Nitrogen Content in Riparian Arthropods is Most Dependent on Allometry and Order

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NITROGEN CONTENT IN RIPARIAN ARTHROPODS IS MOST DEPENDENT ON ALLOMETRY AND ORDER

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ABSTRACT

I investigated the contributions of body mass, order, family, and trophic level to nitrogen (N) content in riparian spiders and insects collected near the Colorado River in western Arizona. Most variation (97.2%) in N mass among arthropods was associated with the allometric effects of body mass. Nitrogen mass increased exponentially as body dry-mass increased. Significant variation (20.7%) in N mass adjusted for body mass was explained by arthropod order. Adjusted N mass was highest in Orthoptera, Hymenoptera, Araneae, and Odonata and lowest in Coleoptera. Classifying arthropods by family compared with order did not explain significantly more variation (22.1%) in N content. Herbivore, predator, and detritivore trophic-levels across orders explained little variation (4.3%) in N mass adjusted for body mass. Within orders, N content differed only among trophic levels of Diptera. Adjusted N mass was highest in predaceous flies, intermediate in detritivorous flies, and lowest in phytophagous flies. Nitrogen content in riparian spiders and insects is most dependent on allometry and order and least dependent on trophic level. I suggest the effects of allometry and order are due to exoskeleton thickness and composition. Foraging by vertebrate predators, such as insectivorous birds, may be affected by variation in N content among riparian arthropods.

Key Words: nutrients, spiders, insects, trophic level, exoskeleton, cuticle

RESUMEN

Se investiguo las contribuciones de la masa de cuerpo, orden, familia y el nivel trófico al contenido de nitógeno (N) en arañas e insectos riparianos (que viven en la orilla del rio u otro cuerpo de agua) recolectadaos cerca del Rio Colorado en el oeste del estado de Arizona. La mayoría de la variación (97.2%) en la masa (N) entre los artrópodos fue asociado con los efectos alométricos de la masa de cuerpo. La masa de nitrógeno aumentó exponencialmente con el aumento de masa-seca del cuerpo. La variación significativa (20.7%) en la masa N ajustada por la masa del cuerpo se explica según el ordén del artrópodo. La masa ajustada N fue mas alta en Orthóptera, Hymenóptera, Araneae, Odonata y mas baja en Coleoptera. Al clasificar los artrópodos por familia comparado con el ordén no explica la variacion mayor significativa (22.1%) en el contenido de N. Los niveles tróficos de los herbívoros, depredadores y detritívoros en todos los ordenes explica la pequeña variación (4.3%) en la masa N ajustada por la masa del cuerpo. Entre los ordenes, el contenido N varía solamente entre los niveles tróficos de Diptera. El valor ajustado de la masa de N fue mayor para las moscas depredadores, intermedio para las moscas detritívoras y menor para las moscas fitófagas. El contenido de nitrógeno en arañas e insectos riparianos es mas dependiente sobre la alometría y ordén y menos dependiente sobre el nivel trófico. Sugiero que los efectos de alometría y ordén son debidos al grosor y la composición del exo-esqueleto. El forraje por los depredadores vertebrados, como aves insectivoras, puede ser afectado por la variación del contenido N entre los artrópodos riparianos.

Nitrogen concentrations in organisms are dependent on trophic level. This is most apparent between plants and herbivores, because N comprises 0.03-7% of dry mass in plants compared with 8-14% in animals (Mattson 1980). Variation in N concentration among and within plants, and its effects on abundances of herbivores including arthropods, especially agricultural pests, has been frequently examined (reviewed in Mattson 1980; Scriber 1984). Fewer studies have considered variation in N concentration among spiders and insects. Bell (1990) and Studier & Sevick (1992) tabulated measurements of %N in various insects from different studies. Fagan et al. (2002) compared %N between arthropod herbivores and predators by analyzing data compiled from various sources. Concentrations of N in spiders and insects were dependent on trophic level after controlling for body length, representing allometry, and taxonomic group, representing phylogeny (Fagan et al. 2002). Predators generally contained higher %N than herbivores. Predaceous arthropods may concentrate N from food similar to phytophagous arthropods.

Variation in N concentration among spiders and insects may affect foraging by arthropod-feeding vertebrates and the qualities of food they obtain. Diet protein has been implicated as affecting egg production (Ramsay & Houston 1997) and nestling growth (Johnston 1993) in insectivorous birds. Identifying sources of variation in arthropod N content may improve our understanding of the prey composition required to support species of insectivorous wildlife.

I examined variation in N content among spiders and insects collected from trees and shrubs established to restore riparian habitat for insectivorous vertebrates, especially birds. Variation in N mass was partitioned into various sources. I first determined the allometric relationship between N mass and body dry-mass. After adjusting N mass for this relationship, N contents of arthropods were compared among orders and families and among trophic levels across and within orders. I interpreted N contents in relation to exoskeleton scaling and chemical composition and concluded by applying the results to diets of insectivorous birds.

