SULFUR CONTENTS OF SPIDERS AND INSECTS IN DESERT RIPARIAN HABITAT

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Abstract

Sulfur is an essential element in plants and animals. I measured amounts of sulfur in 4 families of spiders and 22 families of insects collected from created riparian habitat next to the Colorado River in western Arizona. Relation between sulfur mass and body dry-mass, S $\mu g = 7.2\,(body\ mg)$, in spiders and insects combined was not allometric. Sulfur concentration, as a mean percentage of body dry-mass, was higher in spiders (1.4%) than in insects (0.65%). Coleoptera contained the lowest sulfur concentration (0.35%) among orders. Sulfur contents also varied among arthropod families but not genera. Similar concentrations of sulfur were measured in insect herbivores (0.64%) and predators (0.73%). Taurine, an amino acid-like compound found in spider venom and silk, likely increased sulfur contents in spiders. Variation in sulfur content among riparian spiders and insects, resulting from concentrations of compounds including taurine, the amino acids methionine and cysteine, and their metabolites, may influence foraging by insectivorous birds.

Key Words: Araneae, Insecta, nutrients, taurine, insectivorous birds

Resumen

El azufre es un elemento esencial para plantas y animales. La cantidad de azufre fue medida en 4 familias de arañas y 22 familias de insectos recogidos de un hábitat ripario creado al lado del río Colorado en el oeste de Arizona. La relación entre la masa de azufre y la masa del cuerpo seco S µg = 7.2 (mg cuerpo), en las arañas junto con los insectos no fue alométrica. La concentración de azufre, como un porcentaje medio de la masa del cuerpo seco, fue mayor en las arañas (1.4%) que en los insectos (0.65%). Los coleópteros contenían la menor concentración de azufre (0.35%) entre las órdenes. El contenido de azufre también varía entre las familias de artrópodos, pero no según el género. Se midieron concentraciones similares de azufre en insectos herbívoros (0.64%) y los depredadores (0.73%). La taurina, un compuesto de aminoácido que se encuentra en el veneno de la araña y la seda, probablemente aumentó el contenido de azufre en las arañas. La variación en el contenido de azufre entre las arañas e insectos riparios, como resultado de las concentraciones de compuestos como la taurina, los aminoácidos metionina y cisteína, y sus metabolitos, pueden influir en el forrajeo de las aves insectívoras.

Palabras clave: Araneae, Insecta, los nutrientes, la taurina, las aves insectívoras

Sulfur (S) is a biologically-essential element that resides primarily in the earth's crust. In contrast to nitrogen (N), another essential element that mostly occurs in the atmosphere, S is taken up by plants primarily as sulfate from decomposed rock. Sulfur forms covalent bonds similar to oxygen, but differs from oxygen by being less electronegative. Biological compounds with S substituted for oxygen are more hydrophobic and more reactive at physiological pH. These properties are evident in 2 amino acids, methionine and cysteine, that contain S and are incorporated into proteins (Brosnan & Brosnan 2006). Methionine increases protein interactions with lipids. Cysteine affects protein shape by producing disulfide bonds within and between polypeptides. Sulfur also occurs in taurine (2-aminoethanesulfonic acid), an amino acid-like compound that is absent in proteins but abundant in varying concentrations in animal tissues (Jacobsen & Smith 1968; Whitton 1987). Taurine primarily inhibits nerve impulses in invertebrates (Jacobsen & Smith 1968) including insects (Hayakawa et al. 1987; Whitton et al. 1988). Most insects require methionine in their diet, whereas cysteine and taurine can be synthesized from methionine (Jacobsen & Smith 1968; Dadd 1973). Metabolites of these compounds also contain S (Jacobsen & Smith 1968; Brosnan & Brosnan 2006). Symbiotes in some insects, such as certain aphids, enable S to be taken up as sulfate (Dadd 1973).

Spiders and insects contain different concentrations of S amino acids, including taurine (Ramsay & Houston 2003). In wolf spiders (Lycosidae), taurine averaged 2.14% of amino acids followed by methionine (1.44%) and cysteine (0.94%). In beetles, methionine averaged 0.82% of amino acids followed by cysteine (0.56%) and

taurine (0.08%). Taurine may be more abundant in spiders due to its presence in silk and venom. Droplets secreted by spiders onto their silk contain various concentrations of taurine and similar S compounds (Townley et al. 2006; Tillinghast & Townley 2008). Taurine is the most-abundant free amino acid in venom of a wandering spider, *Cupiennius salei* Keyserling (Araneae: Ctenidae), and increases venom toxicity (Kuhn-Nentwig et al. 1994, 1998). All juvenile and adult spiders produce silk, and those except Uloboridae produce venom (Foelix 1996).

