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Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers

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Key processes such as trophic interactions and nutrient cycling are often influenced by the element content of organisms. Previous analyses have led to some preliminary understanding of the relative importance of evolutionary and ecological factors determining animal stoichiometry. However, to date, the patterns and underlying mechanisms of consumer stoichiometry at interspecific and intraspecific levels within natural ecosystems remain poorly investigated. Here, we examine the association between phylogeny, trophic level, body size, and ontogeny and the elemental composition of 22 arthropod as well as two lizard species from the coastal zone of the Atacama Desert in Chile. We found that, in general, whole-body P content was more variable than body N content both among and within species. Body P content showed a significant phylogenetic signal; however, phylogeny explained only 4% of the variation in body P content across arthropod species. We also found a significant association between trophic level and the element content of arthropods, with carnivores having 15% greater N and 70% greater P contents than herbivores. Elemental scaling relationships across species were only significant for body P content, and even the P content scaling relationship was not significant after controlling for phylogeny. P content did decrease significantly with body size within most arthropod species, which may reflect the size dependence of RNA content in invertebrates. In contrast, larger lizards had higher P contents and lower N:P ratios than smaller lizards, which may be explained by size-associated differences in bone and scale investments. Our results suggests that structural differences in material allocation, trophic level and phylogeny can all contribute to variation in the stoichiometry of desert consumers, and they indicate that the elemental composition of animals can be useful information for identifying broad-scale linkages between nutrient cycling and trophic interactions in terrestrial food webs.

A central goal in ecological stoichiometry is to determine how food web dynamics and rates of nutrient cycling are constrained by the interaction between local nutrient availability and the requirements of multiple elements by organisms (Sterner and Elser 2002, Moe et al. 2005). A first step in understanding these constraints is to identify patterns of variation in the elemental composition of the organisms that may influence ecosystem processes. Despite considerable advances in understanding ecologically relevant variation in the elemental composition of primary producers, studies on consumer stoichiometry are still relatively rare- particularly in terrestrial systems (Fagan et al. 2002, Sterner and Elser 2002, Schade et al. 2003, Woods et al. 2004, Kay et al. 2006, Hambäck et al. 2009, Mulder and Elser 2009). Identifying patterns of stoichiometric variation in terrestrial consumers, and determining their causes and consequences, should help clarify how nutrient cycling affects and is affected by the composition of terrestrial communities.

Previous studies on terrestrial consumers have shown significant phylogenetic and trophic level differences in whole-body content of major elements (carbon (C), nitrogen (N), and phosphorus (P)) among arthropod taxa (Fagan et al. 2002, Denno and Fagan 2003, Woods et al. 2004). For instance, Fagan et al. (2002) found that recently derived groups of terrestrial insects (Diptera and Lepidoptera) have lower body N contents than more ancestral insect orders, and insect predators have higher body N content than herbivore. In addition, body P content has been shown to differ among trophic levels, although patterns of P content variation differ among systems (Woods et al. 2004, Martinson et al. 2008).

A central hypothesis in ecological stoichiometry theory is the growth rate hypothesis (Sterner and Elser 2002), which proposes that differences in whole-body P content among invertebrate organisms results from differential allocation to P-rich RNA needed for rapid growth. Consistent with this hypothesis, faster-growing invertebrates tend to have higher P-content than (otherwise similar) slower-growing organisms (Sterner and Elser 2002). The growth rate hypothesis also predicts size-related variation in invertebrate P content: because small-bodied organisms tend to have faster growth

rates than larger organisms, body P content should decrease with body size across species (Elser et al. 1996, Sterner and Elser 2002, however see Gillooly et al. 2005). Tests of this prediction have shown mixed results (Elser et al. 2000, Woods et al. 2004, Gillooly et al. 2005, Bertram et al. 2008, Martinson et al. 2008). For example, Cross et al. (2003) and Woods et al. (2004) have reported that both N and P contents in invertebrates decrease with body size, whereas Martinson et al. (2008) found no comparable pattern in terrestrial detritivores. Because of the inconsistencies, additional information is needed to determine the mechanisms of size-related variation in elemental stoichiometry of invertebrates.

The elemental composition of organisms can also vary substantially due to differential allocation to other major biomolecules (e.g. protein, lipids) or structural materials (e.g. chitin, scales and bones) (Elser et al. 1996, Sterner and George 2000, Bertram et al. 2008). In addition, individual organisms often show changes in element content with ontogenetic development (Sterner and Elser 2002, Mulder and Bowden 2007). Variation in elemental composition across ontogeny in invertebrates appears to be influenced by the higher P demand associated with faster growth rates in larval stages (Elser et al. 1996, Sterner and Elser 2002, Schade et al. 2003). Furthermore, intraspecific variation in element content may result from spatial and/or temporal changes in the nutrient content of food resources (Persson et al. 2010). These deviations from strict homeostasis might account for significant elemental composition variation among individuals (Persson et al. 2010), and make differences among species more difficult to detect.

The variation in empirical findings across studies could be partly explained by the fact that most studies have relied on compiled metadata (Fagan et al. 2002, Hambäck et al. 2009, although see Woods et al. 2004). No previous studies have examined mechanisms explaining both body N and P content of multiple invertebrate and vertebrate consumers at the species level within a single system. Moreover, very few studies have examined the extent of interspecific and intraspecific variation in elemental stoichiometry in natural ecosystems. Variation in the elemental stoichiometry of organisms could lead to important constraints in major life history traits and in turn affect key ecological processes, such as trophic interactions and nutrient cycling (Sterner and Elser 2002).