Materials and Methods

Arthropod Collections

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; elevation 143 m) 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 and rooted in containers. The area is straddled by Topock Marsh (16 km^2) and Beal Lake (0.9 km^2), 2 impoundments containing mostly emergent cattails (*Typhus* sp., Typhaceae) and open water. Undeveloped areas of the surrounding floodplain support mostly naturalized tamarisk (*Tamarix ramosissima* Ledeb., Tamaricaceae) shrubs. The floodplain is flanked by Sonoran desertscrub dominated by creosote bush (*Larrea tridentata* (DC.) Cov., Zygophyllaceaae). Maximum temperatures average 42.7ºC during Jul, and minimum temperatures average 5.6ºC during Jan at Needles (DRI 2010).

I collected arthropods from plants and trapped insects in flight. Arthropods were swept with a 38-cm diameter muslin net from planted cottonwood (*Populus fremontii* S. Watson, Salicaceae) and Goodding's black willow (*Salix gooddingii* C. Ball, Salicaceae) trees, planted narrow-leaved willow shrubs (*Salix exigua* Nutt.), volunteer honey mesquite (*Prosopis glandulosa* Torrey, Fabaceae) and screwbean mesquite (*Prosopis pubescens* Benth.) trees, and volunteer arrowweed shrubs (*Pluchea sericea* (Nutt.) Cov., Asteraceae). I also swept arthropods from *T. ramosissima* bordering the plots. Additional arthropods on *S. exigua* were swept from plants growing along a dirt irrigation canal 2 km northwest of the restoration area. Plant species were swept separately except for *Prosopis* spp., which grew together. Each species was swept 10-15 min on 9 dates: 30 Apr, 14 May, 27 May, 08 Jun, 22 Jun, 30 Jun, 21 Jul, 4 Aug, and 18 Aug 2009. All plant species were in flower or fruit except for *P. fremontii*. Arthropods swept from plants were placed into plastic bags, kept in a refrigerator, and killed in a freezer. Flying insects were trapped with a Malaise trap (Santee Traps, Lexington, KY) that was placed in the center of a plot supporting *S. gooddingii* and *P. sericea* and elevated 1 m aboveground with fence posts. Trapped insects were collected into a dry plastic bottle containing a nitrogen-free, diclorvos insecticide strip. Insects were trapped for 6.1-7.3 h during 0855-1640 PDT on each of the above dates except 30 Apr, 14 May, and 18 Aug 2009.

Spiders and insects collected on each date were sorted under a microscope into morphotypes (similar-looking specimens). Representatives of each morphotype were placed into 70% ethanol for identification. I counted and split the remaining specimens of each morphotype into samples each with an estimated maximum dry mass of 10 mg. Individual specimens with dry masses ≥10 mg were placed into separate samples. Arthropod samples for N analyses were cleaned by vortexing in water, transferred to filter paper with a Büchner funnel, dried 2 h at 80ºC, and stored in stoppered vials.

Arthropod Identifications and Trophic Levels

Spiders and insects were identified to the lowest taxon possible, at least to family and typically to genus. Vouchers of adult insects were deposited at the Bohart Museum of Entomology, University of California, Davis, and vouchers of spiders were deposited at the California Academy of Sciences, San Francisco. Arthropod taxa were classified into the trophic levels of herbivore, predator, and detritivore based on published descriptions (Table 1). Holometabolous insects were classified by larval diet. Herbivores included consumers of pollen, nectar, or honeydew (homopteran egesta). Predators included parasites and consumers of already-dead animals.

Arthropod Nitrogen Estimates

The mass of N in each arthropod sample was estimated with the Kjeldahl method adapted from Isaac & Johnson (1976). Samples of dried arthropods were weighed (±0.01 mg) with a microbalance (model C-30, Cahn Instruments, Cerritos, CA) and ground into water with a 5-mL glass tissue homogenizer. Homogenized samples were poured and rinsed with water, to a total volume of 20 mL, into 100-ml digestion tubes. I added 6 mL of concentrated sulfuric acid, containing 4.2% selenous acid, and 3 mL of 30% hydrogen

TABLE 1. ADULT ARTHROPODS COLLECTED FROM RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR NITROGEN CONTENT.

