

## LETTER

# Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems

Jens O. Riede,<sup>1\*</sup> Ulrich Brose,<sup>1</sup>  
Bo Ebenman,<sup>2</sup> Ute Jacob,<sup>3</sup> Ross  
Thompson,<sup>4</sup> Colin R. Townsend<sup>5</sup>  
and Tomas Jonsson<sup>6</sup>

### Abstract

Despite growing awareness of the significance of body-size and predator–prey body-mass ratios for the stability of ecological networks, our understanding of their distribution within ecosystems is incomplete. Here, we study the relationships between predator and prey size, body-mass ratios and predator trophic levels using body-mass estimates of 1313 predators (invertebrates, ectotherm and endotherm vertebrates) from 35 food-webs (marine, stream, lake and terrestrial). Across all ecosystem and predator types, except for streams (which appear to have a different size structure in their predator–prey interactions), we find that (1) geometric mean prey mass increases with predator mass with a power-law exponent greater than unity and (2) predator size increases with trophic level. Consistent with our theoretical derivations, we show that the quantitative nature of these relationships implies systematic decreases in predator–prey body-mass ratios with the trophic level of the predator. Thus, predators are, on an average, more similar in size to their prey at the top of food-webs than that closer to the base. These findings contradict the traditional Eltonian paradigm and have implications for our understanding of body-mass constraints on food-web topology, community dynamics and stability.

### Keywords

Allometry, body-size ratio, ecological networks, food-webs, predation, predator–prey interactions.

*Ecology Letters* (2011) 14: 169–178

## INTRODUCTION

Since Charles Elton's seminal work (Elton 1927), an enduring and recently rejuvenated debate on the structure of natural communities has focused on whether and how interactions between predators and their prey are driven by the species' body masses (see Ings *et al.* 2009; Brose 2010 for reviews). Body-size is an important ecological characteristic of organisms (Brown *et al.* 2004) and the distribution of body-sizes in communities influences their structure and functioning (Cohen *et al.* 1993; Neubert *et al.* 2000; Loeuille & Loreau 2004; Jonsson *et al.* 2005; Brose *et al.* 2006a; Rall *et al.* 2008). In particular, ratios between predator size and the average size of their prey (hereafter: body-mass ratios) have an important role in explaining regularities in food-web structure (Warren & Lawton 1987; Cohen *et al.* 2003; Brose *et al.* 2006a; Petchey *et al.* 2008), influencing patterns in interaction strength (Emmerson & Raffaelli 2004; Vucic-Pestic *et al.* 2010) and, consequently, the dynamics and stability of food-webs (Jonsson & Ebenman 1998; Emmerson & Raffaelli 2004; Weitz & Levin 2006; Otto *et al.* 2007; Berlow *et al.* 2009). Hence, predicting how body-mass ratios vary among consumers (or resources) and among and within ecological communities will be important for a better understanding of community structure, dynamics and stability.

Predator–prey body-mass ratios are systematically higher in lake habitats than in marine, stream or terrestrial habitats and vertebrate

predators have, on an average, higher body-mass ratios to their prey than invertebrate predators (Brose *et al.* 2006a; Bersier & Kehrli 2008). However, an unresolved issue is whether predator–prey body-mass ratios systematically change with the mass or trophic level of the predator. Thus, despite growing awareness of the significance of body-mass ratios in ecological networks (Ings *et al.* 2009; Brose 2010) our understanding of how they are distributed within natural food-webs is incomplete. Traditional concepts that have been accepted as a paradigm (Elton 1927) are: (a) predator and mean prey mass are positively correlated, (b) predator masses increase with trophic level and (c) predator–prey body-mass ratios do not vary consistently across trophic levels (i.e., along food chains).

Although these concepts are widely believed to be general features of ecosystems, it is important to remember that (1) the scatter in the relationships among prey mass, predator mass and trophic level can be substantial (e.g., Vander Zanden *et al.* 2000), (2) a few studies have reported different relationships (see below) and (3) concept (c) has not (to our knowledge) been explicitly analysed, neither within nor across ecosystems. Furthermore, in contrast to the accepted wisdom, recent theoretical models of food-web structure, such as the cascade model, the niche model or the allometric diet breadth model (Cohen & Newman 1985; Williams & Martinez 2000; Petchey *et al.* 2008), suggest various and differing scaling relationships among prey mass, predator mass and trophic level. Differences between these opposing

<sup>1</sup>J.F. Blumenbach Institute of Zoology and Anthropology, Systemic Conservation Biology Group, Georg-August University Goettingen, 37073 Goettingen, Germany

<sup>2</sup>IFM Theory and Modelling, Division of Theoretical Biology, Linköping University, S-581 83 Linköping, Sweden

<sup>3</sup>Institute for Hydrobiology and Fisheries Science, University Hamburg, 22767 Hamburg, Germany

<sup>4</sup>School of Biological Sciences, Monash University, Bld 18, Vic. 3800, Australia

<sup>5</sup>Department of Zoology, University of Otago, Dunedin 9054, New Zealand

<sup>6</sup>Ecological Modelling Group, Systems Biology Research Centre, University of Skövde, S-541 28 Skövde, Sweden

\*Correspondence: E-mail: riede@bio.tu-darmstadt.de

concepts are yet to be reconciled. Here, we use a data set of 35 natural food-webs across four ecosystem types (marine, stream, lake, terrestrial) to address the scaling relationships between predator and prey masses, predator trophic levels and predator–prey body-mass ratios (see points a, b, c above). While the first two scaling relationships are more easily and often studied, the dynamically important scaling of body-mass ratios with predator trophic level has been largely ignored. Subsequently, we derive theoretical predictions about the third relationship from the first two relationships, provide empirical tests of these relationships and discuss the implications for community structure, dynamics and stability.

## THEORETICAL PREDICTIONS

Predators normally consume prey of smaller body-mass, which differentiates them from parasitic or parasitoid interactions (Brose *et al.* 2006a). Here we thus assume that predator body-mass,  $M_P$  and mean prey body-mass,  $\overline{M}_R$ , are allometrically related:

$$\overline{M}_R = bM_P^a \quad (1)$$

where  $a$  and  $b$  are constants (Cohen *et al.* 1993; Brose *et al.* 2006b; Bersier & Kehrl 2008). Using eqn 1, the expected predator–prey body-mass ratio,  $\rho$ , can be expressed as a function of predator body-mass:

$$\rho = \frac{M_P}{\overline{M}_R} = b^{-1}M_P^{1-a} \quad (2)$$

In the early 20th century, Elton (Elton 1927) suggested that predator body-mass increases along food chains. In complex food-webs, predator mass should thus increase with the trophic level,  $T$ , as expressed by exponential relationships reported in some studies:

$$\log_{10}M_P = d + cT \quad (3)$$

with constants  $d$  and  $c$  (Woodward & Hildrew 2002; Cohen *et al.* 2003), whereas a few studies have found negative (Burness *et al.* 2001) or no relationships (Layman *et al.* 2005). To consider the relationship between predator–prey body-mass ratios and predator trophic levels, we inserted eqn 3 in eqn 2, which yields:

$$\log_{10}(\rho) = -\log_{10}(b) + d(1-a) + c(1-a)T = f + eT, \quad (4)$$

where  $f$  describes the intercept and  $e$  the slope constant for  $T$  (trophic level).