In this study, we examined variation in body C, N and P content among and within species of desert consumers from four well-delimited food webs from coastal areas of the Atacama Desert, Chile. We focus on the dominant arthropod species and on two lizard species: the only vertebrate predators that occur in these ecosystems. These natural ecosystems that support sufficiently simple and conspicuous food webs provide us with a unique system for studying the ecological stoichiometry of consumers in whole food webs. Here we test general predictions that, across taxa, N and P contents is higher (1) in predators than in herbivores, (2) in more recently derived arthropod orders than in older orders, and (3) in smaller-bodied taxa. We also test, within species, whether (4) N and P contents are higher in early ontogenetic stages than in adults, (5) N and P contents decrease with body size in arthropods, and (6) N and P contents increase with body size in vertebrates.

Material and methods

Sample collection

Arthropods and lizards were collected from four sites in the coastal zone of the Atacama Desert, Chile. The area is characterized by a relatively constant temperature (annual average 18.1°C, annual max. = 20.9°C, annual min. = 15.9°C), a mean annual rainfall of 1.7 mm over the last century (Dirección Meteorológica de Chile), and by the occurrence of fog events mainly during the austral winter (June to August, Cereceda et al. 2008). Fog originates from thick stratocumulus banks below 1000 m which, when intercepted by isolated mountaintops or steep coastal slopes of the Coastal Cordillera, generates a fog immersion zone (Pinto et al. 2006, Cereceda et al. 2008). The increased air moisture and deposition in the fog zone is correlated with the development of isolated vegetation 'islands' that spreads inland through low elevation valleys or passes where fog is also frequent (Pinto et al. 2006, Cereceda et al. 2008). Several terrestrial bromeliad species of the genus *Tillandsia* inhabit southern Perú and northern Chile, which depend exclusively on fog inputs as their primary water source (Pinto et al. 2006). The most noticeable one *T. landbeckii* invades sandy soils covering vast areas and forming specialized communities called 'tillandsiales'. At each of the four *T. landbeckii* stand sites we collected arthropods belonging to 22 species (i.e. Insecta and Arachnida) and two lizard species. All individuals collected were cooled on ice until and taken to the laboratory for analysis. Arthropod's guts were not removed prior to chemical analyses due to their small size, therefore we kept them at 4°C overnight to allow their gut content evacuation (Evans-White et al. 2005). In contrast, we removed the digestive tract of the lizards prior to analyses. Before chemical analyses the individuals were counted and identified to the level of genus or species. We also classified arthropods by trophic level using information from the literature and field observations. We collected larval and adult stages from true flies (*Musca* sp., Diptera), which we used to analyze the effect of ontogenetic stage on body elemental content within this single species.

Sample preparation and nutrient determination

We determined dry mass of individuals using an electronic balance (± 0.1 μg). We measured the phosphorus concentration in whole arthropods and whole lizards using potassium persulfate and sulfuric acid digestion followed by ascorbate–molybdate colorimetry. Prior to digestion, we gently crushed individuals with a Teflon-coated rod while in solution to expose internal tissues to reagents. We performed all P analyses using a flow solution autoanalyzer.

We determined the percent of N and C using a NC analyzer that involves complete combustion of samples. For smaller arthropods (<5 mg dry mass), we performed NC analyses on whole individuals. For larger arthropods and lizards, we analyzed NC levels in subsamples from dried individuals that were first crushed with a mortar and pestle. We determined the percent recovery in P and NC assays by comparison to bovine muscle standards from the Natl Inst.

of Standards and Technology (NIST 8414). We use the term 'P (or C or N) content' to describe P (or C or N) content as a percent of dry body mass. The C:N:P ratios were calculated in molar units. The analyzed number of arthropods and lizards per species ranged from 1 to 42.

Data analysis

We tested the effect of phylogeny on body elemental content (C, N, P and C:N ratios) and body size by calculating phylogenetic independent contrasts (PICs; Felsenstein 1985). The PICs are widely used to correct statistically for potential non-independence of observations (e.g. among species) due to their phylogenic relationships (Felsenstein 2008). Because no comprehensive arthropod phylogeny is available at species level for all our arthropods, we constructed a composite tree including all 22 species of arthropods describing the hypothesized evolutionary relationships among them, using Mesquite 2.72 for phylogenetically based statistical analyses (<http://mesquiteproject.org/mesquite/mesquite.html>). To construct arthropod tree topology we followed Regier et al. (2010) because this is the most complete and updated order-level molecular phylogeny available. Below order level, we used Flook et al. (2000) for Orthoptera; Hunt et al. (2007) for Coleoptera; Han and Ro (2009) and Nihei and Barros de Carvhalo (2007) for Diptera; phylogenetic relationships within Lepidoptera were taken from Wahlberg et al. (2005) and Mitchell et al. (2000). The phylogeny of Arachnidae was drawn from Shultz (2007); Araneae from Coddington and Levi (1991); and Acari phylogeny was based on Dabert et al. (2010). For the few unresolved relationships within genus and species for which we had no information, phylogenetic relationships were inferred from current taxonomy (Felsenstein 1985, Garland et al. 2005). We calculated independent contrasts for continuous traits (i.e. N and P contents, C:N ratios and body size) using the Phenotypic Diversity Analysis Program for Mesquite. We assumed branch lengths were constant (equal to one) as this method met assumptions of PICs analyses (Garland et al. 1992). Contrasts were standardized and positivized on the x-axis and linear regressions performed through the origin (Garland et al. 1992). Contrasts were not calculated for categorical data (i.e. trophic level) because trophic level and phylogeny are closely correlated in arthropods in our data set.