Order or suborder	Family	Genus[1]	Source[2]	No. Samples	No. specimens per sample	Trophic level[3]	Mean body dry mass (mg)	Mean ± SD % N
Araneae	Philodromidae	*Philodromus*	E,S	2	3-4	P	1.93	10.6 ± 0.9
	Salticidae	*Habronattus*	S	2	1	P	6.29	9.3 ± 1.2
		Metaphidippus[6]	S	1	9	P	0.07	13.0
	Thomisidae	*Misumenops*	E	2	1-2	P	2.03	12.1 ± 1.8
	2 families[4,6]	—	S	1	6	P	2.46	14.3
	3 families[5,6]	—	S	2	6-7	P	2.35	13.8 ± 0.1
Odonata	Libellulidae	*Pachydiplax*	P	4	1	P	39.7	12.3 ± 1.0
Orthoptera	Acrididae	*Acridinae*[7]	S	6	1-3	H	13.0	13.9 ± 2.7
	Tettigoniidae	*Scudderia*	S	1	1	H	115.0	14.6
Heteroptera	Largidae	*Largus*	S	1	1	H	49.2	9.2
	Lygaeidae	*Nysius*	S	1	67	H	0.46	9.0
	Pentatomidae	*Brochymena*	F,G,P	4	1	H	55.2	11.0 ± 1.5
		Thyanta	E	1	1	H	17.1	11.6
	Reduviidae	*Pselliopus*	P	1	1	P	14.1	13.3
		Zelus	F,P,S	6	1-3	P	7.20	10.5 ± 2.0
Homoptera	Cicadellidae	*Cicadellinae*	E,F,G	5	1-3	H	6.62	10.1 ± 2.2
		Gyponinae	G	1	2	H	3.36	8.6
		Opsius[6]	T	4	28-41	H	0.68	11.2 ± 1.5
		Typhlocybinae	F	2	19-22	H	0.35	11.4 ± 0.0
		—	S	1	5	H	4.37	14.6
	Cixiidae	*Oecleus*	S	1	4	H	1.24	10.1
	Flatidae	*Ormenis*	G,T	2	2	H	5.72	8.9 ± 1.2
	Membracidae	—	G	1	2	H	5.22	10.6
Neuroptera	Chrysopidae	*Chrysoperla*	F,G,S	9	2-14	P	1.51	9.1 ± 1.5
		—	G	1	11	P	1.37	11.8
	Myrmeliontidae	*Myrmelion*	F	1	1	P	8.99	12.5

[1]Subfamily in Acrididae and subfamily or genus in Cicadellidae.
[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. Reference for all (Borror et al. 1981) except Apioceridae (Cole 1969) and Andrenidae, Formicidae, and Tettigoniidae (Essig 1926).
[4]Salticidae, *Habronattus* sp.; Thomisidae, *Misumenops* sp.
[5]Araneidae, *Hypsosinga* sp.; Salticidae, *Metaphidippus* sp. & *Habronattus* sp.; Thomisidae, *Misumenops* sp.
[6]Adults and immatures.
[7]Immatures.

TABLE 1. (CONTINUED) ADULT ARTHROPODS COLLECTED FROM RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR NITROGEN CONTENT.

Order or suborder	Family	Genus[1]	Source[2]	No. Samples	No. specimens per sample	Trophic level[3]	Mean body dry mass (mg)	Mean ± SD % N
Coleoptera	Bruchidae	*Algarobius*	P	1	6	H	3.01	8.3
	Coccinellidae	*Chilocorus*	F,P	3	2-4	P	4.75	9.8 ± 1.2
		Hippodamia	F,S	3	2-8	P	6.26	6.6 ± 2.8
Diptera	Apioceridae	*Apiocera*	M	1	1	P	52.87	11.4
	Asilidae	*Proctacanthus*	M	1	1	P	42.3	11.7
	Dolichopodidae	*Asyndetus*	M	13	17-113	D	0.39	9.9 ± 2.0
	Lauxaniidae	*Homoneura*	F,G	2	4-5	D	1.31	7.8 ± 1.0
		Minettia	F,G	2	2-6	D	2.37	8.1 ± 4.6
	Sarcophagidae	*Eumacronychia*	F,G	1	2	P	1.68	11.5
	Tabanidae	*Apatolestes*	M	1	1	P	15.0	11.6
		Tabanus	M	13	2-3	P	13.8	10.9 ± 2.2
	Tachinidae	*Zaira*	M	2	1-2	P	7.66	9.2 ± 2.3
	Tephritidae	*Acinia*	F	2	7-9	H	1.01	5.1 ± 1.5
Hymenoptera	Andrenidae	*Perdita*	S	1	2	H	1.74	9.8
	Formicidae	*Formica*	E,S	4	6-16	H	0.76	10.9 ± 1.8
	Halictidae	*Agapostemon*	E	1	1	H	7.42	11.7
		Dieunomia	S	1	3	H	5.57	14.1
		Lasioglossum	E	1	9	H	2.71	16.7
	Sphecidae	*Bembix*	M	1	1	P	33.5	13.4
		Cerceris	M	1	1	P	10.6	8.8
		Tachysphex	M	1	1	P	7.23	8.5
	Tiphiidae	*Myzinum*	E	1	6	P	4.54	21.2
	Vespidae	*Polistes*	G	1	1	P	28.8	14.0

[1]Subfamily in Acrididae and subfamily or genus in Cicadellidae.
[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. Reference for all (Borror et al. 1981) except Apioceridae (Cole 1969) and Andrenidae, Formicidae, and Tettigoniidae (Essig 1926).
[4]Salticidae, *Habronattus* sp.; Thomisidae, *Misumenops* sp.
[5]Araneidae, *Hypsosinga* sp.; Salticidae, *Metaphidippus* sp. & *Habronattus* sp.; Thomisidae, *Misumenops* sp.
[6]Adults and immatures.
[7]Immatures.

peroxide and heated samples 1 h at 400ºC with a block digestor (model 2040, Tecator, Herndon, VA). After cooling, water was added to 60 mL. The ammonia concentration formed in the clear, digested samples was measured by colorimetry, against standards prepared from dried ammonium-sulfate, with a segmented flow analyzer (model FS-4, OI Analytical, College Station, TX). Salicylate, hypochlorite, and sodium nitroprusside were used as the indicator. I converted ammonia concentration to mg N.

