

Phylogenetic signal in predator–prey body-size relationships

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Abstract. Body mass is a fundamental characteristic that affects metabolism, life history, and population abundance and frequently sets bounds on who eats whom in food webs. Based on a collection of topological food webs, Ulrich Brose and colleagues presented a general relationship between the body mass of predators and their prey and analyzed how mean predator–prey body-mass ratios differed among habitats and predator metabolic categories. Here we show that the general body-mass relationship conceals significant variation associated with both predator and prey phylogeny. Major-axis regressions between the log body mass of predators and prey differed among taxonomic groups. The global pattern for Kingdom Animalia had slope >1 , but phyla and classes varied, and several had slopes significantly <1 . The predator–prey body-mass ratio can therefore decrease or increase with increasing body mass, depending on the taxon considered. We also found a significant phylogenetic signal in analyses of prey body-mass range for predators and predator body-mass range for prey, with stronger signal in the former. Besides providing insights into how characteristics of trophic interactions evolve, our results emphasize the need to integrate phylogeny to improve models of community structure and dynamics or to achieve a metabolic theory of food-web ecology.

Key words: allometry; body mass; body-size ratio; food webs; Grafen's ρ ; metabolic theory of food-web ecology; Pagel's λ ; predation; trophic interactions.

INTRODUCTION

A central aim in ecology is to understand the processes underlying community structure, including species interactions in food webs (Lawton and Warren 1988). Early attempts to elucidate food-web patterns were mostly based on niche theory, which postulates that coexisting species must differ to a certain extent in their use of resources (Loreau and Thébaud 2005). More recently it has been suggested that evolutionary constraints might play a more fundamental role in determining trophic interactions and the resulting food-web patterns (e.g., Caldarelli et al. 1998, Cattin et al. 2004, Rossberg et al. 2006, Rezende et al. 2009). Species with recent shared ancestry should therefore tend to have similar functional traits for exploiting similar resources. Despite this, few attempts have been made to link phylogeny and food-web structure (Cousins 1985, Caldarelli et al. 1998, Cattin et al. 2004, Rossberg et al. 2006, Rezende et al. 2009). Body

size, on the other hand, has received greater attention. It represents a key functional trait because size strongly influences the physiological, behavioral, and population ecology of organisms. For example, body size is strongly associated with metabolic rate, growth, locomotory performance, reproduction, the use of space, and population density (e.g., Damuth 1981, Peters 1983, Cohen et al. 2003, Brown et al. 2004, Jetz et al. 2004, Dial et al. 2008). Furthermore, body-size ratios frequently determine the efficiency with which predators encounter, capture, and handle their prey (Werner 1974, Petchey et al. 2008, Brose 2010). Although of course body-mass ratios are very different in other types of interaction, such as for parasites or parasitoids that may be much smaller than their hosts (Lafferty and Kuris 2002), these constraints on predators should lead to regularities in the trophic structure of food webs. For example, larger predators often feed at higher trophic levels, especially in aquatic and marine ecosystems, and body size has been shown to predict many features of empirical food webs (Warren and Lawton 1987, Cohen et al. 1993, Jennings et al. 2001, Petchey et al. 2008, Rohr et al. 2010).

Using a global database of predator and prey body-size relationships, Brose et al. (2006a) showed that the body mass of predators scales with the body mass of their prey following a power law with exponent significantly >1 . In other words, body-size differences between predators and their prey increase with the body

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mass of both (Brose et al. 2006a). As a result, since interaction strength appears to scale with body-mass ratio in trophic interactions (Emmerson and Raffaelli 2004), the scaling of predator–prey interaction strengths should change at higher trophic levels, and with it the effects of interacting species on population dynamics and stability (Otto et al. 2007). Brose et al. (2006a) also demonstrated that average predator–prey body-mass ratios vary among metabolic categories of predators (invertebrates, ectothermic vertebrates, and endothermic vertebrates) and among habitats (marine, stream, lake, and terrestrial systems). However, analysis of the body-mass ratios alone assumes a slope of 1 in the allometric relationship, and thus confounds possible changes in slope, intercept, and average mass. Moreover, the use of broad predator metabolic categories disregards the taxonomic affiliations of the predators and prey, and consequently the evolutionary relationships of the interacting species. Finally, within the general relationship between the body mass of predators and their prey, phylogenetic structure in the data set introduces nonindependence, and failure to account for it may conceal variation among taxonomic groups in the shape of the relationship (Felsenstein 1985).

