Body sizes of animal predators and animal prey in food webs

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Summary

1. We measured the body sizes (weights or lengths) of animal species found in the food webs of natural communities. In *c.* 90% of the feeding links among the animal species with known sizes, a larger predator consumes a smaller prey.

2. Larger predators eat prey with a wider range of body sizes than do smaller predators. The geometric mean predator size increases with the size of prey. The increase in geometric mean predator size is less than proportional to the increase in prey size (i.e. has a slope less than 1 on log–log coordinates).

3. The geometric mean sizes of prey and predators increase as the habitat of webs changes from aquatic to terrestrial to coastal to marine. Within each type of habitat, mean prey sizes are always less than mean predator sizes, and prey and predator sizes are always positively correlated.

4. Feeding relations order the metabolic types of organisms from invertebrate to vertebrate ectotherm to vertebrate endotherm. Organisms commonly eat other organisms with the same or lower metabolic type, but (with very rare exceptions) organisms do not eat other organisms with a higher metabolic type. Mean sizes of prey increase as the metabolic type of prey changes from invertebrate to vertebrate ectotherm to vertebrate endotherm, but the same does not hold true for predators.

5. Prey and predator sizes are positively correlated in links from invertebrate prey to invertebrate predators. In links with other combinations of prey and predator metabolic types, the correlation between prey and predator body sizes is rarely large when it is positive, and in some cases is even negative.

6. Species sizes are roughly log-normally distributed.

7. Body size offers a good (though not perfect) interpretation of the ordering of animal species assumed in the cascade model, a stochastic model of food web structure. When body size is taken as the physical interpretation of the ordering assumed in the cascade model, and when the body sizes of different animal species are taken as log-normally distributed, many of the empirical findings can be explained in terms of the cascade model.

Key-words: allometry of body sizes, cascade model, lognormal distribution, metabolic types, habitat types.

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Introduction

Body size is one of the most obvious features of any animal and one of the most important (Calder 1984; Peters 1983; Reiss 1989; Schmidt-Nielsen 1984).

Size influences how much energy an animal needs, how much food it can gather, and which other organisms can try to eat it, among other aspects of life history. Thus, size constrains animals' feeding interactions on an ecological time-scale and is influenced by feeding interactions on an evolutionary time-scale. Our aim is to describe and understand the connections between the size and the feeding relations of organisms in natural settings. We shall

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report here some steps towards this goal. For background on food webs, see e.g. Pimm (1982), Schoener (1989), Yodzis (1989, Chapter 8) and Pimm, Lawton & Cohen (1991).

The relations between body size and feeding relations have been studied in several ways. Some studies report the weights of predator—prey pairs from different communities and ecosystems, but restrict the data to taxonomically or functionally defined groups, such as vertebrate insectivores, or birds feeding on seeds (e.g. Schoener 1968; Wilson 1975; Peters 1983, p. 277; Vézina 1985). An alternative approach considers the pattern of variation in the weights of predators and prey, not pairwise, but along the full length of a food chain or in an entire food web in a single community or ecosystem. Elton (1927) suggested that in some food chains (e.g. those including marine or aquatic grazers), body size generally increases with increasing remoteness from the green plants; in other food chains (e.g. those including terrestrial herbivores), he suggested, body size generally decreases with increasing remoteness from the green plants. Exceptions to these generalizations come readily to mind. A third approach reports the weights of all (or as many as possible) of the predator—prey pairs in a particular community or ecosystem (e.g. Menge *et al.* 1986; Warren & Lawton 1987).

To investigate further the possibility that there exist general relations between body size and food web structure, we assemble here and analyse data relating body size to feeding links among diverse taxonomic groups of animals in a diversity of food webs. Plants are not included. The data are observational, not based on experimental changes in either animal body size or web structure. Therefore, the data do not permit us to distinguish whether animal body size unidirectionally controls food web structure, or vice versa. In any event, a bidirectional interaction between body size and web structure seems more likely than either unidirectional causation. Our purpose is to describe the interaction quantitatively and to relate it to a model of food web structure known as the cascade model (Cohen, Briand & Newman 1990).

Data

Data set A

One of us (P.Y.) determined the average adult weights (g) of as many as possible of the animal species in the first 40 community food webs of the Briand-Cohen collection, after excluding six webs in which man appeared. The webs of the Briand-Cohen collection are printed in full in Cohen, Briand & Newman (1990, Chapter IV), and are also available in machine-readable form (Cohen 1989a). As in Yodzis (1984), weights were determined using pub-

lished data, scaling formulae, weighing of specimens and, in a few cases, calculation from the geometry of the animals. Some kinds of organisms in the food web data lump too many taxa together, or are too vaguely specified, to permit such a determination. A few of the species involved were too obscure to enable enough information to be gathered.

The data were previously used to test the hypothesis that, other things being equal (including body size), energetically efficient animals such as invertebrate ectotherms are more likely to provide sole support for a consumer than are energetically profligate animals such as endotherms (Yodzis 1984).

For each web, we constructed the subweb containing the species with known weights. We excluded any subweb with species of known weights that had fewer than 10 links because we wanted a 'large' sample of links in each web for the randomization test of the effect of body size, which is described below under Methods. Data set A thus consists of the 18 subwebs of community food webs listed in Table 1 and of the weights associated with each of the 262 species in these webs. From these subwebs and weights, we constructed (prey weight, predator weight) pairs for each of the 354 reported links.