Concentrations of S-containing compounds in spiders and insects may affect development and reproduction of insectivorous birds (Ramsay & Houston 1998, 2003). Growth and breeding by northern bobwhites (*Colinus virginianus* [L.]; Galliformes: Odontophoridae) appear limited by seasonal concentrations of methionine and cysteine in their diet (Peoples et al. 1994). Blue tits (*Parus caeruleus* L.; Passeriformes: Paridae) preferentially feed spiders to nestlings, providing them with additional taurine (Arnold et al. 2007). Diets of breeding willow flycatchers (*Empidonax traillii* [Audubon]; Passeriformes: Tyrannidae) contained similar proportions of spiders (7.4%) despite inhabiting different plant communities (Wiesenborn & Heydon 2007).

I previously measured concentrations of N, another nutrient essential to birds, in spiders and insects collected in desert riparian habitat created for wildlife (Wiesenborn 2011a), including the willow flycatcher. Here I performed a similar study measuring S concentrations in spiders and insects collected at the same locality. The following questions were examined: (1) Does S mass allometrically increase with body mass? (2) What are the relative contributions of class, order, family, and genus to variation in S concentration? (3) Does S concentration vary among trophic levels in insects?

Materials and Methods

Collecting and Identifying Spiders and Insects

Spiders and insects were collected next to the Colorado River within Havasu National Wildlife Refuge in Mohave County, Arizona. Most arthropods were collected at an irrigated 43-ha riparian restoration area (34° 46' N, 114° 31' W; 143 m asl) of planted or volunteer trees and shrubs 12 km southeast and across the river from Needles, California. Plots were planted during 2003-2005 with cuttings that were taken from nearby areas along the river. The area lies between Topock Marsh (16 km²) and Beal Lake (0.9 km²), 2 impoundments containing mostly emergent cattails (*Typha* sp.; Poales: Typhaceae) and open water. Undeveloped areas of the surrounding floodplain support mostly naturalized tamarisk shrubs (*Tamarix ramosissima* Ledeb.; Caryophyllales: Tamaricaceae).

The floodplain is flanked by Sonoran desertscrub dominated by creosote bush (*Larrea tridentata* [DC.] Cov.; Zygophyllales: Zygophyllaceae). Maximum air temperatures at Needles average 42.7 °C during Jul and 17.7 °C during Dec (DRI 2012).

I collected arthropods from plants and trapped insects in flight. Arthropods were swept with a 38-cm diam muslin net from planted cottonwood (*Populus fremontii* S. Watson; Malpighiales: Salciaceae) and Goodding's black willow (*Salix gooddingii* C. Ball; Malpighiales: Salicaceae) trees, volunteer honey mesquite (*Prosopis glandulosa* Torrey; Fabales: Fabaceae) and screwbean mesquite (*Prosopis pubescens* Benth.) trees, and volunteer arrowweed shrubs (*Pluchea sericea* [Nutt.] Cov.; Asterales: Asteraceae). I also swept arthropods from *T. ramosissima* bordering the plots and narrow-leaved willow shrubs (*Salix exigua* Nutt.; Malpighiales: Salicaceae) along a dirt canal 2 km northwest of the plots. Plant species were swept separately except for *Prosopis* spp., which grew together. Each species was swept 10-15 min on 8 dates: 13, 20, & 27 Jul, 10, 17, 25, & 31 Aug, and 14 Sep 2011. All plant species flowered and fruited except for *P. fremontii*. Arthropods swept from plants were contained in plastic bags and killed in a freezer. Flying insects were captured with a Townes-style Malaise trap (MegaView Science, Taichung, Taiwan) that was elevated 1-m aboveground within a plot of *S. gooddingii* and *P. sericea*. Trapped insects were collected into a dry plastic-bottle containing an S-free, diclorvos insecticide strip. Insects were trapped for 50-95 min during 0740-1450 MST on the same 8 dates.

Spiders and insects in each sweeping were sorted under a microscope into groups of similar-looking specimens. Representatives of each group were placed into 70% ethanol for identification. I counted and split the remaining specimens of each arthropod group into samples with an estimated dry mass of 2-50 mg. Arthropod samples for S analysis were cleaned with a small brush and stored in open shell vials.

Spiders and adult insects except Chrysopidae were identified at least to genus. I assumed nymphal Acrididae to be the same species as adult *Melanoplus herbaceus* Bruner swept from the same *P. sericea* plants, the grasshopper's primary host (Strohecker et al. 1968). Spiders were not differentiated as juveniles or adults, whereas insects were identified as nymphs or adults. Vouchers of spiders were deposited at the California Academy of Sciences, San Francisco, and vouchers of adult insects were deposited at the Bohart Museum of Entomology, University of California, Davis.

Measuring Sulfur Contents

Arthropod samples analyzed for S content were dried, weighed, and digested. They were dried 4 h at 95 °C and weighed (±1 μg) with a

microbalance (C30, Cahn Instruments, Cerritos, California). Dried samples > 2 mg were individually digested in a 23-mL microwave acid-digestion vessel (no. 4781, Parr Instrument, Moline, Illinois). I transferred arthropods into the vessel's inner cup and added 2.5 mL of trace-metal grade nitric acid. Samples with dry mass > 30 mg received 3.0 mL of nitric acid. I placed the vessel into a 700 W microwave oven at full power for 20 sec. After cooling for 30 min, the resulting clear liquid was rinsed from the cup and its cap with water into a beaker. I brought the rinse to 50 mL, or to 60 mL if 3.0 mL of nitric acid was used, with a volumetric flask. Different masses (0.576, 1.240, 1.873, 2.322 mg) of methionine (21.5% S, Acros Organics, Fair Lawn, New Jersey), weighed with the microbalance, and a blank were similarly digested to produce a range of S concentrations (2.5-10 µg/mL) for use as standards.