Elton (1927) suggested that predator–prey body-mass ratios do not vary consistently within communities and thus are independent of trophic level. This implies that the term  $e = c(1-a)$  in eqn 4 equals zero, which results if  $c = 0$  or  $a = 1$ . This may occur if predator masses do not vary across trophic levels ( $c = 0$  in eqn 3) or if the mean prey mass increases linearly with predator mass on a log–log scale with a slope of unity ( $a = 1$  in eqn 1). However, assuming a positive relationship between predator mass and trophic level ( $c > 0$  in eqn 3), the body-mass ratio is expected to decrease with trophic level if  $a > 1$  (eqn 1), but should increase with trophic level if  $a < 1$  (eqn 1).

Together, these relationships (eqns 1–4) characterize important aspects of trophic interactions in natural food-webs. In this study, we gathered data from 35 empirical food-webs and analysed the relationships between (1) predator masses and average prey masses (eqn 1), (2) predator masses and trophic levels (eqn 3) and (3)

body-mass ratios and trophic levels (eqn 4). Separate analyses are carried out for four habitat types (marine, stream, lake and terrestrial) and three predator types (invertebrates, ectotherm and endotherm vertebrates).

## METHODS

We analysed the trophic structure and species' body masses of 35 empirical food-webs: 5 marine, 12 stream, 10 lake and 8 terrestrial food-webs [Supporting information (SI)]. The food-web data were collected from three sources. First, seven food-webs are derived from a large global food-web database: Grand Cariçaiie cl control 2, Grand Cariçaiie sc control 2, Sierra Lakes, Skipwith Pond, Tuesday Lake 1984, Weddell Sea and Broadstone Stream. Second, two food-webs are taken from the Ecoweb database: Trelease Woods Illinois and Montane Forest Arizona. Third, for 26 additional food-webs (Carpinteria, Coachella, Small Reef, Little Rock Lake, Alford Lake, Beaver Lake, Bridge Brook Lake, Chub Pond, Connery Lake, Stink Lake, Mondego Estuary, St. Marks, Bere Stream, Calero Creek, Corde, Madre Creek, Coyote Creek, Guadalupe Creek, Alamos Creek, German, Little Kye Burn, Stony, Broad, Hainich HEW1, Ythan Estuary, Florida Islands) we obtained the trophic structure and species' body masses (mainly) from published sources (see Supporting information for an overview of the food-webs studied and the primary references for food-web structure and body masses).

We studied only the predator–prey interactions of the food-webs while excluding herbivore–plant, parasite–host and parasitoid–host interactions, which are characterized by different body-mass ratios than predator–prey interactions (Brose *et al.* 2006a). For each predator, we calculated the mean prey mass ( $\overline{M}_R$ ) as the geometric mean of the body masses of all prey species of the predator, the predator–prey body-mass ratio (hereafter:  $\rho$ ) as the ratio between predator mass  $M_P$  and mean prey mass and predator trophic level ( $T$ ) as the prey-averaged trophic level (one plus the average trophic level of all prey of the consumer) (Williams & Martinez 2004). These prey-averaged trophic levels were calculated using a matrix algebra method (Levine 1980) that sums an infinite geometric series including the contributions from all loops.  $\rho$  is calculated using predator–prey interactions between species, where the predator species has a trophic level higher than two (thus excluding herbivore and detritivore feeding interactions). After  $\log_{10}$  transformation, we normalized all food-web parameters (mean prey masses, predator masses, predator–prey body-mass ratios and trophic levels) independently, to a mean of zero and a standard deviation of unity. This normalization allows lumping food-webs that differ in parameter space (e.g., food-webs with different ranges in body masses).

We grouped the 35 food-webs into four different ecosystem types: marine, stream, lake and terrestrial food-webs. Furthermore, we grouped the predators into three different metabolic types (invertebrates, ectotherm and endotherm vertebrates). These groupings follow prior analyses (Brose *et al.* 2006a; Bersier & Kehrl 2008) suggesting that predator–prey body-mass ratios differ among these categories. First, Pearson correlation analyses were used to assess whether there were statistically significant associations between  $\log_{10}(\overline{M}_R)$  and  $\log_{10}(M_P)$ , between  $\log(M_P)$  and  $T$  and between  $\rho$  and  $T$ . Next, regression analyses were used to estimate the quantitative nature of the scaling between these variables (i.e., estimating constants  $a$ ,  $b$ ,  $c$ ,  $d$ ,  $e$  and  $f$  in the allometric and exponential relationships in eqns 1, 3 and 4). When the causal relationship

between two variables is not clear or both variables are subject to measurement error, Model I regression (ordinary least squares regression: OLS) is not appropriate. Instead, several Type II regression methods have been proposed (see Isobe *et al.* 1990; Warton *et al.* 2006 for reviews). These include ordinary least squares bisector (BIS) and reduced major axis (RMA) regressions. RMA regression has been suggested as the preferred method for line fitting when the independent variable is subject to measurement error and the primary aim of the analysis is estimating the slope of the line that best describes the bivariate scatter in the dependent and independent variables (Sokal & Rohlf 1995; Warton *et al.* 2006; but see Schmid *et al.* 2000). In our study, the results from RMA and BIS regressions were consistent (see Supporting information for details) and the results presented below are focused on RMA regressions whereas BIS results can be found in the Supporting information. The significance of the regression parameters was assessed through error estimates (95% confidence intervals) that were calculated by bootstrapping over 10 000 replicates. We calculated the predicted slope,  $e_{predicted}$  of the relationship between the predator–prey body-mass ratio and trophic level (see eqn 4) for each combination of metabolic predator type and ecosystem type independently and compared these values with the observed values,  $e_{observed}$  from our regressions. Although our theoretical predictions above (eqn 4) suggests that  $\log(\rho)$  should be proportional to  $c(1 - a)T$ , this is for relationships without any error or uncertainties. However, our relationships will include considerable parameter uncertainty and thus, we do not expect the estimated values of the slopes of  $\log(\rho)$  as a function of  $T$  (i.e.,  $e_{observed}$ ) to be equal to  $e_{observed}(1 - a_{observed})$  (where  $a_{observed}$  and  $e_{observed}$  are regression estimates of  $a$  and  $c$  in eqns 1 and 3). Instead, we expect the observed value of the slope of  $\log(\rho)$  as a function of  $T$ , based on RMA regressions, to be