Data set B

Another of us (S.L.P.) independently determined the lengths (cm) of as many as possible of the animal species in prey—predator pairs in 30 webs from a compendium of sink, source and community webs assembled by Anthony W. King & S.L. Pimm (S.L. Pimm, personal communication). Seven webs appear in both data sets A and B: those numbered 19, 23, 25, 33, 35, 38 and 39 in Table 1. The remaining 23 webs in data set B include eight webs from the Briand-Cohen collection (webs numbered 18, 24, 27, 34, 45, 67, 89, 98; see Cohen, Briand & Newman 1990 for sources) and 15 webs from other sources (Beaver 1979 [two webs]; Gardarsson 1979; Hurlbert, Mulla & Willson 1972; Kitching 1983 [two webs]; Larson *et al.* 1978; Marshall 1982; Mayse & Price 1978 [two webs]; Moriarty *et al.* 1973; Readshaw 1971; Richards 1926; Zaret & Paine 1973 [two webs]).

The lengths are best estimates based on various sources, primarily Borror, DeLong & Triplehorn (1981), Migdalski, Fichter & Weaver (1976), Stanek (1962), and Walker (1968). Lengths were used to measure body sizes because they can easily be measured from illustrations. Where a range of lengths was given, the midpoint of the range was used as the estimate. For age-specific groups of organisms, lengths appropriate to the age group were used. Sizes in data set B were determined independently of those in data set A. Data set B consists of 478 pairs giving (prey length, predator length). Each species appears as many times as it has links to other species.

Table 1. Analysis of 18 food webs with at least 10 links having predator and prey of known weight (data set A). Sources of webs are given in Cohen, Briand & Newman (1990)

Web no.	n	L	b	Upper tail	Habitat	Habitat type
2	10	11	0	1	Knysna estuary, South Africa	C
3	17	16	7	0·64	Salt-marsh, Long Island, USA	C
4	11	18	5	0·87	Salt-marsh, California, USA	C
12	10	16	2	0·96	Exposed rocky shore, Washington, USA	C
13	9	19	3	0·96	Protected rocky shore, Washington, USA	C
16	10	11	0	1	Pamlico estuary, North Carolina, USA	C
17	11	18	5	0·90	Coral reefs, Marshall Islands	C
19	14	23	2	1	Moosehead Lake, Maine, USA	A
20	14	18	3	0·99	Antarctic pack ice zone	M
21	7	17	1	1	Ross Sea	M
22	20	26	2	1	Bear Island, Spitzbergen	T
23	11	10	0	0·99	Prairie, Manitoba, Canada	T
25	15	12	2	0·94	Aspen communities, Manitoba, Canada	' T
33	26	20	1	1	Crocodile Creek, Malawi	A
35	9	15	3	0·92	Morgan's Creek, Kentucky, USA	A
37	17	22	7	0·77	Marine sublittoral, southern California, USA	M
38	26	56	2	1	Lake Nyasa, rocky shore, Malawi	A*
39	25	26	0	1	Lake Nyasa, sandy shore, Malawi	A*
Total	262	354	45			

Web no. = serial number of web in the Briand-Cohen collection (Cohen, Briand & Newman 1990).

n, number of species with known weights.

L, number of links in the subweb containing only species of known weight.

b, number of links in which a smaller predator consumes a larger prey.

Upper tail = fraction of times, in 100 random permutations, that the simulated value of b exceeded the observed value of b.

Habitat, location of study.

Habitat type: T, terrestrial; A, aquatic; C, coastal; M, marine.

* The organisms in this web were drawn only from the water offshore, not from the terrestrial boundary for which the web is named, hence the web is classified as aquatic, not coastal.

Classification of species and habitats

Species were classified according to their metabolic type as invertebrate, vertebrate ectotherm, or vertebrate endotherm. All prey–predator pairs in data set A and 468 of 478 pairs in data set B were classified according to the metabolic type of prey and predator. The habitat of each web was classified as terrestrial, aquatic (freshwater), coastal (interfacial), and marine.

Because the webs included in data sets A and B were selected independently and the sizes of the organisms were determined independently, these two data sets provide an internal control for the effects of a difference between investigators. If patterns emerge that are consistent between the two data sets, these patterns are robust in spite of the differing distribution of webs among types of habitat and the differing methods of determining body size.

Methods of analysis

Role of body size in structuring food webs

Our first goal is to assess how weight influences the partners of predator–prey pairs. If bigger species generally eat smaller ones, the number of links in which a smaller species consumes a larger species should be small. For each subweb in data set A, we counted the number of links in which a smaller species consumes a larger species; we call this number b(observed), where b indicates that the weight of the predator is below that of the prey (Table 1).

We then determined whether the observed number of links with bigger prey than predator is small compared to the number of such links that would be expected if body size played no role. For each subweb, we permuted the observed weights randomly using the algorithm RANPER of Nijenhuis & Wilf (1978, p. 62), reassigned the permuted weights to the species, and counted the number of links in which a smaller species consumes a larger species; we call this number b(simulated). We computed b(simulated) 100 times for each web, using independent random permutations of weights. We then counted the number of simulations in which b (simulated) was larger than b(observed) and divided by 100 (the number of simulations) to estimate the probability that a random ordering of species would have smaller species eating bigger ones more often than an ordering of species by weight (Table 1).

*Quantitative relation between prey body size and
predator body size*

Our second goal is to describe and interpret the
relation between prey body size and predator body
size within webs. We plotted prey body size on the
abscissa and predator body size on the ordinate for
all observed links with known prey and predator
sizes, for all subwebs in data set A combined (Fig.
1), for all links in data set B combined (Fig. 2), and
separately for each subweb in data set A. The plots
for the individual subwebs in data set A are not
shown because most subwebs did not have enough
links to form a coherent pattern.