In this study we explore how phylogeny affects body-size relationships between predators and prey. We reanalyze the data set used by Brose et al. (2006a) using taxonomy as a proxy for the phylogenetic affiliations of predators and prey. In addition we test for phylogenetic signal in the relationship between the body mass of predators and the range in body mass of their prey, and that between the mass of prey and the range in mass of their predators. The results emphasize the importance of phylogeny and the need to integrate this information to understand the factors underlying food-web structure and functioning.

MATERIALS AND METHODS

Data set

We extended the global data set of Brose et al. (2005) by adding the taxonomy of each organism, classified according to 18 levels: species, genus, tribe, subfamily, family, superfamily, infraorder, suborder, order, superorder, infraclass, subclass, class, superclass, subphylum, phylum, subkingdom, and kingdom. Between March and June 2006 we retrieved taxonomic affiliation from the Integrated Taxonomic Information System (*available online*),⁶ and we completed the information using the SCAR-Marine Biodiversity Information Network (*available online*),⁷ the Index to Organism Names (*available online*),⁸ the Tree of Life Web Project (*available online*),⁹ the Fauna Europaea (*available online*),¹⁰ and Wikispecies

⁶ <www.itis.gov>

⁷ <www.scarmarbin.be>

⁸ <www.organismnames.com>

⁹ <www.tolweb.org>

¹⁰ <www.faunaeur.org>

(*available online*).¹¹ For the purpose of comparison with Brose et al. (2006a) we restricted our analyses to only part of the global data set, including only predator–prey interactions for which the body masses of both species were measured. We consider only interactions in which both predator and prey were in Kingdom Animalia, and only those that were classified in sufficient detail in the original database to allow us to identify the phylum and class of both taxa involved. Out of 5103 interactions analyzed by Brose et al. (2006a), our resulting database included 4758 interactions, involving 497 predators and 572 prey taxa.

Phylogenetic variation in predator–prey interactions

We evaluated the relationship between predator and prey body masses using major axis regressions (Chapter 10.2 in Legendre and Legendre [1998]). Here, type I regression is not appropriate because on both axes we have nonnegligible measurement error. We chose major axis regression, among the many forms of type II regression, since the measurement unit and error magnitude are the same on both axes. For completeness, we also present results from reduced major axis regression and OLS (ordinary least squares)-bisector regression in Tables A1 and A2 of the Appendix, with highly consistent results. Body masses were measured in grams and \log_{10} -transformed. Regressions were computed for the entire animal kingdom and for subsets of the data comprising interactions involving predators and their prey belonging to individual phyla or classes, for instance chordate predators and arthropod prey, or arachnid predators and insect prey. We consider three data subsets at the phylum level and nine at the class level (Table 1 and Table A3 on the Appendix). Analyses at a finer taxonomic scale were not possible due to small sample sizes. For each regression, the standard errors of the slope and intercept were estimated using a bootstrap procedure ($n = 10\,000$). Inspection of “residuals” (perpendicular distances to the major axis) yielded no indication of departure from linearity.

Phylogenetic signal in predator and prey ranges

We also test for the presence of a phylogenetic signal in the range in body mass of prey for individual predator taxa and the range of predators for individual prey taxa. For example, the body-mass range for a given predator taxon was calculated as the difference in \log_{10} (body mass) between its largest and smallest prey. The presence of a phylogenetic signal was examined using a log-likelihood ratio test between pairs of linear models, both including the \log_{10} (body mass) of the focal species as the explanatory variable, but the first without correlation structure and the second with a correlation structure induced by the phylogeny. Here we apply two commonly used methods to incorporate phylogenetic correlation,

¹¹ <species.wikimedia.org>

TABLE 1. The effect of phylogeny on the intercepts and slopes of major-axis regressions between predator and prey \log_{10} (body mass).