I adjusted estimates of mg N in arthropod samples with chitin samples containing known N masses. Chitin is a nitrogenous polysaccharide $(C_8H_{13}NO_5)_n$ abundant in arthropod exoskeleton, or cuticle (Neville 1975), that typically comprises 25-40% of exoskeleton dry-mass in insects (Richards 1978). Various masses (2, 4, 8, 16, 32, 64 mg) of powdered chitin (Tokyo Chemical Industry) containing 6.89% N were weighed, placed in 20 mL water, digested, and measured for ammonia within each batch (n = 4) of arthropod samples. I increased estimates of mg N in arthropod samples in each batch to correct for the batch's mean underestimate of %N (5.76, 6.23, 6.44, 6.08%) in chitin samples. I calculated %N in arthropod samples as 100(mg N/mg dry mass). Two arthropod samples of *Acinia* and *Chrysoperla* with unusually low N concentrations (<0.9%) were excluded as outliers. Dry mass and mg N of each arthropod sample were divided by the number of specimens in the sample to estimate dry mass and N mass per specimen.

Statistical Analysis

Body masses of arthropods, transformed log(mg) to normalize residuals, were compared among trophic levels with analysis of variance (SYSTAT version 12, San Jose, CA). Nitrogen masses in spiders and insects were analyzed sequentially. I first determined the relationship between N mass and body dry mass by regressing log(mg N) against log(mg body mass) for each arthropod sample. I verified that the relationship was allometric (exponential) by testing with an approximate t test the null hypothesis that the regression coefficient b_1 = 1 (Neter et al. 1996). Transformed N masses were adjusted for their allometric relationship with transformed body mass by adding the residuals from the regression to the overall mean of transformed N mass (Sokal & Rohlf 1981).

Adjusted, transformed N masses were compared among arthropod orders with analysis of variance. Hemiptera were split into suborders Heteroptera and Homoptera, because the digestive systems of most homopterans have filter chambers that concentrate nitrogenous compounds (Borror et al. 1981). I tested if classifying arthropods by family instead of order or suborder explained more variation in adjusted log(mg N) with the general linear test approach (Neter et al. 1996). This approach tests if mean square error in an analysis of variance decreases significantly when the model becomes more complex. Samples containing more than 1 family (3 samples of Araneae, or spiders) were classified only to order.

Arthropod N-contents adjusted for body mass were compared among trophic levels across and within orders or suborders. I compared N masses among trophic levels across orders or suborders with analysis of variance. Separate analyses were performed within Heteroptera, Diptera, and Hymenoptera, the 3 orders or suborders with 2 or more trophic levels each containing more than 1 sample. Analyses within orders or suborders weighted adjusted values of log(mg N) by $1/s^2$ in each trophic level to correct for uneven variances among trophic levels (Neter et al. 1996).

RESULTS

Collected Arthropods

I collected 121 samples of spiders and insects containing 1,490 specimens in 9 orders or suborders, 33 families, and 43 subfamilies or genera (Table 1). All of the arthropods collected were adults except for 8 samples in 3 taxa (families, subfamilies, or genera) with adults and immatures and 6 samples in 1 taxon with only immatures. Body dry-masses of adult arthropods ranged from 0.35 mg in Typhlocybinae leafhoppers (Cicadellidae) to 115 mg in the fork-tailed bush katydid *Scudderia furcata* Brunner (Tettigoniidae).

Two orders or suborders (Orthoptera and Homoptera) of collected spiders and insects were only herbivorous, 3 orders (Araneae, Odonata, and Neuroptera) were only predaceous, and 4 orders or suborders (Heteroptera, Coleoptera, Diptera, and Hymenoptera) included both trophic levels. All Coleoptera were predaceous except for 1 sample. The only detritivores collected were flies (Diptera). Across orders or suborders, herbivores included 42 samples in 22 taxa, predators included 62 samples in 24 taxa, and 17 samples in 3 taxa were detritivores (Table 1). Trophic levels contained arthropods with different body dry-masses (F = 25.5; df = 2, 118; P < 0.001). Predators were largest (back-transformed mean = 6.37 mg) followed by herbivores (4.03 mg) and detritivores (0.55 mg).

