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Trophic links and the relationship between predator and prey body sizes in food webs

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Abstract

The relationship between predator and prey body sizes is an important property of food webs with potential implications for community dynamics and ecosystem functioning. To shed more light on this issue I here analyze the relationships between prey size, predator size and trophic position of consumers, using body size estimates of 697 species in 52 food webs.

First I show that the relationship between predator and prey body sizes across many systems can be different from, and potentially obscure the true relationship within systems. More specifically, when data from all webs are aggregated average prey size is positively correlated to predator size with a regression slope less than unity, suggesting that predators become less similar in size to their average prey the larger the predator is, and consequently that the relative size difference between a predator and its prey should increase with the trophic position of the consumer. However, despite this I find the predator-prey body mass ratio to be negatively correlated to the trophic position of the consumer within many webs. The reason for this is that the across-webs pattern is not representative for the within-web relationship.

Second, I show that the pattern observed is not compatible with a simple null-model for the distribution of trophic links between predators and prey. The observed relationship between predator size and mean prey size is for most webs significantly steeper than that predicted by the cascade model. Furthermore, the observed relationship also deviates significantly (but less so) from an ecologically more realistic model for the distribution of trophic links (the niche model).

The results contradict the traditional Eltonian paradigm that predator-prey body mass ratios do not vary consistently across trophic levels. It is concluded that more studies are needed to establish the generality of the results and explore its dynamical implications.

1. Introduction

Food web studies, both empirical and theoretical, have been an important and active part of community ecology for several decades. Despite this and the fact that food web ecology has developed considerably since quantitative and comparative food web studies began in the late 1970's (Cohen 1977, 1978; Pimm and Lawton 1977, 1978) there is still a lot to be learned about the relationships between predators and their prey and the structure of ecological communities that result from these trophic interactions. Brose et al (2006b), for example, reported systematic differences in predator-prey body size relationships across habitats and consumer types, and Riede et al. (2011) showed a tendency for decreasing predator-prey body mass ratios with increasing trophic position of predators. Because this last finding contradicts the traditional Eltonian paradigm that predator-prey body mass ratios do not vary consistently across trophic levels (Elton 1927) and theoretical studies (Jonsson & Ebenman 1998, Brose et al. 2006a) have shown that predator-prey body mass ratios can influence the dynamics of ecological communities (via interaction strengths) there is a need to see if these findings hold for other communities as well. To this end, I here report the results of an analysis of the relationship between predator and prey body sizes, within a set of real food webs, which confirms the previously found pattern (Riede et al. 2011) in the distribution of predator-prey body size ratios within food webs. More specifically, I focus on how the body sizes are distributed in a large set of documented food webs and show that the body sizes of the prey of predators are not distributed randomly with respect to the trophic position of the predator. Instead, there is a tendency for the relative size difference between a predator and its average prey to decrease with the trophic position of the predator.

1.1. *Body size distributions and predator-prey body mass ratios*

Because many life-history traits and other ecological traits are significantly correlated to body size (e.g. Peters 1983, Calder 1984), this particular species characteristic has been the focus in many ecological studies, at all ecological scales, from individuals to communities (see Brown et al. 2004). In communities, for example, the distribution of body sizes has been linked to both structure and functioning (Cohen et al. 1993, Neubert et al. 2000, Loeuille & Loreau 2004, Jonsson et al. 2005, Brose et al. 2006a, Brose 2008, Rall et al. 2008, Berlow et al. 2009) e.g. by explaining regularities in food web structure (Warren & Lawton 1987, Cohen et al. 2003, Brose et al. 2006b, Petchey et al. 2008, Reuman et al. 2009). Furthermore, how the body sizes and trophic links are distributed in food webs have consequences for the distribution of relative size differences between predators and their prey. This size difference (the predator-prey body size ratio), has been suggested to influence interaction strengths (Emmerson & Raffaelli 2004, Brose et al. 2008, Otto et al. 2008, Vucic-Pestic et al. 2010) and, consequently, the dynamics and stability of food webs (Jonsson & Ebenman 1998, Weitz & Levin 2006, Brose 2008, Otto et al. 2007, Berlow et al. 2009). Hence, predicting how body-mass ratios vary among consumers within ecological communities will be important for a better understanding of community structure, dynamics and stability.

In general, if a predator is defined as an animal consumer that is not a parasite, parasitoid, pathogen or herbivore, predator and prey size are positively correlated so that larger prey on average are taken by larger predators than smaller prey (Vézina 1985, Cohen et al. 1993, Brose et al 2006b). Furthermore, data indicate that predator-prey body-mass ratios are systematically higher in lake habitats than in marine, stream or terrestrial habitats, and that vertebrate predators have on average higher body-mass ratios to their prey than invertebrate predators (Brose et al. 2006b; Bersier & Kehrli 2008). However, whether predators that are larger and/or found higher up in the trophic hierarchy, are more or less similar to their average

prey than predators that are smaller and/or found closer to the base of food webs remain unclear. Thus, despite the growing awareness of the significance of body-mass ratios in ecological networks (Woodward et al. 2005; Ings et al. 2009; Brose 2010) our understanding of how they are distributed within natural food webs is incomplete. A recent study (Riede et al. 2011) of 35 food webs found a tendency for a systematic decrease in the predator-prey body mass ratio with the trophic position of the predator, but additional studies are needed to determine the generality of this finding. Because food web data that includes estimates of body sizes of the species is rare I here make use of an existing data source of 52 community food webs (Cohen et al 1989a) complemented with body size estimates of 697 species (Jonsson 1998) to shed light on this issue.

