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Predators buffer the effects of variation in prey nutrient content for nutrient deposition

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Oikos
128: 360–367, 2019
doi: 10.1111/oik.05685

Subject Editor: Jotaro Urabe
Editor-in-Chief: Dries Bonte
Accepted 3 September 2018

Predator feeding behavior and digestion regulate the flow of nutrients through ecosystems by determining the fate of prey nutrients. Most predators feed on a diversity of prey items, which differ widely in traits including their nutrient content. Yet, relatively little is known of the mechanisms through which variation in prey nutrient content affects the form by which nutrients are deposited into the environment. The overall goal of this study was to test how variation in the nutrient content of prey affected the fate of nutrients following predation by an arthropod carnivore, the Carolina wolf spider *Hogna carolinensis*. We manipulated the macronutrient content of prey by varying the diet on which crickets were fed to produce prey treatments that differed in lipid and protein content. Nutrients were measured as both macronutrients and elements in prey and elements in excreta. We found that there was no effect of diet treatment on the amounts of elements or macronutrients in prey carcasses and excreta despite significant variation in the nutrient content of those prey. This is in contrast to studies of some aquatic systems where mass balance by consumers results in variation in excreta content depending on the nutrient content of food. Wolf spiders assimilated the majority of prey nutrients and deposited relatively small and similar amounts of nutrients following feeding. Hence, while prey can vary widely in nutrient content, our findings suggest that this variation has little effect on the amounts of nutrients deposited by predators.

Keywords: nutrient deposition, prey quality, elements, macronutrients, carnivores

Introduction

Predators regulate resource transfer, trophic interactions, and ecosystem function, including nutrient deposition and mineralization (Schmitz 2007, Hawlena and Schmitz 2010, Schmitz et al. 2010, Hawlena et al. 2012). For example, bears can transfer significant amounts of nutrients from salmon to surrounding terrestrial habitats (Hilderbrand et al. 1999), excreta of seabirds can be a major source of nutrients on islands (Anderson and Polis 1999), and predation risk by spiders can shift the nutrient

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composition of grasshoppers and, ultimately, decomposition processes (Hawlena et al. 2012). However, while studies have shown that predators affect nutrient flows in ecosystems, less remains known about the mechanisms through which predators have these effects.

Predators regulate biogeochemical processes in ecosystems by determining the fate of prey nutrients. Digestible nutrients such as lipid and protein are ingested, digested, and either accumulated into biomass, excreted or respired. Other parts of prey such as structural compounds in the skeleton are either discarded following feeding or deposited in feces. Some of these forms of nutrients may be more readily utilized by microbes, decomposers and primary producers (e.g. excreta) while others may take years to decompose (e.g. prey exoskeleton; Seastedt and Tate 1981).

One factor that could affect how predators regulate the fate of consumed nutrients is the chemical composition of their prey. Prey vary widely in their chemical composition both within and among species (e.g. 5–30% lipid and 20–80% protein; Fagan et al. 2002, Raubenheimer et al. 2007, Lease and Wolf 2010, Wilder et al. 2013). Previous studies of aquatic systems have shown that mass balance can be used to predict the nutrient content of excreta when consumers feed on different foods (Sterner 1990, Elser and Urabe 1999, Sterner and Elser 2002). For example, consuming food with higher N:P than that found in a consumer's body can result in the production of excreta with higher N content (Sterner 1990, Sterner and Elser 2002). While digestive processing of prey is general to all predators, relatively little is known about its importance and how this process varies when feeding on different prey (Croll et al. 2005, Persson and Svensson 2006, Romero et al. 2006, Sin et al. 2008, Gharajehdaghipour et al. 2016).

Spiders are good candidates for studying how digestive processes of predators affect nutrient deposition. First, spiders feed on an estimated 400–800 million tons of prey per year, which likely translates into a significant amount of nutrients deposited from these prey (Nyffeler and Birkhofer 2017). Second, spiders feed using extraoral digestion, which is a process used by the majority of arthropod predators and allows for easier quantification of digestible versus indigestible components of prey (Cohen 1995, Wilder and Eubanks 2010, Wilder et al. 2013). Finally, previous work has already established the importance of nutrition for spiders and provided a foundation upon which the current work can build to gain greater insight into the digestion and utilization of macronutrients (Wilder 2011, Toft 2013). For example, Jensen et al. (2011a) found that wolf spiders grew larger carapaces on more protein-biased diets and weighed more on more lipid-biased diets and that spiders will regulate their lipid and protein intake when possible (Jensen et al. 2011b). Understanding how prey nutrient content affects the quantity and form through which those nutrients are deposited in the environment will complement previous work on how diet affects predator growth and behavior (Wilder 2011, Jensen et al. 2011a, b).

