FLEXIBLE FORAGERS IN FOOD WEBS

Body-mass constraints on foraging behaviour determine population and food-web dynamics

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Abstract

1. In community and population ecology, there is a chronic gap between the classic Eltonian ecology describing patterns in abundance and body mass across species and ecosystems and the more process oriented foraging ecology addressing interactions and quantitative population dynamics. However, this dichotomy is arbitrary, because body mass also determines most species traits affecting foraging interactions and population dynamics.

2. In this review, allometric (body-mass dependent) scaling of handling times and attack rates are documented, whereas body-mass effects on Hill exponents (varying between hyperbolic type II and sigmoid type III functional responses) and predator interference coefficients are lacking. This review describes how these allometric relationships define a biological plausible parameter space for population dynamic models.

3. Consistent with the classic Eltonian description, species co-existence in consumer-resource models and tri-trophic food chains is restricted to intermediate consumer-resource body-mass ratios. Allometric population dynamic models allow understanding the processes of energy limitation and unstable dynamics leading to this restriction. Complex food webs are stabilized by high predator-prey body-mass ratios, which are consistent with those found in natural ecosystems. These high body-mass ratios yield positive diversity-stability and complexity-stability relationships thus supporting the classic picture of ecosystem stability.

4. Allometric-trophic network models, based on body mass and trophic information from ecosystems, bridge the gap between Eltonian community patterns and process-oriented foraging ecology and provide a new means to describe the dynamics and functioning of natural ecosystems.

Key-words: allometric scaling, attack rate, food chain, functional response, handling time, metabolic theory, stability

Introduction

One of the most general patterns documented in organism biology is the scaling of metabolic rate with body mass raised to an exponent of ¾ (Peters 1983). This ¾ power law or Kleiber's rule has been generalized across organism groups as different as unicells, invertebrates and vertebrates and might qualify as one of the rare examples of a biological law (Kleiber 1932, 1961; Peters 1983). As metabolism fuels most biological processes at the level of organisms, physiologists have found the ¾ power-law scaling with body mass, M, for many other biological rates, B, including biomass production reproduction and ingestion (Peters 1983; Brown *et al.* 2004):

$$B \approx M^{0.75}. \qquad \text{eqn 1}$$

This implies that *per biomass* rates, $B'(B' = B/M)$, scale as negative-quarter power laws:

$$B' \approx \frac{M^{0.75}}{M} = M^{-0.25}. \qquad \text{eqn 2}$$

Despite an extensive debate on the exact exponent and the underlying mechanisms (van der Meer 2006), the quarter power-law scaling has been providing a conceptual basis for physiology stretching back to its roots (Kleiber 1932, 1961). This scaling relationship is successful at predicting biological

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rates across a wide range of body masses, but there is much variation in individual data points around this central tendency and different scaling exponents for different groups of organisms.

Similarly, the importance of body mass for population and food-web patterns and processes has been recognized at the roots of modern community ecology (Elton 1927), but in contrast to physiology the principles how body masses determine population and food-web organisation remained largely unexplored over several decades. Pioneering work bridged this gap between Eltonian roots and modern population and food-web ecology (Warren & Lawton 1987; Yodzis & Innes 1992; Cohen *et al*. 1993; Jonsson, Cohen & Carpenter 2005) to reinvigorate allometric (i.e. body mass) scaling models in population and food-web ecology (Berlow *et al*. 2009; Ings *et al*., 2009; Petchey *et al*. 2008; Woodward *et al*. 2005). This review is focused on research addressing how body masses constrain consumer–resource foraging behaviour, and how these constraints determine the dynamics and the stability of populations and food webs.