Is there any reason to expect any regularity or pattern in the size difference between a predator and its prey, for example with respect to trophic levels? It is often considered that large size is advantageous to a consumer because a large predator, relative to the size of its prey, is more likely to overpower and handle the prey efficiently. But at the same time larger prey are, in general, more profitable than smaller prey. Thus, as the size difference between a predator and its prey decreases there should (from the predator point of view) be a change from small, easy-to-capture prey items of low per capita value to large, hard-to-capture prey items of large per capita value. How these considerations should translate into a distribution of predator-prey body mass ratios within communities is unclear. Elton (1927) for example, suggested that predator and prey mass should be positively correlated, and that predator masses would increase with trophic levels. From this he inferred that predator-prey body-mass ratios should not vary consistently across trophic levels (i.e. along food chains). In contrast, theoretical models of food- web structure, such as the cascade model (Cohen and Newman 1985), various versions of the niche model (Williams & Martinez 2000; Banasek-Richter et al. 2004; Cattin et al. 2004) or the allometric diet breadth model (Petchey et al. 2008), suggest

various and differing patterns in the distribution of predator-prey body mass ratios in food webs. Differences between these opposing concepts highlight the need for studies that actually analyze if predator-prey body mass ratios vary systematically with the mass or trophic position of the predator within communities.

2. Methods

I compiled data on the approximate adult body weights of 396 predator consumers (325 trophic species, see below) in 24 of the webs in the ECOWeB database (Cohen 1989a) using literature data (see Jonsson 1998). P. Yodzis kindly supplied data on the body weights of 372 consumers (all trophic species) in 28 additional ECOWeB-webs (these data are as described in Yodzis 1984, see also Cohen et al. 1993), thus making a total of 768 consumer species (697 trophic species) in 52 of the first 70 ECOWeB-webs (see Table 1 for data on the webs that have been used).

2.1. The web data

To get the ECOWeB-webs in a form that suited the purpose of this paper, the original webs were edited somewhat. First, Man was omitted whenever included in a web (webs 48, 49 and 68; see Table 1). Second, since this study only deals with predators (defined as an animal consumer that is not a parasite, parasitoid, pathogen or herbivore), insectivorous plants (web 58) and parasites (webs 25 and 27) reported as consumers were omitted. Third, a few obvious biological impossibilities, such as “marine animals” (web 22) or birds (web 25) being reported as basal species, were omitted by not considering any food chain that started with these species. The paper reports the result based on trophic species (i.e. where trophically identical species have been collapsed to one “trophic species” with the geometric mean size of the

constituting species). However, a parallel analysis showed that conclusions are not dependent on this since splitting trophic species into lower level taxonomic entities (e.g. dividing “Redshank, dunlin, knot” in web 55 into one redshank, one dunlin and one knot species) produced quantitatively similar results.

2.2. Predator-prey body size relationships

Defining basal species to have a *trophic height* (Th) of unity, the trophic height of every consumer j was calculated as the *prey-averaged* trophic height (i.e. one plus the average trophic height of all resource species of the consumer, Williams & Martinez 2004).

Next, *mean prey size* (M_{prey_j}) of predator j (with body mass M_{pred_j}) was defined as the geometric mean body mass of all of the prey species i (with body masses estimates) of the predator, and the *predator-prey body mass ratio* (ρ_j) of predator j , as the ratio between

predator size and *mean prey size* (i.e. $\rho_j = \frac{M_{pred_j}}{M_{prey_j}}$). As in Brose et al (2006) and

Riede et al (2011), the geometric mean is here used to avoid one or a few large prey species in the diet of a predator to dominate the mean prey size and predator-prey body mass ratio of that predator, by giving equal weight to the body sizes of prey on different trophic levels (that tend to have different body size ranges) in the food web.

In a log-log plot of mean prey size as a function of predator size (see Fig. 1) a regression slope equal to unity would suggest that there is no systematic change in the relative size difference (i.e. the predator-prey body mass ratio) between predators and their average prey with increasing predator size. In other words, small predators tend to be as many times larger (or smaller) than their prey as large predators. On the other hand, if the slope is less (greater) than one (and starts below the 1:1 line), this means that the relative size difference between

predators and their prey increases (decreases) with increasing predator size so that larger predators tend to be less (more) similar in size to their prey than small predators.

Thus, the relationship between *predator size* and *mean prey size* was analyzed as well as the relationship between *trophic height* and the *predator-prey body mass ratio*, across all webs as well as within each web. The webs were also grouped into 7 different categories based on the type of habitat (e.g., “marine pelagic” and “terrestrial”, see Table 1 for a complete list of all webs and categories) and the relationship between trophic height and the predator-prey body mass ratio was analyzed.

