

## Chapter 8

# PREDATOR–PREY RELATIONS AND FOOD WEBS

Owen L. Petchey and Jennifer A. Dunne

### SUMMARY

**1** This chapter addresses how knowledge of the body sizes of prey and predators can augment understanding of feeding (“trophic”) interactions among individuals, and the structure and dynamics of complex food webs.

**2** Foraging characteristics of individuals, such as visual acuity and movement speed, can be combined with population-level allometries to predict how frequency of feeding depends on prey and predator body sizes.

**3** Body sizes of prey and predators have long been thought to structure food webs. Cutting-edge models can tell us the types of food webs and interactions that are well predicted by organismal sizes, and conversely when other traits need to be considered and modeled.

**4** Results of population dynamic models show how constraints placed by body size on metabolic rates and interaction strengths can allow otherwise unstable complex food webs to persist.

**5** Situations in which body size appears not to influence trophic relations and food webs may have diverse causes. Ontogenetic diet shifts and averaging of sizes can obscure effects of individual size. Some interactions seem not to depend on size.

**6** Body size has fundamentally important effects on individual interactions, food web structure, and food web dynamics. Effects specific to particular taxonomic groups and ecosystem types are unclear at present, but systematic quantitative analyses are emerging. More will be required to fully understand the trophic consequences of metabolism.

### 8.1 INTRODUCTION

The metabolic theory of ecology (MTE) concerns how body size and temperature affect the metabolic rate of individual organisms, and the ramifications for population-, community-, and ecosystem-level processes and

patterns (Brown et al. 2004). This chapter focuses on explanations of community-level patterns, in particular the structure, dynamics, and stability of networks of trophically interacting species. Trophic interactions and food webs have occupied a prominent place in ecological research, partly because consumption has been

*Metabolic Ecology: A Scaling Approach*, First Edition. Edited by Richard M. Sibly, James H. Brown, Astrid Kodric-Brown.  
© 2012 John Wiley & Sons, Ltd. Published 2012 by John Wiley & Sons, Ltd.

one of the most studied types of interspecific interactions (e.g., Elton 1927; Holling 1959; Emlen 1966; MacArthur and Pianka 1966; Root 1967; Schoener 1971; Luckinbill 1973; Hassell et al. 1976; Cohen 1977; Holt 1977; Pimm and Lawton 1977; Paine 1988; Polis 1991). Consumption is also one of the most obvious, easiest to document, and important interactions for both ecological and evolutionary dynamics.

One of the most influential mathematical theories in ecology, the complexity–stability theory proposed by May (1972), concerns how population stability is related to three properties of food webs: the number of species, the number of interactions, and the average strength of interaction. May’s theory suggests that large complex food webs should be unstable, and challenged ecologists to discover the processes that stabilize the diverse food webs that persist in many natural ecosystems (McCann 2000). As well as addressing May’s rather theoretical challenge, studies of food webs have demonstrated that food web properties, such as connectance, are important determinants of responses to environmental change and species extinction (Dunne et al. 2002; Paine 2002). Thus, an understanding of the processes that govern the structure and stability of food webs has the potential to inform about how ecological communities have responded to and will respond to a rapidly changing world (e.g., Petchey et al. 1999; Montoya et al. 2006; Bukovinszky et al. 2008; Harmon et al. 2009; Woodward et al. 2010a).

The general importance of body size in determining the structure of food webs was recognized by Elton (1927), who observed that predators are usually larger than their prey. This chapter can be considered a review of recent advances that explore and elaborate on Elton’s observations. The first section, on trophic relations, considers how the size of two individuals affects whether or not one eats the other. The following section, on food web structure, discusses how body size, through its effect on trophic interactions, affects food web structure. Finally, in the section on food web dynamics and stability, we explore how the effects of body size on trophic interactions influence the dynamic stability of complex food webs. Thus, the three main sections describe how effects of body size trickle (or flood) up through levels of ecological organization from individuals, to interactions, to whole networks (Fig. 8.1).

Throughout this chapter we provide pertinent examples, but due to limited space we cannot under-

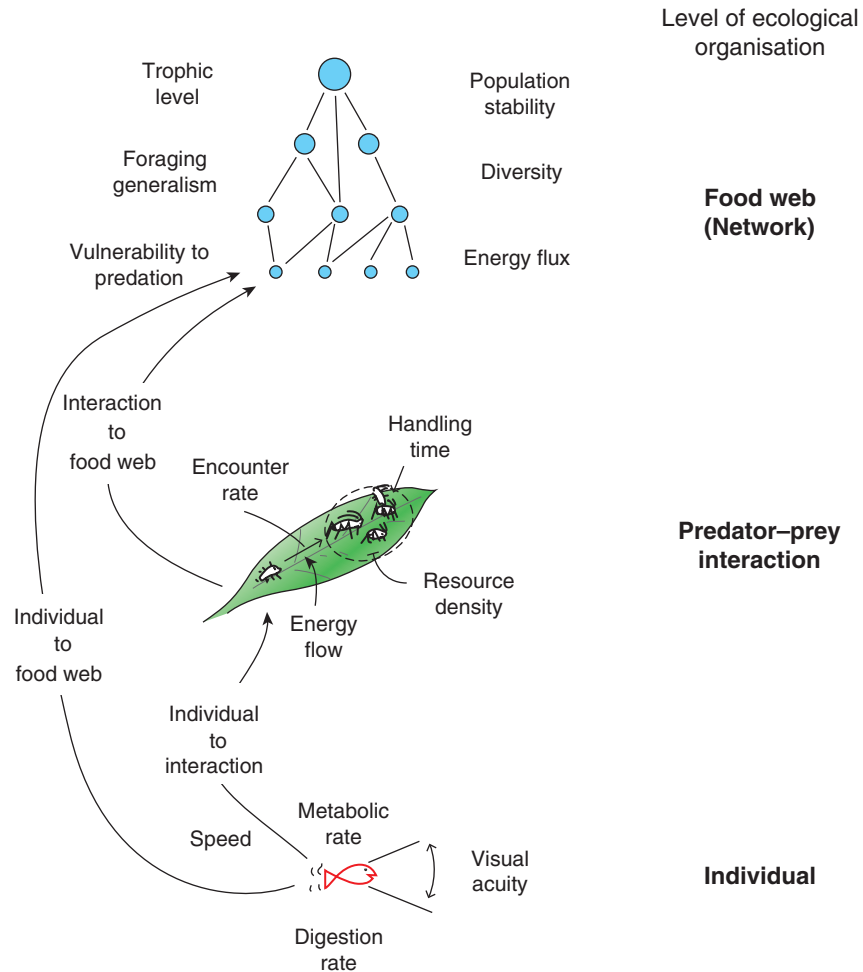
take a comprehensive review. For further examples and discussion we recommend, as a beginning, reviews such as Warren (2005), Woodward et al. (2005a), Dunne (2005), Bersier (2007), Raffaelli (2007), Brose (2010), Stouffer (2010), Petchey et al. (2010b), and Yvon-Durocher et al. (2011a). We use the terms predator and prey throughout, rather than the more generic terms consumer and resource, as most body-size related research thus far has focused on traditional predator–prey interactions, such as fish eating other fish, fish eating zooplankton, or aquatic insect larvae eating other smaller invertebrates. While many of the patterns and concepts we discuss may equally apply to other consumer–resource interactions, such as some types of aquatic herbivory where phytoplankton are eaten by zooplankton and small invertebrates, they will apply less to others, such as uptake of resources by plants (see Enquist and Bentley, Chapter 14) and parasitism (see Hechinger, Lafferty, and Kuris, Chapter 19).