Classic foraging ecology

Defining the roots of modern community ecology, Elton already recognized the dominant structuring force of foraging interactions between species for natural communities: '*If we turned to the sea, or a fresh-water pond, or the inside of a horse, we should find similar communities of animals, and in every case we should notice that food is the factor which plays the biggest part in their lives, and that it forms the connecting link between members of the communities*' (Elton 1927; p. 52). While Elton's work addressed similarities and patterns across species, communities and ecosystem types, subsequent foraging ecology adopted a quantitative approach at describing specific foraging interactions between populations. The varying strength of foraging interactions was conceptualized in functional response models describing the *per capita* (per individual) consumption rate of a consumer depending on resource abundance (Holling 1959). One generalized functional response model is based on Holling's disk equation:

$$F(R) = \frac{bR^h}{1 + iC + bT_hR^h} \qquad \text{eqn 3}$$

where F is the consumer's *per capita* consumption rate, R and C are the abundances of the resource and consumer, respectively, T_h is the handling time that includes the time the consumer needs to pursuit, ingest and digest a resource individual, b is a constant that describes the increase in the attack rate (i.e. the instantaneous search rate), a, with resource abundance ($a \sim bR^{h-1}$), h is the Hill exponent that varies between one (hyperbolic type II functional response) and values larger than one (sigmoid type III functional response), and i is a coefficient varying the strength of predator interference (Holling 1959; Beddington 1975; De Angelis, Goldstein & O'Neill 1975; Real 1977; Skalski & Gilliam 2001; Williams & Martinez 2004; Koen-Alonso 2007). The predator interference term in the denominator is not necessarily linear, and it can also depend on the ratio between predator and prey densities (Abrams & Ginzburg 2000). Over several decades, the Holling school of foraging ecology has established a plethora of quantitative models relating the varying strength of foraging interactions mechanistically to attack and handling parameters (Jeschke, Kopp & Tollrian 2002, 2004). This school of thought provided a quantitative and mechanistic understanding of specific consumer-resource interactions based on one aspect of consumer and resource species: their abundance. Given that the abundance of any species fluctuates substantially in space and time, this focus came at the cost of distracting from regularities across species and communities. In contrast to this quantitative-energetic perspective on foraging interactions, Elton emphasized the importance of another aspect of consumer and resource species: their body masses. '*A little consideration will show that size is the main reason underlying the existence of these food-chains, and that it explains many of the phenomena connected with the food cycle*' (Elton 1927; p. 59). Recently, bridges between this Eltonian size-based perspective on patterns in foraging ecology and quantitative functional response models are increasingly recognized and may unravel surprising regularities across species (Berlow *et al*. 2009; Ings *et al*., 2009; Woodward *et al*. 2005).

Body mass constrains foraging behaviour

While ecologists have documented many different aspects of foraging behaviour, I will subsequently restrict its use to the description of the functional response components of handling, attack and interference (see eqn. 3). The handling time comprises three time components for (i) pursuing and subduing, (ii) ingesting, and (iii) digesting the resource. Considerations of consumer and resource body masses suggest that resources that are large relative to their consumers will take longer to subdue, ingest and digest. Thus, handling time should decrease with increasing consumer-resource body-mass ratios (the ratio between mean individual body masses of consumer and resource). While this trend of decreasing handling time with increasing consumer-resource body-mass ratio is generally supported, some studies reported linear (Hassell, Lawton & Beddington 1976; Spitze 1985) and others power-law or exponential relationships (Thompson 1975; Hassell, Lawton & Beddington 1976; Aljetlawi, Sparrevik & Leonardsson 2004).

Interestingly, metabolic arguments provide predictions on the nature of this relationship. At high (infinite) resource densities, the *per capita* consumption rates are not restricted by attack rates and depend entirely on handling times. The maximum ingestion rates realized at these resource densities are proportional to the inverse of handling time (Yodzis & Innes 1992; Koen-Alonso 2007). As metabolic studies suggest that these maximum ingestion rates follow ¾ power-law relationships with consumer body mass (Peters 1983; Yodzis & Innes 1992; Carbone *et al*. 1999) handling time should follow a neg-
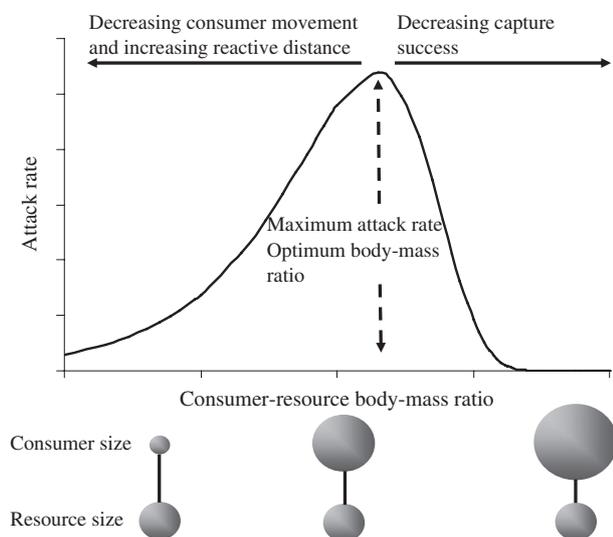
Fig. 1. Hump-shaped relationship between attack rates and consumer-resource body-mass ratios. Underlying processes are indicated at the top of the figure; consumer and resource body masses are illustrated below the *x*-axis.