Allometric Nitrogen Contents

Nitrogen mass in riparian spiders and insects was allometrically related to body dry mass (Fig. 1). Transformed N mass per specimen in arthropod samples was positively related ($F_=$ 4, 066; df = 1, 119; P < 0.001) to transformed body dry-mass per specimen by:

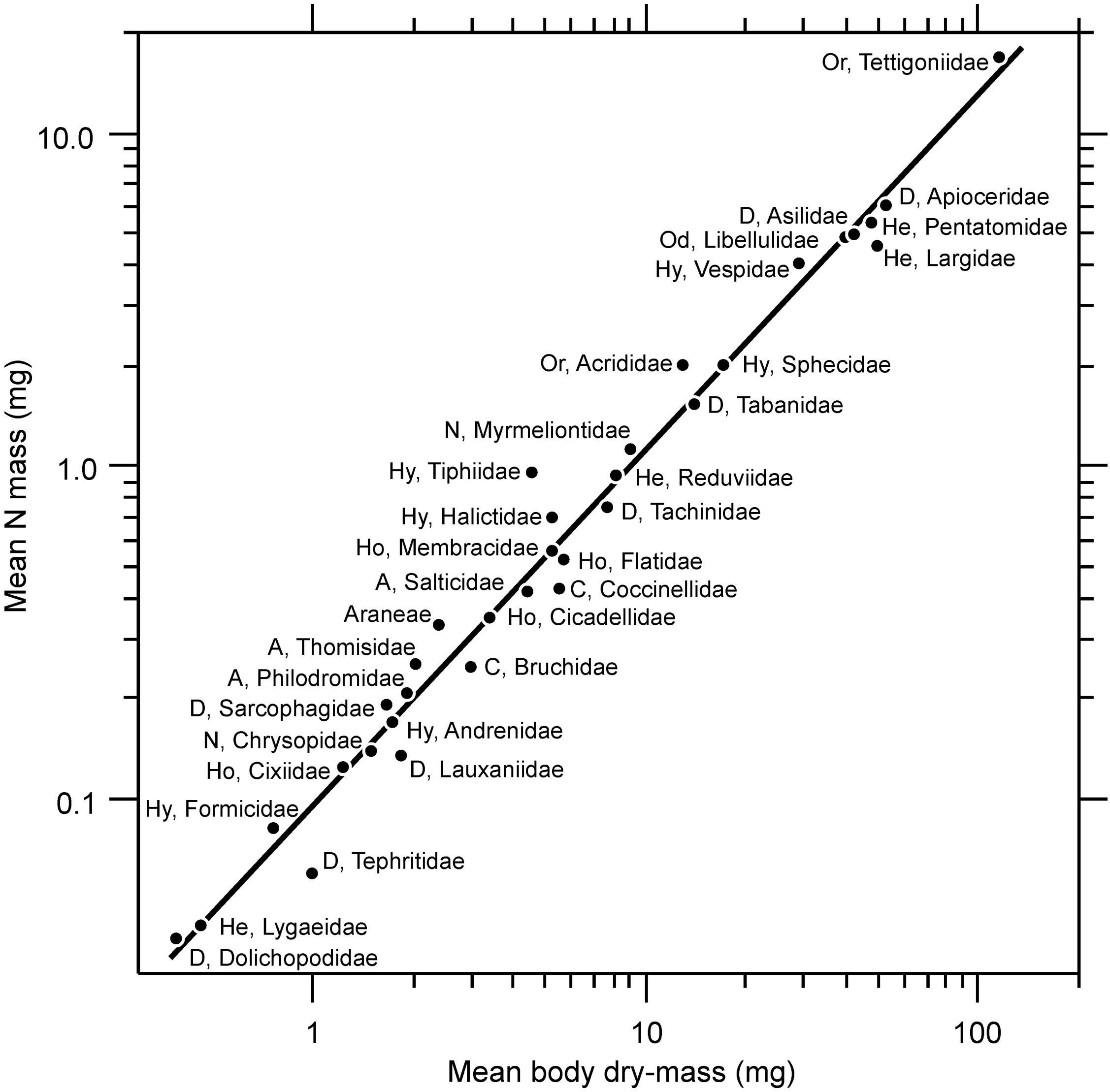

Fig. 1. Mean N mass *vs.* mean body dry-mass in riparian arthropods from the lower Colorado River classified by family. Abbreviations are orders or suborders (in Hemiptera): A, Araneae; C, Coleoptera, D, Diptera; He, Heteroptera; Ho, Homoptera; Hy, Hymenoptera; N, Neuroptera; Od, Odonata; Or, Orthoptera. Single point labeled Araneae represents mixed samples of Araneidae, Salticidae, and Thomisidae. Axes are log scales. Line fit to transformed data by linear regression weighted by sample size.

$$\log \text{mg N} = -1.006 + 1.039(\log \text{mg dry mass})$$

Back-transforming this equation produced:

$$\text{mg N} = 0.0986(\text{mg dry mass})^{1.039}$$

The exponent (1.039 ± 0.016 SD) differs from unity ($t^* = 2.43$; $df = 119$; $P = 0.008$), verifying that the relationship is exponential rather than linear. This allometric relationship explained 97.2% of variation in N mass. Percentage of N in riparian arthropods (Table 1) increased as body mass increased.