The overall goal of this study was to test how variation in the nutrient content of prey affected the fate of nutrients following predation (Fig. 1). We produced four prey types that differed in lipid and protein content by feeding cricket prey with varying diets. Nutrients were measured as both macronutrients and elements in prey and prey carcasses, and elements in excreta. Although prey macronutrients are often estimated from conversion factors based on elements (e.g. protein = nitrogen × 6.25; Jones 1941), these conversions do not differentiate between digestible and indigestible forms, such as protein versus N-rich exoskeleton (Wilder and Eubanks 2010). We hypothesized that spiders would ingest and excrete nutrients in proportions similar to their availability in their prey. In other words, we predicted spiders consuming prey with higher protein content would ingest more protein and excrete more nitrogen than spiders fed prey with higher lipid and lower protein.

Spiders were starved for 10 days prior to trials to standardize hunger level. Extensive evidence suggests that spiders including wolf spiders (Nyffeler and Benz 1988, Wise 1993) regularly experience such food deprivation in nature (reviewed by Wise 1993, 2006). For example, field-collected wolf spiders did not differ in body condition from laboratory conspecifics that were completely deprived of food for three months (Wilder and Rypstra 2008). Another field study estimated that two spider species experienced average starvation periods of 4–8 days (Bilde and Toft 1998).

Methods

Study animals

Spiders, like the majority of arthropod predators, feed using extra-oral digestion (Cohen 1995). Nutrients are liquefied, filtered through the mouth and pharynx, digested, assimilated, respired or excreted as nitrogenous by-products (Foelix 2011). Spiders use digestive enzymes to liquefy edible nutrients (e.g. protein and lipid) and discard prey carcasses following feeding (Foelix 2011). Prey carcasses largely consist of indigestible exoskeleton (Foelix 2011).

For this study, 58 mature female Carolina wolf spiders *Hogna carolinensis* were collected from local fields near Oklahoma State University (Stillwater, OK) in summer 2015. From the field, spiders were transferred to laboratory housing of 473 ml plastic deli cups and were fed two, 1.5 cm sized crickets *Acheta domesticus*) twice per week. Crickets used for maintenance feeding were raised in the laboratory on dog food (Rachel Ray Nutrish). A water-soaked cotton ball and paper-towel bedding were changed twice per week. Wolf spiders and crickets were maintained on a constant 25 ± 1°C and 10D:14L light regime.

Cricket diets and feeding trials

We manipulated the nutrient content of crickets by feeding them different diets varying in carbohydrate, lipid and

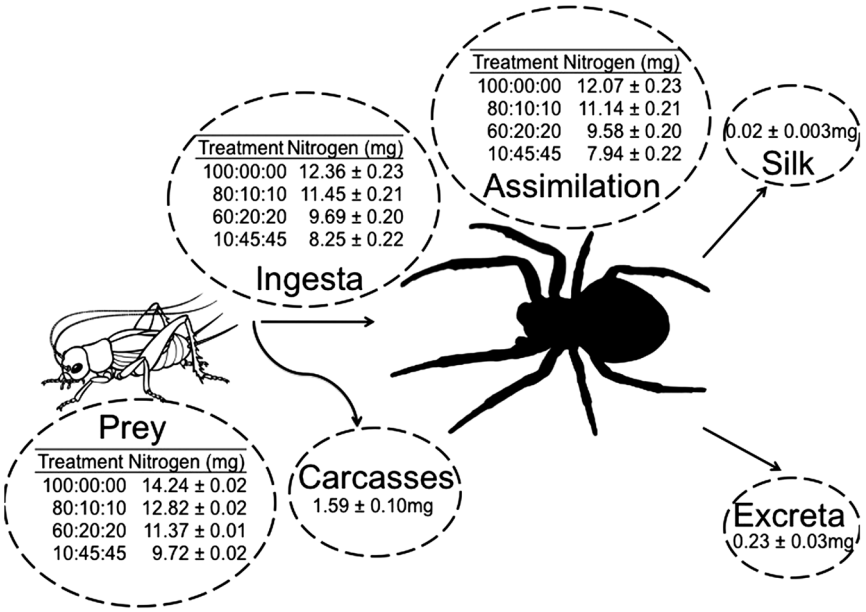

Figure 1. Diagram showing the potential fates of prey nutrients. Nitrogen in prey bodies can be either ingested or deposited as uneaten remains following feeding. Those nutrients that are ingested can then be either assimilated, excreted or deposited as silk. Numbers represent a summary of data from the experiment. Circles with multiple numbers are those compartments where there were significant differences in nutrients between the cricket diet treatments. Circles with only one number are those where there was no significant difference in nutrients between the cricket diet treatments. There was significant variation in the nitrogen content of prey, nutrients ingested by spiders and nutrients assimilated by spiders but there was no significant difference among treatments in prey remains, excreta or silk. Most prey resources were assimilated by spiders rather than deposited.