In order to test for a phylogenetic signal in stoichiometry traits we used the Mantel test (Böhning-Gaese and Oberrath 1999). We created a dissimilarity matrix for stoichiometric traits for each species pair by using Euclidean distance and we also constructed a phylogenetic distance matrix by counting the number of nodes that separate each species pair (Fagan et al. 2002, Woods et al. 2004). The stoichiometric dissimilarity matrices were regressed on the phylogenetic distance matrix and we tested the regression for significance using the Mantel test. We tested the significance of the t value from the Mantel test against a null distribution constructed by Monte Carlo randomizations, whereby the phylogenetic matrix was held constant and species in the stoichiometric matrix were reshuffled randomly (Böhning-Gaese and Oberrath 1999).

We performed a one-way analysis of covariance (ANCOVA) to examine differences in C, N and P contents, and C:N ratios among and within arthropod species, using body size (dry weight in mg) as a covariate. Before analyses consumer body size data were log transformed. In addition, we performed ANCOVAs, with body size as the covariate to test the effects of trophic level and ontogenetic stage on body elemental content. All multiple comparisons between species were performed using a Tukey HSD test. Significance levels were set at $\alpha = 0.05$ for all ANOVAs and ANCOVAs. We used simple linear regression to determine the relationship between body elemental content and log body size across and within species. For these analyses, we included only species with more than six individuals. All mean values are shown with ± 1 SE. All statistical analyses were performed with the statistical package R ver. 2.9.0 (R Development Core Term 2009).

Results

Stoichiometric variation among species

The analysis of body N and P content of 22 arthropod species distributed across ten taxonomic orders (Araneae, Scorpionoidea, Pseudoscorpionoidea, Acari, Solifugae, Orthoptera, Coleoptera, Lepidoptera, Thysanura and Diptera) showed a wide range of variation (Fig. 1). The data revealed almost a two-fold variation in body % N among arthropod species (Fig. 1a), with a mean of 10.7 ± 0.09% N ($F_{21,288} = 3.66$, $p < 0.001$). The highest body % N was recorded for Arachnida: Acari species, with a mean value of 14.8 ± 1.50% N, followed by some Insecta species such as Diptera and Lepidoptera species. Nitrogen content was particularly low for some Coleoptera (Tenebrionidae sp. 3 and sp. 5) with a mean of 9.27 ± 0.30 and 9.13 ± 0.48, respectively. No effect of phylogenetic relatedness in body N content of the arthropod species was found ($r = -0.069$, $p = 0.832$).

Body % P showed greater interspecific variation than body % N, with a four-fold variation among species ($F_{18,265} = 24.56$, $p < 0.001$, Fig. 1b). Mean body % P across all arthropods was 0.79 ± 0.08. Lepidoptera species (Nymphalidae and Noctuidae) showed the highest body P content, with a mean of 1.50 ± 0.30% P, whereas Coleoptera species (Anobiidae sp. 1 and Tenebrionidae sp. 1) and Orthoptera sp. 1 showed the lowest body % P with a mean of 0.37 ± 0.02, 0.37 ± 0.05 and 0.36 ± 0.04% P, respectively. Results from the Mantel test indicate that closely related species had significantly more similar body P content than distantly related species (i.e. there was a significant phylogenetic signal for P ($p < 0.05$)). Phylogenetic relatedness explained 4.13% ($p < 0.05$) of the variance in body P content of the arthropod species.

Differences in body C content among species were small but statistically significant ($F_{21,288} = 5.29$, $p < 0.001$), with a coefficient of variation (CV = SD/mean = 5%). Mean body % C content for all species was 42.45 ± 0.13, and Diptera species had the lowest body % C content with a mean of 39.65 ± 1.00 (Appendix 1 Fig. A1). The C:N stoichiometry of arthropods differed significantly among species ($F_{21,288} = 3.50$, $p < 0.001$) and showed a coefficient of variation of 18%. The C:N ratios ranged from 3.9 ± 0.45