Kingdom, Phylum, Class					
Taxon as predator	Taxon as prey	<i>n</i>	Intercept	Slope	<i>P</i>
Animalia	Animalia	4758	1.89 [1.85, 1.93]	1.20 [1.18, 1.23]	< 0.001
Chordata	Chordata	833	1.72 [1.49, 1.91]	1.03 [0.91, 1.18]	0.611
Actinopterygii	Actinopterygii	296	1.88 [1.65, 2.06]	0.81 [0.70, 0.96]	0.015
Chordata	Arthropoda	1044	3.02 [2.88, 3.17]	0.64 [0.57, 0.73]	< 0.001
Aves	Insecta	154	2.72 [2.64, 2.81]	0.49 [0.43, 0.56]	< 0.001
Reptilia	Insecta	95	2.95 [2.37, 3.95]	1.26 [0.79, 2.10]	0.314
Actinopterygii	Insecta	157	5.50 [5.07, 6.01]	1.35 [1.19, 1.55]	< 0.001
Actinopterygii	Malacostraca	191	4.39 [-23.3, 27.35]	1.99 [-22.84, 22.55]	0.832
Arthropoda	Arthropoda	1994	0.51 [0.26, 0.57]	0.92 [0.86, 0.97]	0.002
Insecta	Insecta	1007	0.14 [-0.02, 0.32]	0.78 [0.72, 0.85]	< 0.001
Arachnida	Insecta	506	1.62 [0.73, 2.82]	1.33 [1.06, 1.70]	0.013
Arachnida	Arachnida	159	-0.99 [-4.23, 2.69]	0.57 [-0.49, 1.77]	0.291
Insecta	Arachnida	91	2.67 [0.59, 10.48]	1.84 [1.17, 4.35]	0.011

Notes: We provide the taxon of the considered subset of predators and prey, the number (*n*) of trophic interactions in the subset, the intercept and slope (in brackets the 95% confidence limit), and the *P* value of the test for the slope differing from 1.

which differ slightly in the way in which they scale trait correlation with divergence time: Pagel's λ (Freckleton et al. 2002) and Grafen's ρ (Grafen 1989). We use taxonomy as a proxy for the phylogeny, with the phylogenetic similarity between two species given by the number of common taxonomic levels divided by the total number of levels plus 1 (Cattin et al. 2004). Both correlation structures also provide information about the strength of the phylogenetic signal, where higher values of λ and ρ indicate a stronger correlation induced by the phylogeny between the trait values of related species. We provide a 95% confidence interval for these parameters, at the upper and lower points at which the profile log likelihood has declined by 1.96 units (Chapter 4 in Davison [2003]).

RESULTS

At the level of Kingdom Animalia, the slope of the major axis regression between predator and prey log body mass was significantly >1 (Table 1). In other words, the relationship between predator and prey body mass follows a power law with exponent >1 , so that predators become disproportionately larger than their prey with increasing body mass. However, this general relationship was not always observed at lower taxonomic levels. At the phylum level, the relationships for chordate predators of arthropod prey and for arthropod predators of arthropod prey both had slopes significantly smaller than one (Table 1, Fig. 1), indicating that the relative size difference between predators and prey decreases with increasing body mass. For chordate predators of chordates, the slope was not significantly different from one.

Similar variation in slope was apparent at the class level (Table 1; Appendix: Fig. A1). Within chordate predators of arthropod prey, there were slopes significantly >1 (Actinopterygii as predators of Insecta), significantly <1 (Aves as predators of Insecta), and

not significantly different from 1 (Reptilia as predators of Insecta and Actinopterygii as predators of Malacostraca). These same three patterns were found within the classes of arthropods as predators of arthropods.