protein content. Crickets were maintained on specific diets for at least one week before being used as prey. Crickets were maintained on diets varying in protein, lipid and carbohydrate (protein:lipid:carbohydrate) at 100:0:0, 80:10:10, 60:20:20 and 10:45:45 percent (see Table 1 for the composition of the diets). Diets were provided to crickets as a powder. To make the diets, we first combined ingredients in a glass container, then we added enough chloroform to saturate the dry ingredients (i.e. to dissolve the lipid and evenly distribute it among the diet), and finally dried the diets at room temperature to evaporate the chloroform. Crickets were provided water ad libitum, which was replaced at least twice weekly.

Table 1. Composition of artificial diet treatments fed to crickets: 100:0:0, 80:10:10, 60:20:20 and 10:45:45 (protein:carbohydrate:lipid percentages) (in grams).

	10:45:45	60:20:20	80:10:10	100:0:0
Egg white	11	89	120	137
Micellar casein	11	89	120	137
Sugar	55	20	7	0
Flour	85	35	14	0
Cellulose	94	51	33	26
Nipagin	1	1	1	1
Vitamin (capsule)	1	1	1	1
Cholesterol	0.5	0.5	0.5	0.5
Fish oil	3	3	3	3
Lard	22	8	3	0
Olive oil	22	8	3	0

Periodically, we collected crickets from each diet to analyze their nutrient content. Prior to analysis of cricket bodies for nutrient content, representative crickets from each treatment were killed via chilling and stored in a freezer, then dried at 60°C for 24 h and weighed.

To standardize feeding level in the trials (Wilder and Rypstra 2008), each wolf spider was starved for 10 days, assigned to a cricket diet treatment, and placed in a 710 ml glass container with a glass fiber substrate. The glass fiber filter used as a substrate in the arenas had the texture of paper and provided a surface for collecting spider excreta that contained no carbon or nitrogen itself. To reduce experimenter bias, spiders were assigned to treatments using a random number generator. A control chamber containing filter paper but no spider was also run alongside each cohort of spiders to test if handling of the paper resulted in C or N contamination, which it did not. To intersperse potentially confounding environmental effects, spider cohorts were rotated within the shelving unit once a week. The experiments were conducted in a room with constant temperature at 25 ± 1°C and 10D:14L light regime.

The wolf spiders were fed two crickets from their assigned treatment group, twice per week, for two weeks. During these feeding trials, prey remains, silk and excreta were collected. Cricket remains were collected from the spider chambers after 24 h using alcohol-sterilized tweezers, deposited in centrifuge tubes, and frozen. Spiders typically finished feeding on prey within 6 h. Silk was removed from the spider

containers weekly by wrapping it around a pair of alcohol-sterilized tweezers, depositing it in centrifuge tubes, and placing them in the freezer.

Several measures of excreta, including total excreta area, individual excreta mass, and density of excreta per unit area, were collected. The experimental chambers were photographed weekly for digitization of the area (cm^2) of spider excreta using ImageJ 1.48v (National Inst. of Health, USA). Excreta tended to spread outward from the point of deposition as it dried. ImageJ was used to trace around the perimeter of each excreta. Counts of all excreta were also calculated. A hole-puncher was used to cut reference (i.e. glass filter only) and filter with excreta samples after pictures were taken. Excreta-free cutouts from spider containers served as within-treatment references. The masses of glass filter paper containing wolf spider excreta were deducted from the mass of similarly sized blank glass filter paper. Then, the density (mass of excreta per unit area of paper) was multiplied by the total digitized area of excreta and multiplied by the proportion of nitrogen to estimate the mass of excreted nitrogen.