We also computed the moments (means and
standard deviations for predator and prey separately,
and the predator−prey correlation) of the logarithm
of body size for the links of each data set (Table 2),
for each type of habitat (Table 2) and for each
combination of prey and predator metabolic type
(invertebrate, vertebrate ectotherm, vertebrate
endotherm) (Table 3). These statistics count each
species with equal weight; species are not weighted
according to their abundance.

Frequency distribution of species weights

We plotted the frequency histogram of the species
sizes. For data set A (Fig. 3, the frequency distri-
bution by weight), each species appears exactly
once. For data set B (Fig. 4, the frequency distri-
bution by length), each species appears as many
times as it is the predator or prey of any link.

Results

Role of body size in structuring food webs

Body size explains a large fraction of the ordering of

species in feeding links. The fraction of links in
which a smaller predator consumes a larger prey in
small: 13% = 45/354 in data set A, 7% = 33/478 is
data set B.

The number of links with smaller predator than
prey is much less than would be expected if the
ordering of species in webs were independent of
body size. According to Table 1, in 15 of 18 webs, at
least 90% of hypothetical webs with identical struc-
ture but randomly permuted weights would have
more than the observed number of links with smaller
predators than prey. In the other three webs, 64−
87% of hypothetical webs would have more than the
observed number of links with smaller predators
than prey. Thus, in most webs the role of size is
dominant. In no case is it small.

There is no evident pattern of association between
the relative importance of size and the type of
habitat in which the web is observed. For example,
webs observed in both marine and terrestrial habitats
are among those where all or nearly all random
permutations produced more links with smaller
consumers than prey. At the other extreme, the
four webs with the lowest 'upper tail' in Table 1
were observed in marine, terrestrial and estuarine
habitats.

*Quantitative relation between prey body size and
predator body size*

Scatter plots of predator size as a function of prey
size (Figs 1 & 2) share four principal features. First,
as already remarked, most links fall above the
straight line where predator size equals prey size.

Second, the average log(predator size) increases
with increasing log(prey size). Ordinary least squares
regression yields, for data set A, $\log_{10}$(predator
weight, g) = $0.3525 \times \log_{10}$(prey weight, g) + 2.2793,
where the standard error of the estimated slope
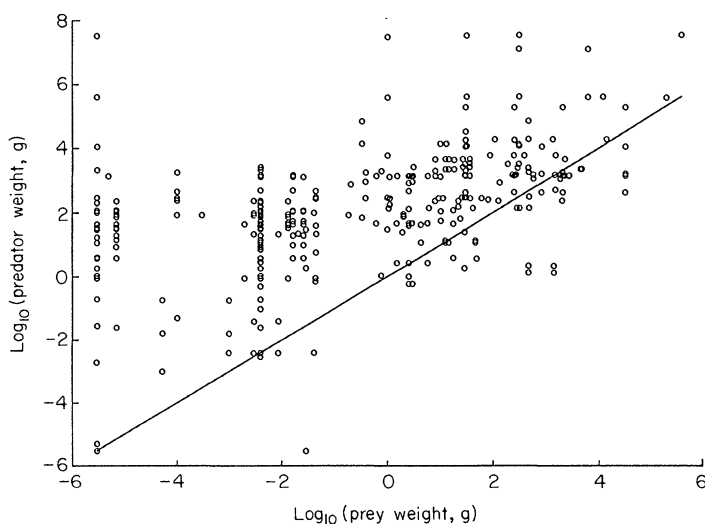
Fig. 1. $\log_{10}$(weight, g) of animal predators as a function of $\log_{10}$(weight) of animal prey for 354 links in 18 community
food webs (data set A; see text). o = one link. Solid line shows where predator weight equals prey weight.
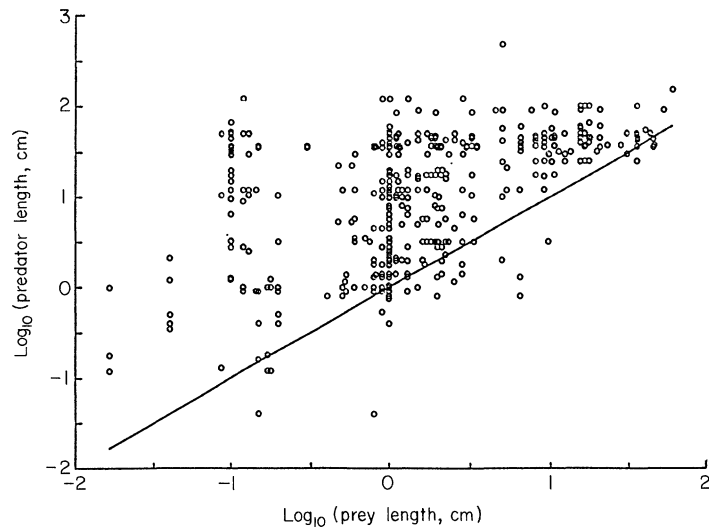
Fig. 2. Log_{10}(length, cm) of animal predators as a function of log_{10}(length) of prey for 478 links in 30 food webs (data set B; see text). o = one link. Solid lines shows where predator length equals prey length.

0·3525 is 0·0321; and, for data set B, log_{10}(predator length, cm) $= 0·4812 \times log_{10}$(prey length, cm) $+$ 0·9334, where the standard error of the estimated slope 0·4812 is 0·0411. For both data sets, the estimated slope is at least 10 standard errors greater than 0.

Third, the slope of mean log(predator size) as a function of log(prey size) is less than 1. According to the estimated regression equations, the slopes for both data sets are at least 10 standard errors less than 1. Thus, if two different sizes of prey are compared, the second larger than the first, then the geometric mean predator sizes increase by a smaller factor than the prey sizes increase. For example, if prey sizes double, the geometric mean predator sizes increase but by less than twice.