Sulfur concentrations in digested samples of arthropods were measured against the methionine standards with an Inductively-Coupled Plasma Atomic Emission Spectrometer (Optima 7300 DV, Perkin Elmer, Waltham, Massachusetts) that surveyed light within 180.614-180.730 nm to detect emission from S at 180.669 nm. Light was detected during an automatic read-time (1-5 sec) for each sample and its intensity quantified as the area under the peak. Operating conditions of the spectrometer included radio frequency power = 1.45 kW, outer argon flow = 15 L/min, nebulizer argon flow = 0.6 L/min, and viewing height = 15.0 mm. Arthropods were analyzed in 6 batches of 12-46 samples using the same methionine standards. Linear correlation coefficients between light intensity and calculated S-concentration in methionine standards were > 0.99.

Sulfur concentration, [S], in each arthropod sample was adjusted for variation among batches by using concentrations in an additional digested blank and an undigested, sulfate Standard Reference Material (SRM), containing 10.16 µg S/mL (ERA, Arvada, Colorado), measured across batches:

$$[S]_{\text{sample, adjusted}} = ([S]_{\text{sample}} + [S]_{\text{blank, mean across batches}}$$

$$- [S]_{\text{blank in batch}} \times ([S]_{\text{SRM, mean across batches}} / [S]_{\text{SRM in batch}}$$

Sulfur concentration in the undigested SRM was inflated to an average 13.4 (range 12.9-14.1) µg/mL across batches, indicating that an average 75.8% of S was recovered from the digested methionine standards. Recoveries of S in the arthropod samples were assumed to be the same as in the methionine standards. Adjusted S-concentration was multiplied by final rinse-volume (mL) to calculate S mass (µg). I also calculated %S of arthropod dry-mass in each sample. One sample of the weevil *Coniatus splendidulus* F. with an exceptionally low S content (0.02%) was omitted.

Relating Sulfur Mass to Body Mass

I examined if S mass was allometrically (exponentially) related to body dry-mass in individual spiders and insects. Arthropod mass, and S mass, was divided by the number of specimens in each sample. I selected a subset of samples of the 2 classes (Arachnida and Insecta) with similar ranges of body dry-mass (1-14 mg) to prevent confounding between class and body dry-mass. I regressed (SYSTAT version 12, San Jose, California) log (*S µg*) against log (*body mg*), with class included as a categorical variable, and determined if the slopes differed between classes by testing the interaction of class × log (*body mg*). Following a non-significant ($P \geq 0.05$) interaction, I regressed log (*S µg*) against log (*body mg*) across all samples. Allometry was determined by testing if the regression coefficient $b_1 \neq 1$ (the exponent of *body mg* in the back-transformed, allometric equation) with an approximate t test (Neter et al. 1996). For plotting, S mass and body dry-mass were averaged within genera.

Comparing Sulfur Contents Among Taxa and Trophic Levels

Sulfur contents of arthropod samples were compared between classes and among orders, families, and genera. I transformed S concentrations with $2[\arcsin(\%S/100)^{1/2}]$. Transformed %S was compared between spiders and insects with an analysis of variance. I repeated the analysis and determined if classifying arthropods by order instead of class, by family instead of order, and by genus instead of family, explained more variation in transformed %S with the general linear test approach (Neter et al. 1996). This approach tests if the mean square error in an analysis of variance decreases significantly when the model becomes more complete (with more model *df*).

Sulfur contents of insects were compared among trophic levels. I classified insects as herbivore, predator, or detritivore with descriptions of primary diet. Descriptions included Essig (1926) for Tettigoniidae, Pentatomidae, Formicidae, and the picture-winged fly *Ceroxys latiusculus* (Loew) (= *Anacampta latiuscula*), Cole (1969) for other Diptera, and Borror et al. (1981) for the remaining taxa. Holometabolous insects were classified by larval diet. Herbivores included consumers of pollen, nectar, or homopteran egesta, and predators included parasites. I compared transformed %S among trophic levels with an analysis of variance and between herbivores and predators with a contrast. These comparisons are not independent of those among taxa, because insect taxon and trophic level are confounded. All reported means, and upper and lower bounds of standard deviations, of %S (except in Table 1) are back-transformed.

TABLE 1. SPIDERS AND INSECTS COLLECTED IN RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR SULFUR CONTENT.

