower amount of unconsumed parts. Hence, sex, feeding level and developmental status all affected prey quality (i.e. the relative concentrations of lipid and protein) but, in some cases, whether or not one prey item or another is of higher quality may depend upon the nutritional needs of the predator (i.e. whether the predator is lipid- or protein-limited). Intraspecific variation in prey quality may be an underappreciated yet important factor affecting predator nutrition, especially in habitats dominated by one species of prey or at times of year when one species of prey is especially abundant.

The nutritional quality of prey is often examined by measuring the amount of nutrients in whole prey...
items (Matsumura et al. 2004, Fagan and Denno 2004, Rickers et al. 2006). However, species that feed using extraoral digestion do not consume the entire prey item but, rather, extract edible portions of the prey and discard other parts. Even predators that ingest an entire prey item likely do not assimilate the entire prey but, rather, extract bioavailable components and egest the rest. Our results show that for lipid content, the amount of lipid extracted using chloroform extraction is almost identical to the amount of lipids that are ingested by spiders (Fig. 4). Hence, lipid measurements from whole prey may be a reasonable estimate of the amount of lipids that spiders consume from prey. However, this may not be the case for nitrogen content. For prey feeding level there was a nonsignificant trend ($0.05 < p < 0.10$) for spiders to extract a greater proportion of the available nitrogen from food-limited than well-fed prey (Fig. 5). For prey developmental status, spiders extracted a significantly higher proportion of available nitrogen from larval than adult mealworms (Fig. 5). Hence, future studies that intend to quantify differences in the nitrogen content of prey should examine ingestion of nitrogen from prey because nitrogen content of whole prey is not necessarily proportional to nitrogen consumed by spiders (e.g. some indigestible compounds such as chitin contain nitrogen).

A discrepancy between whole prey items and what is actually consumed by predators may occur frequently in predator–prey interactions as many species of predators do not consume entire prey items. For example, mammalian predators (e.g. felids and canids), avian predators (e.g. falcons, eagles and hawks), and some reptilian predators will tear off muscle and organ tissue from a prey item and leave behind bone, hair and skin. The feeding mode of some predators involves complete ingestion of prey items, due to a lack of teeth or appendages to tear off pieces of prey, such as in predatory fish, amphibians, snakes and some birds (e.g. kingfishers, pelicans and penguins). However, even when prey are entirely ingested by predators, not all parts of prey may be digested or assimilated. Undigested parts of prey (e.g. hair, bones, chitin) can frequently be identified in the egested pellets of owls or the feces of mammalian predators (Putman 1984). More generally, studies of predator consumption and prey nutritional quality need to consider the inedible or indigestible fractions of prey because the nutritional content of these parts (e.g. carbon and nitrogen in chitin, or calcium and phosphorus in bone) is not biologically available to all predators and should then not be included in measures of the nutritional quality of a prey item.

A number of studies have documented that different species of prey can differ in their quality for predators (Toft and Wise 1999, Oelbermann and Scheu 2002, Rickers et al. 2006). However, variation in quality within a single species of prey has received far less attention in the literature and the relative importance of inter- and intraspecific variation in prey quality is unclear. Our results provide a preliminary comparison into the relative magnitude of inter- and intraspecific variation in prey quality. The average lipid content for species of prey used in this experiment (flies: 21%, crickets: 18%, and mealworms: 20%) did not vary much among species and does not differ much from the mean lipid content of published values for 72 species of insects from eight families (23$\pm2$% lipid; Bernard and Allen 1997, Ramos-Elorduy et al. 1997). However, there was slightly more variation in the mean protein content of our prey species (flies: 40%, crickets: 53%, and mealworms: 36%). Interestingly, the difference between the highest and lowest mean percent protein for our study species (flies – mealworms = 17$\%$ difference) is very similar to the difference in protein content between food-limited and well-fed crickets (16$\%$ difference; Fig. 2). Hence, although we have a limited set of study species, the variation in prey quality within individuals of a single species (i.e. food-limited vs well-fed crickets) in our study was just as large as variation in prey quality among species (i.e. crickets vs mealworms). Further research on a wider range of species is needed to examine the relative importance of inter- and intraspecific variation in prey quality in nature.

A great deal of research has examined nutrient limitation in aquatic systems and revealed the conditions under which primary production and herbivores in different systems are limited by nitrogen and phosphorus.
(Howarth 1988, Sterner and Hessen 1994, Sterner and Elser 2002). However, far less is known about nutrient limitation in terrestrial predatory invertebrates. Observational data suggest that predatory arthropods have a higher concentration of nitrogen in their bodies than herbivorous prey items (Fagan et al. 2002, Fagan and Denno 2004, Matsumura et al. 2004). These data have been used to suggest that predatory arthropods are nitrogen limited in nature by arguing that predators need to consume food with a concentration of nitrogen similar to that of their own body (Denno and Fagan 2003, Fagan and Denno 2004). However, an alternate explanation for higher nitrogen concentrations in predators is that this reflects general food-limitation of predators in nature and, consequently, low levels of lipid content (i.e. carbon) in their bodies. This alternate interpretation suggests that predatory arthropods are carbon (i.e. energy) limited in nature and need to consume prey with higher lipid content. Energy limitation certainly appears to be important for some predatory species as seen by the effect of carbohydrate supplementation on the behavior and growth of some predatory ant species (Davidson 1997, Grover et al. 2007, Helms and Vinson 2008). Experimental studies utilizing artificial diets and prey manipulations in the laboratory and field are needed to provide insight into nutrient limitation in a range of predatory arthropods in nature. A ‘geometrical approach’ such as that used in Raubenheimer et al. (2007) may be particularly useful in examining nutrient limitation in predatory arthropods because it allows one to identify the target intake level of nutrients that predators seek to consume in their diet and a fitness landscape of performance on diets with different nutrient combinations (Raubenheimer and Simpson 1999, Simpson and Raubenheimer 1993, 1995).

Recent research suggests that the nutrient content of prey items may have an important impact on the life history, ecology and evolution of predatory arthropods (Sterner and Elser 2002, Fagan et al. 2002, Denno and Fagan 2003, Fagan and Denno 2004). However, much more research needs to be done to identify which nutritional constituent (or combination of constituents) affects the development and reproduction of predators and the mechanisms through which these effects are mediated. In addition, while many studies have identified fitness effects of consuming different prey, these studies need to be combined with studies of nutrient extraction and assimilation by predators to provide greater insight into what predators are actually consuming from prey. This is especially important for predatory arthropods that use extraoral digestion and discard some parts of prey. However, it may also be important for species that consume entire prey because these species could differentially assimilate or egest certain prey components. Integrative studies combining behavioral, life history and physiological approaches in the laboratory and field will greatly advance our understanding of the role of nutrients for predatory arthropods.

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References