Nitrogen Content in Arthropod Orders

Nitrogen mass adjusted for body mass in riparian arthropods (Fig. 2) differed ($F = 3.64$; $df = 8, 112$; $P < 0.001$) among orders or suborders. These taxonomic levels explained 20.7% of variation in adjusted N mass. Orthoptera (mean 14.0% N), Hymenoptera (12.4% N), Araneae (11.9% N), and Odonata (12.3% N) contained the highest adjusted N contents, and Coleoptera (8.2% N) contained the lowest adjusted N content. Orthoptera were mostly immature slant-faced grasshoppers

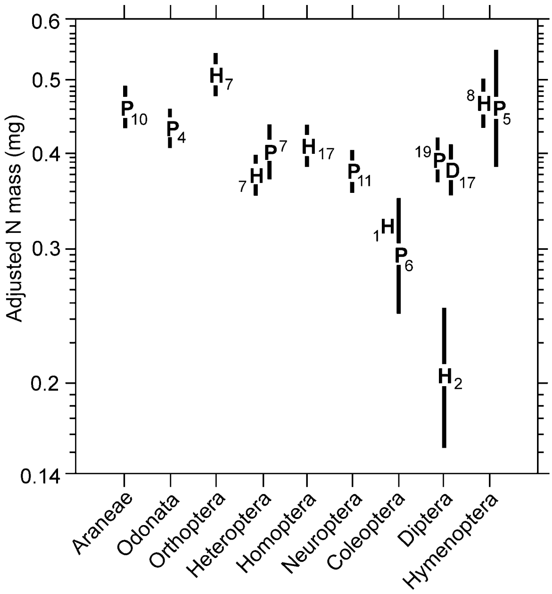

Fig. 2. Nitrogen mass allometrically adjusted for body mass in riparian arthropods from the lower Colorado River classified by order or suborder (in Hemiptera). Letters are means (± SE) and trophic levels: D, detritivores; H, herbivores; P, predators. Adjacent numbers are sample sizes. *Y*-axis is log scale.

(Acridinae) along with the sole katydid *S. furcata*. Hymenoptera included ants (Formicidae), 2 families of bees (Andrenidae and Halictidae), and 3 families of wasps (Sphecidae, Tiphiidae, and Vespidae). Spider samples contained several families (Table 1). The only odonate collected was the dragonfly *Pachydiplax longipennis* Burmeister. Coleoptera included 1 sample of the herbivorous seed beetle (Bruchidae) *Algarobius prosopis* LeConte, collected from *Prosopis* spp., and 6 samples containing 2 species of predaceous ladybird beetles (Coccinellidae), *Chilocorus cacti* L. and the widespread *Hippodamia convergens* Guerin-Meneville. Insects in other orders, including the 2 Hemiptera suborders, contained intermediate N concentrations (Fig. 2).

Classifying arthropods by family instead of order or suborder did not explain more variation in N mass adjusted for body mass. Error variance of adjusted N mass did not decrease ($F = 1.45$; $df = 26, 86$; $P = 0.10$) when arthropods were classified by family compared with order or suborder. Classifying arthropods by family instead of order or suborder explained 22.1%, a 1.4% improvement, of variation in adjusted N mass.

Nitrogen Content in Trophic Levels

Differences in N content among the trophic levels of herbivore, predator, and detritivore depended on classification (Fig. 2). Across orders or suborders, N mass did not vary ($F = 0.62$; $df = 2, 118$; $P = 0.54$) among trophic levels. Trophic levels explained 1.0% of variation in N mass after accounting for body mass. Back-transformed means of adjusted N mass (and mean % N) were 0.413 mg (11.1% N) in herbivores, 0.397 mg (10.9% N) in predators, and 0.380 mg (9.44% N) in detritivores, the smallest arthropods collected. Within orders or suborders, N mass varied among trophic levels in Diptera ($F = 4.60$; $df = 2, 35$; $P = 0.017$) but not in Heteroptera ($F = 0.62$; $df = 1, 12$; $P = 0.45$) or Hymenoptera ($F = 0.13$; $df = 1, 11$; $P = 0.91$). Adjusted N contents in flies (Fig. 2) were lower in herbivores (mean 5.1% N) compared with predators (10.9% N) or detritivores (9.4% N). All phytophagous flies collected were 2 samples of the fruit fly (Tephritidae) *Acinia picturata* (Snow), swept from *P. fremontii*. Adjusted N concentrations in predaceous or parasitic flies (Apioceridae, Asilidae, Sarcophagidae, Tabanidae, and Tachinidae) and detritivorous flies (Dolichopodidae and Lauxaniidae) were similar.