Nutrient analyses

We froze the cricket remains, silk, and excreta following collection. Crickets and remains of crickets following feeding were randomly split between macronutrient and elemental analyses. All silk and excreta were run in elemental analysis. We measured lipid content as the difference in mass before and after sequential soaking and extraction in chloroform over the course of three days (Wilder et al. 2013). Protein content was determined in triplicates using the Bradford Assay on lean, ground samples (Wilder et al. 2013). Although we manipulated the amount of carbohydrates present in cricket diets, nutrient analysis of cricket body composition did not measure carbohydrates as they are typically present in arthropods at low concentrations (Raubenheimer and Rothman 2013). Crickets, like other omnivores, either metabolize or convert ingested carbohydrate to lipid reserves and do not use carbohydrates as a storage molecule in the body (Klowden 2013). Crickets, predation remains, silk and spider excreta were evaluated for carbon and nitrogen content. The percentages present were quantified from combustion in an elemental analyzer.

Nutrient ingestion was estimated by first calculating the expected nutrient content of prey fed to spiders using the wet mass of the prey and data from control prey items (i.e. linear regressions of wet mass versus nutrients). The nutrient content of prey remains was then deducted from the initial amount of nutrients present in the prey fed to the spiders to calculate the amount of nutrients ingested.

Statistical analysis

We tested if variation in the macronutrient content of prey (four treatments) affected amounts (mg/100 mg prey) of resources ingested, egested, excreted and silk produced by the wolf spiders. To meet the assumptions of parametric statistics, percentage datasets were logit transformed. Multivariate analysis of variance (MANOVA) was first used to determine if there was an overall effect of the diet treatments on multiple responses. Following significant MANOVA effects, individual ANOVAs were run for each response variable. Statistics were assessed using JMP 12 software package (SAS Inst.).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2qj6g41> (Barnes al. 2018).

Results

Prey content

We found significant differences in the lipid (ANOVA; $F_{3,51}=21.81$, $p < 0.0001$) and protein (ANOVA; $F_{3,51}=26.27$, $p < 0.0001$) content of crickets fed the different experimental diets, which confirmed the effectiveness of our diet manipulation treatments (Fig. 2A). Crickets fed the highest protein food had the highest protein in their body and crickets fed the highest carbohydrate and lipid food had the highest lipid content in their bodies. Additionally, elemental analysis showed significant differences in nitrogen (ANOVA; $F_{3,54}=39.20$, $p < 0.0001$) and carbon (ANOVA: $F_{3,54}=16.75$, $p < 0.0001$; Fig. 2B) among cricket treatments. Carbon content of crickets was higher in the higher carbohydrate and lipid diets, while nitrogen content was greatest in the higher protein treatments. The mean wet mass of crickets fed to spiders was highest in the 60:20:20 treatment, lowest in the 100:0:0 treatment and intermediate in the other treatments (ANOVA; $F_{3,54}=4.28$, $p=0.009$). Yet, the dry mass of crickets fed to spiders did not differ significantly among the diet treatments (ANOVA; $F_{3,50}=2.68$, $p=0.06$), which suggests that crickets differed in water content but not total amount of nutrients provided to spiders.

Wolf spiders mass

The initial wet mass of spiders before receiving their experimental diets did not differ among treatments (ANOVA; $F_{3,55}=1.01$, $p=0.40$). Further, the mean wet masses of spiders on prey treatments did not differ after the first week (ANOVA; $F_{3,53}=2.35$, $p=0.08$) or final week of feeding (ANOVA; $F_{3,51}=1.52$, $p=0.22$). The mean change in mass between start to completion of the feeding trials did not differ by treatment (ANOVA; $F_{3,52}=0.35$, $p=0.79$).

Ingestion

From the MANOVA, we found a significant effect of prey treatment on the fates of nutrients (MANOVA; $F_{12,64}=15.36$, $p < 0.0001$). We found that spiders fed higher lipid prey ingested more lipid (ANOVA; $F_{3,27}=136.92$, $p < 0.0001$) and spiders fed higher protein prey ingested more protein