$$e_{RMA} = c_{RMA} \sqrt{1 + a_{RMA}^2 - 2r_{\log M_p, \log M_r} a_{RMA}} \quad (5),$$

where  $r_{X,Y}$  is the Pearson product moment correlation coefficient between variables  $X$  and  $Y$ . See Supporting information for a derivation of this relationship. The significance of the correlation between  $e_{predicted}$  from eqn 5 and  $e_{observed}$  from regressions was evaluated with a Pearson correlation analysis.

## RESULTS

Generally, a lack of data hindered analyses of the relationships for endotherm vertebrates in lakes and streams. Moreover, data for terrestrial ectotherm and endotherm vertebrates were scarce. First, we analysed the relationship between predator mass and mean prey mass. After log–log transformation of the data, the slope of the linear relationship equals the exponent,  $a$  of the power-law relationship in eqn 1. We found significant, positive relationships with slopes larger than unity across most ecosystems and predator groups (Table 1, Fig. 1 see below for exceptions to this pattern). This indicates that prey become disproportionately larger for larger predators and that larger predators should be more similarly sized to their prey than small predators. Subsequently, we studied the relationship between  $\log_{10}$  predator mass and predator trophic level to obtain estimates of the slope  $c$  in eqn 3. We found significant, positive relationships (Table 1, Fig. 2) across all ecosystem types and predator metabolic types, except for terrestrial and stream vertebrates, which exhibited a lack of significance (Table 1). In all other cases, these analyses demonstrate systematic increases in predator mass with predator trophic level

across all ecosystem and predator types. Finally, we analysed the relationship between the  $\log_{10}$  predator–prey body-mass ratio and trophic level to obtain empirical estimates of the slope of this relationship that could be compared with the theoretical prediction  $c(1 - a)$  in eqn 4 and  $e_{predicted}$  in eqn 5. We found significant, negative relationships (Table 1, Fig. 3) across most combinations of ecosystem and predator types (with a few exceptions, see below). This suggests that the relative size difference ( $\log_{10}$  body-mass ratio) between a predator and its prey decreases with trophic level of the predator.

Looking more detailed at the results, there are interesting exceptions to the general trends outlined above. First, there is one group of marine invertebrates feeding on small resources despite intermediate to high body-mass of these consumers (data points at the bottom of Fig. 1a). These outliers of the scaling relationship are mainly benthic suspension feeders and scavengers, which stresses that the scaling relationships presented here best characterize predatory interactions. Second, our analyses also demonstrates that stream communities systematically follow a different scaling pattern to other systems, with slopes smaller than unity (stream invertebrates: slope = 0.71, stream ectotherm vertebrates: slope = 0.79, Table 1, Fig. 1). Third, the negative relationship between the  $\log_{10}$  predator–prey body-mass ratio and trophic level was non-significant for stream ectotherm vertebrates ( $P = 0.08$ ) and stream invertebrates ( $P = 0.63$ , Table 1). Fourth, there was only one exception to the general trend of decreasing size difference between a predator and its prey with increasing predator trophic level: we found a non-significant positive relationship for terrestrial endotherm vertebrates ( $P = 0.09$ ).

The correlation between observed values from regressions,  $e_{observed}$  and predicted values for  $e_{predicted}$  from eqn 5 that accounts for error propagation is very high (Pearson correlation coefficient = 0.99, Table 2). Consistently, the more simple prediction of the slope not accounting for error propagation [i.e.,  $c(1 - a)$  in eqn 4] yielded only slightly weaker correlations ( $r = 0.89$ ,  $P = 0.007$ , based on the seven significant slopes, Table 2).

## DISCUSSION

Our analyses of the relationships between predator and prey mass, body-mass ratios and trophic levels have shown that across different types of ecosystems and predators some generalities hold: (1) the  $\log_{10}$  of average prey mass increases with the  $\log_{10}$  of predator mass with a slope larger than unity, (2) the  $\log_{10}$  of predator mass increases with predator trophic level and (3) the  $\log_{10}$  of the predator–prey body-mass ratio (i.e., the ratio of predator mass to average prey mass) decreases with predator trophic level. Our theoretical derivations show that the third relationship is the consequence of the first two relationships, which is supported by our empirical data. Exceptions to these patterns were identified for stream ecosystems and for endotherm consumers in terrestrial ecosystems and potential reasons for these deviations are discussed below.

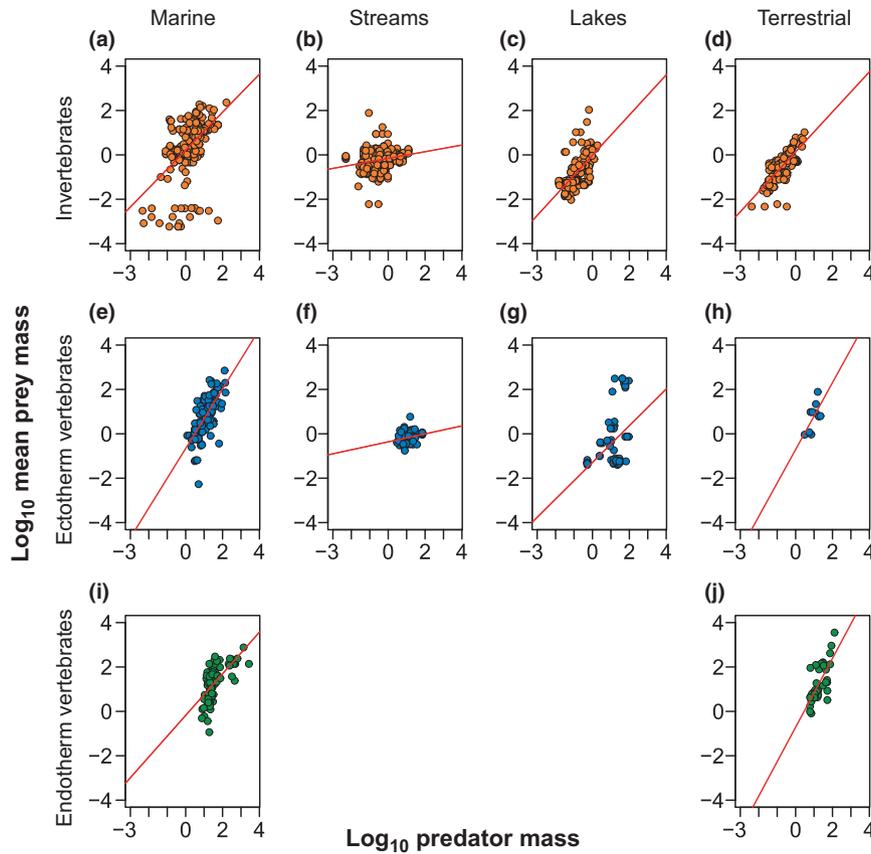
Our analyses are based on the largest allometric food-web data base (including information on trophic links between consumers and resources and the species' body masses) compiled so far. Despite this wealth of data, some combinations of ecosystem type and metabolic group were under-represented. While endotherm vertebrates in streams and lakes are naturally rare, the scarcity of data for terrestrial vertebrates will most likely be removed by future food-web compilations.