Fourth, with a few exceptions, the links are distributed over a triangle (in the plane with abscissa given by prey size and ordinate given by predator size) bounded below by the equality of predator and prey sizes, above by the maximum predator size,

and on the left by the minimum prey size. The smaller the prey size, the larger the scatter in predator sizes. The larger the predator size, the larger the scatter in prey sizes. (This observation suggests that one assumption underlying the probabilistic interpretation of ordinary least squares regression may be violated. The assumption that the standard deviation of residuals with respect to the regression line is independent of the abscissa could not be true if the data points uniformly filled a triangular region. However, the apparent heteroscedasticity as a function of the abscissa is not dramatic. The estimated slopes for both data sets A and B are so many standard errors removed from 0 and one that the inference of *a positive slope less than 1* is robust to possible small violations of the conventional assumptions of ordinary least squares regression.)

Correlates of habitat

In both data sets, in all habitats (Table 2), the

Table 2. Number of links and moments of log_{10}(body size) for prey and predators, according to habitat type. For data set A, body size is weight in g; for data set B, body size is length in cm. Data set B included no marine webs

Habitat	L	Mean		Standard deviation		Prey−predator correlation
		prey	predator	prey	predator	
Data set A						
Terrestrial	48	0·0946	2·1595	2·8205	1·9779	0·7383
Aquatic	140	−2·1415	1·3074	2·2371	1·5994	0·4028
Coastal	109	0·5286	2·2887	1·9300	1·2394	0·2278
Marine	57	1·1192	3·6695	2·8074	2·4158	0·2784
All links	354	−0·4911	2·1054	2·6993	1·8927	0·5037
Data set B						
Terrestrial	162	0·3438	0·9940	0·6997	0·8457	0·7813
Aquatic	306	−0·0021	0·9850	0·6846	0·6669	0·2774
Coastal	10	0·6854	1·3516	0·8726	0·3554	0·7957
All links	478	0·1295	0·9957	0·7159	0·7286	0·4728

L, number of links.

geometric mean size of predators exceeds that of prey by a substantial factor. The geometric mean sizes of both prey and predators increase as the habitat of webs changes from aquatic to terrestrial to coastal to marine. (Data set B includes no marine webs.) Within each type of habitat, prey and predator sizes are always positively correlated. (The null hypothesis of no correlation has probability less than 0·01 in each habitat in each data set, except for coastal and marine habitats in data set A; the probability is less than 0·05 for coastal and marine habitats in data set A.)

Correlates of metabolic type

When the links are categorized by the metabolic types of prey and predator (Table 3), there is a cascade-like ordering of types: invertebrates are not reported as eating vertebrates (except for three links in data set A), and vertebrate ectotherms are not reported as eating vertebrate endotherms, but all the reverse possibilities are commonly observed. For each type of link, the geometric mean size of predators exceeds that of prey by a substantial factor.

The sizes of prey (but not of predators) always increase as the type progresses from invertebrate to vertebrate ectotherm to vertebrate endotherm.

Prey and predator sizes are positively correlated in links from invertebrate prey to invertebrate predators. (The null hypothesis of no correlation has probability less than 0·01 in both data sets). In links with other combinations of prey and predator metabolic types, the correlation between prey and predator body sizes is rarely large when it is positive, and in some cases is even negative. Apart from the positive correlation between invertebrate prey size and invertebrate predator size, there is little consistency between the two data sets in the sign or magnitude of the correlations.

Frequency distribution of species weights

The frequency distributions of species log(sizes) (Figs 3 & 4) are unimodal, with slightly more extremely small species than extremely large species on a logarithmic size scale. As previously noted, each species appears once in data set A but as many times as it is the predator or prey of any link in data

Table 3. Number of links and moments of $\log_{10}$(body size) for prey and predators, according to metabolic types of prey and predators (invertebrate, vertebrate ectotherm, vertebrate endotherm) of prey and predators. For data set A, body size is weight in g; for data set B, body size is length in cm. Of 478 links in data set B, 468 links are classified by type here

Prey type	Moment*	Predator type					
		Invertebrate		Vertebrate ectotherm		Vertebrate endotherm	
Data set A							
Invertebrate	L	81		136		34	
	m	−1·1270†	0·5630†	−1·9551	1·7510	−1·1292	3·4326
	SD	2·1196	2·2152	2·5086	1·0407	2·4017	2·0072
	Corr	0·6835		0·3367		0·2369	
Vertebrate ectotherm	L	3		42		21	
	m			1·8661	3·3632	2·1671	3·1026
	SD			1·0470	0·5985	0·8532	2·0493
	Corr			0·3066		−0·3347	
Vertebrate endotherm	L	0		0		37	
	m					2·5350	3·4548
	SD					1·1112	1·3069
	Corr					0·7414	
Data set B							
Invertebrate	L	147		141		70	
	m	−0·2194	0·0828	−0·2040	1·2495	0·0022	1·3447
	SD	0·5424	0·4713	0·4789	0·3858	0·4728	0·2846
	Corr	0·4858		−0·0942		0·0143	
Vertebrate ectotherm	L	0		35		23	
	m			1·0517	1·6684	0·8266	1·6006
	SD			0·4891	0·3353	0·3777	0·1802
	Corr			0·0272		0·0143	
Vertebrate endotherm	L	0		0		52	
	m					1·1556	1·6295
	SD					0·2146	0·2067
	Corr					0·1843	

