Oecologia (2019) 190:1–9
https://doi.org/10.1007/s00442-018-4308-y

HIGHLIGHTED STUDENT RESEARCH

Consequences of prey exoskeleton content for predator feeding and digestion: black widow predation on larval versus adult mealworm beetles

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Received: 17 April 2018 / Accepted: 16 November 2018 / Published online: 26 November 2018

Abstract

Predators often feed on a wide range of prey that can vary in behavior, morphology, and physiology. The net benefits that predators gain from prey are likely related to both prey nutrient content and prey morphology or defenses. For invertebrates, the exoskeleton is a morphological trait that varies widely among species and during ontogeny and could affect nutrient extraction by predators. The goal of this study was to determine how prey exoskeleton content affected predator nutrient intake, assimilation, and excretion by comparing spiders feeding on either larval or adult mealworms of similar size. We found that the proportion of prey energy invested in digestion was greatest in spiders consuming adult mealworm beetles which had higher amounts of exoskeleton than larvae. Further, spiders extracted a greater proportion of elements, macronutrients, and energy from the larval mealworms, which had lower amounts of exoskeleton. Interestingly, total nitrogen content of prey was not a predictor of nitrogen assimilation as spiders assimilated more nitrogen from the larval mealworms, which had lower total nitrogen content. While adult beetles had higher total nitrogen content, their discarded remains of prey had large amounts of nitrogen that was nutritionally unavailable for spiders (i.e., exoskeleton). These results suggest that prey exoskeleton can affect assimilation efficiency by predators, and that a combination of macronutrient and elemental analyses may be needed to examine the quality of prey for predators and the potential consequences of predation for nutrient flows (e.g., consumer assimilation, egestion, and excretion) in ecosystems.

Keywords Nutrition · Exoskeleton · Arthropods · Metabolic rate · Specific dynamic action

Introduction

Many predators are polyphagous and their potential prey can vary in a number of traits including: nutrient content, behavior (e.g., evasion), morphology, crypsis, and toxicity (Denno and Fagan 2003; Fagan and Denno 2004). These traits could impact predator–prey interactions in a number of ways. First, prey traits can affect the ability of predators to locate or subdue prey. Second, prey traits can affect prey choice by affecting the attractiveness of prey to predators (e.g., toxicity). Third, once a prey is captured, prey traits can affect handling time and the ability of predators to efficiently extract nutrients from prey. One factor that could influence prey capture and handling is prey exoskeleton content. Prey can vary substantially in exoskeleton content (9–60% of dry mass) from soft prey (e.g., larval insects such as caterpillars) to heavily sclerotized prey (e.g., beetles; Kaspari and Joern 1993; Lease and Wolf 2010). Prey exoskeleton has been suggested to be a factor that affects the ability of predators to

Communicated by Sylvain Pincebourde.

Arthropods vary widely in quality as prey. We show that exoskeleton content may be animportant factor mediating predator digestion and nutrient assimilation through itseffects on prey quality.

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subdue prey and affect the choice of prey by predators. Yet, less is known about the role of prey exoskeleton content for mediating predator digestion and nutrient extraction.

Many vertebrate and invertebrate predators feed on arthropods. In particular, spiders are among the most abundant and diverse carnivores within terrestrial ecosystems. Spiders also consume a significant amount of prey worldwide, which has been estimated to be 400–800 million tons per year (Nyffeler and Birkhofer 2017). Spiders, like most arthropod predators, feed using extraoral digestion (Cohen 1995). This feeding mode clearly separates undigested parts of prey (e.g., egesta) and excreta and provides a model system for studying how indigestible components (i.e., exoskeleton) of prey affect the ingestion of digestible nutrients. Digestible nutrients (e.g., lipid and protein) are liquefied; filtered through the mouth and pharynx; digested; and assimilated, respired or excreted as nitrogenous by-products (Foelix 2011). Predators that feed using extraoral digestion can be very efficient at liquefying nutrients in the soft tissues of prey, leaving behind uneaten prey remains, which are largely composed of indigestible exoskeleton. The inability of spiders to digest exoskeleton, like many other predators of invertebrates, means that the energy and protein (e.g., cross-linked proteins bound in the chitinous matrix, which can be up to half the weight of exoskeleton) in this compound are not nutritionally available to spiders (Klowden 2013). While previous research has examined the use of digestible nutrients in prey, less well-known are the consequences of prey exoskeleton content for the energetic costs of prey handling, digestion, and nutrient extraction by spiders.