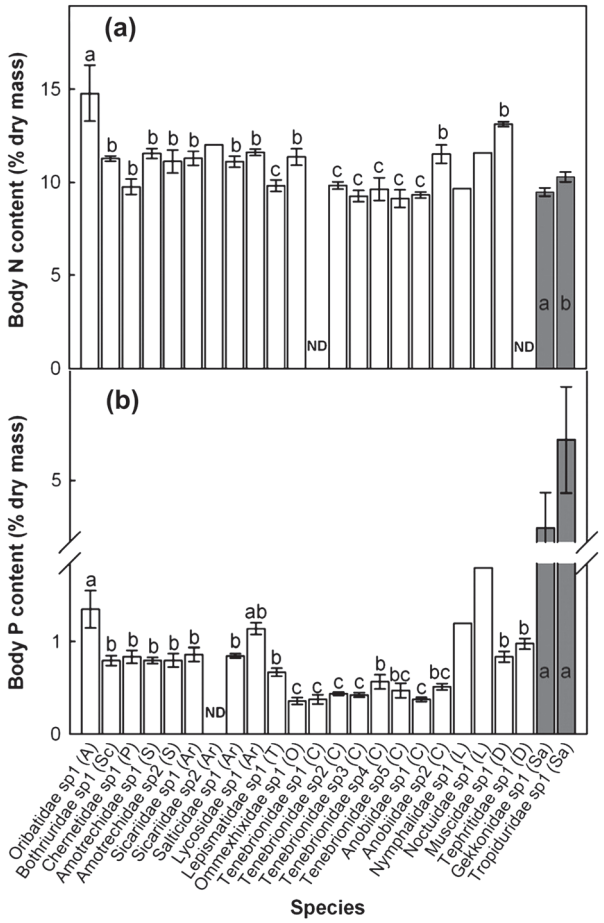

Figure 1. Mean (±SE) nutrient content across species: (a) nitrogen as a percentage of dry weight, and (b) phosphorus as a percentage of dry weight. Different letters above their bars were judged significantly different by ANCOVA. Tukey HSD was used for post hoc analysis of differences among species. Letters inside parenthesis after family names indicate the taxonomic order: (A) Acari, (Sc) Scorpionoidea, (P) Pseudoscorpionoidea, (S) Solifugae, (Ar) Araneae, (T) Thysanura, (O) Orthoptera, (C) Coleoptera, (L) Lepidoptera, (D) Diptera and Sauria (Sa). Grey bars show vertebrate species. ND indicates no available N % data for Tenebrionidae sp. 1 (C) and for Tephritidae (D). No available % P data for Sicariidae sp. 2 (Ar). The species belonging to Noctuidae and Nymphalidae (L) were not included in statistical analyses (n = 1). Lizards were analyzed independently from arthropods.

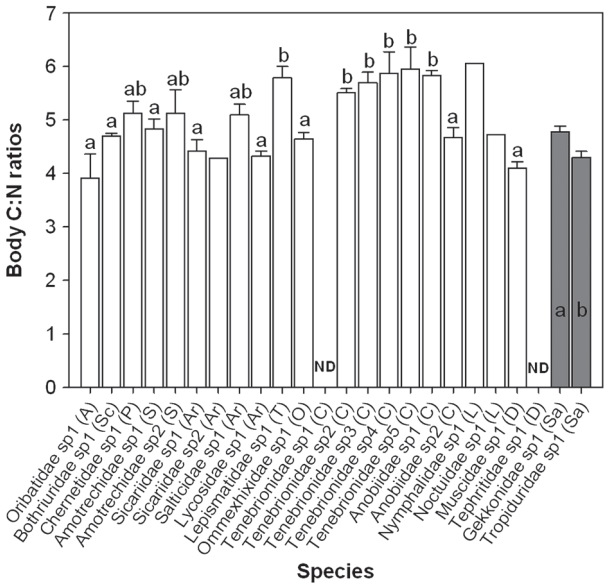

Figure 2. Mean (±SE) C:N molar ratios across species. Different letters above their bars were judged significantly different by ANCOVA. Tukey HSD was used for post hoc analysis of differences among species. Letters inside parenthesis after family names indicate the taxonomic order: (A) Acari, (Sc) Scorpionoidea, (P) Pseudoscorpionoidea, (S) Solifugae, (Ar) Araneae, (T) Thysanura, (O) Orthoptera, (C) Coleoptera, (L) Lepidoptera, (D) Diptera and Sauria (Sa). Grey bars show vertebrate species. Lizards were analyzed independently from arthropods.

in Acari species to 6.1 in Lepidoptera species (Fig. 2). No effect of phylogenetic relatedness in body C content and C:N ratios of the arthropod species was found ($r = –0.072$, $p = 0.729$ and $r = 0.152$, $p = 0.248$, respectively).

Lizards showed an average of 9.75 ± 0.55% N and 4.56 ± 0.10% P in their bodies (Fig. 1). The *Phrynosaura reichei* (Tropiduridae) showed significantly higher body N content than the *Phyllodactylus gerrhopygus* (Gekkonidae) ($F_{1,22} = 7.78$, $p < 0.05$), but they did not differ in body P content ($F_{1,26} = 3.48$, $p = 0.070$). The lizard *P. reichei* had significantly lower body C:N ratios than *P. gerrhopygus* ($F_{1,24} = 11.88$, $p < 0.01$).

The comparison of the body element content among trophic levels showed higher N ($F_{2,292} = 30.9$, $p < 0.001$, Fig. 3) and P contents ($F_{2,281} = 97.64$, $p < 0.001$, Fig. 3), and also lower C:N ($F_{2,292} = 27.52$, $p < 0.001$) and N:P ratios ($F_{2,54} = 7.86$, $p < 0.001$) for carnivorous arthropods compared to herbivorous arthropods. Herbivores had a mean of 9.84 ± 0.13% N and 0.50 ± 0.02% P whereas carnivore mean was 11.36 ± 0.11% N and 0.85 ± 0.02% P. In detritivore species, N content was 10.34 ± 0.41%, which was significantly different from carnivores ($p < 0.01$), and P content was 0.81 ± 0.08%, which was significantly different from herbivores ($p < 0.001$). Trophic level explained 19% of the variation in body N and 41% of the variation in body P content.

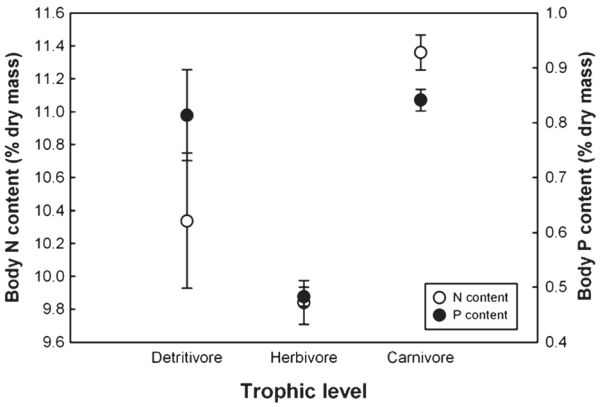

Figure 3. Mean (±SE) body N (open circles) and P (closed circles) content P for detritivores, herbivores and carnivores. Tukey HSD was used for post hoc analysis of differences among trophic levels.