Order[1]	Family	Genus	Source[2]	No. Samples	No. specimens per sample	Trophic level[3]	Mean body dry mass (mg)	Mean ± SD %S
Araneae	Araneidae	Eustala	F	1	2	P	2.7	1.1
		Neoscona	E,S	2	1	P	10.8	1.7 ± 0.1
	Thomisidae	Diaea	E,G,S	5	1-3	P	4.8	1.5 ± 0.7
		Mecaphesa	S	2	1	P	4.4	1.0 ± 0.1
		Misumenops	G	2	3-5	P	1.5	1.4 ± 0.2
	Miturgidae	Cheiracanthium	F	1	1	P	2.1	1.2
	Salticidae	Habronattus	E,G,M,P,S,T	18	1-5	P	4.1	1.4 ± 0.3
		Phidippus	E,S	2	1-2	P	7.7	1.4 ± 0.1
		Sassacus	F	1	2	P	1.3	1.3
Orthoptera	Acrididae	Melanoplus[4]	S	16	1	H	19.1	0.78 ± 0.15
	Tettigoniidae	Insara	S	2	1	H	69.6	0.63 ± 0.09
Hemiptera	Pentatomidae	Brochymena	F,P	3	1	P	51.9	0.49 ± 0.10
		Thyanta	E	1	1	H	16.2	0.93
	Reduviidae	Zelus	F,P,S	4	1	P	5.2	0.70 ± 0.37
	Membracidae	Stictopelta	P	2	1	H	15.7	0.59 ± 0.16
	Cicadellidae	Opsius[5]	T	4	3-15	H	0.84	1.00 ± 0.25
	Cixiidae	Oecleus	F,G	2	2-6	H	1.3	0.59 ± 0.01
	Acanaloniidae	Acanalonia	F,G,S	7	1	H	6.1	0.73 ± 0.51
Neuroptera	Chrysopidae	—	F	2	1	P	3.2	0.65 ± 0.27
Coleoptera	Buprestidae	Acmaeodera	P	4	1	H	33.6	0.36 ± 0.06
	Oedemeridae	Oxacis	F	1	1	D	2.0	0.18
	Chrysomelidae	Algarobius	P,S	2	2	H	2.9	0.23 ± 0.13
		Metachroma	E,G	2	1	H	5.0	0.37 ± 0.09
	Curculionidae	Coniatus	T	8	6-24	H	0.92	0.42 ± 0.12

[1]Araneae are juveniles and adults; other orders are adults unless noted.
[2]E, *Salix exigua*; F, *Populus fremontii*; G, *Salix gooddingii*; M, Malaise trap; P, *Prosopis glandulosa* or *P. pubescens*; S, *Pluchea sericea*; T, *Tamarix ramosissima*.
[3]D, Detritivore; H, Herbivore; P, Predator.
[4]Nymphs.
[5]Nymphs and adults

TABLE 1. (CONTINUED) SPIDERS AND INSECTS COLLECTED IN RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR SULFUR CONTENT.

Order[1]	Family	Genus	Source[2]	No. Samples	No. specimens per sample	Trophic level[3]	Mean body dry mass (mg)	Mean ± SD %S
Diptera	Tabanidae	*Tabanus*	F,G,M,S	13	1	P	15.0	0.87±0.16
	Dolichopodidae	*Asyndetus*	M	1	6	P	0.47	0.12
	Syrphidae	*Syritta*	M	3	1	D	2.5	0.35 ± 0.20
	Ulidiidae	*Ceroxys*	F,M	4	1-2	H	4.6	0.79 ± 0.49
	Tachinidae	*Zaira*	M	3	1	P	7.3	0.95 ± 0.02
Hymenoptera	Formicidae	*Formica*	P,S	11	5-19	H	0.82	0.78 ± 0.42
	Tiphiidae	*Paratiphia*	S	1	1	P	4.2	0.63
	Vespidae	*Polistes*	M,P	3	1	P	26.9	0.70 ± 0.13
	Apidae	*Apis*	M	1	1	H	20.6	0.68

[1]Araneae are juveniles and adults; other orders are adults unless noted.
[2]E, *Salix exigua*; F, *Populus fremontii*; G, *Salix gooddingii*; M, Malaise trap; P, *Prosopis glandulosa* or *P. pubescens*; S, *Pluchea sericea*; T, *Tamarix ramosissima*.
[3]D, Detritivore; H, Herbivore; P, Predator.
[4]Nymphs.
[5]Nymphs and adults

RESULTS

I collected 34 samples of 56 spiders in 4 families and 9 genera and 100 samples of 341 insects in 6 orders, 22 families, and 23 genera (Table 1). The most abundant spiders collected were the jumping spiders *Habronattus* (Araneae: Salticidae), with the adults identified as *Habronattus tranquillus* (Peckhams). They were found on 5 of the 6 plant-species swept and in the Malaise trap. The most abundant insects collected were *C. splendidulus*, weevils recently introduced onto *T. ramosissima* in the U.S. (Eckberg & Foster 2011). All insects collected were adults except for the leafhopper *Opsius stactogalus* Fieber, also specific to *T. ramosissima*, and *M. herbaceous*. Body dry-mass of spiders and insects (Fig. 1) ranged from 0.47 mg in the dolichopodid fly *Asyndetus* to 69.6 mg in the katydid *Insara elegans* (Scudder).