The energetic cost of handling, digesting, and assimilating nutrients has been termed specific dynamic action (SDA). The SDA coefficient refers to the proportion of the total ingested energy that is spent as SDA. Two open areas of research in this area are the physiological factors contributing to variation in SDA and the characterization of SDA in novel organisms (McCue 2006). Although SDA has been investigated in numerous taxa (Jobling 1983; McCue 2006; Secor 2009), studies of SDA in spiders are particularly sparse. Nespolo et al. (2011) was one of the first to measure SDA in spiders and found that spiders do elevate respiration following digestion (i.e., they do have an SDA response). Jensen et al. (2010) studied SDA in wolf spiders and found no effect of prey macronutrient content on spider respiration. Links between metabolism, nutrient allocation, and nutrient flows will likely produce key insights into predator feeding and digestion and its consequences for ecosystems.

The overall goal of this study was to determine how prey exoskeleton content affected nutrient extraction and the metabolic costs of digestion (i.e., SDA) in a predator. We did so by feeding similarly sized larval or adult *Tenebrio molitor* beetles to black widow spider (*Latrodectus mactans*) females, which are generalist, web-building spiders. By using these prey treatments, we were able to test the effects of exoskeleton content (i.e., low in larvae and high in adults) on ingestion, egestion (uneaten remains of prey), assimilation, and excretion while controlling for prey size, species identity, and prey diet (Fig. 1). Further, we measured the metabolic costs of processing a meal (i.e., SDA) using closed-system respirometry. We predicted that spiders consuming prey with a greater amount of exoskeleton (i.e., adult beetles) would extract fewer resources from their prey, leaving a greater proportion of nutrients in the prey remains. We also predicted that SDA would increase with exoskeleton content due to the potentially higher costs of puncturing and sucking nutrients from prey with rigid exoskeletons.

Methods

Study species

Tenebrio molitor larvae were purchased from a commercial distributor (Fluker Farms, Louisiana) and used to create a breeding population that produced a constant supply of larvae and adults. The colony of mealworm larvae and beetles were maintained on a diet of wheat germ and provided potatoes as a water source. The colony was maintained at constant 25 ± 1 °C and 14L:10D light regime.

Female black widows (*Latrodectus mactans*) were collected from residences in Stillwater, Oklahoma, during summer 2016. These spiders produced egg sacs in the laboratory

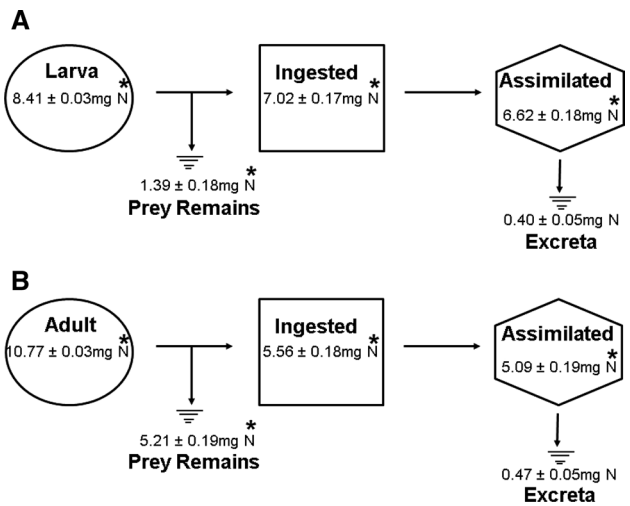

Fig. 1 Diagram showing the fates of mealworm larva (**a**) and adult beetle (**b**) nitrogen, standardized for a 100 mg dry mass prey (circles). Nitrogen in prey can be either ingested (squares) or deposited as uneaten remains of prey following feeding. Those nutrients that are ingested can then be either assimilated (hexagons) or excreted. Nutrient deposition fates (i.e., prey remains and excreta) are indicated by ground symbols. Values are expressed as mean ± SE and asterisks indicate significant differences between prey treatments

and the spiderlings were reared to maturity ($n = 30$). The spiders were maintained at a constant 25 ± 1 °C and 14L:10D light regime in the laboratory. They were lightly misted with water and fed twice per week on vinegar flies (*Drosophila melanogaster*) and crickets (*Acheta domesticus*) of roughly half of each spider's body mass. Once mature, laboratory-reared female spiders were housed in 946 mL (32 oz), clear plastic deli containers. In the field, black widow spiders often feed on Coleopterans (Salomon 2011). All applicable institutional and/or national guidelines for the care and use of animals were followed.