Stoichiometric variation within species

Differences in elemental content within species from different sites were small, but seven species from the whole-data set (out of 13 species analyzed) showed high intraspecific variability in body N or P content (Table 1). The body N and P content of some Coleoptera and Arachnida species differed significantly (showing about two-fold to five-fold variation for each taxa). Body N, P content and C:P ratios did not differ between larval and adult stages for Diptera (for N content, $F_{1,18} = 0.968$; $p = 0.338$; for P content, $F_{1,16} = 0.629$, $p = 0.439$ and for C:P ratios $F_{1,7} = 0.278$, $p = 0.614$), in contrast to body C:N ratios that were much higher for larval individuals than for adults ($F_{1,18} = 18.30$, $p < 0.001$, Appendix 1 Fig. A2).

There were significant allometric relationships for P content (but not N content) across all arthropods in the data set (Table 2). However, the allometry for body P content was not significant after correcting for phylogeny (Table 2). At the species level, all arthropods showed a negative body P content allometry (Fig. 4a, Table 2), but this relationship was significant for only seven (of 13) species (Table 2). In contrast, there was a significant positive allometric scaling of body N content for the Scorpionoidea species. Both lizard species showed a significant positive relationship between P content and body size (Fig. 4b, Table 2). The body N:P ratios showed a negative allometry for both species ($r^2 = 0.59$, $p < 0.05$ for *P. reichei* and $r^2 = 0.453$, $p < 0.01$ for *P. gerrhopygus*).

Discussion

Our results show that terrestrial consumers in desert food webs differ widely in their element content both within and among species. Evolutionary and ecological factors appear to explain differences among arthropod species. We found a significant effect of trophic level on the elemental stoichiometry of arthropods, with carnivores having higher body N and P content than herbivores. Ontogeny did explain some, but not much, of the variation in the element content of Diptera. Our findings suggest that differences associated with phylogenetic relateness, structural material allocation, trophic level and body size contribute to extensive natural inter- and-intraspecific variation in the elemental stoichiometry of consumers in desert environments.

Stoichiometric variation among species

Body N content showed two-fold variation among species, whereas body P content varied from two to five-fold among species. These differences are not simple correlates of phylogenetic relatedness. Within our dataset we found no phylogenetic signal for N and C:N ratios. These results are consistent with those from a broad-scale literature survey by Fagan et al. (2002), who found that arthropod N content was not related to phylogeny at lower taxonomic levels. Our results, along with those of Fagan et al. (2002), strongly suggest a lack of fine-grained phylogenetic signal for arthropod

Table 1. Results of analysis of covariance of intra-specific variation in body N and P content of consumers across sites. Significant differences are in bold. $^{*}p < 0.05$, $^{**}p < 0.01$.

Species	Source of variation	Range of variation (%)	DF	F-value	p-value
Bothriuridae (Sc)	nitrogen	9.11 – 13.15	3,38	0.420	0.742
	phosphorus	0.60 – 1.36	3,12	0.897	0.484
Ammotrechidae sp. 1 (S)	**nitrogen**	8.65 – 15.23	**3,35**	**2.878**	**0.050***
	phosphorus	0.50 – 1.29	3,33	0.900	0.542
Ammotrechidae sp. 2 (S)	nitrogen	9.27 – 13.64	1,7	0.189	0.677
	phosphorus	0.50 – 1.21	1,9	0.625	0.450
Salticidae (Ar)	nitrogen	7.77 – 12.89	1,15	0.242	0.630
	phosphorus	0.58 – 1.23	**3,37**	**3.855**	**0.017***
Lycosidae (Ar)	**nitrogen**	9.79 – 14.61	**1,27**	**7.270**	**0.003****
	phosphorus		ND		
Sicariidae sp. 1 (Ar)	nitrogen		ND		
	phosphorus	0.47 – 1.67	2,14	1.358	0.296
Lepismatidae (T)	nitrogen	7.10 – 12.88	2,23	0.680	0.516
	phosphorus	0.47 – 1.01	2,12	2.374	0.135
Tenebrionidae sp. 2 (C)	**nitrogen**	7.47 – 12.58	**3,31**	**4.440**	**0.010****
	phosphorus	0.25 – 0.63	2,26	1.453	0.252
Tenebrionidae sp. 3 (C)	nitrogen	6.73 – 11.60	1,12	2.467	0.142
	phosphorus	0.13 – 0.70	**1,26**	**7.948**	**0.009****
Anobiidae sp. 1 (C)	nitrogen	7.93 – 10.67	1,24	3.420	0.077
	phosphorus	0.22 – 0.55	**1,20**	**11.064**	**0.003****
Muscidae (D)	**nitrogen**	8.20 – 14.67	2,17	4.833	**0.022***
	phosphorus	0.60 – 1.12	1,16	0.283	0.602
Tropiduridae (Sa)	nitrogen	9.08 – 11.62	1,7	3.176	0.118
	phosphorus	3.57 – 7.00	2,8	1.298	0.320
Gekkonidae (Sa)	nitrogen	8.44 – 10.76	3,13	0.335	0.800
	phosphorus	3.14 – 6.10	3,11	1.103	0.383

Order codes: (Sc) Scorpionoidea, (S) Solifugae, (Ar) Araneae, (T) Thysanura, (C) Coleoptera, (D) Diptera, and the two lizard species belonging to (Sa) Sauria. ND indicates no data available for P and N analysis for Lycosidae sp. 1 and Sicariidae sp. 1, respectively.