Consistent with former studies (Cohen *et al.* 1993; Brose *et al.* 2006a; Bersier & Kehrl 2008), we found that predator and prey

**Table 1** Slopes and intercepts for the RMA regressions of  $\log_{10}$  mean prey mass (MPM) vs.  $\log_{10}$  predator mass (PM),  $\log_{10}$  predator mass (PM),  $\log_{10}$  predator–prey body-mass ratio ( $\rho$ ) vs. trophic level (TL). Significance is indicated by Pearson correlation analyses for the relationships and by the upper and lower confidence interval (CI) for each slope and intercept. The number of species for each combination is indicated by *n*. Upper and lower confidence intervals for the intercepts and slopes were obtained by bootstrapping over 100 000 cases

	Marine food-webs			Stream food-webs			Lake food-webs			Terrestrial food-webs		
	MPM vs. PM	PM vs. TL	$\rho$ vs. TL	MPM vs. PM	PM vs. TL	$\rho$ vs. TL	MPM vs. PM	PM vs. TL	$\rho$ vs. TL	MPM vs. PM	PM vs. TL	$\rho$ vs. TL
<b>Invertebrates</b>												
<i>r</i>	0.49	0.34	-0.24	0.21	0.22	-0.02	0.65	0.49	-0.17	0.75	0.25	-0.29
<i>P</i> -value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.63	< 0.001	< 0.001	0.03	< 0.001	< 0.001	< 0.001
Intercept	0.01	0.35	-0.31	0.16	-0.35	-0.75	0.43	-0.68	-0.58	0.37	-0.85	-0.35
Upper/lower CI	1.54/-0.18	0.46/0.26	0.29	0.61/0.09	-0.67	0.14	1.2/0.2	-0.78	0.55	1.08/0.27	0.81	0.63
Slopes	1.76	0.53	-0.82	0.71	0.81	-1.04	1.40	0.82	-0.89	1.20	0.60	-0.52
Upper/lower CI	2/1.54	0.61/0.46	3.02/-0.97	0.83/0.61	0.91/0.71	1.12/-1.18	1.61/1.2	0.93/0.72	0.59	1.33/1.08	0.69/0.53	0.69
<i>n</i>	<b>234.00</b>			<b>388.00</b>			156.00			<b>179.00</b>		
<b>Ectotherm vertebrates</b>												
<i>r</i>	0.68	0.46	-0.57	0.23	0.19	-0.25	0.39	0.32	-0.69	0.65	0.30	-0.68
<i>P</i> -value	< 0.001	< 0.001	< 0.001	0.11	0.19	0.08	< 0.001	0.01	< 0.001	0.04	0.40	0.03
Intercept	-1.35	0.77	1.02	-1.03	1.06	1.60	-2.77	1.02	1.98	-1.52	0.78	0.83
Upper/lower CI	1.7/-1.75	0.85/0.68	1.14/0.89	0.56/-1.31	1.2/0.91	1.81/1.44	1.61/-1.31	1.2/0.85	2.19/1.75	1.28/-1.86	1.31/0.6	1.07/0.59
Slopes	1.98	0.41	-0.58	0.79	0.63	-0.83	2.13	0.76	-1.48	2.33	0.21	-0.36
Upper/lower CI	2.32/1.7	0.47/0.36	0.70	1.07/0.56	0.94/-0.6	0.48	2.85/1.61	0.97/0.58	0.01	3.79/1.28	0.34/-0.25	0.48
<i>n</i>	<b>117.00</b>			<b>50.00</b>			<b>68.00</b>			<b>16.00</b>		
<b>Endotherm vertebrates</b>												
<i>r</i>	0.62	0.61	-0.27	NA	NA	NA	NA	NA	NA	0.72	0.15	0.28
<i>P</i> -value	< 0.001	< 0.001	0.01	NA	NA	NA	NA	NA	NA	< 0.001	0.38	0.09
Intercept	-1.04	1.20	1.09	NA	NA	NA	NA	NA	NA	-1.50	1.20	0.48
Upper/lower CI	1.2/-1.72	1.29/1.11	1.27/0.92	NA	NA	NA	NA	NA	NA	1.8/1.86	1.45/1.06	0.51/0.07
Slopes	1.50	0.42	-0.49	NA	NA	NA	NA	NA	NA	2.17	0.34	0.51
Upper/lower CI	1.99/1.2	0.51/0.31	0.69	NA	NA	NA	NA	NA	NA	2.46/1.8	0.45/-0.45	0.74/0.35
<i>n</i>	<b>84.00</b>			NA	NA	NA	NA	NA	NA	<b>37.00</b>		

*r*, Pearson correlation coefficient; *n*, number of species.