Feeding trials

Our study used a standardized starvation period to clear the spider gut of previous meals. Spiders were fasted for 14 days prior to each feeding trial. In the field, spiders often experience starvation periods greater than 1 week (Bilde and Toft 1998). For example, in another species of spider, body condition of individuals collected from the field was not significantly different from laboratory individuals that were completely deprived of food for 3 months (Wilder and Rypstra 2008). In addition, a starvation period is critical for motivating spiders to feed and ensuring that the results of the study measure maximum extraction ability when feeding on the prey treatments. On day 9 of the fast, we measured spider body masses (± 1 mg) and transferred them to individual metabolic chambers to quantify baseline metabolic rate prior to feeding trials (see below). Spiders were then ordered by decreasing mass; even numbers were assigned to mealworm larvae and odd numbers were assigned to adult beetle treatment groups. This assignment, rather than one designated at random, ensured similarity of spider mass between prey treatment groups. Five procedural control chambers were established the same as the experimental groups, minus the organisms (i.e., prey and spiders absent), to test if handling protocol affected CO_2 readings (which it did not).

Following the 14-day fast, spiders were fed a single pre-weighed prey item (i.e., larval or adult beetle). The wet mass of each larva (80.9 ± 3.2 mg) and beetle (78.0 ± 3.1 mg) was selected from the breeding colony such that there was no difference in mass between the prey treatments ($t_{1,27} = 0.65$, $p = 0.52$). Prey mass in proportion to the spider mass (i.e., relative prey mass) did not differ, either. More specifically, there were no differences between relative prey mass of larvae (25.8 ± 1.9%) and beetles (24.0 ± 1.8%; $t_{1,27} = 70$, $p = 0.49$). The mass of late-development larval insects such as mealworms is often similar to or larger than that of recently eclosed adults as metamorphosis involves the metabolism of a significant amount of tissue for energy.

After prey were introduced, spiders were observed every 3 h and the time at which prey were discarded was recorded. The discarded prey remains were removed and weighed after 9 h to ensure that all spiders had standardized time available to feed on prey. All spiders had finished feeding by 9 h. Excreta production was monitored daily for the next 5 days. When excreta were found in the spider containers, the excreta were collected (see "Nutritional analyses" and the container was exchanged for a clean one. Spiders generally captured prey within 30 s, completed extraoral digestion in 6 h, and produced most of their excreta within 24 h. One black widow failed to feed and was excluded from subsequent analyses.

Metabolic rate

We measured spider metabolism using closed-system respirometry to quantify accumulated CO_2. Use of this measure assumes that spiders in both treatments are using the same substrates for respiration, which is reasonable given that spiders in both treatments were treated identically prior to feeding trials. Respiration, feeding, and excreta production of spiders were monitored within tall 946 mL deli containers with lids modified to include sealable ports. The lower half of each container was lightly abraded with sandpaper to permit climbing and web production, but the upper half was left smooth to minimize climbing and interference with the container ports.

Standard metabolic rate (SMR) of post-absorptive spiders was measured every 12 h (09:00 and 21:00) for the final two consecutive days of the fast. After the spiders were presented with prey, the chambers were re-sealed and respiration measurements were collected at an interval of 3 h for the duration of the next 12 h. All prey were removed at 9 h to prevent decomposition of prey from affecting respiration measurements. Following this sampling duration, measurements were resumed at the 12-h interval for the next 5 days. The 5-day post-feed sampling duration exceeded the time required for metabolic rates to return to baseline.

At the end of each respirometry period, we flushed the metabolic chambers using a small aquarium aerator pump after which we recorded CO_2 levels within each chamber. The experimental groups' chambers were rotated within the shelving unit at the end of each sampling period and locations of individual chambers were randomly assigned to intersperse potential spatial variability within the housing space. Respiration was measured in accumulated CO_2 (ppm) using an Li-840A CO_2/H_2O gas analyzer (LI-COR Biosciences) and converted into percent by dividing by 10,000. To calculate VCO_2, this was then divided by 100 and multiplied by the volume of the container (946 mL). The metabolic rate was calculated as the end minus start (i.e., just after chambers were flushed with the aquarium pump) respiration readings, divided by the sampling duration. We assumed that similar ratios of lipids and carbohydrates were used for sustaining SDA. Metabolic rate was converted to

energy using the conversion factor 24.65 kJ L CO_2^{-1} (Chown et al. 2007).

We characterized multiple components of the post-feeding metabolic profile. The peak VCO_2 was defined as the highest metabolic rate (CO_2 h^{-1}) following feeding. The scope was calculated as peak VCO_2 divided by the baseline SMR. CO_2 production during each time interval was converted to units of energy and summed for calculation of SDA. The end of SDA response was conservatively identified as the time step at which post-feeding respiration was no longer statistically different from the SMR. The SDA coefficient was determined by dividing the ingested prey energy by SDA.

Nutritional analyses

We froze the whole prey, prey remains, and excreta until analyses. Whole prey and remains were then dried at 60 °C for 24 h, bisected, and weighed. Then, each half was randomly assigned to either macronutrient or elemental analysis. Excreta were suspended in 0.1 M sodium hydroxide prior to elemental analysis (Hamdy 1972).