Trophic levels of insects (Table 1) included 66 samples of herbivores in 14 genera, 30 samples of predators in 7 genera and Chrysopidae, and 4 samples of detritivores in 2 genera. Most herbivore samples were *M. herbaceous*, *C. splendidulus*, and the ant *Formica xerophila* M. R. Smith. Most predator samples were *Tabanus* deer flies and *Zelus* assassin bugs. The 2 detritivores collected were the wood-consuming, false blister beetle *Oxacis* and the dung-decomposing syrphid *Syritta pipiens* L.

Relation between Sulfur Mass and Body Dry-Mass

Sulfur mass was linearly related to body dry-mass in both spiders and insects. Slopes of transformed S-mass regressed against transformed body-mass did not differ ($F = 0.21$; $df = 1, 75$; $P = 0.65$) between the 2 arthropod taxa. When spiders and insects were combined, S mass and body dry-mass (Fig. 1) were related ($F = 618$; $df = 1, 132$; $P < 0.001$) by log $(S\ \mu g) = 0.86 + 1.024[\log (body\ mg)]$. Body dry-mass explained 82% of variation in S mass. The b_1 coefficient of 1.024 did not differ from one ($t = 0.59$; $df = 132$; $P = 0.56$), signifying that the relation between S mass and body mass was not allometric. Setting $b_1 = 1$ and back-transforming the regression equation produced $S\ \mu g = 7.2(body\ mg)$.

Sulfur Contents Among Taxa and Trophic Levels

Variation in S content among arthropods (Table 1) depended upon taxonomic rank. Sulfur concentrations differed between spiders and insects ($F = 107$; $df = 1, 132$; $P < 0.001$), and these 2 taxa, representing different classes, explained 45% of variation in %S (Fig. 2). Mean S concentrations, as percentages of dry mass, were 1.4% in spiders and 0.65% in insects. Classifying arthropods by order instead of class explained a significant ($F = 6.99$; $df = 5, 127$; $P < 0.001$) proportion of ad-
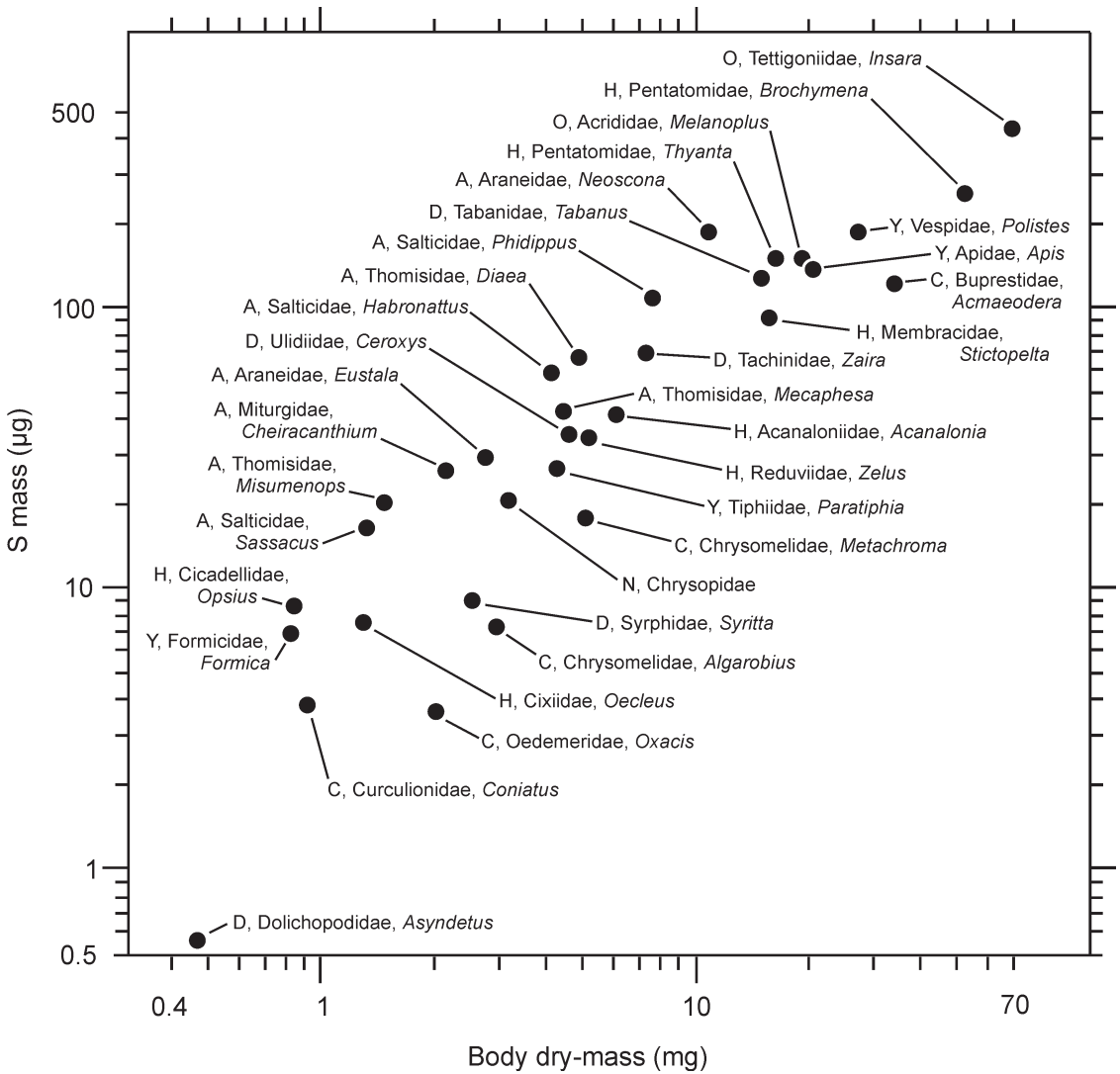
Fig. 1. Mean sulfur mass vs. mean body dry-mass of spiders and insects collected in riparian habitat near the Colorado River in Arizona. Axes are log scales. Single letters are orders: A, Araneae; C, Coleoptera; D, Diptera; H, Hemiptera; N, Neuroptera; O, Orthoptera; Y, Hymenoptera. All specimens are adults except Araneae are juveniles and adults, *Melanoplus* are nymphs, and *Opsius* are nymphs and adults.