## 8.2 TROPHIC RELATIONS

The fundamental building blocks of food webs are the links formed when one individual consumes another, for example an individual bat eating a moth, or a ladybird larva eating an aphid (Fig. 8.1). These trophic links are fundamentally metabolic, since they represent the channels along which energy and materials flow. Components of these interactions, such as encounter, capture, handling, and digestion rates, scale with body size. These properties of trophic links make possible a number of approaches for a metabolic and size-oriented research.

### 8.2.1 Metabolic requirements

Consumption must satisfy energy and mass balance; for example, the metabolic requirements of an individual multiplied by the trophic transfer efficiency gives the energy needed from its prey. Dividing this by the energy content of each resource gives the “killing rate” (number of prey eaten per time) required to sustain metabolism, which can be related to prey size and predator metabolic rate (Peters 1983). A similar approach uses individual body size to give metabolic rate which, multiplied by the trophic transfer efficiency, gives required daily ingestion rate of an individual, which gives required killing rates (Emmerson et al.

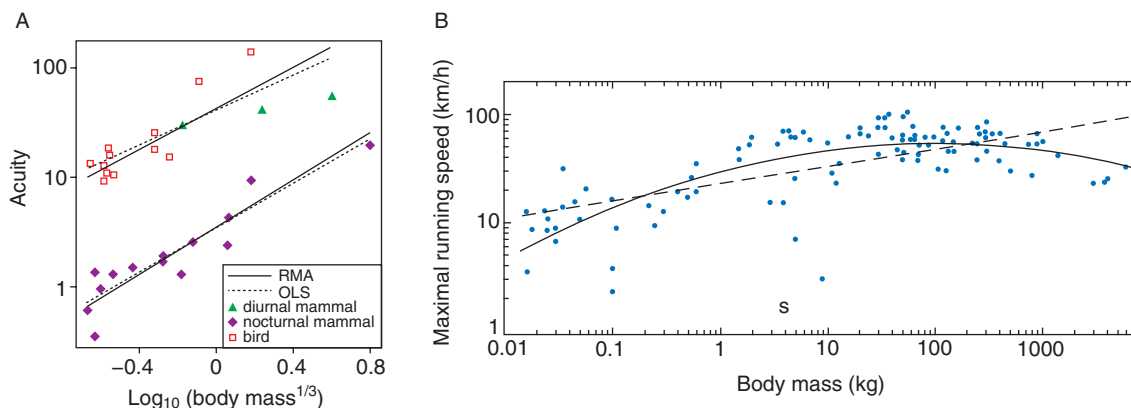


**Figure 8.1** Food webs are composed of individuals and the trophic interactions among them. Their structure, dynamics, and response to perturbations depend on characteristics of the individuals within them, such as size, movement rate, visual acuity, and digestion rate, and also properties of interactions between pairs of individuals, such as handling times and attack rates. The scaling with body size of characteristics of individuals and interactions places considerable constraints on the structure, dynamics, and response to perturbations exhibited by models of ecological networks. We illustrate fish at one level and insects at another to suggest that the allometric scaling of foraging traits is not limited to aquatic organisms or ecosystems.

2005). Simple calculations such as these, based on the fundamental metabolic nature of consumption, can be very powerful. For example, these killing rates can be transformed into various measures of per-capita interaction strength and energy flow, and thus estimates of strengths that can explain the stability of complex food webs (de Ruiter et al. 1994; Neutel et al. 2002).

### 8.2.2 Foraging trait allometries

Killing or consumption rates can also be explored using a more bottom-up approach, by breaking consumption down into a chain of events (e.g., Gergs and Ratte 2009). First a predator must encounter its prey. The frequency with which it does so depends at least on the