We determined lipid content as change in mass following sequential soaking and extraction in chloroform over the course of 3 days (Wilder et al. 2013). Protein content was determined in triplicate using the Bradford assay on lean, ground samples (Wilder et al. 2013). Protein analysis using the Bradford assay on invertebrates only measured the protein present in the soft tissues of the prey (Wilder et al. 2013). Exoskeleton can have considerable protein content; however, proteins present within the exoskeleton are unavailable to consumers because they are bound within the inedible matrix of chitin. Hence, sclerotized proteins in the exoskeleton are not included in our measures of protein. Carbohydrates were not measured as they are typically present at low levels in arthropods (Raubenheimer and Rothman 2013). Nutrient dry masses were converted to energy using standard conversion factors (protein = 17 kJ/g, and lipid = 37 kJ/g; Raubenheimer and Rothman 2013).

Lipid extracted whole prey, lipid from prey, uneaten remains of prey, and spider excreta were evaluated for carbon and nitrogen content. We removed lipid from prey items before elemental analysis because high lipid content of prey, especially mealworm larvae, can make it difficult to homogenize samples. Hence, to calculate the total carbon content of whole prey we also measured the carbon content of the purified lipids that were extracted from prey and, based on the lipid content of prey, factored this back into the calculation of prey total carbon content. The C and N in samples were quantified from combustion in an elemental analyzer (Elementar Americas, Inc., Mt. Laurel, NJ, USA).

We used wet mass and nutrient content of control larvae and beetles to develop linear regression equations. From the linear equations, we were able to use the wet mass of prey fed to spiders to estimate the masses of each nutrient contained in the prey before it was fed to a spider. Wet mass was strongly related to carbon mass ($F_{1,18} = 68.44$, $p < 0.0001$, $R^2 = 0.79$), nitrogen mass ($F_{1,18} = 43.29$, $p < 0.0001$, $R^2 = 0.71$), lipid mass ($F_{1,18} = 26.40$, $p < 0.0001$, $R^2 = 0.59$), and protein mass ($F_{1,18} = 59.14$, $p < 0.0001$, $R^2 = 0.77$) in larval mealworms. Wet mass was also significantly linked to carbon mass ($F_{1,18} = 163.01$, $p < 0.0001$, $R^2 = 0.90$), nitrogen mass ($F_{1,18} = 672.02$, $p < 0.0001$, $R^2 = 0.97$), lipid mass ($F_{1,18} = 8.49$, $p = 0.0093$, $R^2 = 0.32$), and protein mass ($F_{1,18} = 12.01$, $p < 0.0032$, $R^2 = 0.43$) in adult beetles. Ingesta was calculated as the elements and macronutrients estimated in prey before they were fed on by spiders minus the contents of the prey remains. Elemental assimilation was calculated as the carbon and nitrogen estimated to be in prey before they were fed on by spiders minus the carbon and nitrogen in the prey remains and excreta. Energy assimilation was calculated as the difference in initial prey energy minus energy in prey remains and SDA.

We determined exoskeleton mass from lean (i.e., lipid extracted) whole mealworm larvae and adult beetles. *Tenebrio* were soaked in 8 mL of 0.1 M sodium hydroxide, and sonicated in a hot water bath at 80 °C for 2 h. Sodium hydroxide dissolved the soft tissue in the body (Lease and Wolf 2010). Finally, mealworm larvae and adult beetle exoskeletons were removed, dried at 60 °C, and re-weighed to quantify exoskeleton mass. Exoskeleton content was quantified as exoskeleton mass divided by the dry mass of the prey.

Statistics

Differences in prey mass, nutrient content, and energy were examined using *t* tests and ANOVA in JMP 12 software package (SAS Institute, Cary, NC, USA). The peak, scope (peak divided by baseline VCO_2), and SDA coefficient (elevated metabolic rate energetic expenditure relative to prey energy) were also tested using this software package. The SDA was compared between prey types using repeated measures mixed models MANCOVA in the SAS 9.4 statistics program (SAS Institute, Cary, NC, USA), with spider mass as a covariate. the least squares means of the SMR and post-feeding metabolic rates were plotted from the mixed models MANCOVA. Termination of the SDA was the time step at which respiration no longer significantly differed from the baseline, determined from differences of least squares means post hoc tests.

Results

Prey content

The chemical composition of mealworm larvae and adult beetles differed considerably. Larvae had over three times higher lipid and slightly higher protein than adult beetles. Consequently, mealworms had significantly higher energy content compared to adult beetles (Table 1). Larval mealworms also contained slightly higher carbon and slightly lower nitrogen content than adult beetles (Table 1). Adult beetles had almost twice as much exoskeleton content compared to mealworm larvae (Table 1). However, water content did not differ between adult beetles and mealworm larvae (Table 1).