ditional variation (12%) in S content (Fig. 2). Within insects, mean S concentrations differed most between Coleoptera (0.35%) and the other 5 orders (0.72%). A significant ($F = 1.96$; $df = 19$, 108; $P = 0.016$) proportion of additional variation (11%) in S concentration also was explained when arthropods were classified by family instead of order (Fig. 2). This additional variation was partly due to lower mean S concentrations in Dolichopodidae (0.12%) and Syrphidae (0.33%) compared with the other 3 families of Diptera (0.85%). Classifying arthropods by genus instead of family did not explain a significant ($F = 1.23$; $df = 8$, 100; P = 0.29) proportion of additional variation (2.6%) in S content. Class, order, family, and genus described 70% of variation in %S.

Insect herbivores, predators, and detritivores contained different ($F = 5.40$; $df = 2$, 97; $P = 0.006$) concentrations of S. Trophic level explained 10% of variation in transformed S concentration. Concentrations of S (mean, ± SD) were lower in the 2 detritivores (0.29, 0.13-0.50%) than in herbivores (0.64, 0.37-0.99%) and predators (0.73, 0.48-1.03%). Sulfur contents of herbivores and predators did not differ ($t = 1.35$; $df = 97$; $P = 0.18$).
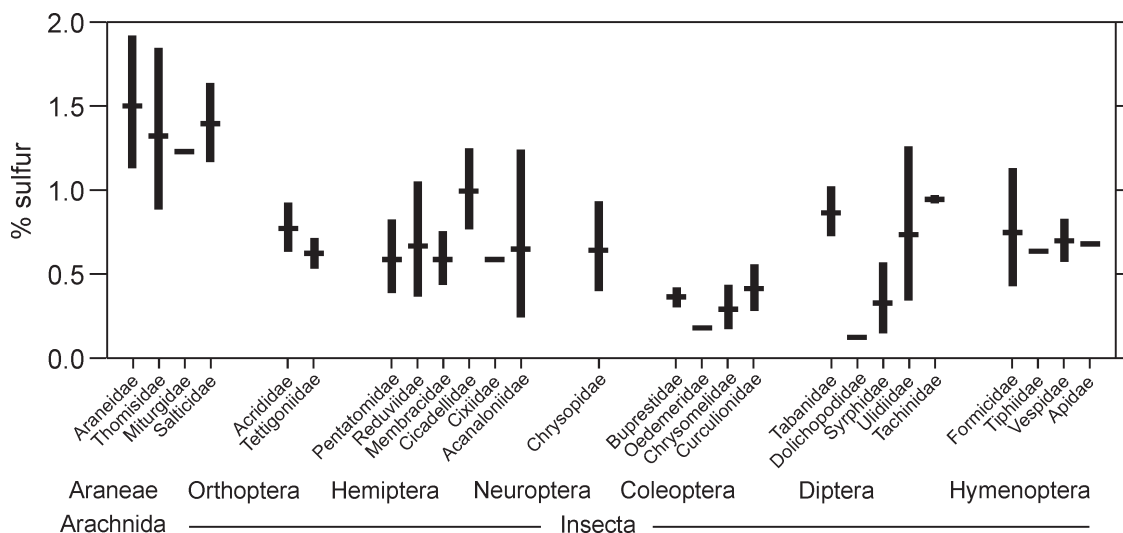
Fig. 2. Sulfur contents as a percentage of body dry mass in spiders and insects collected in riparian habitat near the Colorado River in Arizona. Horizontal bars are means and vertical bars are ± SD's. Means and upper and lower bounds of SD's are back-transformed from percentages transformed $2[\arcsin(\%S/100)^{1/2}]$. All families are adults except Araneae are juveniles and adults, Acrididae are nymphs, and Cicadellidae are nymphs and adults.