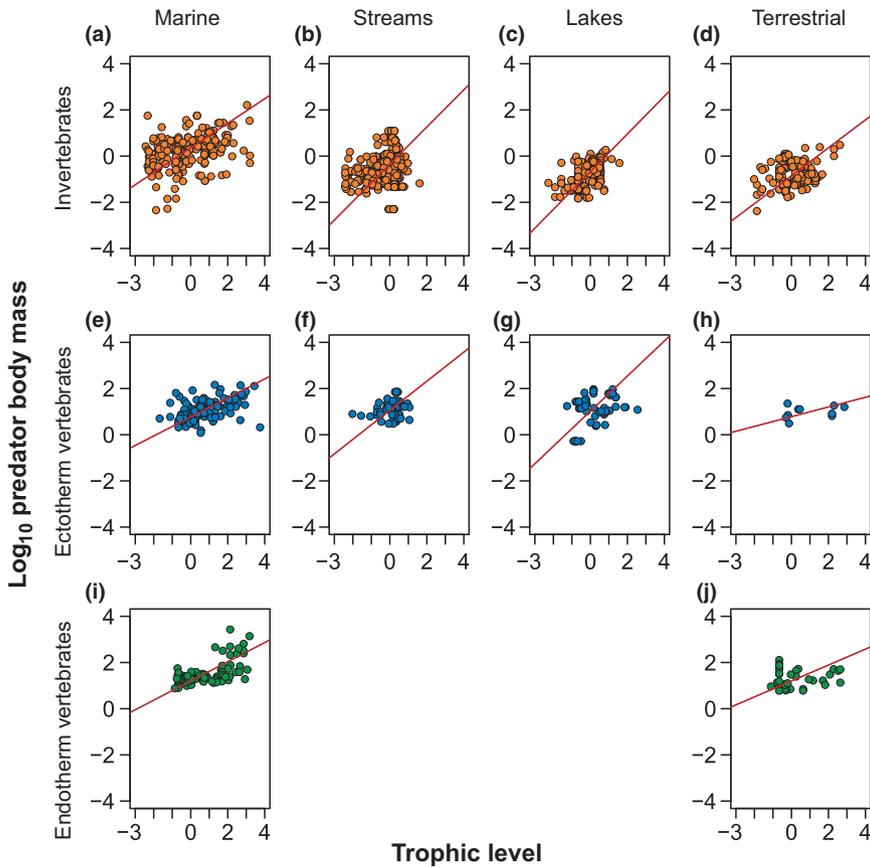


**Figure 1** The relationship between  $\log_{10}$  mean prey mass [gram] and  $\log_{10}$  predator mass [gram]. The panels show different metabolic predator types – invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) – and different ecosystems types – marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 1 for details). Prior to analyses, data were normalized for each web independently.

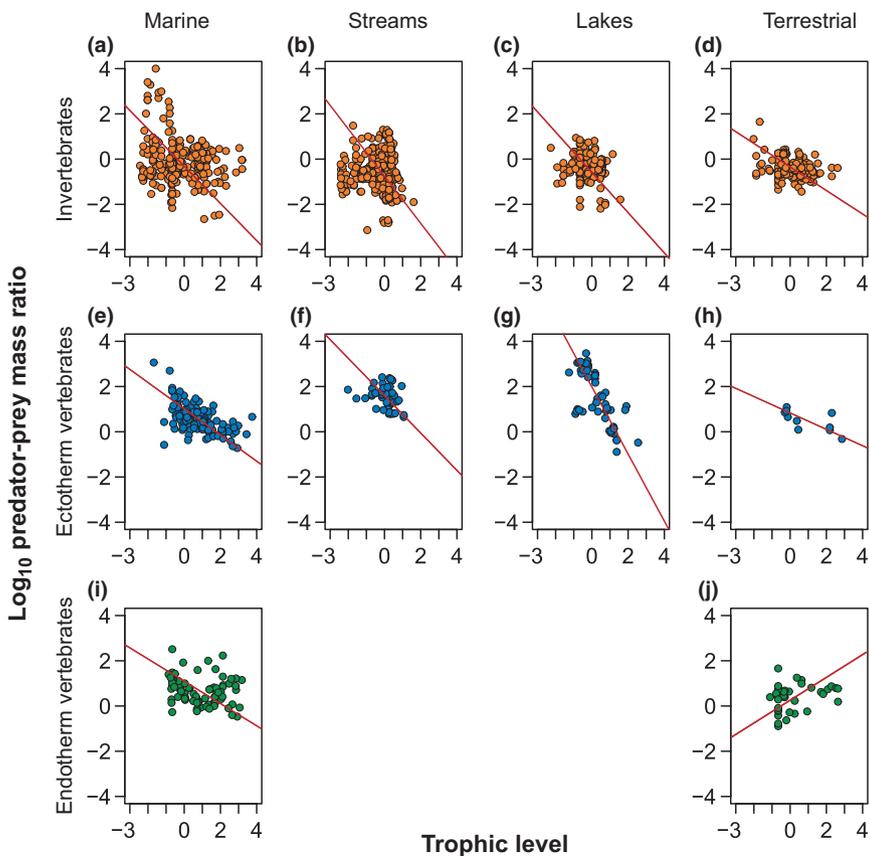
masses are positively correlated. Our study generalizes this finding across combinations of ecosystem types (marine, lake, terrestrial) and predator types (invertebrate, ectotherm and endotherm vertebrate). The relationship had a slope larger than unity across all of these combinations of metabolic types and ecosystems except for streams. Some notable outliers of this relationship were characterized as marine benthic omnivorous suspension feeders (sponges, bryozoans, hydrozoans and ascidians) and scavengers (e.g., polychaetes, gastropods, echinoderms and amphipods) that consume small resources despite their large body-mass. These outliers highlight that the scaling relationship presented here is particularly suited to describe interactions among predators and their prey, whereas other consumer types may follow different scaling relationships. In stream ecosystems, invertebrate and piscivorous predator species consumed a larger range of prey body masses than predators in other ecosystems. This causes a shallower slope (smaller than unity) for the relationship between predator body-mass and average prey body-mass in stream ecosystems. While previous analyses of this relationship for data pooled for ecosystem and predator types suggested exponents smaller than unity (Brose *et al.* 2006a), recent analyses accounting for differences among predator types found exponents larger than unity (Bersier & Kehrli 2008). Note that these prior studies (Brose *et al.* 2006a; Bersier & Kehrli 2008) addressed the relationship between predator mass and average prey mass, whereas the present study has reversed the axes of this relationship to allow a closer match between theoretical derivations and empirical

tests. Our analyses, based on a much larger set of natural food-webs, support the conclusion that the exponents are prevalently larger than unity (Bersier & Kehrli 2008; Costa 2009). This indicates regularity in community structure that holds across ecosystems except for streams: prey becomes disproportionately larger with increasing predator mass and larger predators tend to be more similarly sized to their prey than small predators.