ative ¾ power-law relationship with consumer body mass. In contrast, the time needed to ingest and digest a resource should be directly proportional to its mass suggesting a negative, linear relationship between resource body mass and handling time, but systematic evaluations of this relationship are lacking. In addition to these energetic arguments, adaptive behaviour can provide an alternative explanation for the saturation in the functional response (Abrams 1990).

The second component of the functional response, the attack rate, also depends on three characteristic sub-components: (i) the reactive distance between consumer and resource, (ii) the speed of movement of consumer and resource, and (iii) the capture success. Unfortunately, considerations of consumer and resource body-mass effects on attack rates are not straightforward and unambiguous (Fig. 1). When consumers are small relative to their resources (small consumer–resource body-mass ratios) the reactive distance is high and the consumer movement is slow (Aljetlawi, Sparrevik & Leonardsson 2004). When consumers are large relative to their resources (high consumer–resource body-mass ratios) the capture success is low (Brose *et al.* 2008). Consistent with the classic pattern that '*The food of every carnivorous animal lies therefore between certain size limits, which depend partly on its own size and partly on other factors. There is an optimum size of food which is the one usually eaten...*' (Elton 1927; p. 60) this suggests a hump-shaped relationship between attack rates and consumer–resource body-mass ratios with a maximum attack rate at intermediate (optimum) body-mass ratios (Fig. 1), which is also rooted in optimal-foraging and niche theory (Wilson 1975).

Such hump-shaped relationships have been documented for a wide range of consumer–resource interactions including terrestrial predators of aphids (Hassell, Lawton & Beddington 1976), aquatic invertebrate predators of Daphnia

(Hassell, Lawton & Beddington 1976; Spitze 1985) or tadpoles (Vonesh & Bolker 2005), perch preying on zooplankton (Wahlstrom *et al.* 2000), marine benthic isopods consuming amphipods (Aljetlawi, Sparrevik & Leonardsson 2004) and terrestrial epigeic arthropod predators (Brose *et al.* 2008). These studies suggest a broad generality of the hump-shaped relationship between attack rates and consumer–resource body-mass ratios (Fig. 1). However, documentation of this pattern in experimental studies requires extending the axis of body-mass ratios to very small and very high ratios. Continuous increases or decreases in attack rates found in some studies (e.g. see examples in Hassell, Lawton & Beddington 1976; Thompson 1975) might be caused by a limited range of body-mass ratios included, which restricts the pattern to the increasing or decreasing part of the hump. Moreover, the optimum body-mass ratio characterizing the maximum attack rate of the consumers appears to differ between consumer groups, but systematic explorations of optimum body-mass ratios and the scaling exponent indicating the width of the hump-shaped curve across different consumer and resource groups are still lacking.

One key parameter of functional response models is the Hill exponent, *h* (see eqn. 1), which can be gradually varied to convert hyperbolic, type II ($h = 1$) into increasingly more sigmoid type III ($h > 1$) functional responses (Real 1977). An important stabilizing feature of such increases in the Hill exponent is the slight relaxation of consumption at low resource densities, which leads to accelerating consumption rates with increasing prey density. The relaxation of feeding at low resource density is evocative of a variety of well-documented ecological mechanisms including prey switching and refuge seeking (Abrams 1987; Crawley 1992). Additionally, the sigmoid shape of functional responses with $h > 1$ yields a density-dependent predation probability at low resource density (Crawley 1992). This strong top-down pressure can control the prey population to low equilibrium densities if the attack rate is high, whereas low attack rates lead to oscillatory dynamics (Oaten & Murdoch 1975; Rall, Guill & Brose 2008). Considerations of consumer and resource body mass suggest that resource species could more easily employ refuges to hide from their consumers when they are small relative to their consumers (high consumer–resource body-mass ratio). This suggests that the Hill exponent of the functional response could increase with the predator-prey body-mass ratio in structured environments (i.e. those with a habitat structure with potential refuges) that provide refuges for the resource population. To my knowledge, however, this potential body-mass effect on Hill exponents has not been tested yet.