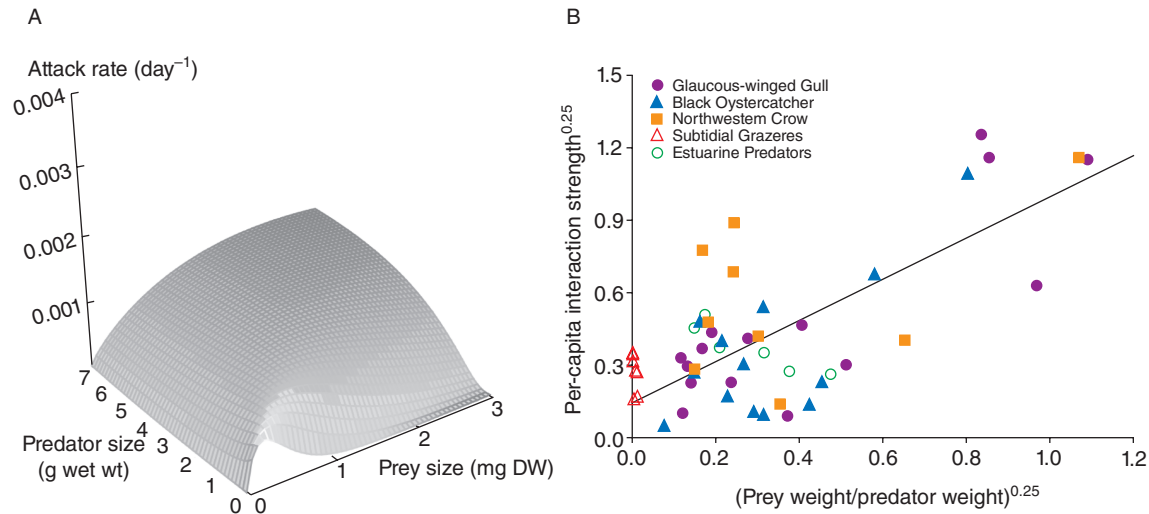
**Figure 8.2** The scaling of individual foraging relevant traits with body size. (A) The distance over which organisms can detect or perceive a prey individual depends on body size. (Reproduced from Kiltie 2000 by permission of John Wiley & Sons, Ltd.) (B) Running speed of mammals increases with body size, at least up to an optimum size, and then decreases. (Reproduced from Garland 1983a.) (Also see appendix VIb in Peters 1983.)

density of individuals of the prey species and the predator's ability to detect a prey individual. Population density scales negatively with individual size, such that smaller individuals are generally more common in an area than larger individuals (White et al. 2007; Reuman et al. 2008). Smaller prey individuals may, however, be harder to detect than larger ones, as a result of access to more, smaller, hiding places. These effects of body size will to some extent compensate for each other, and reduce the effect of prey size on the rate at which they are encountered. (Note that considerable care is required when mathematically defining encounter rates; for example, some definitions include capture success, which will also depend on predator and prey size (Brose 2010).) Thus, two allometries, one about a population characteristic (density of prey) and one about an individual characteristic (visibility of prey to predators), can be combined to predict the effect of prey sizes on encounter rate, an important component of predator-prey interactions.

Characteristics of predator individuals, including their body size, will also affect encounter rates via their effect on the ability to detect prey individuals. McGill and Mittelbach (2006) provide a simple geometric model of encounter rates as a function of prey size and predator size. In their model a predator's ability to detect prey individuals is influenced by its visual acuity, which scales positively with body size (Kiltie 2000). Visual acuity determines the distance at which a prey

of a particular size can be detected or encountered (i.e., reactive distance; Brose 2010) (Fig. 8.2A). The speed at which organisms move also scales positively with size at least up to an optimum (Fig. 8.2B), hence larger predators can search an area for prey faster than smaller predators (Garland 1983b; Andersen and Beyer 2006). McGill and Mittelbach's model predicts that encounter rate scales positively with both predator and prey size. They provide three tests of the predictions of the model, all focused on data from predatory fish. First, the model predicts correctly the observed functional form of the relationship between encounter rate and body size. Second, the model correctly predicts lower importance of predator size and greater importance of prey size in more complex habitats. Finally, the model makes good numerical predictions of observed intraspecific variation in encounter rates, with  $r^2 = 0.69$ . Although the model is based on fish foraging in open water and has only been tested with intraspecific data, these results are encouraging. It seems possible that encounter rates can be predicted using allometric relationships and relatively simple mathematical assumptions.

Many additions could be made to increase the realism (and complexity) of this type of model. One is an effect of prey and predator size on the likelihood that a predator can successfully capture a prey individual. A small predator may have a hard time subduing a prey individual larger than itself, and a large



**Figure 8.3** The scaling of interactions with predator and prey size. (A) Larger predators attack prey more frequently, all else being equal, though very large predators may be less likely to capture very small prey, leading to a humped relationship between successful encounter rate and predator size. (Reproduced from Aljetlawi et al. 2004 by permission of John Wiley & Sons, Ltd.) (B) Per-capita interaction strengths (the log-ratio measure of interaction strength,  $\log(\text{resource abundance in presence of consumer}/\text{abundance in absence of consumer})/\text{consumer abundance}$ ) scale positively with predator–prey size ratio. (Reproduced from Wootton and Emmerson 2005, copyright 2011 Annual Reviews.)

predator may have trouble handling a very small prey (filter feedings excepted). These ideas predict a hump-shaped scaling of capture success with both predator and prey size (Weitz and Levin 2006), and Brose (2010) provides numerous examples of hump-shaped scalings (e.g., Fig. 8.3A). Brose points out that these hump-shaped scalings of capture success (and hence encounter and attack rates) are consistent with Elton's observation that there is an optimum size of food usually eaten. Therefore documenting and integrating the allometries of vision, locomotion, abundance, and capture success can provide predictive models about whether and how often predator–prey interactions occur (Gergs and Ratte 2009; Hayward, Gillooly, and Kodric-Brown, Chapter 6).

Another addition would be to tackle the scaling of handling times, defined in foraging theory as the component of foraging time spent consuming and not searching. One can easily imagine that handling time increases with prey size and decreases with predator size. There are, however, few if any datasets about interspecific variation in handling times (Petchey et al. 2008a; Rall et al. 2011). Furthermore, the concept itself may be difficult to operationalize due to the many

biological processes that can influence handling times (e.g., biomechanics, ingestion rate, egestion rate, and digestion rate).