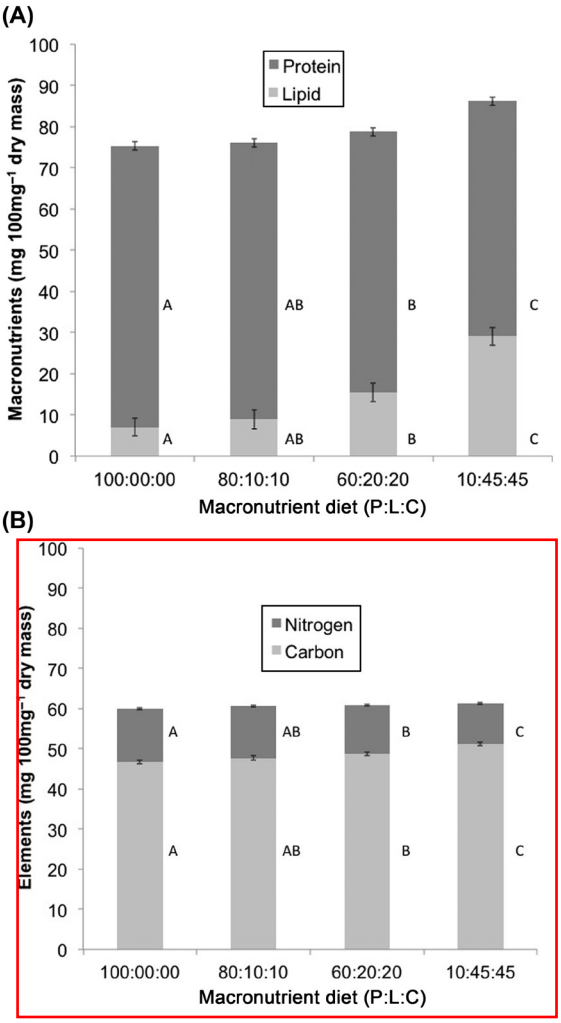

Figure 2. Macronutrient (A) and elemental (B) composition of crickets on artificial diet treatments (protein:carbohydrate:lipid percentages) (Mean ± 1 SE). Bars with different letters were significantly different from each other in post hoc analyses.

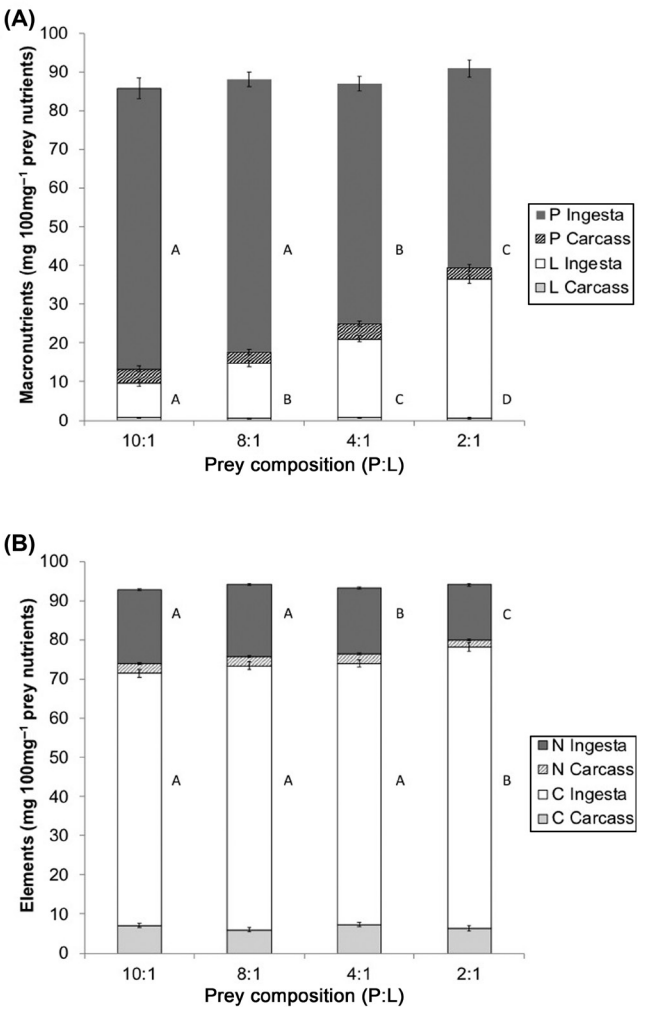

Figure 3. Prey macronutrients (A) and elements (B), relative to the total prey nutrients, in the wolf spider's cricket prey remains and ingesta by prey composition (protein:lipid from Fig. 2A). (mean ± 1 SE). Bars with different letters were significantly different from each other in post hoc analyses.

(ANOVA; $F_{3,27}=15.72$, $p<0.0001$; Fig. 3A). The MANOVA also indicated that prey treatment affected elemental fates (MANOVA; $F_{12,106}=71.52$, $p < 0.0001$). There were differences in nitrogen (ANOVA; $F_{3,43}=77.68$, $p < 0.0001$) and carbon ingestion (ANOVA; $F_{3,43}=8.97$, $p=<0.0001$; Fig. 3B). The ingestion of carbon by spiders was greatest when fed high lipid prey and nitrogen ingestion was highest when fed higher protein prey.