2.3. *The cascade and niche models*

The cascade model was proposed by Cohen and Newman (1985) as “a stochastic theory of community food webs” that would explain observed food web patterns. It is a simple, but still usefull null-model (Gotelli and Graves 1997) for the distribution of trophic links, without detailed biological mechanisms, that results of the present analysis can be compared with. Essential to the cascade model is the idea that species can be arranged in a trophic cascade so that one species feeds only on those species below it (in the cascade) *with equal probability*. It has been suggested that the ordering in this cascade could be based on body size (Warren and Lawton, 1987; Cohen 1989b). If it is assumed that species higher in the trophic cascade are larger than species lower in the cascade, a prediction of the cascade model is that larger consumers are found higher up in food chains and eat prey over a larger range of body sizes than do small consumer species. Here, an analysis was made to see if the cascade model is able to generate the same relationship between predator size and mean prey size as that found in the 52 food webs used here. Thus, for every web, 1000 random predation matrices of the same size, with the same number of upper triangular links (i.e. links where predator size exceeds prey size) and the same body size distribution as the real web, was generated, using

the cascade model. That is, the upper-triangular links were randomly redistributed in the upper triangular section of the predation matrix and for every randomized replicate of a real web new *mean prey sizes* was calculated for every predator. The regression slope for the relationship between *predator size* and *mean prey size* was then calculated for every randomized web. Furthermore, the proportion of these 1000 random webs with a regression slope greater than the slope calculated for the real food webs (considering only upper triangular links since the cascade model cannot generate lower triangular links, see below) was determined. This proportion is also the probability of drawing, from the distribution of randomized web-slopes, a regression slope of the same size, or larger, as the observed slope of the particular ECOWeB-web. Furthermore, because the cascade model is a very simple model, based only on one mechanism (predators only eat prey smaller than themselves with equal probability), and real webs include examples where the predator is smaller than one or several of its prey species, I also compared the observed predator-prey relationships with those predicted by the niche model (Williams & Martinez 2000) that can produce lower triangular links in the predation matrix. The niche model randomly assigns a niche value (n_i), as well as a feeding niche range (r_i) with center c_i , to every species (with $c_i \leq n_i$). Every species with a niche value falling within the feeding niche of another species is included as prey of that species with equal probability. Thus, for every web, 1000 random niche model webs of the same size and connectance (C), and with the same body size distribution as the real web, was generated, by drawing for each species, n_i from a uniform distribution between $[0\ 1]$, r_i from a beta distribution between $[0\ n_i]$ (with shape parameters $\alpha=1$ and $\beta=(1-2C)/2C$), and c_i from a uniform distribution between $[r_i/2\ n_i]$. Next the proportion of these 1000 niche model webs with a regression slope greater than the slope observed in the real food webs (considering both upper and lower triangular links) was determined.

3. Results

3.1. *The relationship between predator and mean prey body sizes*

Fig. 1 shows the relationship between *predator size* and *mean prey size* (on a log-log scale) for all 52 webs combined. The relationship is highly significant ($r^2=0.45$, $p<0.001$) with an estimated regression slope less than unity ($b=0.80$), indicating that the larger the predator, the less similar in size its average prey is. For individual webs the pattern is not so conclusive since the estimated regression slopes range from less than zero in a few cases to almost three (Table 1). However, both the mean regression slope and the fraction of webs with a slope greater than one increase as the smallest webs (in terms of number of predator-prey pairs with estimated body sizes of the predator and at least one of its prey) are gradually eliminated from the analysis ($r^2=0.70$, $p=0.008$ and $r^2=0.59$, $p<0.035$ respectively). This means that the probability of observing larger predators to be more similar in size to their prey than smaller predators is greater in a web if the number of reported predator-prey links is large.

3.2. *Predator-prey body mass ratios and trophic position*

Across all webs there is a significant negative correlation ($r^2=0.024$, $p=0.0019$) between the predator-prey body mass ratio and the trophic height of a predator (Fig. 2A), although it is evident that there is a large range in body mass ratios for small values of the trophic height. Most of the individual webs are small, with an even smaller number of consumer-prey pairs with estimated body sizes. (Only 15 of the 52 webs have body size data on 10 or more consumers with at least one prey, see Table 1.) Thus, the relationship between trophic position and the predator-prey body mass ratio for single webs range from statistically significantly negative to even positive (Table 1), but, the proportion of webs with a negative relationship increases with web size ($r^2=0.39$, $p<0.023$; i.e. as the smallest webs, in terms of the number of

consumer-prey pairs with estimated body sizes in the web, are gradually eliminated from the analysis). Furthermore, of the five webs with body size data on more than 15 consumers with at least one prey, all show a negative relationship (Fig. 2B-F), and for three of these the relationship is statistically significant.