### 8.2.3 Predator–prey size ratios

In addition to this first-principle, bottom-up approach, one can observe allometries of trophic interactions directly. For example, the empirical relationship between mean prey size and mean predator size across various mammal, bird, lizard, and amphibian taxa indicates that predators eat prey with 0.2 to 10% of their body size, and that prey body size scales with predator size with an exponent of about 1.17 (i.e.,  $M_{\text{prey}} \propto M_{\text{predator}}^{1.17}$ ). Many other near-linear predator–prey size scaling relationships have been documented (e.g., Vezina 1985; Warren and Lawton 1987; Cohen et al. 1993; Memmott et al. 2000; G. C. Costa 2009; Brose et al. 2006a). A recent compilation of predator–prey size ratios supports these findings, but also indicates an exponent of less than 1 in stream communities (i.e., prey of large predators are relatively small; Riede et al. 2011). A recent compilation of prey and predator

(mostly fish and squid) sizes goes one step further, by reporting the observed body sizes of interacting individuals (Barnes et al. 2010), rather than mean values for interacting populations. The allometry results from these two approaches can differ (Woodward and Warren 2007), as a result of intraspecific (often ontogenetic) size variation and phenomena such as the smallest individuals of the predator species not eating the largest individuals of the prey species (also see Isaac, Carbone, and McGill, Chapter 7). A focus on individuals' body sizes indicates that, in most cases, prey become relatively smaller as predator size increases (i.e., predator–prey body-size ratios increase with predator body size). (Though the opposite seems to be true of terrestrial carnivores; Vezina 1985.) This leads to the prediction that trophic transfer efficiency (production of predators divided by production of prey) decreases with increasing predator size (Barnes et al. 2010), an example of how one foraging allometry can make predictions about another (also see Jennings, Andersen, and Blanchard, Chapter 21; Hechinger, Lafferty, and Kuris, Chapter 19).

Predator–prey size ratios might represent a shortcut for estimating interaction strengths. Wootton and Emmerson (2005) reported scalings of per-capita interaction strengths with predator–prey size ratios for avian predators, subtidal grazers, and estuarine predators (Fig. 8.3B). These findings have been somewhat corroborated in a recent study (O’Gorman et al. 2009). Very recent studies of feeding rates confirm effects of both size and taxonomic identity (Rall et al. 2011). At present the causes of this interspecific variation in the allometries of interaction strength are poorly understood.

### 8.2.4 Other consumer–resource interactions

The bulk of research on allometries of feeding relationships has focused on a particular type of predator, sometimes termed “true predators” or carnivores. Herbivores, parasites, parasitoids, pathogens, and other types of consumer exhibit different allometries (e.g., see Hechinger, Lafferty, and Kuris, Chapter 19). For example, the sizes of emerging parasitoids are strongly positively related to aphid host size, with an allometric scaling exponent close to 0.75 for primary, hyper- and mummy parasitoids (Cohen et al. 2005). The foraging allometries of the full range of consumer–

resource types needs to be documented and modeled with the same detail as more classic predator–prey relationships reviewed here.

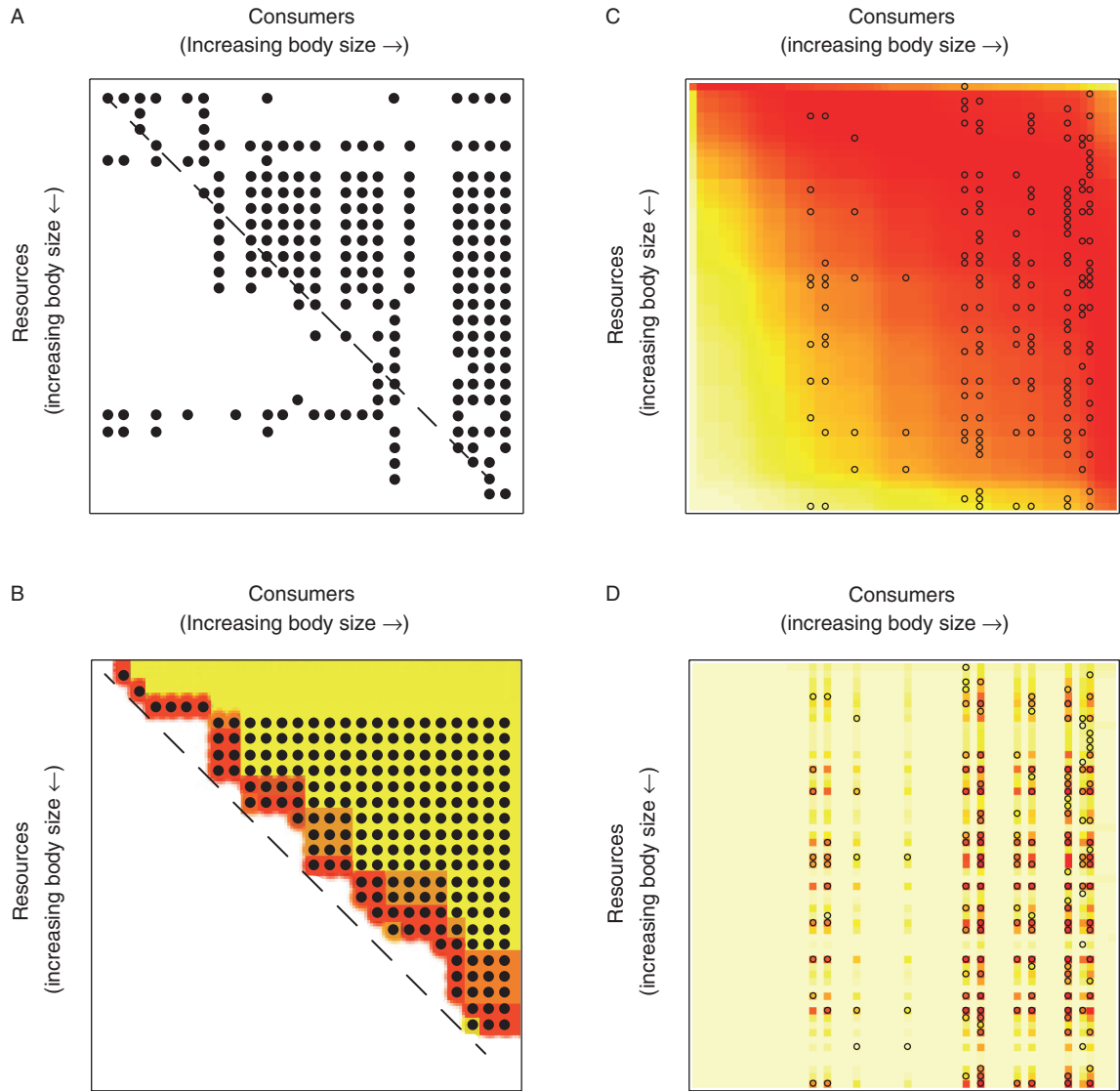
## 8.3 FOOD WEB STRUCTURE

Food webs characterize complex networks of trophic interactions among large numbers of co-occurring species. When visualized as species (nodes) connected by trophic links (lines) representing energy and material flow due to food consumption, food webs can appear overwhelmingly complex. However, careful presentation and analysis can make sense of this apparent complexity, revealing structural regularities and organizing principles (Fig. 8.4A).