Variation in consumer density may affect the functional response via interference behaviour, which has been documented for numerous consumer types (Skalski & Gilliam 2001). Increases in consumer body mass should increase the strength of interference for any consumer density, but systematic explorations of this relationship are still lacking.

Body-mass effects on consumer–resource dynamics

In a pioneering study, Yodzis & Innes (1992) formulated a plausible bioenergetic consumer–resource interaction model based on allometric (body-mass dependent) ¾ power-law scaling of the physiological parameters of respiration, maximum ingestion and biomass production (Peters 1983; Brown *et al*. 2004). With respect to foraging behaviour as described by functional responses this implies allometric power-law scaling of the handling time while ignoring hump-shaped or other allometric scaling relationships of attack rates. Analytical solutions of this power-law consumer–resource model showed that neither the feasibility boundary (delimiting the parameter space of species persistence) nor the Hopf boundary (delimiting the parameter space of equilibrium population dynamics) depend on body masses (Yodzis & Innes 1992; Rall, Guill & Brose 2008). However, the periods of the oscillations (i.e. the time-scale of the consumer-resource system) scale with consumer body mass raised to the 1/8 exponent and resource body mass raised to the 1/8 exponent (Yodzis & Innes 1992).

Prior Lotka-Volterra or Rosenzweig-McArthur consumer-resource models comprise similar parameters that were usually sampled randomly and independently from each other without accounting for their allometric scaling. A significant improvement of allometric scaling models is that they allow parameterizing the model with plausible parameters based on species body masses. For instance, McCann & Yodzis (1994) demonstrated that the parameters of a prior study on population dynamics in a tri-trophic food chain implied the unrealistic assumption of a predator-prey body-mass ratio higher than 10^3 for an invertebrate predator feeding on an ectotherm vertebrate prey. Further analyses revealed that varying the predator-prey body-mass ratio in a biologically plausible parameter space (thus varying the respiration and consumption rates) can drive a tri-trophic food-chain from limit cycles into chaotic dynamics (McCann & Yodzis 1994). Interest-ingly, this study demonstrated that the parameters of con-sumer-resource models are not random. Additionally, allometric scaling models also suggest that biological parame-ters of consumer-resource models are not independent from each other: as all parameters are closely correlated to the spe-cies body masses, assigning one parameter implies a body mass of this species, which subsequently parameterizes the remaining parameters of this species (Fig. 2). Thus, independent-random parametrization of consumer-resource models is biologically implausible and should be avoided.

Recently, Weitz & Levin (2006) introduced an allometric consumer-resource model with power-law scaling of the phys-iological rates (e.g. population growth rate) and a hump-shaped relationship between the rate of successful attack and the consumer-resource body-mass ratio. In particular, these hump-shaped attack rates find substantial empirical support (Hassell, Lawton & Beddington 1976; Spitze 1985; Wahl-strom *et al*. 2000; Aljetlawi, Sparrevik & Leonardsson 2004; Vonesh & Bolker 2005; Brose *et al*. 2008) and thus provide an improvement over prior models with constant attack rates. Analyses of this consumer-resource model revealed that (i) consumer-resource co-existence is restricted to specific body-mass ranges that coincide with empirical mass ranges (Brose *et al*. 2006a), and (ii) the feasibility and Hopf boundaries depend on consumer and resource body masses (Weitz & Levin 2006).