Discussion

Allometric Nitrogen Contents

The allometric relationship between N mass and body mass in riparian arthropods resembles a similar relationship between exoskeleton mass and body mass in terrestrial arthropods. Anderson et al. (1979) dissected the exoskeletons from 3 species of immature and adult spiders, weighing between 25 mg and 1.2 g, and determined exoskeleton dry-mass and body wet-mass were positively related by:

$$\text{g exoskeleton} = 0.078(\text{g body mass})^{1.135}$$

Body mass in spiders explained 94.1% (their *r*-value squared) of variation in exoskeleton mass. Anderson et al. attributed this allometric relationship to scaling. The exoskeleton of terrestrial arthropods must increase in thickness as body weight increases to support the organism and withstand the stresses of bending and twisting (Prange 1977; Anderson et al. 1979).

Allometric relationships between N mass and body mass, and between exoskeleton mass and body mass, may be primarily due to exoskeleton N. Trim (1941) estimated N concentrations of 11.8% in abdominal cuticles of 2 Orthoptera species, approximating the mean concentration (10.7%) in riparian arthropods. A large proportion of N in terrestrial arthropods likely resides within the exoskeleton due to its greater density compared with internal tissues and hemolymph. The allometric relationship between exoskeleton mass and body mass may have produced the similar relationship between N mass and body mass.

A linear increase in N mass in internal tissues as body mass increases would dampen the exponential increase in cuticular N mass. The lower exponent relating N mass to body mass (1.039) compared with the exponent relating cuticle mass to body mass (1.135) may reflect this dampening.

Nitrogen Contents in Orders or Suborders

Exoskeleton composition may have contributed to different N concentrations among orders of spiders and insects (Fagan et al. 2002). Arthropod cuticle is composed primarily of protein and chitin (Neville 1975), and concentrations of N are higher in the former. For example, I estimated %N in arthropod cuticular protein from percentages of amino acids in pronotal and abdominal cuticles of adult *Tenebrio* beetles (Andersen et al. 1973; reported in Table 3.4 in Neville 1975) by assuming the amino acids were bonded into polypeptides. The estimated N concentration of cuticular protein (17.4%) exceeded that of chitin (6.89%). Based on the maximum range of chitin concentration (10-60% of dry mass) in insect cuticle (Richards 1978; see also Table 1 in Hackman 1974), and assuming cuticle is entirely chitin and protein, N concentrations in insect exoskeleton may vary from 11.1% to 16.4%.

Greater concentrations of protein in arthropod cuticle, producing higher N contents, have been associated with concentrations of resilin (Andersen 1979). Resilin is a flexible, elastic protein that occurs in cuticle in near-pure concentrations or combined with other proteins and chitin (Richards 1978). I estimated as above that resilin contains 19.0% N from percentages of amino acids in resilin from *Schistocerca* grasshoppers (Andersen 1966; reported in Table 3.4 in Neville 1975). Various mechanical structures in arthropods are elastic due to resilin (Table 2.1 in Neville 1975). Resilin is especially prevalent in the wing tendons and hinges of Odonata and Orthoptera (Andersen & Weis-Fogh 1964), primitive orders with synchronous flight muscles. Andersen and Weis-Fogh also detected resilin in the abdominal sclerites of *Schistocerca* grasshoppers, presumably allowing the abdomen to stretch. Abundances of resilin in riparian Odonata and Orthoptera may have contributed to their high N contents. Although resilin has not been found in spiders (Andersen & Weis-Fogh 1964), the high degree of abdominal stretching by spiders (Browning 1942) suggests their cuticles contain a similar elastic protein. Cuticles of Coleoptera are likely less elastic. A dominant feature of beetles is the elytra, hardened front-wings that act only to cover the folded hind-wings and abdomen. The likely absence of resilin and resultant high concentrations of chitin, in elytra may have lowered %N in Coleoptera.

Nitrogen Contents in Trophic Levels

I did not detect an overall difference in N concentration among herbivorous, predaceous, and detritivorous arthropods after accounting for the allometric effects of body mass. Trophic level did not appear to generally affect arthropod %N. This contradicts the overall difference in N concentration between herbivorous and predaceous arthropods detected by Fagan et al. (2002). Different results may have been due to statistical methodology. Fagan et al. controlled for body length and taxonomic group, to account for phylogeny, whereas I controlled only for body mass. Controlling for phylogeny is difficult, because different frequencies of herbivores compared with predators among taxonomic groups cause trophic level and phylogeny to be confounded. Phylogeny and trophic level cannot be statistically separated.

Similar N contents between trophic levels agree with the concept that most insects satisfy nutrient requirements by adjusting food intake (Waldbauer 1968; reviewed in Simpson et al. 1995). An example in riparian arthropods may be found in the 2 suborders of Hemiptera, insects with piercing-sucking mouthparts. Phytophagous Heteroptera, such as *Lygus* leaf bugs (Backus et al. 2007), typically rupture, dissolve with saliva, and ingest mesophyll from a variety of plant structures. All Homoptera are herbivorous, and many homopterans feed on phloem which is high in water and carbohydrates but low in other nutrients including N. The *Opsius stactogalus* Fieber leafhoppers collected here increase food intake, concentrate nutrients within their filter-chamber digestive tracts (Wiesenborn 2004), and void excess water and sugars. Concentrations of N in Homoptera, phytophagous Heteroptera, and predaceous Heteroptera were similar despite different diets and physiologies.