Prey remains

There were no effects of diet treatments on lipid (ANOVA; $F_{3,27}=0.56$, $p=0.65$) or protein (ANOVA; $F_{3,27}=0.60$, $p=0.62$; Fig. 3A) remaining in the prey carcass. There was very little lipid and protein remaining in the carcasses when they were discarded by the spiders (e.g. typically less than 5% of the amount present in whole prey; Fig. 1). Similarly, we did not detect a ifference in the carbon content of prey carcasses between the treatments (ANOVA; $F_{3,43}=1.46$, $p=0.24$; Fig. 3B), but egested nitrogen was greater in the highest protein diet treatment than the lowest protein diet treatments (ANOVA; $F_{3,43}=3.22$, $p=0.03$).

Silk

The quantity and composition of silk produced by wolf spiders did not differ by prey treatment. Overall, silk production was low, as might be expected for wandering spiders (Fig. 1). The mass of silk produced by spiders did not differ by prey diet treatments (mean= 0.62 ± 0.13 mg; ANOVA; $F_{3,39}=1.05$, $p=0.38$). Proportions of nitrogen (mean = 10.2 ± 0.53 mg 100 mg^{-1} silk) and carbon (34.9 ± 1.37 mg 100 mg^{-1} silk) in silk did not differ between the prey treatments (ANOVA; $F_{3,17}=0.77$, $p=0.53$ and $F_{3,17}=0.05$, $p=0.99$, respectively).

Excretion

The content and quantity of nutrients in the wolf spider excreta did not differ by prey diet (Fig. 1, 4A–B). The number of excreta produced (mean= 12.36 ± 0.98 excreta per spider) did not differ between prey treatments (ANOVA; $F_{3,46}=1.58$, $p=0.21$), but was linearly related to the area of excreta (regression; $F_{1,49}=9.01$, $p=0.004$, $R^2=0.16$). Regardless of prey diet, wolf spider nitrogen and carbon content within spider excreta were not significantly different among treatments (ANOVA; $F_{3,30}=1.70$, $p=0.19$ and $F_{3,30}=0.84$, $p=0.48$, respectively). The data for elemental content of excreta included three data points with much higher nitrogen and carbon content than the rest of the data set, which contributed to higher SE in the data. If these three data points are excluded, there is still no significant effect of treatment on nitrogen and carbon content of excreta (ANOVA; $F_{3,27}=0.87$, $p=0.47$ and $F_{3,27}=0.25$, $p=0.86$, respectively).

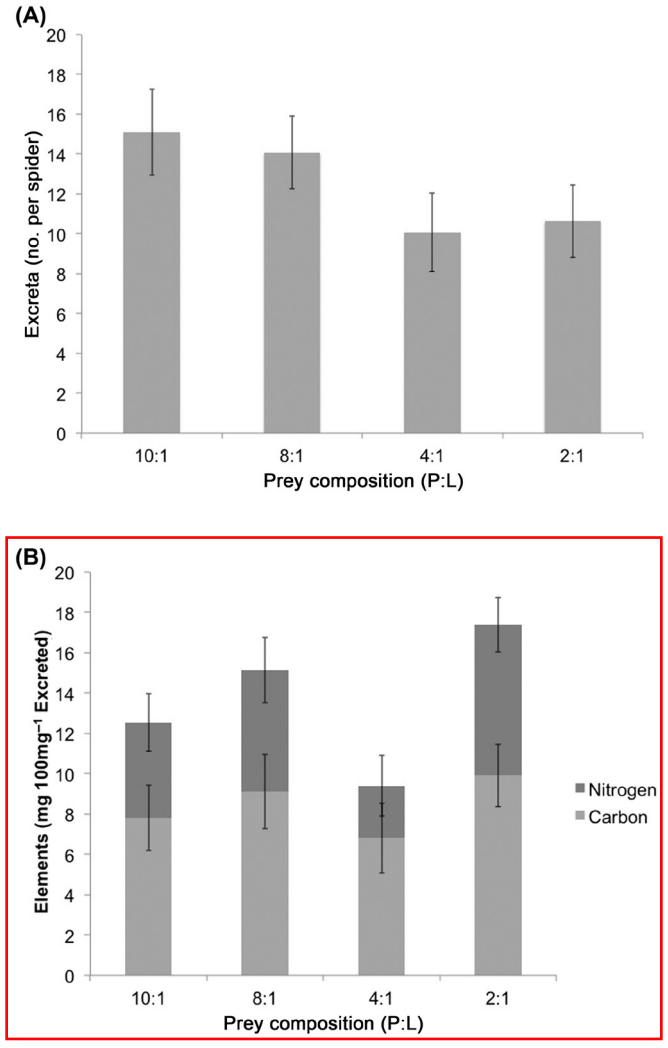

Figure 4. Quantity (A) and elemental composition (B) of excreta produced by wolf spiders fed prey of different composition (protein:lipid from Fig. 2A) (mean ± 1 SE).