3.3. Predictions for the relationship between predator and prey body size based on the cascade and niche models

When the trophic links in each web were redistributed 1000 times, using the cascade model, this produced more often than not in many webs more shallow slopes than the one observed in the real web (for the relationship between predator size and mean prey size, Table 1). Particularly for large webs the cascade model consistently predicts shallower slopes than the ones found in the real webs. As an example, Fig. 3 shows the relationship between predator and mean prey size, as well as the distribution of regression slopes for 1000 randomized cascade webs for a single web (web 41).

The results for all webs are summarized in Fig. 4A as a frequency histogram of the probabilities that the cascade model would generate regression slopes for the relationship between predator size and mean prey size greater than the ones actually observed. Thus, for 20 of the 49 webs with body mass data on three or more predator-prey pairs, the probability is less than 0.1 (meaning that for 90% of the randomized replicates of a real web, mean prey size does not increase as fast with increasing predator size as in the real web). Furthermore, for seven of the 12 webs with body mass data on more than 10 species, the probability is less than 0.1. The distribution of probabilities is thus highly skewed, with a dominance of low probabilities. The probability of having 20 or more proportions less than 0.1 (out of 49) is

$\sim 1.57 \times 10^{-8}$ (assuming that the proportions are binomially distributed around 0.5). (The probability of having seven or more proportions less than 0.1, out of 12, is $\sim 5.02 \times 10^{-5}$.)

Furthermore, when niche model replicates were generated for each web, the distribution of proportions of regression slopes steeper than the observed is still somewhat skewed (Fig. 4C) but less so than for cascade model webs. For 10 webs with body mass data on three or more predator-prey pairs, the probability is less than 0.1, and for 19 webs the probability is less than 0.2. The probability of having 10 or more proportions less than 0.1 (out of 49) is ~ 0.02 while the probability of having 19 or more proportions less than 0.2, is $\sim 9.56 \times 10^{-8}$.

4. Discussion

Darwin's entangled bank has been widely used as a metaphor for the complexity of ecological systems but how much of this complexity do we understand? A food web graph is one way to try to capture some of this complexity by describing who eats whom in a community, but the usefulness of such traditional connectance webs alone for a deeper understanding of the structure and functioning of ecosystems is limited. That is, an ecological community is much more than the trophic interactions among its species, and modern approaches in food web ecology try to link food web characteristics and species traits, such as body size, to increase our understanding of food web structure, dynamics and functioning. For example, based on correlations between body-mass ratios and interaction strengths (Persson et al. 1998; Aljetlawi et al. 2004; Emmerson & Raffaelli 2004; Reuman & Cohen 2005; Wootton & Emmerson 2005; Brose et al. 2008; Vucic-Pestic et al. 2010) it may be possible to predict dynamics and stability of communities from the distribution of predator-prey body mass ratios within a food web (Jonsson & Ebenman 1998, Emmerson & Raffaelli 2004, Weitz & Levin 2006, Otto et al. 2007, Brose 2008, Berlow et al. 2009, Boit et al. 2012). Hence, understanding how body-mass

ratios are distributed within ecological communities could increase our understanding of some of the constraints on food-web stability (De Ruiter et al. 1995; McCann et al. 1998; Neutel et al. 2002; Brose et al. 2006; Rooney et al. 2006; Neutel et al. 2007; Otto et al. 2007; Brose et al. 2008; Rall et al. 2008). To this end, I here report the results of an analysis of the distribution of predator-prey body size ratios within a set of real food webs that show that predator and prey species tend to become more similarly sized with increasing body mass and trophic height of the predator.

4.1. The relationship between predator and mean prey body sizes

The analysis presented here for the relationship between predator and mean prey size showed a discrepancy between the relationship across all webs and within individual webs. Across all webs the slope of the regression line was less than unity, suggesting that predators become less similar in size to their prey with increasing size, while within many web the slope was found to be greater than unity, indicating that predators become more similar in size to their prey with increasing size. Furthermore, the probability of observing a relationship between predator and mean prey size with a slope closer to, or greater than one, was found to increase as the number of predator-prey links in a web increased. This suggests (i) that larger and potentially more well-documented, webs are more likely than smaller webs to show predator-prey size relationships where mean prey size increases faster than predator size and (ii) that aggregating data from many webs and from many types of system may hide the “true” (and more interesting) relationship within individual webs and lead to wrong conclusions about the relationship between predator and prey body sizes within food webs.

4.2. *Predator-prey body mass ratios and trophic position*

Across all webs the negative relationship between predator-prey body mass ratios and trophic position is weak and there is a large range in predator-prey body mass ratios for small values of the trophic height of consumers (Fig. 2A). However, the data come from many different types of communities (e.g. both pelagic and terrestrial) differing among other things in the kind of dominating primary producer (e.g. phytoplankton vs. trees). This suggests that the relationship between the predator-prey body size ratio and trophic position of the consumer might best be analyzed in every web separately, or by breaking the data into different kinds of systems, e.g. by habitat type. Different kinds of habitats may impose different restrictions on the consumers, for example in terms of the size difference of a consumer relative to its prey. To test this, the webs were grouped into seven different habitat types (benthic, estuarine, lentic, lotic, pelagic, terrestrial and mixed, see Table 1) and the relationship between trophic height and the predator-prey body mass ratio was analyzed within each ecosystem category (Table 2). For all of these habitat types the relationship was negative, and stronger than across all webs, suggesting once more that aggregating data from many types of system, although increasing the number of data points, actually may make it more difficult to reveal what the “true” relationship is within individual webs or ecosystem types. This conclusion is also supported by Riede et al. (2011) who found the strength of the relationship between trophic height and the predator-prey body mass ratio to be different for different ecosystem and consumer types.