* L, number of links; m, mean; SD, standard deviation; Corr, correlation coefficient.
† Wherever two numbers are listed side by side, the left number describes the prey and the right number describes the predator. Here, for example, in data set A, in the 81 links where an invertebrate species eats an invertebrate species, the mean $\log_{10}$(weight, g) of the prey species is −1·1270 and the mean $\log_{10}$(weight, g) of the predator species is 0·5630.
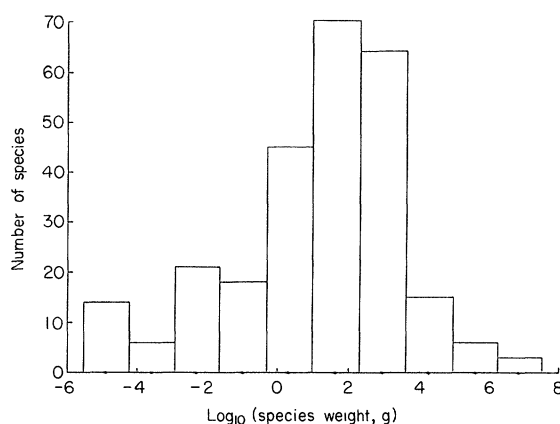
Fig. 3. Frequency histogram of $\log_{10}$(weight, g) of 262 animal species in subwebs of 18 community food webs (data set A; see text).
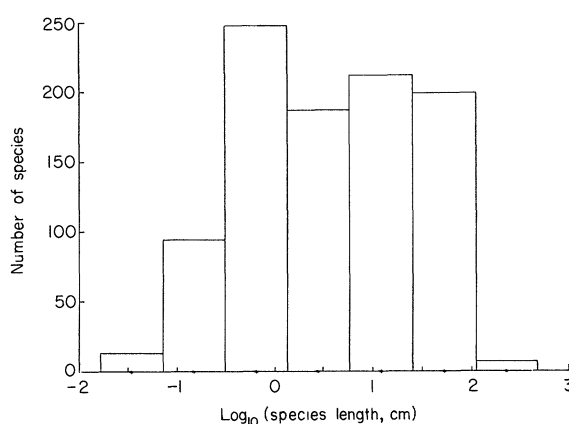
Fig. 4. Frequency histogram of $\log_{10}$(length, cm) of animal species in subwebs of 30 food webs (data set B; see text).

set B. The approximate log-normality of species sizes supports the use of the arithmetic mean of the logarithms of size (which is the logarithm of the geometric mean of the original measurements) to summarize the sizes of groups of species.

The means and the standard deviations of $\log_{10}$ (size) for all species of each data set are given in Table 4 in columns 1 and 2. In columns 3 and 4 of Table 4, these figures are converted back to the original scale of measurement by taking each figure in turn as an exponent of 10. Thus, the geometric

mean weight of the species in data set A (counting each species equally) is 10·7 g, while the geometric mean length of the species in data set B (counting each species as often as it appears as a predator or as a prey) is 3·7 cm.

Discussion

CONNECTIONS BETWEEN THE DATA SETS

The similarity in overall appearance between Figs 1 and 2 has a simple approximate explanation. Size is measured by weight (g) in data set A, by length (cm) in data set B. If each animal is approximated by a sphere of water, then weight (g) = $(\pi/6) \times \text{length}^3$ (cm^3), so $\log_{10}(\text{weight}) \approx -0·3 + 3 \times \log_{10}(\text{length})$. Under this crude approximation, the coordinates of Fig. 2 should translate roughly to the corrdinates of Fig. 1 simply by multiplying both axes of Fig. 2 by three. To a surprising extent, the translation works! More quantitatively, if one computes $W = (\pi/6)L^3$ when L is the geometric mean length of all species, of prey only and of predators only in data set B, one obtains estimated geometric mean weights of 25 g, 1 g and 508 g, which differ from the corresponding observed geometric mean weights in data set A (11 g, 0·3 g and 127 g) by considerably less than an order of magnitude.

The similarity in overall appearance between Figs 3 and 4 also has a simple approximate explanation, based in part on the previous paragraph and in part on the cascade model. This stochastic model aims to explain the large-scale patterns of feeding links in collections of food webs (Cohen, Briand & Newman 1990). The cascade model supposes that in a community of S species, the species are labelled from 1 to S in such a way that any species has a positive probability of eating any species lower in the ordering, but zero probability of eating any species higher in the ordering. Explicitly, for any two species i and j, if $j > i$, then there is a probability $p > 0$ that j eats i, i.e. there is a directed link from i to j, and a probability $1 - p$ that j does not eat i, but there is a probability 0 that i eats j, and all links are statistically independent.

The previous argument that weight is approxi-

Table 4. Mean and standard deviations of species' sizes. The entries in columns 3 and 4 are not the mean and standard deviation computed in the original scale of measurement, but rather 10 raised to the power given by the mean and standard deviation of $\log_{10}$ of the original measurements

Variable	Number of species	$\log_{10}$ of original measurement (1) m	$\log_{10}$ of original measurement (2) SD	Original scale of measurement $(3) = 10^{(2)}$ m	Original scale of measurement $(4) = 10^{(2)}$ SD
Data set A species	262	1·0308	2·5159	10·7346	328·0102
Data set B species	956	0·5626	0·8420	3·6526	6·9496

m, mean; SD, standard deviation.

mately proportional to length cubed explains why the abscissa values of Fig. 3, log(weights), should be three times the abscissa values of Fig. 4, log(lengths). Why should the frequency histograms be similar in form? Each species in Fig. 3 (data set A) is sampled once, whereas each species in Fig. 4 (data set B) is sampled as many times as it appears as a predator or prey (consumer or resource) of any link. According to the cascade model, if the probability of a link between two species is p and there are S species in the web, then each species will appear as a prey (resource) or as a predator (consumer) in $(S-1)p$ links, on the average. That is, according to the cascade model, every species has an equal chance of being represented in a random sample of links (as predator or prey), and by definition every species has an equal chance of being represented in a random sample of species. Therefore, the cascade model predicts that a sufficiently large random sample of species and a sufficiently large random sample of links will give identical frequency distributions, or histograms, of body size (apart from sampling fluctuations and apart from possible differences in scale).