DISCUSSION

Sulfur concentrations in Araneae and Coleoptera were approximately twice those predicted from protein and amino acid concentrations (including taurine) measured in wolf spiders and beetles by Ramsay & Houston (2003). In wolf spiders, mean percentages of methionine, cysteine, and taurine in amino acids multiplied by their S contents (21.5, 26.5, and 25.6%), added and multiplied by mean protein content (60.2% of dry mass), produced an estimated S concentration of 0.67%. Sulfur content in beetles (50.5% protein) was similarly calculated as 0.17%. This discrepancy may be due to the absence of taurine in protein (causing a calculation error), different taxa analyzed, different analytical methods, measurement error, or to S-containing compounds other than the 3 amino acids. Various compounds containing S occur during metabolism of methionine, cysteine, and taurine (Jacobsen & Smith 1968; Brosnan & Brosnan 2006). One of these, S-adenosylmethionine, is a ubiquitous coenzyme involved in the synthesis of a wide range of biochemicals (Brosnan & Brosnan 2006).

Lack of an allometric relation between S mass and body mass in spiders and insects suggests S-containing compounds are not dominated by those within the cuticle, such as the protein components methionine and cysteine. An allometric relation between N mass and body mass was detected in arthropods from the same locality (Wiesenborn 2011a). I attributed this allometry to increasing exoskeleton thickness as body mass increased. This further indicates that a substantial portion of S resides in taurine and S amino-acid metabolites, compounds that would not occur in the exoskeleton.

Greater S concentration in spiders agrees with the order's greater taurine content compared with insects. Higher S content appears characteristic of Araneae, similar to silk and venom production, because it was observed across the 4 families and 9 genera analyzed. Less S in Coleoptera compared with other insects corresponds with the low N content detected in the order (Wiesenborn 2011a). Low concentrations of S and N in beetles may be due to the elytra, rigid cuticular structures that likely contain a large proportion of body dry-mass. Exoskeleton rigidity has been associated with the abundance of chitin, a polysaccharide devoid of S that complexes with protein and comprises 20-50% of exoskeleton dry-mass (Andersen 1979). High chitin contents in elytra would decrease S and N concentrations in beetles. Spider and insect families appeared to be more variable in S content than in N content. In contrast to %S, concentrations of N did not vary among families more than among orders (Wiesenborn 2011a).

The small sample-size of detritivores prevents concluding that they contain lower S concentrations than insect herbivores or predators. Analysis of only 2 detritivores, the oedemerid *Oxacis* and syrphid *Syritta*, resulted from the collection methods of sweeping plants and capturing flying

insects. Low S content also was measured in *Asyndetus*, minute flies in Dolichopodidae that may feed on detritus. Dolichopodid larvae live within soil, beneath bark, or in decaying vegetation (Cole 1969). Although diets of *Asyndetus* are unknown, adults and most larvae of the few dolichopodids examined are predaceous (Cole 1969; Robinson & Vockeroth 1983). Low S contents in *Syritta* and *Asyndetus* contributed to the significant variation in %S among arthropod families. Similar S contents between herbivorous and predatory insects suggest the element does not concentrate in higher trophic levels. Greater N content on average in predators compared with herbivores has been detected in a variety of insects (Fagan et al. 2002) but not in riparian spiders and insects (Wiesenborn 2011a).

Insectivorous birds in desert-riparian habitat foraging in relation to prey S contents would be most likely to discriminate between spiders and insects. Preferentially feeding spiders to nestlings may be difficult, because nesting and spider abundance may be asynchronous. Populations of spiders on *S. exigua* and *P. fremontii* planted for habitat generally increased during the growing season and peaked in August (Wiesenborn 2011b). Birds can utilize S-containing compounds directly or, like insects, produce cysteine from methionine, and taurine from cysteine (Jacobsen & Smith 1968; Ramsay & Houston 2003). Not all S-containing compounds in arthropods would be available to birds. Methionine and cysteine in sclerotized cuticle, indigestible by birds, would not be utilized. Other sources of these compounds and taurine, along with their metabolites, could be used by birds to meet their own nutrient requirements or those of their offspring.

REFERENCES CITED

ANDERSEN, S. O. 1979. Biochemistry of insect cuticle. Annu. Rev. Entomol. 24: 29-61.

ARNOLD, K. E., RAMSAY, S. L., DONALDSON, C., AND ADAM, A. 2007. Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. Proc. R. Soc. B Biol. Sci. 274: 2563-2569.

BORROR, D. J., DE LONG, D. M., AND TRIPLEHORN, C. A. 1981. An Introduction to the Study of Insects, 5th ed. Saunders College Publishing, Philadelphia. xi + 827 pp.

BROSNAN, J. T., AND BROSNAN, M. E. 2006. The sulfur-containing amino acids: an overview. J. Nutr. 136: 1636S-1640S.