4.3. *The cascade model and the relationship between predator size and mean prey body size*

Cohen et al. (1993) asserted that the relationship between prey size and predator size found in their study was compatible with the predictions of the cascade model. However, I have here shown that the relationships between predator and prey body sizes in a much larger data set deviates significantly from the predictions of the cascade model. Fig. 1 showed that, across all webs, the larger the predator, the less similar in size its average prey is expected to be. This actually is in line with the predictions of the cascade model, with larger predators taking a broader range of prey sizes and thus, on average, relatively smaller prey than smaller-bodied predators. However, for many individual webs the relationship between predator and mean prey size tended to have slopes *greater* than one, meaning that larger predators instead take prey that, on average, are more similar in size to themselves than smaller predators. In addition to contradicting the finding across all webs (Fig. 1), this also suggests that trophic links in these larger webs are not distributed as assumed by the cascade model. This suspicion was confirmed by the analysis showing that cascade model replicates of most webs produced regression slopes (for the relationship between predator and mean prey size) that were more shallow than the observed slope in the real webs, and the distribution of proportions of cascade model slopes steeper than the observed was highly skewed (Fig. 4A). The expected distribution of probabilities, if the cascade model is to describe predator-prey relationships correctly (according to the ones found here), is a binomial distribution with (mean and) mode at 0.5. Clearly, the observed distribution (Fig. 4) does not conform to this expectation. Thus, the cascade model fails to reproduce the same pattern in the relationship between predator size and mean prey size as the one found in 52 food webs. For any single web, the pattern could have arisen by chance, but the result across the whole set of webs is highly improbable, leading to the conclusion that the trophic links are not distributed as assumed by the cascade

model. Instead larger predators eat, on the average, larger prey than expected, resulting in a steeper relationship between predator size and mean prey size. Thus, the equal predation probability assumption of the cascade model does not seem to be ecologically defensible. The equal predation probability assumption of the cascade model was tested by Neubert et al. (2000) against four heterogeneous alternatives (predation probabilities differing between rows, columns or diagonals basically). In a restricted set of 16 food webs for which adequate data was available, the null hypothesis (equal predation probability) could be rejected in favor of any of these alternatives in seven out of 16 webs at a significance level of $p \leq 0.06$. This result is corroborated by the findings here.

The niche model has been widely used to model the structure of complex food webs and in a comparative study (Williams & Martinez 2008) was found to perform better than several other alternative models, including the nested hierarchy model (Cattin et al 2004) and the generalized cascade model (Stouffer et al. 2005). Despite this success in reproducing various food web properties (Williams & Martinez 2008) and improvement over the simple cascade model, in terms of predicting the relationship between predator and prey size, found here, the observed relationship in individual webs still deviate significantly from those predicted by the model (Fig. 4B). This suggests that the niche mechanisms driving the model are lacking some important process or constraint that affects the diet of real predators.

4.4. The web data

The ECOWeB-webs have been criticised for a number of reasons (e.g. Paine 1988, Peters 1988, Martinez 1994). Although new and better resolved webs are available today, these webs rarely contain data on the body sizes of the species within them (but see Brose et al. 2005). Furthermore, although many ECOWeB-webs may be incomplete descriptions of real

communities they share this feature with probably all other documented webs this far. Thus, much can still be learned from analyzing the ECOWeB-collection, at least when the focus is not on food web level statistics, but instead on species level characteristics such as the size difference between predators and their prey. In other words, hypotheses about the distribution of predator-prey body size ratios within food webs, can be initially tested against this data source, awaiting new and better food web data.

The ECOWeB-webs, as most other published food webs tend to be better resolved at the top than at the bottom and as a consequence there might be proportionately more large than small prey species recorded in the diet of a large predator. Thus, there is a possibility that the pattern documented here (of decreasing body mass ratios between a predator and its average prey, with increasing trophic height of a consumer, e.g. Fig. 2), is an artefact caused by poor resolution at lower trophic levels in food webs. However, the webs analyzed do include small species at the same time as comparison with cascade model replicates showed that there is an underrepresentation of links between large predators and the small species present. In other words, even among the species actually reported in the ECOWeB-webs, trophic links are not distributed at random between predators and their potential (smaller sized) prey, with the result that the relative size difference between predators and their average prey decreases with the size and trophic height of the predator. This suggests that poor resolution is not a (major) explanation for the results found.