Macronutrient and elemental digestion

Following feeding, the prey remains of adult beetles weighed significantly more than the prey remains of larvae ($t_{1,27} = -12.44$, $p < 0.0001$). Spiders ingested greater lipid ($t_{1,22} = 17.11$, $p < 0.0001$) and protein ($t_{1,22} = 3.24$, $p = 0.0038$) from mealworm larvae compared to adult beetles (Fig. 2). Spiders left behind a greater amount of protein in prey remains following feeding on adult beetles ($t_{1,22} = -3.74$, $p = 0.01$) compared to larvae, but there was no difference in lipid in prey remains between prey types ($t_{1,22} = 1.04$, $p = 0.31$; Fig. 2). The uneaten remains of adult beetles also contained greater carbon ($t_{1,27} = -5.26$, $p < 0.0001$; Fig. 3a) and nitrogen ($t_{1,27} = -5.22$, $p < 0.0001$; Fig. 3b) compared to those of mealworm larvae. Excreta from black widows fed mealworm larvae and adult beetles did not differ in dry mass of carbon ($t_{1,27} = -0.32$, $p = 0.75$) or nitrogen ($t_{1,27} = -0.08$, $p = 0.94$; Fig. 3a, b). Overall black widow assimilation was greater when feeding on mealworm larvae, compared to adult beetles, in both carbon ($t_{1,27} = 6.08$, $p < 0.0001$) and nitrogen ($t_{1,27} = 2.40$, $p = 0.02$; Fig. 3a, b).

Table 1 Nutritional composition (mean ± SE) of *Tenebrio molitor* larvae and adult beetles, expressed relative to dry mass. Total nitrogen includes content within the exoskeleton

Component	Larvae	Beetles	$t_{1,42}$	p
Lipid (mg)	10.1 ± 0.17	2.9 ± 0.18	29.13	**< 0.0001**
Protein (mg)	23.8 ± 0.43	21.0 ± 0.45	4.49	**< 0.0001**
Exoskeleton (mg)	3.8 ± 0.14	7.2 ± 0.15	− 16.64	**< 0.0001**
Water (mg)	50.7 ± 1.45	47.8 ± 1.38	− 1.47	0.15
Carbon (%)	51.5 ± 0.05	49.0 ± 0.05	37.50	**< 0.0001**
Nitrogen (%)	8.3 ± 0.06	10.7 ± 0.05	− 31.46	**< 0.0001**
Energy (kJ g^{-1})	22.5 ± 0.10	15.5 ± 0.10	67.00	**< 0.0001**

Significant differences between prey types (*t* test) are shown in bold

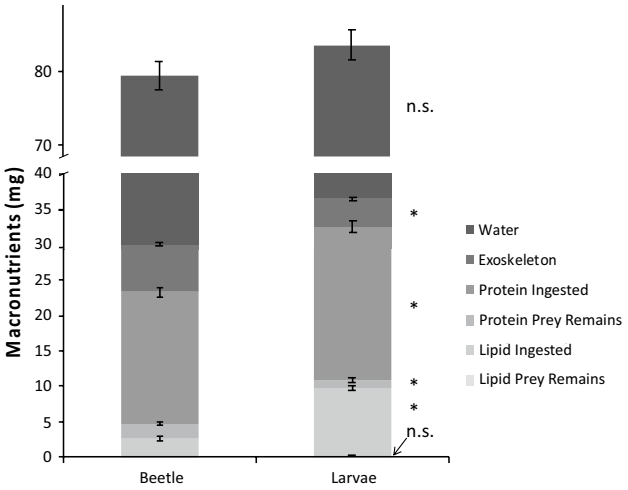

Fig. 2 Partitioning of prey macronutrients (wet mass) by black widows into the spider's prey remains and ingesta by prey treatment. Asterisks indicate significant differences between prey treatments. Lipid content in prey remains was low and non-significant between prey types, indicated by an arrow