Body-mass effects on food-chain dynamics

Natural food webs are characterized by energy transfer across multiple trophic levels and one of the most basic and simple description of this process is captured by linear food chains. Model analyses showed that population dynamics and the persistence of three-species food chains respond to varying consumer-resource body-mass ratios (McCann & Yodzis 1994; Jonsson & Ebenman 1998). Moreover, allometric consumer-resource models can be used to predict the strength of trophic cascades across trophic levels (Shurin & Seabloom
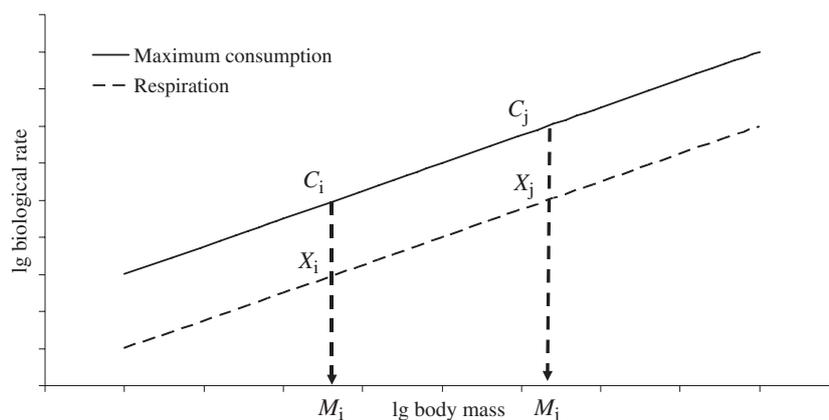

Fig. 2. Three-quarter power-law relationships between the maximum consumption rate, C, the respiration rate, X, and the body mass, M, of a species. Species i with body mass M_i has the respiration rate X_i and the maximum consumption rate C_i; species j with the body mass M_j has the respiration rate X_j and the maximum consumption rate C_j. Assigning a species one of these parameters (M, X, C) simultaneously defines the remaining parameters. In contrast, independent-random sampling of X and C could lead to combinations of C_i and X_j, which imply different body masses. Thus, independent-random parameterization of the biological rates for population dynamic models is implausible.
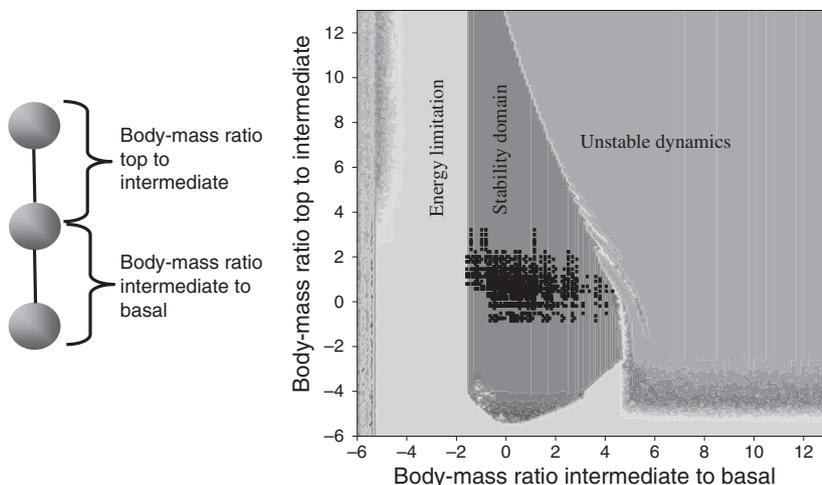
Fig. 3. The stability domain of species co-existence in tri-trophic food chains is limited by energy availability and unstable dynamics towards low and high body-mass ratios, respectively. The black points illustrate empirical food chains of the Skipwith Pond food web as an example.

2005). This study showed that effects of predator removal (third trophic level) on plant biomass (first trophic level) increase with the herbivore-plant body-mass ratio, whereas it is independent of the predator-herbivore body-mass ratio. This offers a simple explanation why trophic cascades occur more frequently in aquatic-pelagic ecosystems (with high zoo-plankton-phytoplankton body-mass ratios) than in terrestrial ecosystems (with low herbivore-plant body-mass ratios) (Shurin *et al.* 2002; Shurin & Seabloom 2005).