An exception was Diptera. Herbivorous flies, all Tephritidae, contained lower N concentrations than predaceous or detritivorous flies after considering body mass. Fagan et al. (2002) compared phylogenetic categories of herbivorous insects and found lower N concentrations in Diptera and Lepidoptera, combined as the recent lineage Panorpida, after accounting for body length. The database analyzed by Fagan et al. included the herbivorous flies Bibionidae, Chloropidae, and Drosophilidae, each in a different superfamily separate from Tephritidae. The diversity of phytophagous Diptera found to contain low N concentrations suggests N contents in flies generally vary by trophic level. Fagan et al. (2002) suggested several explanations for lower N contents in herbivores than in predators. These included the direct effects of diet N, indirect effects of trophic niche unrelated to diet, and selection for low body N in response to low diet N. The *A. picturata* tephritids that I collected develop as larvae in the flower heads of *Pluchea* spp. (Foote et al. 1993), corresponding with the flowering *P. sericea* at the study site. Infestations by *A. picturata* reduce seed production (Alyokhin et al. 2001), suggesting larvae eat ovaries or seeds. The species does not appear to concentrate N from food, because its N concentration (5.1%) is within the range (1-7% of dry mass) reported for seeds (Mattson 1980). The structural or biochemical features correlated with low N concentration in *A. picturata* and other plant-feeding flies are unknown. Low exoskeleton mass in tropical, herbivorous beetles has been attributed to low diet N, short larval-development time, and high fecundity (Rees 1986). Equivalent N concentrations in predaceous or parasitic flies and detritivorous flies suggest their diets contain similar amounts of N.

Arthropod Nitrogen as a Nutrient for Birds

Not all N in arthropods is digested by insectivorous birds. Bird diets are frequently determined by identifying undigested fragments of exoskeleton in fecal samples (e.g., Wiesenborn & Heydon 2007). Digestion of arthropod cuticle by vertebrates likely depends on its sclerotization (Karasov 1990). Sclerotized proteins are bonded together, frequently with chitin, forming an irreversibly-hardened cuticle that cannot be hydrolyzed into amino acids (Richards 1978). Unsclerotized proteins, like resilin, can be hydrolyzed (Richards 1978). Relative proportions of sclerotized and unsclerotized proteins vary greatly among species (Richards 1978) producing cuticles with different digestibilities. Arthropod orders with high amounts of elastic protein, such as Odonata and Orthoptera and probably Araneae, may provide insectivorous birds with high concentrations of digestible protein.

Riparian arthropods presented insectivorous birds with prey containing a range (5.1-14.0%) of N concentrations. Foraging by insectivorous birds in relation to prey N concentration can be difficult to discern, because birds frequently forage in response to prey availability which is transitory and hard to estimate. Selective foraging may be inferred by comparing arthropods eaten by adults with those concurrently captured by adults but fed to nestlings. Insectivorous nestlings depend on diet nutrients in addition to calories (Johnston 1993). Adult great tits (*Parus major* L.) and blue tits (*Parus caeruleus* L.) in woodlands ate mostly Lepidoptera larvae but provided 3-9 day-old nestlings with more spiders, earwigs (Dermaptera), and flies (Cowie and Hinsley 1988). Including other arthropods, especially spiders, as prey may have augmented the low N content of Lepidoptera (Fagan et al. 2002). Spiders also provide different amino-acid compositions (Ramsay & Houston 2003).

The importance of prey N-concentration to insectivorous birds that feed on more-diverse prey is less clear. An example is the southwestern willow flycatcher (*Empidonax traillii* (Audubon) ssp. *extimus* Phillips), a migrant that winters in Central America and breeds in southwestern U.S. riparian habitats. Adult flycatchers ate mostly heteropterans, flies, and beetles but fed more odonates and beetles to nestlings (Drost et al. 2003). Diet N may be increased by including odonates, especially dragonflies due to their large biomass. Diets of nestling flycatchers in other localities contained more Diptera than those of adults (Durst et al. 2008) or prey compositions similar to adults (Wiesenborn & Heydon 2007). The high-N orders of Araneae, Odonata, and Hymenoptera, taken together, were eaten with similar frequency by flycatchers at different localities and habitats. These orders comprised 21% of prey in California (Drost et al. 2003), 31% of prey in Arizona (Durst et al. 2008), and 21% of prey at 3 localities in Arizona and Nevada (Wiesenborn & Heydon 2007).

In summary, N concentrations in riparian arthropods are primarily dependent on body mass and order and less dependent on trophic level. Variation in prey N concentration may affect foraging by insectivorous birds and the qualities of food they obtain.

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