4.5. Conclusions

This paper has concentrated on the relationship between predator and mean prey size, whether this implies any pattern in predator-prey size ratios at different trophic positions of a consumer, and if two topological food web models (the cascade and niche models) can

reproduce the observed pattern. The analysis of body size data in 52 food webs shows that there is a tendency for the predator-prey body mass ratio to decrease with the trophic height of a consumer. It is also shown that the relationship between predator and prey size deviates significantly from what is expected by both the cascade and niche models. Large predators tend to eat prey of larger average size than would be the case if trophic links were distributed randomly between a consumer and all species smaller than the consumer (i.e. according to the cascade model).

The generality of the results reported here are supported by two recent studies that find similar results using different data sets. Costa (2009) report that for marine predators, mean prey size increases with predator size on a log-log scale, with a slope greater than one, which means that large marine predators will be more similarly sized to their average prey than small marine predators. This is a pattern previously reported also for terrestrial carnivores (Vézina 1985). These results also suggest that the predator-prey body mass ratio decreases with predator trophic level for many marine as well as terrestrial predators (if predator trophic level increases with body size). Furthermore, using body mass estimates of 1313 animal predators of different metabolic groups, sampled in 35 natural food webs of different ecosystem types, Riede et al. (2011) found that the geometric mean prey mass increased with predator mass with a power-law exponent greater than unity, and that the predator-prey body-mass ratio in most ecosystem types decreased with the trophic level of the predator. All of these studies indicate a regularity in community structure that holds across ecosystems: prey become disproportionately larger with increasing predator mass, and larger predators closer to the top of food webs tend to be more similarly sized to their prey than smaller predators closer to the base of food webs. Recent theoretical and empirical approaches in food-web ecology, linking predator-prey interaction strengths to the predator-prey body mass ratio (Jonsson & Ebenman 1998, Emmerson & Raffaelli 2004, Brose et al 2006a), suggest dynamical implications of this

pattern: Based on metabolic theory predator-prey per capita interaction strengths are predicted to be positively correlated to the predator-prey body mass ratio (Emmerson et al. 2005, Berg et al. 2011). This suggests that, on average, the strongest per capita trophic interactions are to be expected near the base of food chains, whereas weaker interactions should characterize the links at the top of food chains (where predator-prey body mass ratio are found to be smaller than near the base). Such a pattern in the distribution of interaction strengths have been found to increase resilience of food chains (Jonsson & Ebenman 1998) and enhance stability of food webs (Brose et al 2006a). Recently, O’Gorman et al. (2010) used field experiments to study the correlation between theoretical predictions based on metabolic theory and empirical estimates of interaction strengths, and found significant correlations between the two metrics.

Future studies using better web data will have to test the hypothesis that decreasing predator-prey body size ratios with increasing trophic level is a general feature of ecological systems, and more sophisticated models of trophic structure that include mechanisms that reproduce and explain this pattern need to be looked for. With more studies like this, that analyze the distribution of trophic links within food webs and explores differences between systems, we may in the end obtain a better understanding of community structure, dynamics and stability.

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Table 1

Table 1. List of webs from the ECOWeB-collection (Cohen 1989a) used. The web number as they appear in Cohen *et al* (1990) is denoted by #, n_1 is the number of trophic species after editing (see methods), n_2 is the number of (trophic) consumers with known body mass and estimates of the body size of at least one prey species, r is the Pearson coefficient of correlation for the relationship between trophic height of the consumer and the predator-prey body mass ratio, p is the significance level, a is the regression slope for the relationship between predator size (log body mass) and mean prey size (mean log body mass), and $P_{cascade}$ and P_{niche} respectively, are the proportions of 1000 cascade and niche model replicates (see methods) with a slope greater than the one calculated for the real web. The classification of the webs into different types of systems follow Schoener (1989) with the exception of web #21 (which was not classified by Schoener).

#	web name (description & location)	trophic height vs.				predator size			habitat type
		websize		predator-prey		vs.			
		body mass ratio		mean prey size					
		n_1	n_2	r	p	a	$P_{cascade}$	P_{niche}	
2	Knysna estuary, South Africa	14	5	-0.32	0.60	2.41	0.002	0.008	estuarine
3	Salt marsh, NY, USA	24	10	-0.10	0.78	0.54	0.638	0.692	estuarine
4	Salt marsh, CA, USA	13	9	-0.79	0.01	1.14	0.519	0.355	terrestrial
5	Salt marsh, GA, USA	6	2	- [†]	- [†]	- [†]	- [†]	- [†]	estuarine
9	Lough Ine Rapids, Ireland	9	4	0.54	0.46	0.08	0.048	0.732	benthic
10	Exposed rocky shore, USA	3	1	- [†]	- [†]	- [†]	- [†]	- [†]	benthic
11	Protected rocky shore, USA	5	1	- [†]	- [†]	- [†]	- [†]	- [†]	benthic
12	Exposed rocky shore, WA, USA	9	3	0.93	0.24	-0.07	0.000	0.844	benthic
13	Protected rocky shore, WA, USA	9	3	0.97	0.15	-0.07	0.000	0.851	benthic