Discussion

In nature, prey vary widely in elemental and macronutrient content (Fagan et al. 2002, Wilder et al. 2013). Our results show that predator assimilation buffers the effects of variation in prey nutrient content for nutrient deposition following predation. Regardless of the initial nutrient content of prey, spiders deposited the same amounts of C and N in prey carcasses, silk, and excreta (Fig. 1). We found that wolf spiders on higher protein diets ingested higher protein and nitrogen than wolf spiders on higher lipid diets. But, there was no effect of prey nutrient content on the amount of nutrients or elements in prey carcasses and excreta, and both of these products comprised a small proportion of total prey nutrients (Fig. 1). These results highlight the value of integrating data on digestive physiology into predictions for how predators or other consumers might influence nutrient cycling.

Spiders have often been hypothesized to be food-limited in nature and, hence, may have faced strong selection for efficient extraction and use of nutrients (reviewed by Wise 1993, 2006). In the current study, most of the macronutrients in the prey were ingested by predators (83–88%), rather than deposited in the prey remains. In addition, excreta production was relatively low. We estimate that spiders would immediately return only approximately 16–19% of total prey nitrogen to the patch in which they reside, while the rest (81–85%) would be assimilated. The high relative magnitude of these assimilation estimates is corroborated by other studies of resource assimilation efficiency in arthropod carnivores (81.4% in the wolf spider *Pardosa lugubris*; (Edgar 1971) and 83–90% in damselflies; Lawton 1970). Furthermore, a large proportion of the nutrients deposited by the wolf spiders was in the form of exoskeleton (i.e. prey carcasses), which can take years to decompose (Seastedt and Tate 1981). The food-limited conditions used in our study likely reflect conditions experienced by many spiders and other predators in nature (Wise 1993). Yet under high feeding levels, some spiders have been observed to engage in superfluous killing (i.e. killing but not eating prey) or selective extraction of nutrients from prey (Riechert and Maupin 1998, Mayntz et al. 2005). It is possible that these patterns of nutrient extraction and deposition might differ under higher feeding levels, such as predators feeding on agricultural pests or during outbreaks of prey.

Our results show that combining macronutrient and elemental approaches can help better predict nutrient fates during trophic interactions. Spiders do not consume entire prey items. Rather, they liquefy and ingest soft tissues of prey and discard the indigestible parts (i.e. exoskeleton). As demonstrated in our results, spiders are very efficient at extracting nutrients from prey and discarded prey remains are almost entirely composed of exoskeleton. While exoskeleton has a large amount of C-rich chitin, it can also contain a large amount of N due to cross-linked proteins that are bound in the chitin matrix and, hence, inaccessible to both spiders and our soft-tissue protein assay (Klowden 2013). If we had estimated protein using the standard 6.25 conversion factor,

these estimates would have been approximately 6–15% greater than that of our estimates using the Bradford protein assay, similar to what has been observed in previous research of crickets and other arthropods (Finke 2007). Analysis of elements alone cannot distinguish between N in the soft tissues of prey and N in the indigestible exoskeleton. Yet, the combination of macronutrient and elemental approaches could be used to partition N in prey into protein-N versus non-protein-N, which can then be used to better predict the fate of prey nutrients (e.g. ingested versus egested). Such distinctions may be especially important when examining the diet of predators that feed on diverse prey that vary substantially in exoskeleton composition (e.g. caterpillars versus adult beetle).