Table 2. Scaling of body elemental content in arthropods and lizards with body size. The results show regressions on phylogenetic independent contrasts (PICs) for whole arthropod data set and analogous results from non-phylogenetically controlled data for 15 arthropod species and two lizard species. The r^2-values, slope and p-values are indicated. Statistically significant relationships are in bold ($p < 0.05$). Only species with more than six individuals were used in regression analyses.

	N			P			C:N ratios		
Species	r^2	slope	p	r^2	slope	p	r^2	slope	p
Whole arthropod data set (phylogenetically controlled)	0.050	−0.004	0.648	0.004	−0.48	0.811	0.004	0.04	0.797
Whole arthropod data set (non-phylogenetically controlled)	0.020	−0.14	0.052	**0.046**	**−0.22**	**0.000**	0.007	0.08	0.315
Bothriuridae sp. 1 (Sc)	**0.275**	**0.52**	**0.004**	0.225	−0.47	0.166	0.064	−0.26	0.202
Ammotrechidae sp. 1 (S)	0.141	0.38	0.086	**0.146**	**−0.32**	**0.037**	**0.111**	**−0.33**	**0.291**
Ammotrechidae sp. 2 (S)	0.516	−0.72	0.108	0.364	−0.60	0.231	0.471	0.69	0.132
Sicariidae sp. 1 (Ar)	0.284	0.53	0.277	**0.389**	**−0.62**	**0.006**	0.009	0.10	0.857
Salticidae sp. 1 (Ar)	0.023	−0.51	0.774	**0.133**	**−0.97**	**0.022**	0.027	0.44	0.647
Lycosidae sp. 1 (Ar)	0.000	−0.01	0.956		ND		0.097	0.31	0.350
Lepismatidae sp. 1 (T)	0.026	−0.16	0.583	0.228	−0.48	0.084	0.033	0.18	0.534
Ommexhixidae sp. 1 (O)	0.009	0.10	0.778	0.143	−0.52	0.356	0.005	0.07	0.838
Tenebrionidae sp. 2 (C)	0.269	−0.52	0.057	**0.520**	**−0.72**	**0.000**	**0.526**	**0.73**	**0.005**
Tenebrionidae sp. 3 (C)	0.000	0.02	0.951	**0.141**	**−0.38**	**0.049**	0.030	−0.17	0.590
Tenebrionidae sp. 4 (C)		ND		0.473	−0.69	0.131		ND	
Tenebrionidae sp. 5 (C)	0.588	−0.77	0.075		ND		0.389	0.62	0.186
Anobiidae sp. 1 (C)	0.204	0.45	0.163	0.116	−0.34	0.305	0.189	−0.43	0.213
Anobiidae sp. 2 (C)	0.519	−0.72	0.169	**0.198**	**−0.44**	**0.048**	0.713	0.84	0.070
Muscidae sp. 1 (D)	0.020	0.45	0.742	0.036	−0.60	0.746	0.390	−0.622	**0.018**
Gekkonidae sp. 1 (Sa)	0.284	−0.53	0.140	**0.500**	**0.67**	**0.006**	0.064	−0.25	0.362
Tropiduridae sp. 1 (Sa)	0.392	−0.63	0.070	**0.510**	**0.71**	**0.014**	0.183	0.43	0.189

Order codes: (Sc) Scorpionoidea, (S) Solifugae, (Ar) Araneae, (T) Thysanura, (O) Orthoptera, (C) Coleoptera, (D) Diptera and the two lizard species belonging to (Sa) Sauria. ND indicates no data available for the analysis.

N content. Although the interpretation of phylogenetic signal remains in dispute (Losos 2008, Revell et al. 2008), one possible cause of this result is that life history traits influencing body N content may evolve relatively fast as a response to environmental conditions (Fagan et al. 2002). The biochemical and morphological correlates of body N (and C:N) differences among taxa are still poorly described. Possible correlates include differential exoskeleton investment and cuticle composition (e.g. protein-to-chitin ratios) (Sterner and Elser 2002).

We also found a small, but statistically significant, phylogenetic signal for P. This result is consistent with a survey of North American desert arthropods by Woods et al. (2004), who found that recently derived orders (Lepidoptera and Diptera) had higher body P content than other groups. The relatively high body P content for Lepidoptera and Diptera in our data set suggests that this may be a general pattern, at least in dry ecosystems.

Invertebrate predator N content in our survey was higher than that of herbivores and detritivores; this result is similar to comparisons made in other systems (Fagan et al. 2002, Matsumura et al. 2004, Kagata and Ohgushi 2007). Interestingly, we also found that invertebrate predators have on average higher body P content than herbivores and detritivores. This finding contrasts with the results of Woods et al. (2004), who did not find differences in P content between trophic levels (herbivores vs carnivores).

Contrary to general expectations on allometric relationships in arthropod element content, we found no consistent relationship between N content and body size of arthropods when all taxa were pooled together. Phylogenetically corrected and uncorrected analyses yielded different results for P content; only when phylogenetic relatedness was not considered did we find a significant (negative) relationship between P content and body size. Although our data set is limited to 22 species, the weak association between whole-body P content and body size is consistent with the analysis of Gillooly et al. (2005), who modeled size-related changes in the relative proportion of P-rich RNA (required for rapid growth) versus P associated with other body pools such as phospholipids that are invariant with body size.

To our knowledge, no other data about lizard nutrient stoichiometry has been published. Summarizing available data on larger vertebrates, Sterner and Elser (2002) reported that, in birds and mammals, body N content ranged from 8 to 12%, P content from 1.5 to 4.5%, and N:P ratios from 5 to 15. Our data on lizards fall within these ranges, suggesting a relatively high constancy in nutrient content across vertebrate species.