Across all ecosystem and predator types we found positive relationships between predator mass and trophic level. This correlation was not significant for vertebrates in stream and terrestrial ecosystems. This lack of a significant relationship for stream vertebrates is consistent with prior studies (Layman *et al.* 2005), indicating a potential general difference between stream and other ecosystems. The broader feeding niches of opportunistic, omnivorous predatory fishes in streams (Winemiller 1990) could be responsible for this systematic difference. In contrast, we anticipate that the lack of significant correlations for terrestrial vertebrates may be explained by the limited amount of data available. Interestingly, our results contrast with a prior study documenting the lack of a relationship between predator mass and trophic level in a marine food-web (Jennings *et al.* 2001). The highly significant relationships documented here across communities suggest that from the previously anticipated ones, marine food-webs might be less different from other ecosystems. Except for stream and terrestrial vertebrates, our analyses have provided support for the classic paradigm (Elton 1927) that those predators in food chains become progressively larger in size.



**Figure 2** The relationship between  $\log_{10}$  predator masses [gram] and predator trophic level. The panels show different predator metabolic types – invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) and different ecosystems types – marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 1 for details). Prior to analyses, data were normalized for each web independently.



**Figure 3** The relationship between  $\log_{10}$  predator–prey body-mass ratio and predator trophic level. The panels show different predator metabolic types – invertebrates (top), ectotherm vertebrates (middle) and endotherm vertebrates (low panels) and different ecosystems types – marine (left), stream (second), lake (third) and terrestrial ecosystems (right panels). The solid lines represent the RMA regressions (see Table 1 for details). Prior to analyses, data were normalized for each web independently.

**Table 2** Observed and predicted predator–prey body-mass ratios. Predicted slopes, without error propagation based on eqn 4 and with error propagation are based on eqn 5) for each combination of metabolic predator type and ecosystem type

		Observed slopes empirical	Predicted slopes with eqn 4	Predicted slopes with eqn 5
Marine	Invertebrates	-0.82	-0.4	-0.82
Stream		-1.04	0.23	-0.89
Lake		-0.89	-0.32	-0.87
Terrestrial		-0.52	-0.12	-0.49
Marine	Ectotherm	-0.58	-0.4	-0.62
Stream	vertebrates	-0.83	0.13	-0.71
Lake		-1.48	-0.86	-1.5
Terrestrial		-0.36	-0.28	-0.39
Marine	Endotherm	-0.49	-0.21	-0.49
Terrestrial	vertebrates	0.51	-0.4	0.56

On the assumption that the size increase of predators and their prey per trophic level is constant and similar, this classic paradigm also suggests that the mean predator–prey body-mass ratio should be invariant with respect to predator trophic level (Elton 1927). In contrast, our analyses demonstrate that the correlation between trophic level and body-mass ratio is negative for all combinations of ecosystem and predator types except for terrestrial endotherm vertebrates. We anticipate that this exception is caused by data scarcity in this group.

In contrast, the lack of significance in this correlation for stream invertebrates suggests a systematic difference in the body-mass structures. We can only speculate as to the mechanisms (or lack of mechanisms) that may result in this pattern. Forces generated by flowing water and hydrological disturbance are known to constrain body-size in stream invertebrates, (e.g., Townsend 1989; Townsend *et al.* 1997, Snook & Milner 2002), as does size of stream substrates (Bourassa & Morin 1995). Streams differ from the other systems reviewed in the community that is predominantly comprised of larval stages of flying adults. If selective pressure for size is mainly exerted on adult stages, this could explain the lack of a pattern for larvae. Finally, there is the potential for omnivory to alter body-size relationships. Omnivory is a recurrent feature of food-webs, but is rare in stream systems (Thompson *et al.* 2007). This reflects the relatively short food chains in streams, which may reduce the potential for large size disparities between predators and prey. Other mechanisms are certainly possible and more detailed study of the constraints on size ratios in streams is warranted.

Our theoretical derivations relate the general decrease in predator–prey body-mass ratios with trophic level to the combination of increases in predator mass with trophic level and increases in mean prey mass with predator mass with an exponent larger than unity. As eqn 4 is a function of eqns 1–3, we should expect error propagation in the regression parameters. That is, the uncertainties in estimates of parameters  $e$  and  $f$  will actually be a function of uncertainties in parameters  $a$ ,  $b$ ,  $c$  and  $d$ . As a result of this we should not be surprised by the considerable scatter in Fig. 3. More specifically, it can be shown (see Supporting information) that the error estimates of the slopes in Figs 1–3 are expected to propagate in a multiplicative fashion from Figs 1–3.

Accordingly, our results should be interpreted as qualitative scaling models, whereas quantitative predictions of body-mass ratios remain less accurate. Together, our theoretical derivations and empirical tests

demonstrate the broad generality of decreasing body-mass ratios with increasing trophic level. Thus, species with high trophic levels such as top predators are more equal in size to their average prey than predators with low trophic levels. This finding generalizes across ecosystem and predator types (with the possible exception of terrestrial endotherms and stream invertebrates) with profound implications for our understanding of food-web structure, the distribution of predator–prey interaction strengths and community stability, as discussed below.

It is interesting to note that the positive correlation between prey and predator mass across all species and systems (ignoring streams) is compatible with theoretical models of food-web topology such as the cascade model (Cohen & Newman 1985), whereas the more specific results presented here deviate from patterns produced by these models. Under the cascade model, species are arranged in a trophic cascade on a hypothetical niche axis (e.g., according to body-size) (Cohen & Newman 1985) and trophic links are distributed at random between a species and every other species with lower rank (smaller body-size). In consequence, small predators can feed only on a few prey, whereas larger predators can feed on a much larger range of prey (including the smaller prey of small predators). Hence, large predators should have a larger variance in the size of their prey than small consumers (see Wilson 1975) and they should be more dissimilar in size to their average prey (mean log size) than small predators. Indeed, this is what previous studies (Cohen *et al.* 1993; Brose *et al.* 2006a) on the relationship between prey and predator size found while lumping predator types. Consistent with another recent study (Bersier & Kehrli 2008), however, we found the opposite relationship when accounting for different predator and ecosystem groups. This supports a prior finding that the cascade model is unable to reproduce the empirical relationship between mean predator–prey body-mass ratio and predator trophic level (Jonsson 1998). Potential explanations for this disparity include: (1) the trophic hierarchy of natural food-webs is independent of body masses and (2) trophic links are not distributed as assumed by the cascade model (i.e., randomly among every species smaller than a particular consumer species). The positive relationship between predator body-mass and trophic level in our study contrasts with the first explanation, whereas the second explanation is consistent with prior conclusions that the equal predation probability assumption of the cascade model does not generally hold across food-webs (Neubert *et al.* 2000). More recent models of trophic structure, namely the niche (Williams & Martinez 2000), nested-hierarchy (Cattin *et al.* 2004), generalized cascade model (Stouffer *et al.* 2005) and minimum potential niche model (Allesina *et al.* 2008) incorporate additional restrictions on the distribution of trophic links but our results indicate that even the assumptions of these models may have to be modified. Under these models, the consumers feed on prey that fall within a feeding range on the niche axis. As the centre of this feeding range, also representing the average body-mass of the prey, is randomly chosen within a range between zero and the niche value of the consumer, these models produce a pattern that the ratio between a predator's niche value and the average niche value of the prey (i.e., the centre of the feeding range) increases with the predator's niche value. Assuming similarity among niche values and body masses, this suggests that predator–prey body-mass ratios and predator body masses should be positively correlated, which is opposed by our empirical results. While there is thus only limited concordance between our empirical results on the body-mass structure of natural food-webs and some emergent patterns of static food-web models,

their consistency with a more recent allometric diet breadth model using body-mass data to predict feeding links (Petchey *et al.* 2008) remains to be explored.