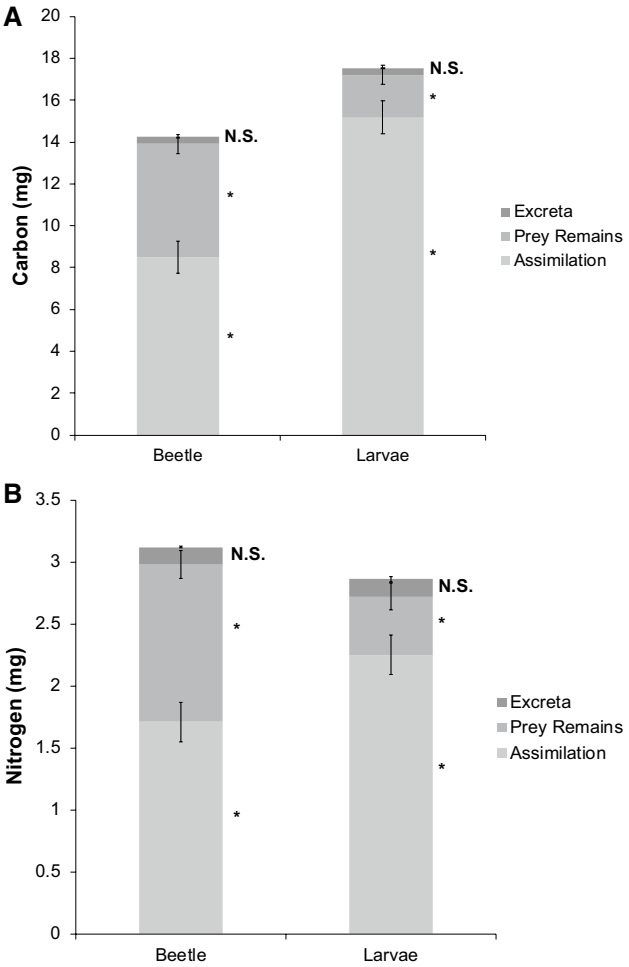

Fig. 3 Allocation of elements within assimilation, prey remains, and excreta by black widows (**a**, **b**). Asterisks indicate significant differences between prey treatments

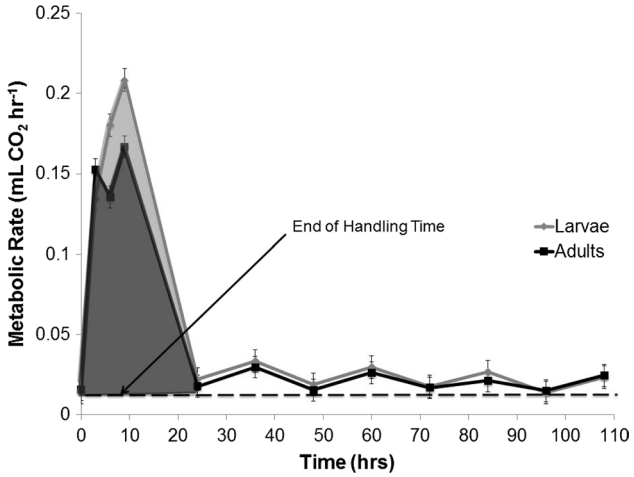

Fig. 4 Digestive metabolic responses in black widows. The metabolic rate at time zero represents the mean SMR over two consecutive days completing the fast, and dashed lines represent the SMR (baseline) extended across the digestive response. Gray profiles represent digestion of *Tenebrio* larvae and black profiles represent digestion of beetles

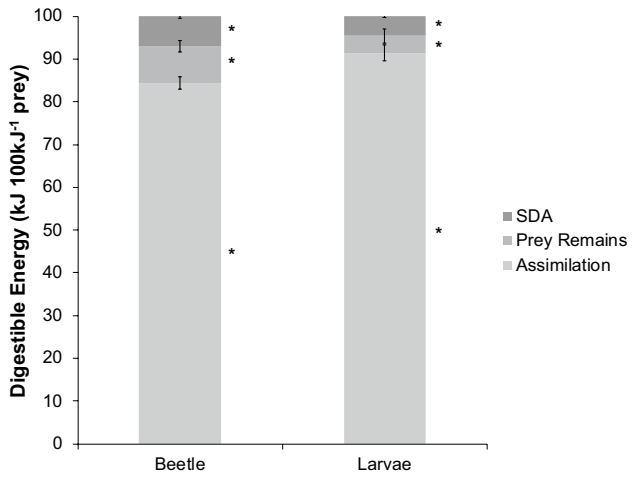

Fig. 5 Allocation of digestible prey energy among assimilation, prey remains, and SDA by black widows. Asterisks indicate significant variation between prey treatments

Digestive energetics

Spider mass ($F_{1,25} = 3.98$, $p = 0.06$) and time ($F_{11,275} = 5.93$, $p < 0.0001$), but not treatment ($F_{1,25} = 1.04$, $p = 0.32$), influenced the black widow post-feeding metabolism profile (Fig. 4). Within this profile, peak metabolism occurred at 9 h post-feeding and was greater in spiders digesting larvae than adult beetles ($t_{1,275} = 4.25$, $p < 0.0001$). Widows fed adult beetles both expended greater proportions of the digestible prey energy on SDA ($t_{1,27} = -3.90$, $p = 0.0006$; Fig. 5) and deposited more energy in prey remains ($t_{1,22} = -2.17$, $p = 0.04$). Consequently, widows assimilated relatively less energy ($t_{1,22} = 2.96$, $p = 0.0073$; Fig. 5) and had significantly higher SDA coefficients (Table 2) when feeding on adult beetles compared to larvae.