Investigating “community-level” allometries is one method for revealing such regularities. For example, one can examine how trophic level, generalism (richness or diversity of prey of a species), and vulnerability (richness or diversity of predators of a species) vary with its average body size. Trophic level of predators has been observed to increase with body size (Riede et al. 2011; Romanuk et al. 2011), and to also show no consistent pattern (Layman et al. 2005). Foraging generalism tends to increase with size of predator, and vulnerability to predation to decrease with predator size (Digel et al. 2011). These (and other) community-level allometries are reviewed in Yvon-Durocher et al. (2011a), Jennings, Andersen, and Blanchard (Chapter 21) and Isaac, Carbone, and McGill (Chapter 7). Rather than re-review these empirical patterns, we will discuss how such patterns may emerge from interspecific variation in body size.

### 8.3.1 The cascade, niche, and related food web models

Very simple models have been used to generate food-web-like network structures representing the feeding relationships among species. One of the earliest and simplest models of food web structure, the cascade model, ranked species along an arbitrary axis, and allowed them to feed only on species with lower rankings (Cohen et al. 1990). More recent variations include the niche model (Williams and Martinez 2000), the nested hierarchy model (Cattin et al. 2004), and generalized versions of the cascade model (Stouffer



**Figure 8.4** Examples of when body size more or less explains who eats whom in ecological networks. Each panel shows a network in the form of a predation matrix. Consumers are in columns and are ordered by body size from left to right. Resources are in rows and are ordered by body size from top to bottom. Feeding interactions are indicated by a black circle. Thus, for example, a consumer's diet is given in a column of the matrix. (A) The observed interactions of Coachella Valley food web (Polis 1991) and (B) the predicted interactions based on a deterministic model of allometric foraging behavior and optimal foraging theory. (Reproduced from Petchey et al. 2008a by permission of the National Academy of Sciences.) (Darker colors indicate a more energetically profitable interaction.) (C) and (D) both show observed interactions (black circles) in a laboratory-based food web – “Sheffield” in the supplementary material of Rohr et al. 2010). Darker reds indicate the predictions of models, so that coincidence of black circles and dark red indicates good prediction. (C) Interactions are poorly predicted by body size. (Reproduced from Rohr et al. 2010 by permission of University of Chicago Press.) (D) Inclusion of traits other than body size greatly increases predictive power. (Reproduced from Rohr et al. 2010 by permission of University of Chicago Press.)

et al. 2005), all of which do a remarkably good job of generating networks that have structure similar to that observed in food webs from a variety of habitats.

These somewhat more complicated models retain the cascade model's ranking of species on a one-dimensional axis, with predator species feeding mostly on species with lower ranks. Subsequent analyses of the structure of food webs have revealed that species and their diets can be closely mapped onto a single dimension (Stouffer et al. 2006). It has been repeatedly suggested that this single dimension may correspond to body size. Indeed, as section 8.2.3 reviews, it has been empirically observed that non-parasite predators tend to feed on organisms smaller than themselves, which would result in a feeding hierarchy in a food web. Also, predators tend to feed on prey within a certain body-size range (Stouffer et al. 2011; Zook et al. 2011), which corresponds to the feeding niche concept embodied in the niche model (Williams and Martinez 2000; Stouffer et al. 2006) but not the other models. Thus, body size appears related to both the hierarchical and niche structuring of empirical food webs.

### 8.3.2 Size-based food web models

The models mentioned above are simple and do not include body size explicitly. Since the probability of feeding can depend on the sizes of the potential predator and prey, this may be useful to include in more realistic models. This type of model can be fit to observed data about food web structure and species body sizes, and provides a measure of how well the model can explain the data. The fitting procedure is similar in principle to fitting a power-law equation to the relationship between metabolic rate and body size. Such models could be termed “allometric food web structure models.” (Allometric food web dynamics models will be discussed in section 8.4.) Rohr et al.'s (2010) allometric food web structure model (of many of the same empirical food webs) displayed quite variable explanatory power; at worst it predicted 2.9% of trophic links correctly, and at best 49%. However, it only includes three parameters so is quite parsimonious.

More complex models are of course possible! For example, one can first translate predator and prey sizes into encounter rates, handling times, and ener-

getic contents. These traits can then be fed into models of diet choice, such as the contingency model of optimal foraging, to produce a prediction of which of the available prey species a predator species will feed upon (Emlen 1966; MacArthur and Pianka 1966). Such a model of the structure of 15 empirical food webs found that from about 5% to 65% of the trophic links were successfully predicted (e.g., Fig. 8.4B) (Petchey et al. 2008a; Thierry et al. 2011). More phenomenological models (e.g., Allesina 2011) have similar explanatory power and it remains to be seen whether optimal foraging is really necessary for predicting food web structure, or whether simpler phenomenological models are just as predictive and useful (Petchey et al. 2011). Furthermore, trade-offs between time spent foraging and on other activities may be important (see Hayward, Gillooly, and Kodric-Brown, Chapter 6).

### 8.3.3 Hybrid models

Other approaches for testing the importance of body size for food web structure are combinations of the two general approaches outlined above. For example, the “probabilistic niche model” (Williams et al. 2010) fits the three parameters of the niche model (Williams and Martinez 2000) for each species in order to maximize the match between predicted and observed food web structure. An allometric version of this probabilistic model reproduces fewer links correctly than a non-allometric version, but at the benefit of having 29 fewer parameters estimated.