COLE, F. R. 1969. The Flies of Western North America. University of California Press, Berkeley. xi + 693 pp.

DADD, R. H. 1973. Insect nutrition: current developments and metabolic implications. Annu. Rev. Entomol. 18: 381-420.

DESERT RESEARCH INSTITUTE (DRI). 2012. Western U.S. Climate Historical Summaries. Western Regional Climate Center, Reno, Nevada [http://www.wrcc.dri.edu/Climsum.html; accessed 27 Jun 2012].

ECKBERG, J. R., AND FOSTER, M. E. 2011. First account of the splendid tamarisk weevil, *Coniatus splendidulus* Fabricius, 1781 (Coleoptera: Curculionidae) in Nevada. Pan-Pac. Entomol. 87: 51-53.

ESSIG, E. O. 1926. Insects of Western North America. The MacMillan Company, New York. xi + 1035 pp.

FAGAN, W. F., SIEMANN, E., MITTER, C., DENNO, R. F., HUBERTY, A. F., WOODS, H. A., AND ELSER, J. J. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. Am. Nat. 160: 784-802.

FOELIX, R. F. 1996. Biology of Spiders, 2nd ed. Oxford University Press, New York. 330 pp.

HAYAKAWA, Y., BODNARYK, R. P., AND DOWNER, R. G. H. 1987. Effect of taurine on excitation-induced changes in brain and hemolymph octopamine levels in *Periplaneta americana*. Arch. Insect Biochem. Physiol. 5: 129-137.

JACOBSEN, J. G., AND SMITH, L. H., JR. 1968. Biochemistry and physiology of taurine and taurine derivatives. Physiol. Rev. 48: 424-511.

KUHN-NENTWIG, L., SCHALLER, J., AND NENTWIG, W. 1994. Purification of toxic peptides and the amino acid sequence of CSTX-1 from the multicomponent venom of *Cupiennius salei* (Araneae: Ctenidae). Toxicon 32: 287-302.

KUHN-NENTWIG, L., BÜCHELER, A., STUDER, A., AND NENTWIG, W. 1998. Taurine and histamine: low molecular compounds in prey hemolymph increase the killing power of spider venom. Naturwissenshaften 85: 136-138.

NETER, J., KUTNER, M. H., NACHTSHEIM, C. J., AND WASSERMAN, W. 1996. Applied Linear Statistical Models, 4th ed. McGraw-Hill, Boston. xv + 1408 pp.

PEOPLES, A. D., LOCHMILLER, R. L., BOREN, J. C., LESLIE, D. M., JR., AND ENGLE, D. M. 1994. Limitations of amino acids in diets of northern bobwhites (*Colinus virginianus*). Am. Midl. Nat. 132: 104-116.

RAMSAY, S. L., AND HOUSTON, D. C. 1998. The effect of dietary amino acid composition on egg production in blue tits. Proc. R. Soc. Lond. B Biol. Sci. 265: 1401-1405.

RAMSAY, S. L., AND HOUSTON, D. C. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. Ibis 145: 227-232.

ROBINSON, H., AND VOCKEROTH, J. R. 1981. Chapter 48, Dolichopodidae, pp. 625-639 *In* J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth and D. M. Wood [eds.], Manual of Nearctic Diptera, vol. 1. Monograph No. 27, Agriculture

Canada, Biosystematics Research Centre, Ottawa. iii + 674 pp.

STROHECKER, H. F., MIDDLEKAUFF, W. W., AND RENTZ, D. C. 1968. The Grasshoppers of California (Orthoptera: Acridoidea). Bull. California Insect Survey, vol. 10. Univ. California Press, Berkeley. v + 177 pp.

TILLINGHAST, E. K., AND TOWNLEY, M. A. 2008. Free amino acids in spider hemolymph. Comp. Biochem. Physiol. B 151: 286-295.

TOWNLEY, M. A., TILLINGHAST, E. K., AND NEEFUS, C. D. 2006. Changes in composition of spider orb web sticky droplets with starvation and web removal, and synthesis of sticky droplet compounds. J. Exp. Biol. 209: 1463-1486.

WHITTON, P. S., STRANG, R. H. C., AND NICHOLSON, R. A. 1987. The distribution of taurine in the tissues of some species of insects. Insect Biochem. 17: 573-577.

WHITTON, P. S., NICHOLSON, R. A., AND STRANG, R. H. C. 1988. Effect of taurine on neurotransmitter release from insect synaptosomes. J. Neurochem. 51: 1356-1360.

WIESENBORN, W. D. 2011a. Nitrogen content in riparian arthropods is most dependent on allometry and order. Florida Entomol. 94: 71-80.

WIESENBORN, W. D. 2011b. Biomasses of arthropod taxa differentially increase on nitrogen-fertilized willows and cottonwoods. Restor. Ecol. 19: 323-332.

WIESENBORN, W. D., AND HEYDON, S. L. 2007. Diets of breeding southwestern willow flycatchers in different habitats. Wilson J. Ornithol. 119: 547-557.