Interestingly, there was no significant relationship between the \log_{10} (body mass) of species and the range in \log_{10} (body mass) of either their prey or their predators ($P = 0.368$ for the range of prey vs. the body mass of predators; $P = 0.132$ for the range of predators vs. the body mass of prey; both linear regressions using Pagel's λ correlation structure). However, there was a significant phylogenetic signal in these ranges (Table 2). Pairs of closely related species are therefore more similar in the body-mass ranges of their predators and of their prey than are pairs of randomly chosen species. Furthermore, this phylogenetic signal seems to be stronger when considering the prey range for predators than when considering the predator range for prey (the difference was significant when considering Grafen's ρ , but the confidence intervals overlapped for Pagel's λ).

DISCUSSION

Our analysis of Brose et al.'s (2005) database reinforces the importance of evolutionary history for an understanding of predator-prey interactions and thus the structure of trophic networks. Firstly, phylogeny (examined here as taxonomic affiliation) had a significant association with predator-prey body-mass ratios. Slopes of the relationship between predator and prey \log (body mass) for individual pairs of phyla and classes differed significantly from the general relationship for Kingdom Animalia. Secondly, there was a significant phylogenetic signal in the range of \log (body mass) of prey of each predator taxon as well as the range of \log (body mass) of predators of each prey taxon.

As in the analysis of Brose et al. (2006a), the general relationship between predator and prey log body mass had slope significantly >1 , meaning that predators

become disproportionately larger than their prey as body mass increases. An interesting question is why this observed relationship is a power law (or log-log linear). Classical allometric relationships (e.g., metabolic rate in Kleiber's law) have been interpreted based on physical laws (e.g., West et al. 1997). Because predators use various morphological features such as diverse mouth parts and appendages to capture, handle, and ingest prey, an allometric relationship would be expected since body parts scale with body size. Given the diversity of prey-capture strategies, one might expect great variability around this relationship, and indeed we found that the slopes for pairs of phyla and classes differed significantly. In several cases, slopes were significantly smaller than 1, implying that consumers and their resources become more similar in size with increasing body mass. Furthermore, it is clear that the taxonomic affiliations of both predators and prey affect the relationship, with significant differences in slope between chordate predators of chordates and chordate predators of arthropods, and also between chordate and arthropod predators of arthropods.

From a functional morphological standpoint, it is not surprising that slopes vary among taxonomic groups: these differences surely reflect different physiological constraints. For example, birds are more constrained in body size than fishes due to the high energy demands of flight, which leads to a decreasing power-to-mass ratio, and hence maneuverability and acceleration, as body mass increases (Dial et al. 2008). This can explain the difference in slope between birds and fishes when eating insects (Table 1), with a slope significantly smaller than 1 for birds and larger than 1 for fishes. Within the general limits on body size, functional morphology may further constrain predator-prey interactions. The differences in scaling of these behaviors are probably related to the mode of prey capture and handling, and how this is affected by habitat. For instance, the extent to which predator size must increase in order to handle larger prey will be affected by whether toxins are used, whether prey are ingested intact, and whether the habitat offers a surface against which prey can be subdued.

Interestingly, the range in prey $\log(\text{body mass})$ for predators, and the range in predator $\log(\text{body mass})$ for prey, are not related to $\log(\text{body mass})$ of the focal species. This result suggests that the upper and lower bounds of body mass of the prey or the predators of a species are linearly related to its body mass. If body mass of the focal species does not play a role, phylogeny does: closely related species are significantly more similar in the ranges in body mass of their prey and predators than are randomly chosen species. This phylogenetic signal is stronger in prey range for predators than in predator range for prey, suggesting that prey range is more evolutionarily constrained. At first sight, this contrasts with the findings of Bersier and Kehrli (2008) and of Rossberg et al. (2006), who suggested that the phylogenetic signal is stronger for

species in their role as prey than as predator. However, these previous analyses were based on the specific identity of predators and prey with which each species interacted, and not on their body-size ranges. Therefore, it appears that diets tend to be labile in the prey species involved, but the evolution of diets causes little change in the range of prey body sizes. By the same token, the set of predator species that feed on a given prey taxon is evolutionarily more conserved, but when changes occur, it is with larger variability in the range of predator body sizes.