### 8.3.4 Does size explain food web structure?

The results of these modeling exercises suggest that sometimes body size strongly explains food web structure, and other times it does not. This is not simply a consequence of the common perception that aquatic food webs are size structured, and terrestrial food webs are not. Indeed, size provides a very good explanation of the structure of a terrestrial food web of plants, insects, arachnids, and other predators, in the Coachella Valley (Polis 1991; Petchey et al. 2008a) (Fig. 8.4B). Two terrestrial food webs were, however, quite rather poorly predicted, though this is probably



because they are dominated by host–parasitoid interactions, for which the contingency model of optimal foraging is inappropriate.

Another surprise was the relatively poor ability (~40% of links correctly predicted) of the model to explain the structure of the Broadstone Stream food web (a food web containing macroinvertebrate predators). Interactions in this food web are known to be extremely size-dependent (Woodward et al. 2005b). However, if the Broadstone food web is recompiled by size only, ignoring individuals' taxonomic identity, the model was then able to predict over 80% of the trophic links correctly. The model failed to predict the taxonomic version because aggregation of individuals into species ignored large ontogenetic changes in body size and diet. Hence, the use of individual- versus population-level data can fundamentally alter our understanding of body-size effects on food web structure (Werner and Gilliam 1984; Woodward and Warren 2007; Woodward et al. 2010b; Yvon-Durocher et al. 2011a). More generally, we must carefully ensure that assumptions of our models are not violated by the data we test them against.

Differences in the explanatory power of size-based foraging could have at least two other sources. First, organismal traits other than size may determine who interacts with whom. For example, herbivorous insects may be more limited by plant chemical defenses than by some measure of plant size. Rohr et al. (2010) were able to greatly increase the explanatory power of their food web model by allowing each species to be represented by its body size and two other traits (Figs 8.4C, D). These other traits, related to phylogenetic differences, modified how likely were predators to consume and prey to be consumed. It is possible that they described differences in biological characteristics such as microhabitat use, camouflage, specialized defenses, and offensive adaptations. A second explanation of poor performance of these models is that they have allowed only one allometry per food web. Perhaps size has different implications for different types of interactions and taxa. Differences in allometries of foraging traits among different types of predators, such as homeotherms and ectotherms, are not included in current models, and indeed are poorly documented (Petchey et al. 2008a). However, adding different allometries and/or foraging strategies will increase the complexity of the model, which may help to explain specific deviations from a general pattern, but draws us further from simple, general explanations.

## 8.4 FOOD WEB DYNAMICS AND STABILITY

Characterizing the structure of food webs as a network of the feeding interactions (links) among species (nodes) is a simple and powerful way to think about complex relationships among species. However, each species and each interaction is also changing through time in ecosystems; for example, the population of a species increases and decreases. These food web “dynamics” are influenced by body size, which in turn influences the stability of the whole system of interaction species. Understanding the dynamics of food webs is helping us to understand how many species can coexist and persist, even as their populations fluctuate (Dunne et al. 2005), and how species interactions mediate ecosystem functioning (Cardinale et al. 2008). Because it is very hard to track many co-occurring species' abundances through time in natural ecosystems, modeling has been a very important tool for understanding the relationship between dynamics and body size.

### 8.4.1 A bioenergetic foundation for dynamics and stability

In a seminal paper in 1992, Yodzis and Innes presented an allometric approach to modeling consumer–resource dynamics. Each population has a particular metabolic type and a characteristic body size, and is modeled as a stock of biomass that decreases due to losses to predation and metabolism, and increases due to gains from feeding or primary production. Most metabolic parameters are allometrically scaled: intrinsic growth rate of the resource, respiration rate of the consumer, and maximum consumption rate of the resource by the consumer all scale with body size to the 3/4 power (Peters 1983; Brown et al. 2004). Thus, the Yodzis and Innes “bioenergetic” approach uses abstractions based on a few interdependent, easy to measure, body-size based parameters as a way to model complex interspecific dynamics in a reasonably simple and biologically plausible way. This provides for greater biological realism than that expressed by randomly parameterized Lotka–Volterra models, and at the same time reduces the “plague of parameters” that typically afflicts multispecies population dynamic models (Yodzis and Innes 1992).

A number of studies based on this approach examined how different factors affect the stability of populations in small trophic modules, for example in short food chains (reviewed in Dunne et al. 2005). Subsequent research increased the size of the networks modeled and updated the allometric equations used (Brose et al. 2003; Williams and Martinez 2004; Martinez et al. 2006). These studies explored the impact of factors such as diversity and network structure on the persistence of species in model systems, a key measure of community stability (Martinez et al. 2006). However, these studies lacked a realistic body size distribution: they implicitly assigned a single body size to all taxa, leaving unanswered the question of how predator–prey body-size ratios affect species persistence in food webs.

#### 8.4.2 Predator–prey size ratios and stability

Body-size ratios among certain kinds of predators and prey are well documented, for example invertebrate predators are ~10 times larger than their prey, and ectotherm vertebrate predators are ~100 times larger than their prey (Brose et al. 2006a). When a dynamic bioenergetic model includes various predator–prey body-size ratios, from inverted ratios (predators 100 times smaller than prey; sometimes referred to as micropredators) to very large (predators up to 100 000 times the size of their prey), the persistence of species tended to saturate at body-size ratios quite close to the empirically observed values (10–100; Brose et al. 2006b) (Fig. 8.5A). The effect of predator–prey body-size ratio on persistence was much stronger than effects of network structure, metabolic type, species richness, or other factors.