Besides prey remains, the other major source of nutrient deposition following feeding is excreta. Our results show that N deposition in excreta is not related to the N or protein content of the spider's meal. Our results are in contrast to previous studies that have shown that dietary nutrient content of food affects the nutrient content of consumer excreta (Sterner 1990, Elser and Urabe 1999, Sterner and Elser 2002). Relationships between nutrient intake and excreta composition are more likely to occur when animals are well-fed and consuming more nutrients than can be utilized in the body. Yet, our experiments were conducted on spiders during the breeding season and under relatively food-limited conditions, as appears to be common for wolf spiders and other spiders in nature (Nyffeler and Benz 1988, Wise 1993, Wilder and Rypstra 2008). A long evolutionary history of food limitation may have selected for spiders to store as many nutrients as possible from each prey, even if it is biased in nutrient content, and to excrete as few nutrients as possible. In addition, producing eggs would provide females with a tissue source into which nutrients can be invested, which may also explain the high assimilation efficiency and low excreta production by spiders in our study. Similarly high assimilation efficiency and low excreta production might also be predicted for juveniles that are actively growing and building tissue.

Our results also show high variation in excreta nitrogen content. We believe this is a function of variation among individual spiders in excretion and not measurement error because: 1) measures of nitrogen in whole prey and prey remains have low variation, which suggests we can measure nitrogen precisely, 2) other measures of spider excretion (i.e. number of excreta produced and area of the substrate covered by excreta) are also highly variable, and 3) subsequent experiments measuring excreta of this species using different methods have found similarly high variation in excreta nitrogen content (Barnes and Wilder unpubl.). Although it is not yet clear why excreta production varies among these spiders, this study showed that excreta comprise a very small component of the overall nitrogen budget of the spiders (i.e. 1.6–2.3 % of total prey N, Fig. 1). Thus, even there had been statistically significant differences, they would likely have little ecological significance.

While the amount of nutrients deposited from individual prey may be small, there still may be situations where spiders or other predators have a significant effect on nutrient cycling. For example, even small deposited amounts of nutrients could have disproportionately large effects on ecosystem processes if they affect the structure and function of microbial communities (Hawlena et al. 2012). For example, in a grassland ecosystem, relatively small changes in the nutrient content of grasshopper carcasses had large effects on carbon mineralization, presumably through their effects on microbial communities (Hawlena et al. 2012). Second, while individual deposits of nutrients may be small, sedentary predators may deposit nutrients in a relatively small area over an extended period of time and, hence, have a significant impact on local nutrient deposition relative to patches without a predator. Finally, spiders may deposit larger amounts of nutrients when they feed on prey larger than can be fully consumed or prey that are over abundant (Samu and Bíró 1993, Riechert and Maupin 1998). Evidence also suggests that some species can preferentially extract particular nutrients from prey to meet their diet requirements, which would result in deposition of carcasses with biased concentrations of unconsumed nutrients (Mayntz et al. 2005). Further research is needed to examine how these and other conditions affect the amount of nutrients deposited by spiders and how these deposited nutrients affect ecosystem processes.

Predators are expected to accelerate nutrient cycling by consuming prey and converting the nutrients in prey tissue to nutrients that are immediately deposited in the environment in forms that may be rapidly incorporated by microbes and plants (Romero et al. 2006, Schmitz et al. 2010). It is important to understand how this effect of predators may be altered by changes in the nutrient content of their food, as prey nutrient content can vary widely within and among species both spatially and temporally (Fagan et al. 2002, Raubenheimer et al. 2007, Lease and Wolf 2010, Wilder et al. 2013). Whether or not predator excretion is affected by variation in the nutrient content of prey has important consequences for understanding how variation in trophic interactions will affect the flow of nutrients through ecosystems. Studies of aquatic systems have shown that mass balance between food and consumer can be used to predict the nutrient content of excreta (Sterner 1990, Elser and Urabe 1999, Sterner and Elser 2002). Yet, the results of the current project demonstrate that spiders only release a small fraction of prey nutrients as excreta and the nutrient content of this excreta is not affected by the nutrient content of prey. Hence, spatial and temporal variation in the nutrient content of prey will have little if any effect on the ratio of nutrients deposited by this spider. In the future, expanded research will be necessary to resolve the consequences of prey nutrient content for predator ingestion and excretion among a wider range of taxa, and whether the pattern observed in the current study represents a special case for spiders or more general differences between aquatic and terrestrial systems.

Acknowledgements – We would like to thank the Wilder Lab group for assistance in the lab and stimulating discussions. We thank Kim Jensen for comments on a previous draft of the manuscript. We are grateful to Punidan Jeyasingh and group for use of elemental analysis equipment. We thank Sue Fairbanks, Sarah DuRant and Punidan Jeyasingh for constructive comments on this paper.
Funding – Funding was provided by the Department of Integrative Biology at Oklahoma State University and European Research Council grant (ERC-2013-StG- 337023 (ECOSTRESS) to DH).

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