Thus far the argument is exact, though it is stated informally. Now we make some approximate remarks. Unfortunately, neither the sample of species in data set A nor the sample of links in data set B can be strictly random, because plants are excluded. If the sampling of species and links were random, conditional on the exclusion of plants from the sample of species and as possible resources in the sample of links, one would expect herbivorous animals to appear relatively less often in a sample of links (such as data set B, Fig. 4) than in a sample of species (such as data set A, Fig. 3). The exact theoretical magnitude, according to the cascade model, of the difference between sampling by species and sampling by links due to the exclusion of plants requires a calculation that has yet to be done, but the similarity between Figs 3 and 4 suggests that the difference is not large.

HYPOTHESIS OF ORDERING IN THE CASCADE MODEL

Independently, and about the same time, Warren & Lawton (1987) and Cohen (1989b) suggested that the ordering of predation by body size could provide a physical basis for one previously uninterpreted hypothesis of the cascade model. They proposed that if the size (weight, length, or other quantitative measure) of species i in the cascade model is s_i, $i = 1$, $2, \ldots, S$, then $s_i < s_j$ whenever $i < j$.

Warren & Lawton (1987) were the first to provide direct evidence that the labelling posited in the cascade model could (almost) correspond to increasing body size. They carried out laboratory feeding trials combining one predator species and one prey species at a time, using all 15 common species from an acid pond community. The web they constructed had 45 links, of which six went from a longer prey species to a shorter predator species. They pointed out that 'length is not an equally good indicator of size across a range of very differently shaped species'. Moreover, feeding observed in a confined test chamber with a single species of predator and a single species of prey may not necessarily reflect feeding in nature.

Warren (1988, pp. 83–85) investigated body sizes and feeding interactions in the field, using gut contents of specimens captured from the Wash Dyke community to infer feeding. To index body size, he computed the average length over five sampling dates. For 20 taxa, he found 92 links, of which 13 were directed from a larger resource to a smaller consumer. Warren's randomizations of these data showed (p. 85) that 'the upper triangularity in the food web matrix is significantly related to size.'

These pioneering studies posed a challenge. Would their conclusions be valid for most food webs, with links observed under natural circumstances, and with sizes measured by criteria other than length? The results shown in Table 1, Fig. 1 and Fig. 2 confirm the conclusions of Warren & Lawton (1987) and Warren (1988) in every essential respect. For the great majority of food webs in the data sets assembled here, most predator–prey links involve a smaller prey species and a larger predator species, whether size is measured by length or by weight.

Nevertheless, in our data sets, as in the webs of Warren & Lawton (1987) and Warren (1988), there remains a small minority of links (about 1 in 10) from larger prey to smaller predators. As Warren & Lawton (1987) suggested, length and weight may be less than perfect measures of size, and some other variable, highly but imperfectly correlated with length and weight, could be the actual variable responsible for the ordering assumed in the cascade model. Some measures, such as mouth size, accurately measure constraints on the predator but not on the prey (P. Warren, personal communication). If some other variable is the responsible factor, it remains to be identified.

The web reported by Warren & Lawton (1987) and almost all of the webs in the Briand-Cohen collection, including the subset considered in data set A, are acyclic, as the cascade model assumes. So the possibility exists that some factor orders the animal species nearly perfectly. That factor may yet turn out to be body size, perhaps measured in some more appropriate way, such as by volume or maximal linear dimension.

Certain kinds of animal taxa are probably underrepresented in food web data, notably ecto- and endo-parasites, insect parasitoids and group hunters (see e.g. Lawton 1989a). In these cases, the individual consumers are typically smaller than their

prey. (For group hunters, the aggregate mass of the hunting group may be a more appropriate measure of size.) If such taxa were fully represented in food web data, the role of size might have to be re-examined. Moreover, plants have been completely omitted from the data assembled here, and may well complicate the patterns observed among animals.

TRIANGULAR JOINT DISTRIBUTION OF PREDATOR SIZES AND PREY SIZES

Wilson (1975) presented data to show that larger predators consume a wider range of prey sizes than do smaller predators. The data in Figs 1 and 2 confirm Wilson's finding.

Because animal predators generally consume animal prey smaller than themselves, body size provides a natural interpretation of the ordering assumed in the cascade model, at least for the animal species. With this interpretation, the cascade model provides a convenient tool to analyse the consequences of ordering trophic relations by body size. We shall now demonstrate that the physical interpretation of the cascade model in terms of body size explains three features of Figs 1 and 2 mentioned above: (1) average log(predator size) increases as log(prey size) increases; (2) the slope is less than 1; and (3) the smaller the prey size, the larger the scatter in predator sizes. We also give a simulation to illustrate all three properties.

1. Consider species i, viewed as a potential prey of all the species above it in the cascade ordering. All those species are bigger than species i according to the physical interpretation of the ordering. The probability that species j eats species i is p if $j > i$, so the average log(size) of species that eat i (μ_i) is

$$\mu_i = \frac{p \, \log(s_{i+1}) + \ldots + p \, \log(s_s)}{p(S - i)}$$

$$= \frac{\log(s_{i+1}) + \ldots + \log(s_s)}{(S - i)}, \qquad 1 \leq i < S.$$

As i increases, the species with smaller sizes are successively omitted from the numerator on the right, so the average size increases. This proves (1). Since a positive regression slope is equivalent to a positive correlation, the cascade model predicts the sign of the positive correlations shown in Table 2, assuming that the cascade model applies to all habitats. (The cascade model is silent, or neutral, regarding the signs of the correlation coefficients in Table 3, because the model makes no explicit assumptions about the trophic roles of the three metabolic types.)