Predator-prey body size ratios in food webs

14	Mangrove swamp 1, HI, USA	8	4	0.33	0.67	0.37	0.626	0.590	estuarine
15	Mangrove swamp 3, HI, USA	7	3	-0.63	0.56	0.61	0.633	0.499	estuarine
16	Pamlico estuary, NC, USA	14	6	-0.50	0.31	0.81	0.606	0.550	estuarine
17	Coral reefs, Marshal Islands	14	8	-0.38	0.36	1.54	0.156	0.168	benthic
19	Moosehead Lake, ME, USA	17	12	-0.06	0.84	0.71	0.671	0.610	lentic
20	Antarctic Pack Ice zoon	19	13	0.05	0.88	0.46	0.397	0.393	pelagic
21	Ross sea	9	7	0.74	0.06	0.33	0.440	0.657	pelagic
22	Bear Island, Spitzbergen	28	12	0.29	0.36	0.79	0.000	0.012	mixed
23	Prairie, Manitoba, Canada	15	9	-0.43	0.25	0.71	0.364	0.459	terrestrial
24	Willow forest, Manitoba, Canada	11	5	-0.10	0.87	0.33	0.048	0.532	terrestrial
25	Aspen community, Manitoba, Canada	24	10	0.31	0.32	0.80	0.090	0.169	terrestrial
27	Wytham wood, England	22	10	-0.07	0.82	0.29	0.176	0.564	terrestrial
33	Crocodile creek, Malawi	29	12	-0.02	0.95	0.44	0.716	0.535	lentic
34	River Clydach, Wales	12	3	-0.40	0.60	0.56	0.199	0.266	lotic
35	Morgan's creek, KY, USA	13	7	0.25	0.59	-0.01	0.990	0.964	lotic
36	Mangrove swamp 6, HI, USA	19	7	-0.16	0.73	1.55	0.317	0.283	estuarine
37	Marine sublittoral, CA, USA	24	17	-0.72	0.00	1.77	0.010	0.040	benthic
38	Lake Nyasa, rocky shore, Malawi	31	18	-0.39	0.11	0.48	0.991	0.930	lentic
39	Lake Nyasa, sandy shore, Malawi	33	15	-0.46	0.08	1.90	0.023	0.108	lentic
41	Tropical seas, epipelagic zoon	18	16	-0.70	0.00	1.07	0.138	0.201	pelagic
42	Upwelling areas, Pacific ocean	15	9	-0.38	0.31	0.73	0.264	0.199	pelagic
43	Kelp bed community, CA, USA	20	9	-0.34	0.30	2.74	0.026	0.060	benthic
44	Marine coastal lagoons, Guerrero, Mexico	12	5	-0.81	0.09	2.05	0.000	0.012	mixed
47	Swamp, FL, USA	27	19	-0.20	0.40	0.60	0.001	0.631	mixed
48	Nearshore marine 1, Aleutian Islands	13	5	-0.14	0.80	0.51	0.237	0.202	benthic
49	Nearshore marine 2, Aleutian Islands	12	4	0.06	0.93	-0.09	0.871	0.846	benthic
50	Sandy beach, CA, USA	14	5	0.77	0.13	0.15	0.794	0.837	benthic
51	Shallow sublittoral, Cape Ann, MA,	24	11	0.48	0.09	0.67	0.049	0.135	estuarine

Predator-prey body size ratios in food webs

USA

52	Rocky shore, Torch Bay, AL, USA	20	8	0.33	0.36	0.13	0.546	0.851	benthic
53	Rocky shore, Cape Flattery, WA	22	7	0.31	0.46	0.19	0.422	0.808	benthic

USA

54	Western rocky shore, Barbados	14	2	0.92	0.03	- [†]	0.000	0.000	benthic
55	Mudflat, Ythan estuary, Scotland	12	7	-0.92	0.00	1.21	0.094	0.047	estuarine
56	Mussel bed, Ythan estuary, Scotland	10	5	-0.91	0.03	0.97	0.208	0.169	estuarine
58	Sphagnum bog, Russia	17	6	0.25	0.49	0.60	0.029	0.114	mixed
59	Trelease woods, IL, USA	29	12	0.11	0.73	0.64	0.084	0.195	terrestrial
60	Montane forest, AZ, USA	33	15	0.16	0.56	1.14	0.007	0.028	terrestrial
61	Barren regions, Spitzbergen	8	3	0.56	0.62	0.20	0.684	0.517	terrestrial
62	Reindeer pasture, Spitzbergen	11	3	-0.07	0.96	0.81	0.029	0.032	terrestrial
63	River Rheidol, Wales	18	6	-0.44	0.38	-0.15	0.94	0.989	lotic
64	Linesville creek, PA, USA	19	6	-0.12	0.78	-0.04	0.843	0.838	lotic
65	Yoshino river rapids, Japan	12	3	0.02	0.98	0.03	0.891	0.818	lotic
66	River Thames, England	10	4	-0.94	0.06	2.87	0.000	0.005	lotic
68	Loch Leven, Scotland	22	8	-0.60	0.05	1.19	0.120	0.129	lentic

[†] No regression and/or correlation could be performed because of too few data points ($df < 1$) or no variation in the independent variable. (Data from these webs were however used in the total analysis, with all webs combined.)