Discussion

Ecological stoichiometry predicts that predators may benefit from prey with higher N content (Fagan et al. 2002; Denno and Fagan 2003; Fagan and Denno 2004). Our results did not agree with this prediction. Spiders ingested more N when they fed on the prey, larval mealworms, that had lower total N content in its body. This is because a significant portion of the adult beetles consisted of exoskeleton, which is indigestible to the predators and which can contain significant amounts of N (Klowden 2013; Finke 2007). For prey of a given size, prey types that have more exoskeleton will necessarily have less digestible nutrients. Consequently, spiders that fed on larvae with relatively smaller exoskeleton content ingested more macronutrient, elements, and energy than spiders that consumed adult beetles. Hence, measures that fail to distinguish between indigestible exoskeleton and digestible nutrients (e.g., total elemental content of whole prey) will likely be inaccurate measures of prey quality. Understanding the consequences of prey exoskeleton content for predator digestion and assimilation is important as arthropod prey vary widely in exoskeleton content and many predators feed on a diversity of prey (Kaspari and Joern 1993; Fagan and Denno 2004; Lease and Wolf 2010).

Nutrient currencies and the exoskeleton

While elements did not provide a reliable indicator of prey quality, analysis of macronutrients (i.e., lipid and proteins) in whole prey items provided a better predictor of what would be assimilated versus discarded following feeding by predators. Spiders consumed nearly all lipid and protein in prey and the discarded remains were nearly completely composed of indigestible exoskeleton (Fig. 2). After deducting prey remains and SDA energy from the original prey content, we found that spider energetic assimilation efficiency ranged between 84 and 91% (Fig. 5). Prior attempts have been made to use total nitrogen content of prey as a measure of their nutrient content or quality for predators (Denno and Fagan 2003; Fagan and Denno 2004). Yet, the conclusions of these studies were contradicted by parallel studies that measured the macronutrient content of prey and digestion by predators

Table 2 Metabolic variables (mean ± SE) of black widows fed *Tenebrio molitor* larvae and adult beetles

Component	Larvae	Beetles	*t*	*p*
N	14	15		
Spider body mass (g)	0.3340 ± 0.02	0.3430 ± 0.02	− 0.27	0.78
Prey size (g)	0.0809 ± 0.003	0.0780 ± 0.003	0.65	0.52
Prey size (% body mass)	25.8 ± 1.9	24.0 ± 1.8	0.69	0.50
SMR VCO_2 (mL h^{-1})	0.0139 ± 0.007	0.0156 ± 0.007	− 0.16	0.87
Peak VCO_2 (mL h^{-1})	0.2084 ± 0.007	0.1666 ± 0.007	4.25	**< 0.0001**
SDA duration (h)	24	24		
Scope	15	10.7		
SDA (kJ)	0.04 ± 0.002	0.03 ± 0.002	1.74	0.09
SDA coefficient (%)	4.93 ± 0.50	7.74 ± 0.48	− 4.04	**0.0004**
Handling time (h)	8.36 ± 0.4	8.20 ± 0.3	0.32	0.75
Passage rate (h)	24.0 ± 0	24.0 ± 0	–	–

Significant differences between prey types (*t* test) are shown in bold

(Wilder and Eubanks 2010; Wilder et al. 2013). The current results comparing assimilation based on nitrogen and protein measures explain why previous studies provided different conclusions (i.e., prey vary in exoskeleton content, which can be a significant pool of indigestible nutrients including N). Furthermore, this suggests that further work is needed to better reconcile or combine elemental and macronutrient currencies for measuring nutrients.

Elements are an important currency because they can be followed from individuals to ecosystems throughout the cycle. Yet, elements may not be as useful for predicting variation in feeding preferences and nutrient use efficiencies as macromolecules when food items vary significantly in the amounts of elements (e.g., N) present in digestible (e.g., protein) and indigestible (e.g., exoskeleton) molecules. A way to have the best of both worlds might be to use biochemical measures (e.g., protein and exoskeleton) to quantify different pools of nitrogen (e.g., digestible N versus indigestible N) in prey (Leroux et al. 2012).