Our analysis is not without its limitations, and a number of caveats should be recognized. The data come from topological food webs that represent links simply as present or absent, rather than quantitative data that take into account link strength. As a result, when estimating the slope of the body-mass relationship all prey are weighted equally, with no consideration of their relative importance. Also, single estimates of body mass and diet are used for each species, regardless of intraspecific variation in body mass or size structuring of trophic interactions. Finally, we stress again that we treat only predator-prey interactions, and that very different body-mass relationships would be expected in the interactions of herbivores, parasites, or detritivores with their resources.

The general body-mass relationship demonstrated by Brose et al. (2006a) suggested that body-mass ratios should provide an important element in food-web models. These ratios constrain feeding interactions: small prey may contain insufficient energy to be worth the costs of capture and handling, whereas some prey are too large to be captured, handled, and ingested. The structure of food webs emerges from multiple trade-offs that influence foraging profitability, and a recent model combining optimal foraging theory with allometric relationships for traits such as resource density and handling time provided a reasonable fit to topological food webs (Petchey et al. 2008). Similarly, a model based on a universal predator-prey body-mass ratio allowed 6–46% of trophic links to be correctly fitted in nine of the largest available topological food webs (Rohr et al. 2010).

Our results suggest that incorporation of phylogenetic information would allow considerable refinement of food-web models. Brose et al. (2006a) have already demonstrated that average predator-prey body-mass ratios vary among metabolic categories of predators (invertebrates, ectothermic vertebrates, and endothermic vertebrates) and among habitats (marine, stream, lake, and terrestrial systems). Furthermore, Riede et al. (2011) found differences among these same categories in the slope of the relationship between predator and average prey $\log(\text{body masses})$. However, all combinations except those from stream food webs had slopes <1 , leading them to argue that this reveals regularity in community structure. Here we show that even the use of very crude taxonomic information at the phylum or

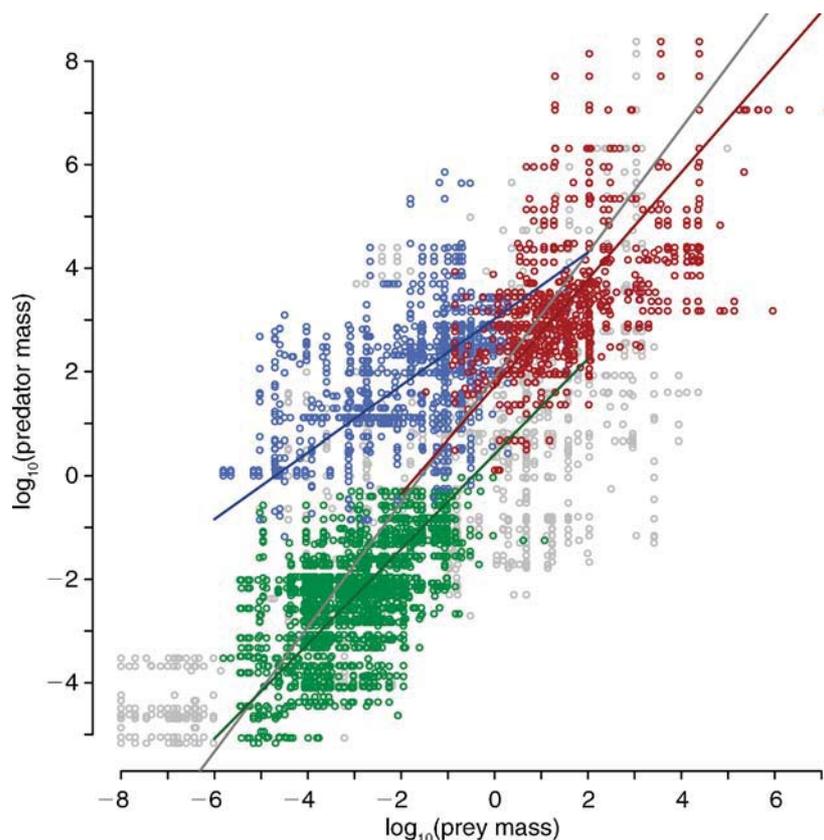


FIG. 1. The relationship between the \log_{10} (body mass) of predators and prey. The gray line shows the general relationship for the full data set of Animalia as predator and prey. Three subsets are reanalyzed separately: in red for chordate predators and chordate prey, in blue for chordate predators and arthropod prey, and in green for arthropod predators and arthropod prey. The circles in gray represent interactions falling outside of these three subsets.