Table 2

Table 2. Coefficient of correlation (r) and significance level (p) in data set A (trophic species data, see methods) for the relationship between the trophic height of a predator consumer and the average predator-prey body mass ratio (mean $\log_{10}$ body mass ratio, see methods for definition of these metrics) in 52 food webs (see Table 1) classified into seven habitat types according to Schoener (1989). The number of predator consumers with estimated body masses of at least one prey species is denoted by n .

	r	p	n
habitat type:			
benthic	-0.1531	0.1752	80
estuarine	-0.3457	0.0059	62
lentic	-0.3079	0.0141	63
lotic	-0.2811	0.1396	29
pelagic	-0.2818	0.0639	44
terrestrial	-0.0279	0.8100	77
mixed	-0.1902	0.2337	41

Figure captions

Fig. 1. Mean prey size (mean $\log_{10}$ prey body mass) as a function of predator size ($\log_{10}$ predator body mass) for 395 predator consumers (trophic species, i.e. data set A, see methods) in 52 food webs (see Table 1). $r^2=0.4517$ ($p<0.001$). Prey size equals predator size along the solid line. (Dashed line is the least squares regression line $Y=0.8007X-2.7371$.)

Fig. 2. The predator-prey body mass ratio (mean $\log_{10}$ body mass ratio) between a predator consumer and its prey as a function of the average trophic position of the predator. (A) 395 predator consumers (trophic species) in 52 food webs (see Table 1), $r^2=0.0243$, $p=0.0019$. (B) 17 predator consumers in web 37, $r^2=0.51$, $p=0.0012$, (C) 17 predator consumers in web 38, $r^2=0.15$, $p=0.12$, (D) 15 predator consumers in web 39, $r^2=0.37$, $p=0.022$, (E) 16 predator consumers in web 41, $r^2=0.49$, $p=0.0024$, (F) 18 predator consumers in web 47, $r^2=0.042$, $p=0.42$.

Fig. 3. (A) The relationship between predator size ($\log_{10}$ predator body mass) and mean prey size (mean $\log_{10}$ prey body mass) in web 41 (see Table 1). Prey size equals predator size along the solid line. Dashed line is the least squares regression line ($Y=1.0664X-3.5262$). (B-C) The distribution of regression slopes for the relationship between predator size ($\log_{10}$ predator body mass) and mean prey size (mean $\log_{10}$ prey body mass) in web 41 (see Table 1) for (B) 1000 cascade model realisations and (C) 1000 niche model realizations (see methods). Vertical line shows the observed regression slope (1.07) for the real web.

Fig. 4. The frequency distribution of the proportion of randomly constructed “cascade webs” (see methods) with a regression slope greater than the one found in 48 food webs (see Table 1,

646 each having body size data on three or more predator consumers with at least one prey
647 species).
648

Figure 1

Fig. 1. Mean prey size (mean $\log_{10}$ prey body mass) as a function of predator size ($\log_{10}$ predator body mass) for 395 predator consumers (trophic species, i.e. data set A, see methods) in 52 food webs (see Table 1). $r^2=0.4517$ ($p<0.001$). Prey size equals predator size along the solid line. (Dashed line is the least squares regression line $Y=0.8007X-2.7371$.)

658 Figure 2

Fig. 2. The predator-prey body mass ratio (mean log₁₀ body mass ratio) between a predator consumer and its prey as a function of the average trophic position of the predator. (A) 395 predator consumers (trophic species) in 52 food webs (see Table 1), $r^2=0.0243$, $p=0.0019$. (B) 17 predator consumers in web 37, $r^2=0.51$, $p=0.0012$, (C) 17 predator consumers in web 38, $r^2=0.15$, $p=0.12$, (D) 15 predator consumers in web 39, $r^2=0.37$, $p=0.022$, (E) 16 predator consumers in web 41, $r^2=0.49$, $p=0.0024$, (F) 18 predator consumers in web 47, $r^2=0.042$, $p=0.42$.

668 **Figure 3**

Fig. 3. (A) The relationship between predator size ($\log_{10}$ predator body mass) and mean prey size (mean $\log_{10}$ prey body mass) in web 41 (see Table 1). Prey size equals predator size along the solid line. Dashed line is the least squares regression line ($Y = 1.0664X - 3.5262$). (B-C) The distribution of regression slopes for the relationship between predator size ($\log_{10}$ predator body mass) and mean prey size (mean $\log_{10}$ prey body mass) in web 41 (see Table 1) for (B) 1000 cascade model realisations and (C) 1000 niche model realizations (see methods). Vertical line shows the observed regression slope (1.07) for the real web.

680 **Figure 4**

681
682
683 **Fig. 4.** Frequency distributions of the proportion of (A) cascade model webs and (B) niche
684 model webs, with a regression slope for the relationship between mean prey size and predator
685 size, greater than the one found in 49 food webs (see Table 1, each having body size data on
686 three or more predator consumers with at least one prey species).
687
688