Although our results show some associations between body element content, phylogeny, trophic level, and body size among species, the underlying basis of these associations is still poorly understood. There are two main categories of explanation for these patterns: functional and economical (Kay et al. 2005, Kay and Vrede 2008). Functional mechanisms that have been offered to explain species differences in N and C:N ratios include differential exoskeleton investment and cuticle composition (e.g. protein to chitin ratios); for example, flying insects may have reduced cuticle investment that trades off support and protection for increased agility and decreased metabolic costs during flight (Fagan et al. 2002, Lease and Wolf 2010). Similarly, the growth rate hypothesis (which functionally links P content to growth rate) has been offered as an explanation for the high

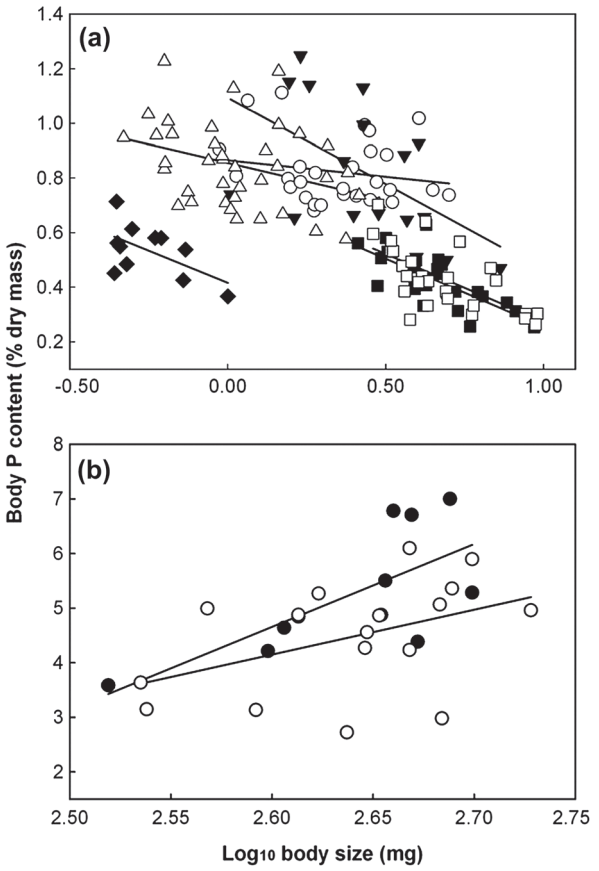

Figure 4. Allometric relationship of P content in arthropod and lizard species: (a) Allometry of P content in arthropod species: ○ Ammotrechidae sp. 1 (S), ▼ Sicariidae sp. 1 (Ar), △ Salticidae sp. 1 (Ar), ■ Tenebrionidae sp. 2 (C), □ Tenebrionidae sp. 3 (C) and ◆ Anobiidae sp. 2 (C) and (b) Allometry of P content in lizard species: ○ *Phyllodactylus gerrhopygus* and ● *Phrynosaura reichei*. Note difference in scale of each figure. See Table 2 for statistical results.

P contents of Lepidoptera and Diptera because these taxa need high rates of growth and reproduction to efficiently exploit ephemeral food resources (Woods et al. 2004). Differences in element content among consumers have also been explained using economical mechanisms. For instance, recent surveys suggest a major role of the elemental factors of the microhabitat (soil abiotics) in the distribution of larger organisms (Mulder and Elser 2009). Moreover, carnivores may have higher N content than herbivores because they generally have higher assimilation efficiencies than herbivores (Lehman 1993, Sterner and Elser 2002), and intraguild predation may allow predators to enhance their N-intake by feeding on N-rich preys (Fagan et al. 2002, Denno and Fagan 2003). In addition, the significant difference in P content between predators and herbivores in our survey could be a consequence of the fact that plant resources in our desert sites have particularly low P content (González unpubl.). Clarifying the relative importance of functional and economic selection pressures on body element composition is a major research challenge in ecological stoichiometry (Kay et al. 2005). Progress toward this end can be made with comparisons of element stoichiometry, higher-order biochemistry, and functional traits (Kay et al. 2006), coupled with studies linking dietary nutrition to the element content of organisms and trait expression (Behmer 2009).

Stoichiometric variation within species

We found that both N and P content showed extensive variation within individual arthropod species. This variation suggests that, although individual consumers might maintain compositional homeostasis through selection ingestion, assimilation, and excretion, compositional set points may vary predictably with individual trait differences. To date, studies examining within-taxa variation in terrestrial consumers are still rare, however, some reports exist on the variation of stoichiometry across development stages and body sizes (Kay et al. 2006, Back et al. 2008, Bertram et al. 2008). Although empirical studies suggest that the element content of invertebrates is strongly associated with ontogeny (Sterner and Elser 2002), there is some evidence that show no influence of development stage on body element content of insects (Fagan et al. 2002). Here we did not find any significant difference on N or P content between ontogenetic stages; however, larvae had significant higher C contents and C:N ratios than adult flies. The larval stage of holometabolus insects (e.g. Diptera) is characterized by conversion of carbohydrates to fat bodies, which supports the rapid growth of the larvae and fuels the animal through the subsequent non-feeding (pupal) period (Aguila et al. 2007). These findings suggest that higher amount of larval-stored fat increase larval C content and C:N ratios (with no changes in body N content) in holometabolous insects, whereas hemimetabolous insects do the opposite. Such life-history differences between holometabolous and hemimetabolous insects will likely play a main role in influencing ontogenetic differences in insect stoichiometry and, thus should be considered in future studies.