Thus, predator–prey body-size ratios appear fundamentally important for the persistence and coexistence of species in complex trophic networks. But why does allometric scaling, including body-size ratios, facilitate species persistence? Perhaps it is simply that predators that forage on only very small prey cannot meet their energetic requirement, and predators that forage on large prey are condemned by the paradox of enrichment (population stability decreasing with increasing productivity; Oksanen et al. 1981). High persistence in model systems appears restricted to intermediate range of possible predator–prey body-size ratios (Otto et al. 2007). Empirical data focused on predator–prey interactions support these conclusions, as 97.5% of inver-

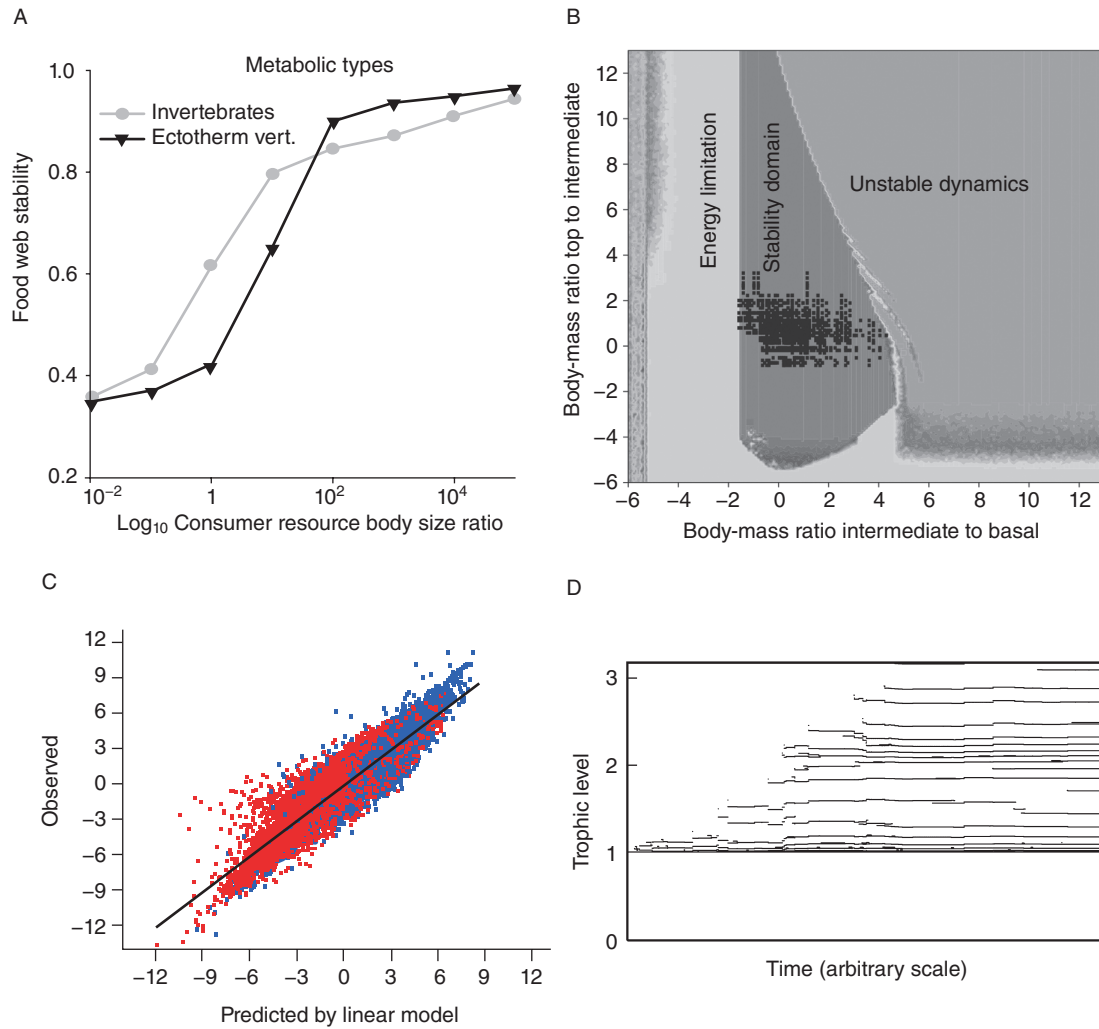
tebrate food chains from five food webs fall within a “stability domain” of intermediate body-size ratios (Fig. 8.5B) (Otto et al. 2007). In model food webs, allometric scaling increases intraspecific competition relative to metabolic rates for higher body-sized species and reduces biomass outflow from prey to predator when the predator is larger than the prey, resulting in increased persistence.

#### 8.4.3 Simplicity from complexity

The “allometric food web dynamics model” approach described before (Brose et al. 2006b) has been used to explore other aspects of the dynamics and stability of complex ecological networks with realistic topologies. For example, studies have examined keystone effects (Brose et al. 2005), competitive exclusion among producer species (Brose et al. 2008), the paradox of enrichment (Rall et al. 2008), the relative roles of network structure, models of primary production, functional response, generalist behavior (Williams 2008), and interaction strength (Berlow et al. 2009). The latter study systematically conducted every possible single-species knockout in 600 networks with  $S$  (species richness) of 10–30, as a means of quantifying the interaction strength for each species pair, in terms of the change in biomass of one species in response to the removal of another species. Per-capita interaction strengths were well-predicted by a simple linear equation with only three variables: the two species’ biomasses and the body size of the removed species (Fig. 8.5C; Berlow et al. 2009). When tested with empirical data from an experiment in an intertidal ecosystem, the equation successfully predicted the interaction strengths of taxa when trophic interactions, rather than spatial competition, dominated (Berlow et al. 2009). The relationship between interaction strength and body size may be connected with a recent finding that the keystone status of a species is closely linked to its body size (Berg et al. 2011).

#### 8.4.4 Evolutionary dynamics added

Other kinds of dynamical models have also explored the importance of body size for the evolution and persistence of species in complex ecological networks (e.g., Loeuille and Loreau 2006; Guill and Drossel 2008; Rossberg et al. 2008; Stegen et al. 2009). These studies



**Figure 8.5** Allometries at the individual and interaction level constrain the dynamics of ecological networks. (A) Persistence of species as a function of predator–prey body-size ratios, in dynamical models of food webs parameterized for invertebrates and ectotherm vertebrates. (Reproduced from Brose et al. 2006b by permission of John Wiley & Sons, Ltd.) (B) The stability domain of species coexistence in tritrophic food chains is limited by energy availability and unstable dynamics towards low and high body-size ratios, respectively. The black points illustrate food chains of the Skipwith pond food web as an example. (Reproduced from Brose 2010 by permission of John Wiley & Sons, Ltd.) (C) Observed  $\log_{10}$  per capita interaction strength versus that predicted by a multiple linear regression (based on population biomasses of the removed and target species and the body size of the removed species) in an “allometric food web dynamics model”. Red points correspond to low population biomasses of the removed species, and blue points to high population biomasses. (Reproduced from Berlow et al. 2009 by permission of the National Academy of Sciences.) (D) Trophic levels ( $y$ -axis) of species that evolve during  $10^8$  time steps ( $x$ -axis) at high niche width and competition intensity, in an eco-evolutionary model in which adaptation works on body size. (Reproduced from Loeuille and Loreau 2005 by permission of the National Academy of Sciences.)