Digestion and SDA

The digestive metabolic response of many consumers to various prey types has been investigated (Jobling 1983; McCue 2006; Secor 2009). In previous studies of prey types, "hard-bodied" prey (e.g., *Zophobas* beetle larvae with chitinous exoskeletons) were generally more energetically costly to digest than "soft-bodied" prey (e.g., *Lumbricus* earthworms) by amphibians (Secor and Faulkner 2002; Secor and Boehm 2006) and reptiles (Britt and Bennett 2008). That is, consumers experienced greater SDA (i.e., digestive metabolism), peak metabolism, and duration of SDA when digesting more chitinous prey in these studies. Broadly, greater energetic costs of digestion could also reduce the allocation of limited energy to activity and other budget components (Boggs 2009). Such costs and their consequences on life history should be considered when examining the quality of different prey for predators.

Organisms incapable of chewing, such as black widows, may require greater effort to puncture or suck contents from within the relatively rigid arthropod prey exoskeleton that do not readily collapse as nutrients are removed. Black widows would therefore be predicted to have increased handling costs reflected by SDA. However, only peak digestive respiration and SDA coefficients (i.e., proportion of energy expended on digestion to meal energy) differed between prey treatments. The spiders did not differ in handling time between mealworm larvae or adult beetles. The end of prey handling time generally corresponded with the times at peak respiration (Fig. 4), suggesting that the greatest energetic cost contributing to SDA primarily occurred during extraoral digestion. Interestingly, the observed effect was opposite to our predictions. We predicted greater costs for spiders feeding on prey with greater exoskeleton content, but observed higher peak SDA when spiders fed on the mealworms with less exoskeleton content. The higher peak SDA when feeding on larval mealworms is likely related to the significantly higher amounts of nutrients that spiders consumed from these prey. It is not yet clear if this cost is due to increased prey handling (e.g., greater action of the muscular sucking stomach), greater enzyme production, and/or other costs associated with digesting a larger meal. Regardless of the exact reasons for the higher peak digestive respiration, higher macronutrient ingestion by spiders that fed on larvae can explain the higher SDA coefficients of those spiders. Hence, our findings suggest that the primary consequence of increases in prey exoskeleton content is reduced nutrient intake and not necessarily a large increase in digestive metabolism.

Ecological implications

It is assumed that predators favor prey with light armor because of lower handling costs (Secor 2009). Our findings do not agree with this prediction because black widow spiders that use extraoral digestion did not pay extra handling costs when consuming the armored adult beetles. Yet, we showed that predators using extraoral digestion may still prefer prey items with smaller exoskeleton content just because of their higher content of digestible macronutrients. This consideration should be included in future studies of predator food choices.

The exoskeleton content of prey may affect also nutrient deposition by predators with implications for ecosystem nutrient cycling. Spiders assimilated less and deposited more nitrogen, as both protein and exoskeleton, in prey remains when feeding on prey with higher exoskeleton content. While prey differed in both nutrient content (i.e., larvae had more lipid and protein than adults) and exoskeleton content, the nutrient content of prey appeared to have no effect on feeding and digestion. In both prey types, spiders ingested > 90% of digestible nutrients (i.e., lipid and protein) and most of the prey remains were exoskeleton. Spiders actually left behind slightly more protein in the high exoskeleton prey that had less protein in its body, which is likely due to the difficulty of digesting protein in the prey legs and other parts of the body soft tissue may have been difficult to access. Some spiders can be choosy of nutrients in prey, but this is most likely in situations where prey are abundant (Mayntz et al. 2005). However, abundant data suggest that spiders are often food limited in nature (reviewed in Wise 1993). Our results are similar to findings of other studies of food-limited spiders feeding on prey items. Regardless of the balance of macronutrients in prey (i.e., lipid and protein), spiders ingest nearly all macronutrients and leave behind only exoskeleton (Wilder et al. 2013). Although exoskeleton is slow to decompose, these nutrients likely still, eventually, provide a significant contribution to nutrient cycling in ecosystems—especially, given worldwide estimates of prey consumption by spiders (Seastedt and Tate 1981; Nyffeler and Birkhofer 2017). Hence, in addition to nutrient content of prey, our results suggest that future studies of prey quality and foraging by spiders and other polyphagous predators should also measure and consider the role of prey exoskeleton in the costs and consequences of feeding on different prey.

Acknowledgements We would like to thank the Wilder Lab group for assistance in the laboratory and stimulating discussions. We are grateful to Dr. Punidan Jeyasingh and group for use of elemental analysis equipment. We thank Drs. Sue Fairbanks and Punidan Jeyasingh for constructive comments on this paper. 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).

Author contribution statement CLB, DH, MDM, and SMW conceived and designed the experiments. CLB performed the experiments. CLB and SMW analyzed the data. CLB, DH, MDM, and SMW wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest

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