class level reveals much greater variation in the relationship between predator and prey body mass. Such variation with phylogeny may explain patterns seen in the recently published latent-traits model of food-web structure (Rohr et al. 2010): when fitting presence/absence data for trophic interactions on the basis of an optimal predator-prey body-mass ratio, the addition of latent traits improved the fit of the model, and these traits were correlated with taxonomy. Finer-scale taxonomic resolution would surely reveal further variation. For instance, adaptations in host use lead to

phylogenetic structuring of insect-plant and host-parasitoid interactions (e.g., Ehrlich and Raven 1964, Hawkins 1994). However, there are insufficient data to analyze current food-web collections at finer resolution.

Body size is a key ecological trait, so understanding how its influence changes with phylogeny is a necessary step towards general theories of community structure and functioning (Siemann et al. 1996, Price 2003, Cattin et al. 2004, Loeuille and Loreau 2005). For example, in combination with previous work, our results suggest that body-mass ratios, and hence the strength of trophic

TABLE 2. Phylogenetic signal in the range in \log_{10} (body mass) of prey for the predator species and the range in \log (body mass) of predators for the prey species.

Phylogenetic correlation structure	Prey range for predators			Predator range for prey		
	Parameter	AIC	P	Parameter	AIC	P
Without		2207			2457	
Grafen's ρ	$\rho = 0.143$ [0.088, 0.210]	2131	<0.001	$\rho = 0.035$ [0.015, 0.070]	2415	<0.001
Pagel's λ	$\lambda = 0.457$ [0.348, 0.547]	2126	<0.001	$\lambda = 0.374$ [0.249, 0.491]	2410	<0.001

Notes: All six models include the \log_{10} (body mass) of the focal species as an explanatory variable. The first row ("Without") includes only this term. For phylogenetic regressions using either Grafen's ρ or Pagel's λ as the parameter, we provide the estimated strength of the phylogenetic signal and its 95% confidence limit (in brackets), the model AIC, and a test of the importance of phylogeny given by the P value of the log-likelihood ratio test between the phylogenetic regression and the model without phylogenetic correlation.

interactions, may vary systematically with habitat type, trophic level, and phylogeny. This has fundamental implications for analyses of food-web stability (Brose et al. 2006b, Otto et al. 2007, Banasek-Richter et al. 2009). The ecology of a species can be understood as the interplay of phylogenetic constraints that increase ecological similarity, and adaptations that cause interspecific divergence (Price 2003, Bersier and Kehrlı 2008). It is the functional similarity of related species that makes taxonomy a useful predictor of ecology, and the nested hierarchy of phylogeny may underlie much of the hierarchical structure of food webs. For example, Rossberg et al. (2006) showed that many aspects of food-web structure could be viewed in a phylogenetic context whereby newly evolving species avoid direct competition with closely related species. Moreover, Rezende et al. (2007, 2009) demonstrated that phylogenetic relationships play a major role in structuring plant–pollinator and plant–frugivore mutualistic networks as well as food webs. In conclusion, the organization of natural communities can only be explained by considering evolutionary history in concert with the contemporary environmental setting. Widening classical allometric studies of species characteristics to encompass the scaling of interactions would allow food-web ecology to be unified with the metabolic theory of ecology (Brown et al. 2004) and optimal foraging theory (Petchey et al. 2008). However, given the phylogenetic associations that we demonstrate here, this endeavor will not succeed without taking evolutionary history into account. Dobzhansky’s famous quote – that “nothing makes sense in biology except in the light of evolution” (Dobzhansky 1964:449) – is clearly as relevant for food-web ecology as for other domains.

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APPENDIX

Tables with the results of two alternative methods of type II regression (Tables A1 and A2), information on the range in body size of the analyzed taxa (Table A3), and a figure showing relationships between the log(body mass) of predators and prey for subsets at the class level (Fig. A1) (*Ecological Archives* E092-188-A1).