assembled food webs via stochastic speciation events, and the resulting species interacted according to population dynamic equations. In one model, adaptation worked on a single trait, body size, and resulted in persistent, complex food webs (Loeuille and Loreau 2006). The relative roles of predation, which resulted in species with distinct body sizes, and interference competition, which resulted in homogenization of body sizes, influenced food web structure by altering the degree to which species sorted into more or less distinct trophic levels (Fig. 8.5D). An extension of this approach incorporated metabolic temperature dependencies (Allen et al. 2006) as a means of extending metabolic theory to macro-evolutionary patterns (Stegen et al. 2009). Evolutionary models have also explored the emergence of body-size–abundance scaling relationship (Rosenberg et al. 2008), and have linked the niche value of the niche model (Williams and Martinez 2000) to species body size and used evolutionary game theory to determine individuals' foraging efforts (Guill and Drossel 2008). All of these approaches produced complex, persistent food webs and provide some initial insights on the interplay of ecological dynamics, evolutionary dynamics, and body size.

#### 8.4.5 Stability explained?

Thus it seems that body size and its effects on vital rates and interactions among species provides an elegant, if not completely understood, explanation for the stability (persistence) of at least some complex food webs comprising predators and their prey. Furthermore, allometric scaling appears to be related to other stabilizing mechanisms, such as weak interactions (McCann et al. 1998) and weak long loops (Neutel et al. 2002). Perhaps allometric scaling across levels of ecological organization, and feedback among levels, will provide one of the most powerful responses to May's diversity–stability challenge. Ultimately, however, we need to include in explanations of species persistence and coexistence the diversity of trophic interactions in food webs (Lafferty and Kuris 2002), and also the diversity of non-trophic interactions among organisms.

### 8.5 WAYS FORWARD

We hope that the previous sections have convinced readers that body size places constraints on predator

foraging behavior, on interactions between prey and predators, on the structure of food webs, and on the dynamics and persistence of populations and communities. As mentioned, we have explicitly focused on particular types of interspecific interactions, primarily predation, and it remains to be seen what constraints body size places on other types of trophic interactions, or indeed other types of interspecific interaction (e.g., parasitic and mutualistic interactions) (Stang et al. 2006; Ings et al. 2009; Warren et al. 2010).

Other holes in need of filling include the following.

- 1** The importance of body size for the response of ecological networks to perturbations such as climate change (Rall et al. 2008; Petchey et al. 2010a), species loss and secondary extinctions (Dunne and Williams 2009), species invasions (Romanuk et al. 2009), and changes in ecosystem function (Cardinale et al. 2008) have yet to be widely studied or experimentally tested (though see O'Gorman et al. 2009; Woodward et al. 2010a). Experimental manipulative tests of interaction and food web models are lacking. While some models have faced such tests (e.g., Emmerson and Raffaelli 2004), many remain experimentally untested.
- 2** Effects of temperature on trophic interactions and food web structure are relatively unexplored, either theoretically or experimentally. Recent theoretical analyses suggest different activation energies (see White, Xiao, Isaac, and Sibly, Chapter 1) of metabolism and consumption will lead to stabilizing effects of temperature on population dynamics (Vucic-Pestic et al. 2011). Predictions of the effects of temperature on food web structure and metabolic balance of ecosystems are also sensitive to differences in activation energies of different processes (Petchey et al. 2010a; Yvon-Durocher et al. 2010). These findings suggest that warming might change dynamics above and beyond simply speeding them up.
- 3** A systematic review of foraging allometries, and continued experimental investigation of these allometries and their response to environmental change, would provide the data required to make specific predictions about effects of adaptation to environmental change (Brose 2010). At present we can make general predictions, but have insufficient knowledge about foraging allometries to make predictions that account for taxonomic composition of a specific food web.
- 4** Although general opinion says that aquatic communities, at least pelagic ones, are more size structured than terrestrial ones, thorough analyses comparing ecosystems are rare (Digel et al. 2011; Riede et al.

2011). Furthermore, analyses across multiple levels of ecological organization would be extremely informative (Yvon-Durocher et al. 2011a).

**5** A greater appreciation of intraspecific variability, ontogenetic diet shifts, and their consequences for food web persistence is needed. It is abundantly clear that the perception of food web structure (Woodward et al. 2010b) and dynamics (Persson et al. 1998; Rudolf and Lafferty 2011) are fundamentally altered by size/stage-structuring, yet most observed food webs do not include any kind of data about intraspecific variation. Particularly interesting approaches involve elegant mathematical modeling of individual-level processes that result in community structure and dynamics (e.g., De Roos et al. 1992; Hartvig et al. 2011).

**6** Dynamical models can be augmented and improved through insights from empirical and experimental work (e.g., Arim et al. 2010; Vucic-Pestic et al. 2010) and theoretical work (Weitz and Levin 2006). For example, the population dynamics of such models do not systematically incorporate hump-shaped attack

rates, certain parameters are not yet allometrically scaled, and differences among predator groups are not addressed (Brose 2010).

**7** The relationship of species persistence to diversity and complexity in dynamical models remains unclear and seems to be sensitive to small differences in the modeling approach (Brose et al. 2006b; Kartascheff et al. 2010). Furthermore, it is unclear what are the feedbacks and paths of causation that connect individuals, interactions, and population persistence. Do prey–predator size ratios drive dynamics, or does selective extinction drive observed size ratios?

## ACKNOWLEDGMENTS

This research was partially supported by a Royal Society University Research Fellow awarded to OLP, by the University of Zurich, and NSF grants DBI-0850373 and DBI-1048302 and a National Academies/Keck Futures Initiative grant to JAD.