2. The slope of average log(predator size) as a function of log(prey size) depends on the frequency distribution of species by body size. In the Appendix, we derive a general formula (A1) for the derivative of the mean log(size) of the predators of a given prey species as a function of the log(size) of the prey species, in the limit as the number of species in the web becomes large. We show that this derivative is 1/2 when log(size) is uniformly distributed between 0 and 1, is 1 when log(size) is exponentially distributed, and is less than 1 in the realistic case when log(size) is normally distributed. This proves (2).

3. Finally, according to the cascade model, the possible predators of species i range from species $i + 1$ to species S, and the actual predators are uniformly distributed over this possible range, so the smaller species i (that is, the smaller its label i), the bigger is the expected range in size of its predators. This proves (3).

The following simulation illustrates properties (1), (2) and (3) listed above. Based on Figs 3 and 4, the simulation supposes that the weights of species are log-normally distributed (Aitchison & Brown 1957), i.e. that the log(weights) are normally distributed. Further, in the simulation, the mean and the standard deviation of the normal distribution of log(weights) are set equal to those observed for data set A, namely, 1·0308 and 2·5159, respectively.

For each web listed in Table 1, we constructed a simulated web with a number n of animal species equal to the number reported in Table 1 (which is the number with known weight). We assigned feeding relations according to the cascade model by constructing an $n \times n$ matrix with all elements 0, then independently changing each element above the main diagonal to 1 with a probability $p = L/[n(n - 1)/2]$ chosen so that the expected number of links $pn(n-1)/2$ would just equal the observed number L of links. We chose n random variates $x_1, \ldots, x_n$ from the above normal distribution of animal $\log_{10}$(weights), sorted them in increasing order $x_{(1)} < x_{(2)} < \ldots < x_{(n)}$ (the parentheses around the subscripts indicate 'smallest,' 'second smallest', and so on), and assigned species i the weight $10^{x_{(i)}}$ g. We then tabulated the pairs (log(prey weight), log (predator weight)) for all links in the simulated web: if the element in row i and column j of the simulated food web matrix had been changed to 1 (which occurred with probability p), then one simulated pair of $\log_{10}$(weights) was $(x_{(i)}, x_{(j)})$.

After carrying out this calculation for all 18 webs in Table 1, we plotted the pairs (log(prey weight), log(predator weight)) for all webs together in Fig. 5, exactly as we did for the real webs of data set A. The properties (1), (2) and (3) of the real data sets in Figs 1 and 2 are clearly evident in Fig. 5.

Conclusions

Measurements of the body sizes (weights or lengths) of animal species found in the food webs of natural communities from a variety of habitats show that about 90% of the feeding links among the animal species with known sizes involve a larger predator consuming a smaller prey. Body size or some variable
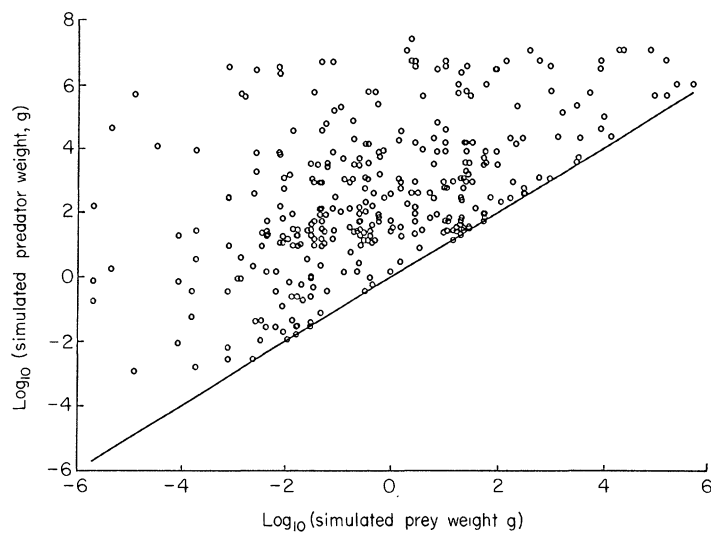
Fig. 5. Log_{10}(weight, g) of animal predators as a function of log_{10}(weight) of animal prey in 18 simulated community food webs. o = one simulated link. Solid line shows where predator weight equals prey weight.

highly correlated with it is far more closely associated with the direction of predation among animals in nature than could be accounted for by chance alone.

Body size may be a good (though not perfect) interpretation of the ordering of animal species assumed in the cascade model, a stochastic model of food web structure. When body size is taken as the physical interpretation of the ordering assumed in the cascade model, and when the body sizes of different animal species are taken as log-normally distributed, many of the empirical findings can be explained in terms of the cascade model.

This work is a step towards integrating food webs with the rest of ecological theory (Cohen 1991). An obvious next step is to connect food web structure and body sizes with species abundances (e.g. Morse, Stork & Lawton 1988; Lawton 1989b; Blackburn, Harvey & Pagel 1990).

Acknowledgements

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Appendix

The aim of this Appendix is to give a general formula for the derivative of the mean log(size) of the predators of a prey species as a function of the log(size) of the prey species in the cascade model, then to prove that this derivative is less than one when the log(size) of species is normally distributed.