Recent theoretical and empirical approaches in food-web ecology have related predator–prey body-mass ratios to their interaction strengths and energy fluxes through the feeding links. Some studies based on metabolic theory have proposed power-law increases in interaction strengths with body-mass ratios (Emmerson & Raffaelli 2004; see O’Gorman *et al.* (2010) for a recent study of the correlation between theoretical predictions based on metabolic theory and empirical estimates of interaction strengths). In combination with the results of the present study this suggests that the strongest interactions should be found between small species at the lowest trophic levels of food-webs, whereas weak interactions should characterize the links between large species at higher trophic levels. However, studies of foraging ecology have reported hump-shaped relationships with the strongest interactions at intermediate body-mass ratios (Wilson 1975; Persson *et al.* 1998; Vucic-Pestic *et al.* 2010). Based on the results of the present study, we suppose that the strongest interactions should be located at intermediate trophic levels. While these lingering gaps between metabolic and foraging ecology need to be reconciled, the results of the present study will allow systematic predictions on the distribution of interaction strengths across food-webs. Furthermore, general differences concerning size structure between stream ecosystems and other food-webs need to be addressed in subsequent studies.

## CONCLUSIONS AND CAVEATS

Charles Elton (1927) laid the foundation for what today is called ‘food-web ecology’ by introducing the concept of food chains and food cycles as well as suggesting the importance of body-size in animal community organization. As pointed out by Warren (2005), the conventional wisdom in ecology accepts Elton’s observations and suggestions that animal predators are in general both larger and less abundant than their prey. However, these ideas were not pursued in great detail until recently when body-size has come into focus in many food-web studies (Cohen *et al.* 1993; Brose *et al.* 2006b; Otto *et al.* 2007). The central question of the present study was thus whether Elton’s paradigm is an adequate description of natural communities. Based on our analyses of 35 natural food-webs, we agree with Elton that (1) predator body-mass and mean prey mass are positively correlated and (2) predator body-mass increases with trophic level. However, we disagree with Elton’s claim that predator–prey body-mass ratios are invariant with trophic level (i.e., along food chains). Instead, based on the first two points, our theoretical derivations demonstrated that this is unlikely and our data support systematic decreases in body-mass ratios with trophic level.

Herbivorous and detritivorous interactions were ignored in this study. Herbivores and detritivores rarely consume their entire resource, but rather parts of its biomass. Our choice not to focus on these groups was motivated by systematic differences in interactions among ecosystem types: in contrast to their aquatic counterparts, terrestrial herbivores and detritivores are often much smaller than their resources. Prior studies have shown that the consumer-resource body-mass ratio of aquatic consumers on plants or on detritus is several magnitudes higher than the predator–prey body-mass ratios in the same system (Brose *et al.* 2006a). These higher body-mass ratios at the food-web base would strengthen the trend of

decreasing body-mass ratios with trophic level in aquatic ecosystems, whereas the lower ratios might blur the relationship in terrestrial ecosystems. Rather than focusing on these well-known differences between terrestrial and aquatic ecosystems, we decided in this study to document surprising regularities in the predator–prey body-mass structure of natural food-webs that hold across terrestrial and aquatic ecosystems.

In contrast to Elton’s paradigm, we conclude that predator and prey species become more similarly sized with increasing body-mass and trophic level of the predator. Is this difference important? Based on correlations between body-mass ratios and interaction strengths (Persson *et al.* 1998; Emmerson & Raffaelli 2004; Vucic-Pestic *et al.* 2010), our results suggest a systematic distribution of interaction strengths across food-webs. Ultimately, these interaction strength distributions will be crucially important for understanding constraints on food-web stability (Brose *et al.* 2006b; Neutel *et al.* 2007; Otto *et al.* 2007; Rall *et al.* 2008). Modifying Elton’s paradigm of the body-size structure of natural communities may thus allow us to gain a better understanding of community structure, dynamics and stability.

## ACKNOWLEDGEMENTS

Valuable comments and helpful suggestions that improved earlier versions of the manuscript have been provided by Annie Jonsson. Sorting the data collection was supported by Christoph Digel and Franziska Grischkat. Financial support for this study is partly provided by funds to B. E. and T. J. from the Bank of Sweden Tercentenary Foundation and the Swedish Natural Science Research Council, by the Irish Research Council to U.J. and to J.O.R. and U.B. by the German Research Foundation (BR 2315/4-1, 9-1).

## REFERENCES

- Allesina, S., Alonso, D. & Pascual, M. (2008). A general model for food web structure. *Science*, 320, 658–661.
- Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl Acad. Sci. USA*, 106, 187–191.
- Bersier, L.F. & Kehrli, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecological Complexity*, 5, 132–139.
- Bourassa, N. & Morin, A. (1995). Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *J. North Am. Benthol. Soc.*, 14, 393–403.
- Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Funct. Ecol.*, 24, 28–34.
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F. *et al.* (2006a). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.
- Brose, U., Williams, R.J. & Martinez, N.D. (2006b). Allometric scaling enhances stability in complex food webs. *Ecol. Lett.*, 9, 1228–1236.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Burness, G.P., Diamond, J. & Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proc. Natl Acad. Sci. USA*, 98, 14518–14523.
- Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427, 835–839.
- Cohen, J.E. & Newman, C.M. (1985). A Stochastic-theory of community food webs. 1. Models and aggregated data. *Proc. R. Soc. Lond., B, Biol. Sci.*, 224, 421–448.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.*, 62, 67–78.

- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003). Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA*, 100, 1781–1786.
- Costa, G.C. (2009). Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 90, 2014–2019.
- Elton, C. (1927). *Animal Ecology*. Reprint, 2001, University of Chicago Press edn, Sidgwick & Jackson, London.
- Emmerson, M.C. & Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.*, 73, 399–409.
- Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F. *et al.* (2009). Ecological networks – beyond food webs. *J. Anim. Ecol.*, 78, 253–269.
- Isobe, T., Feigelson, E.D., Akritas, M. & Babu, G.J. (1990). Linear regression in astronomy. *Astrophys. J.*, 364, 104–113.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T.W. (2001). Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J. Anim. Ecol.*, 70, 934–944.
- Jonsson, T. (1998). *Food webs and the distribution of body sizes*. PhD Thesis, Linköping Studies in Science and Technology, Dissertation No. 535. Department of Biology, IFM, Linköpings Universitet, Linköping, Sweden.
- Jonsson, T. & Ebenman, B. (1998). Effects of predator-prey body size ratios on the stability of food chains. *J. Theor. Biol.*, 193, 407–417.
- Jonsson, T., Cohen, J.E. & Carpenter, S.R. (2005). Food webs, body size, and species abundance in ecological community description. *Adv. Ecol. Res.*, 36, 1–84.
- Layman, C.A., Winemiller, K.O., Arrington, D.A. & Jepsen, D.B. (2005). Body size and trophic position in a diverse tropical food web. *Ecology*, 86, 2530–2535.
- Levine, S. (1980). Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.*, 83, 195–207.
- Loeuille, N. & Loreau, M. (2004). Nutrient enrichment and food chains: can evolution buffer top-down control? *Theor. Popul. Biol.*, 65, 285–298.
- Neubert, M.G., Blumenshine, S.C., Duplisea, D.E., Jonsson, T. & Rasmussen, B. (2000). Body size and food web structure: testing the equiprobability assumption of the cascade model. *Oecologia*, 123, 241–251.
- Neutel, A.M., Heesterbeek, J.A.P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldewey, C. *et al.* (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599–602.
- O'Gorman, E.J., Jacob, U., Jonsson, T. & Emmerson, M.C. (2010). Interaction strength, food web topology and the relative importance of species in food webs. *J. Anim. Ecol.*, 79, 682–692.
- Otto, S.B., Rall, B.C. & Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, 450, 1226–1229.
- Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. & Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theor. Popul. Biol.*, 54, 270–293.
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA*, 105, 4191–4196.
- Rall, B.C., Guill, C. & Brose, U. (2008). Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, 117, 202–213.
- Schmid, P.E., Tokeshi, M. & Schmid-Araya, J.M. (2000). Relation between population density and body size in stream communities. *Science*, 289, 1557–1560.
- Snook, D.L. & Milner, A.M. (2002). Biological traits of invertebrates and hydraulic conditions in a glacier-fed catchment (French Pyrénées). *Arch. Hydrobiol.*, 153, 245–271.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*, 3rd edn. W.H. Freeman & Co., New York.
- Stouffer, D.B., Camacho, J., Guimera, R., Ng, C.A. & Amaral, L.A.N. (2005). Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86, 1301–1311.
- Thompson, R.M., Hemberg, M., Starzomski, B.M. & Shurin, J.B. (2007). Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88, 612–617.
- Townsend, C.R. (1989). The patch dynamics concept of stream community ecology. *J. North Am. Benthol. Soc.*, 8, 36–50.
- Townsend, C.R., Scarsbrook, M.R. & Dolédec, S. (1997). The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnol. Oceanogr.*, 42, 938–949.
- Vander Zanden, J.M., Shuter, B.J., Lester, N.P. & Rasmussen, J.B. (2000). Within-among –population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Science*, 57, 725–731.
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010). Allometric functional response model: body masses constrain interaction strengths. *J. Anim. Ecol.*, 79, 249–256.
- Warren, P.H. (2005). Wearing Elton's wellingtons: the importance of body size in food webs. In: *Dynamic food webs multispecies assemblages, ecosystem development and environmental change* (ed. de Ruiter, P.C., *et al.*). Elsevier, Boston, pp. 128–136.
- Warren, P.H. & Lawton, J.H. (1987). Invertebrate predator-prey body size relationships – an explanation for upper-triangular food webs and patterns in food web structure. *Oecologia*, 74, 231–235.
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biol. Rev. Camb. Philos. Soc.*, 81, 259–291.
- Weitz, J.S. & Levin, S.A. (2006). Size and scaling of predator-prey dynamics. *Ecol. Lett.*, 9, 548–557.
- Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.
- Williams, R.J. & Martinez, N.D. (2004). Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.*, 163, 458–468.
- Wilson, D.S. (1975). Adequacy of body size as a niche difference. *Am. Nat.*, 109, 769–784.
- Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.*, 60, 331–367.
- Woodward, G. & Hildrew, A.G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.*, 71, 1063–1074.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** The relationship between  $\log_{10}$  mean prey mass and  $\log_{10}$  predator mass. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained from BIS regression.

**Figure S2** The relationship between  $\log_{10}$  predator mass and trophic level. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained from BIS regression.

**Figure S3** The relationship between  $\log_{10}$  predator–prey body-mass ratio and trophic level. The red solid line represents the slope obtained from RMA regression, the blue dashed line represents the slope obtained from BIS regression.

**Figure S4** Predicted slopes for the relationship between predator–prey body-mass ratio against observed values. (Table 2). In panel (a) and (b) the prediction is calculated with eqn 4 [ $c(1-a)$ ], in panel (c) and (d) the prediction is calculated with eqn 5. Furthermore in (b) and (d) are all possible combinations out of ecosystem and metabolic predator types considered, in (a) and (c) only significant observed slopes. The performance was evaluated with Pearson correlation analyses (results are in each panel). To summarize, equation S4 gives a very accurate prediction for the slope of the RMA regression between predator–prey body-mass ratio and trophic level.

**Table S1** Overview of all food-webs sources used in this study, with references of predation matrix and body-sizes.

**Table S2** Slopes and intercepts for the ordinary least squares bisector regressions (BIS) of  $\log_{10}$  mean prey mass (MPM) vs.  $\log_{10}$  predator mass (PM),  $\log_{10}$  predator mass (PM) vs. trophic level (TL) and predator–prey body-mass ratio ( $\rho$ ) vs. trophic level (TL). Significance is indicated by Pearson correlation analyses and the upper and lower confidence interval for each slope. Furthermore, the number of species for each combination is indicated by  $n$ . Upper and lower confidence

intervals for the intercepts and slopes were obtained by bootstrapping over 100 000 cases.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Sergio Navarrete

Manuscript received 11 August 2010

First decision made 20 September 2010

Manuscript accepted 7 November 2010