At the intraspecific level we found that smaller invertebrates have higher P content. Current explanations for such allometries focus on the functional link between growth rate and body P content (Elser et al. 1996, Sterner and Elser 2002, Woods et al. 2004, Bertram et al. 2008). The allometric patterns in lizards are consistent with existing data showing that body P content is an increasing function of body size in most vertebrates (Dantas and Attayde 2007, Hendrixson et al. 2007). In contrast, body N content and N:P ratios have shown a negative, positive or no relationship with body size in fishes (Sterner and George 2000, Hendrixson et al. 2007, Torres and Vanni 2007). These findings suggest that some fishes and lizards may have less relative allocation of N into muscles, but also the endoskeletal mass investment seems to be variable across vertebrate species (Lease and Wolf 2010). Consequently, the scaling of structural support and elemental stoichiometry in vertebrates exhibit slightly different allometric responses across taxonomic groups, which could be partly driven by evolutionary history (Hendrixson et al. 2007).

Overall, our study analyzed nutrient content variation in both invertebrate and vertebrate species in desert ecosystems within a well-delimited geographical area. To our knowledge, our study is the first to assess inter- and-intra specific

consumer stoichiometry from terrestrial food webs extending beyond a single nutrient and invertebrate consumers. Our results support previous findings indicating that taxonomic and ecological factors have an important influence on the natural variation of consumer C:N:P stoichiometry. This work sets the stage for studies on the functional and economical causes of these differences, which in turn can be used to identify broad connections between nutrient cycling and the structure of consumer communities.

Implications for food web structure and nutrient cycling

Much of the work in ecological stoichiometry lies in the understanding of the patterns and mechanisms of organism elemental composition as the departing point for identifying the occurrence and magnitude of consumer–resource elemental imbalances. These elemental imbalances between consumers and their resources are particularly important because impose stoichiometric constraints on consumers, providing powerful mechanisms that shape food web structure and dynamics (Sterner and Elser 2002, Hall 2009). Although substantial evidence has shown that stoichiometry of herbivore–plant interaction is strongly imbalanced and influence both herbivore fitness and species interactions (Hall 2009), stoichiometric mismatches and their consequences for higher trophic levels have received far less attention. There is some evidence, however, that suggest an increase to nutrient-richer biomass as we progress from plants up through the food web, revealing stoichiometric imbalances at predator–prey interactions (Denno and Fagan 2003, Matsumura et al. 2004). In fact, individual/population growth limitation driven by stoichiometric imbalances are also a real possibility for predators (Fagan et al. 2002). These observations are particularly important in light of evidence that suggest how nutrient limitation may contribute to the evolution of intraguild predation and lead to changes in the stability and complexity of food webs (Fagan et al 2002). Furthermore, rates and magnitudes of nutrient recycling by consumers are affected by the stoichiometry of the organisms and by the elemental mismatch between them and that of their resources (Sterner and Elser 2002). Therefore, our study calls for further research into the patterns and mechanisms that explain how elemental stoichiometry varies across taxa and ecosystems, as well as its influence on food-web structure and ecosystem functioning.

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Appendix 1

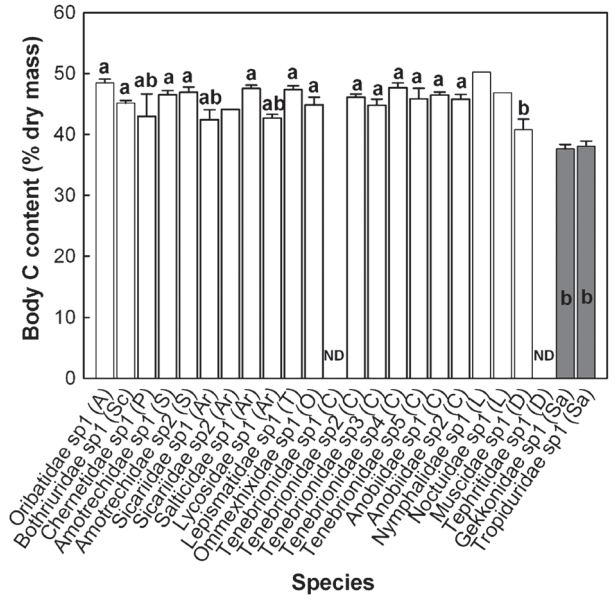

Figure A1

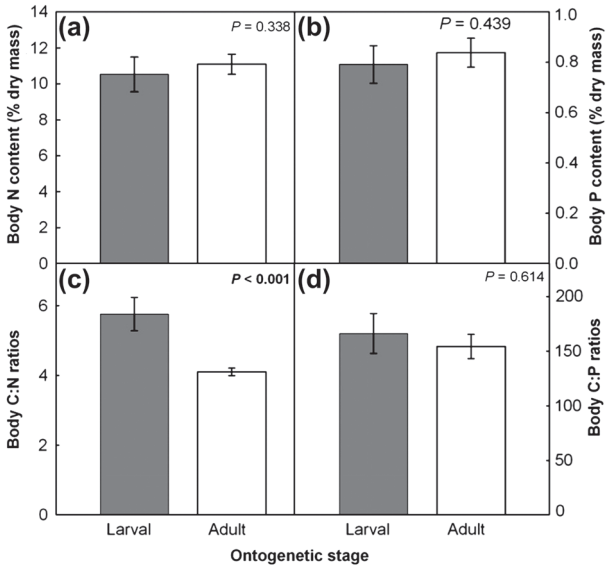

Figure A2

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