Let the number of species be so large that we may assume that the logarithm x of body size has a smooth probability density function $f(x)$, i.e. for $a < b$,

$$\text{Prob}\{a \le x \le b\} = \int_a^b f(x)\,dx.$$

Let $\mu(z)$ be the average log(size) of predators that eat a prey species when the log(size) of the prey species is equal to z. According to the cascade model, all species larger than z are equally likely predators on a prey of log(size) equal to z, so

$$\mu(z) = \frac{\displaystyle\int_z^\infty x f(x)\,dx}{\displaystyle\int_z^\infty f(x)\,dx} \equiv \frac{H(z)}{G(z)},$$

where we define

$$H(z) = \int_z^\infty x f(x)\,dx, \qquad G(z) = \int_z^\infty f(x)\,dx.$$

Then

$$\mu'(z) \equiv \left[\frac{d\,\mu(x)}{dx}\right]_{x=z} = \frac{G\,H' - H\,G'}{G^2}$$

$$= \frac{(\mu(z) - z)f(z)}{G(z)}. \qquad\qquad \text{eqn A1}$$

This last expression is easy to evaluate when f is uniform or exponential, cases which are unfortunately unrealistic. In the uniform case, if $f(x) = 1$ on $[0, 1]$ and $f(x) = 0$ elsewhere, then $\mu'(z) = 1/2$ on $[0, 1]$. In the exponential case, if $f(x) = e^{-x}$ on $[0, \infty)$, then $\mu'(z) = 1$ on $[0, \infty)$.

When body sizes are log-normally distributed, we standardize $\log(\text{size})$ x to have standard deviation equal to 1 so that $f(x) = Ce^{-x^2}$, where $C = \pi^{-1/2}$. Then

$$H(z) = \int_z^\infty Cxe^{-x^2}dx = -(C/2)\int_z^\infty d(e^{-x^2}) = (C/2)e^{-z^2}.$$

Hence

$$\mu(z) = \frac{1}{2}\frac{e^{-z^2}}{\int_z^\infty e^{-x^2}dx}.$$

Then $\mu'(z) < 1$ if and only if

$$\mu'(z) = \frac{1}{2}\frac{-2ze^{-z^2}\left(\int_z^\infty e^{-x^2}dx\right) + e^{-z^2}e^{-z^2}}{\left(\int_z^\infty e^{-x^2}dx\right)^2} < 1$$

or

$$F_1(z) := 2e^{z^2}\left(\int_z^\infty e^{-x^2}dx\right)^2 + 2z\int_z^\infty e^{-x^2}dx - e^{-z^2} > 0.$$

Now our goal is to prove that $F_1(z) > 0$ for all real z. We consider two cases: first, $z \in [0, \infty)$, then $z \in (-\infty, 0)$. To see that $F_1(z) > 0$ for $z \in [0, \infty)$, observe that

$$F_1(0) = 2\left(\int_0^\infty e^{-x^2}dx\right)^2 - 1 = 2\left(\frac{1}{2}\int_{-\infty}^\infty e^{-x^2}dx\right)^2 - 1$$

$$= \frac{1}{2C^2} - 1 = \frac{\pi}{2} - 1$$

and $F_1(\infty) = 0$ because

$$\lim_{z\to\infty} e^{z^2}\left(\int_z^\infty e^{-x^2}dx\right)^2 = \lim_{z\to\infty}\frac{\left(\int_z^\infty e^{-x^2}dx\right)^2}{e^{-z^2}}$$

$$= \lim_{z\to\infty}\frac{\int_z^\infty e^{-x^2}dx}{z} = 0,$$

where the second equality uses l'Hôpital's rule. So $F_1(z) > 0$ if $F'_1(z) < 0$ on $[0, \infty)$. Taking the derivative of $F_1(z)$ gives

$$F_1'(z) = 4ze^{z^2}\left(\int_z^\infty e^{-x^2}dx\right)^2 - 2\int_z^\infty e^{-x^2}dx.$$

So $F_1'(z) < 0$ if and only if

$$2z\int_z^\infty e^{-x^2}dx < e^{-z^2}. \qquad\qquad \text{eqn A2}$$

If we define

$$F_2(z) := e^{-z^2} - 2z\int_z^\infty e^{-x^2}dx,$$

then $F_2(0) = 1 > 0$ and $F_2(\infty) = 0-0 = 0$, so it suffices to show that $F_2'(z) < 0$ on $[0, \infty)$. But

$$F_2'(z) = -2ze^{-z^2} - 2\int_z^\infty e^{-x^2}dx + 2ze^{-z^2}$$

$$= -2\int_z^\infty e^{-x^2}dx < 0$$

for all z. Hence $F_2(z)$ is a decreasing function that tends asymptotically to 0 as $z\to\infty$, and therefore $F_2(z) > 0$ for all $z \in [0, +\infty)$. Hence $F_1'(z) < 0$ and $F_1(z) > 0$ on $[0, \infty)$. This proves $\mu'(z) < 1$ on $[0, \infty)$.

Now consider $z \in (-\infty, 0)$. In a similar way, it can be shown that $F_1(z) > 0$ for all $z < 0$ and that $F_1(-\infty) = +\infty$. Then eqn A2 obviously holds because the left side on eqn A2 is negative while the right side is positive. Since $F_1(0) = \pi/2-1 > 0$, it follows that $F_1(z) > 0$ everywhere, and hence $\mu'(z) < 1$ for all z.

The formulas above assume that the probability that any predator eats a given prey is the same for all the predators which eat that prey. The formulas are therefore independent of that probability, even if that probability is different from one prey to another. Thus, the formulas are valid for all generalizations of the cascade model where the predation probability is determined by the prey, including all the so-called 'prey-dominant' and superlinear homogeneous models considered by Cohen (1990).