Systematic explorations of population dynamics in tri-trophic food chains demonstrated that the co-existence of three species in a food chain is restricted to a persistence domain of intermediate predator-prey body-mass ratios (Fig. 3, Otto, Rall & Brose 2007). Consumer persistence is not feasible at low body-mass ratios when predators are small and have a high *per biomass* rate of metabolism that is not balanced by the resources available. Increasing body-mass ratios increase the consumer body masses, which decreases their *per biomass* rate of metabolism (see eqn. 2). This enables the persistence of all three species while driving the populations into chaotic population dynamics until the accelerating oscillations eventually eliminate the consumer species. The persistence domain of body-mass ratios (i.e. consumer-resource body-mass ratios yielding persistence of all three species) is thus constrained by bottom-up energy availability towards low body-mass ratios and unstable population dynamics towards high body-mass ratios (Fig. 3). This prediction of the allometric population dynamic model finds support for more than 97% of the food chains across different natural food webs (Otto, Rall & Brose 2007). While these analyses were based on consumer-resource models with allometric power-law scaling, the consequences of hump-shaped attack rates for the dynamics of tri-trophic food chains remain to be explored. Nevertheless, these results suggest that the population dynamics in multi-species systems should depend on their body-mass structure.

Body-mass effects on food-web dynamics and stability

In natural ecosystems, species are connected to each other via feeding links composing a food-web topology that is much

more complex than simple food chains. Moreover, these nat-ural food webs have a characteristic body-mass structure (Woodward *et al.* 2005; Brose *et al.* 2006a). For instance, one regularity across ecosystem types is that invertebrate and ver-tebrate predators are on geometric average roughly ten and hundred times, respectively, larger than their prey (Brose *et al.* 2006a). Despite some exceptions to this pattern (e.g. pack hunters), this simple regularity imposes an allometric structure on the food web: (i) body masses increase with tro-phic levels, (ii) species are hierarchically organized on a body-mass axis with higher ranked species predominantly feeding on lower ranked species, and (iii) the number of resources (i.e. the generality) and consumers (i.e. the vulnerability) increase and decrease, respectively, with the body mass of a species (Otto, Rall & Brose 2007). Interestingly, this body-mass structure may account for the specific link structure defining who eats whom in natural food webs (Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008).

In addition, consumer-resource body-mass ratios can also be used to parameterize allometric population dynamic mod-els of complex food webs (Brose, Berlow & Martinez 2005; Loeuille & Loreau 2005; Brose, Williams & Martinez 2006b; Brose 2008; Guill & Drossel 2008; Rall, Guill & Brose 2008). Evolutionary food-web models (models that start with a sin-gle population to increase the number of populations by evo-lutionary emergence) showed that the body-mass structure is necessary to yield complex food web structures with multiple trophic levels (Loeuille & Loreau 2005; Guill & Drossel 2008). Systematic variation of body-mass ratios in dynamic models of complex food webs (models that start with an ini-tial complex network structure) demonstrated that species persistence (i.e. the fraction of the initial populations that per-sisted during the simulations) is low at low body-mass ratios (when predators are smaller than or equally sized as their prey), but persistence increases steeply with increasing body-mass ratios (Brose, Williams & Martinez 2006b). This increase saturates at body-mass ratios of 10 and 100 for inver-tebrate and vertebrate predators, respectively, which is highly consistent with the geometric average body-mass ratios found in natural food webs (Brose *et al.* 2006a). Moreover, persis-tence decreases with species richness at low body-mass ratios

(indicating negative diversity-stability relationships), whereas it exhibits a slight increase in persistence at high body-mass ratios (indicating positive diversity-stability relationships, see Brose, Williams & Martinez 2006b). In the same vein, additional analyses revealed positive complexity-stability relationships in complex food webs with an empirically supported body-mass structure (Rall, Guill & Brose 2008). While some initial results stress the importance of predator interference for food-web stability (Rall, Guill & Brose 2008), detailed information about allometric scaling of interference prevents final conclusions. However, these results reconcile lingering gaps between the perspectives of theoreticians using random interaction matrices implying low body-mass ratios around unity to predict negative diversity-stability relationships and empiricists documenting positive diversity-stability relationships in natural food webs with high body-mass ratios. In addition, complex food webs with realistic body-mass structure prevent competitive exclusion among producer species at the base of the food web (Brose 2008).

Together, these studies demonstrate that regularities in the body-mass structure provide stability of complex and diverse natural food webs. The models employed accounted for body-mass effects on the biological rates of respiration, production and maximum consumption, whereas additional body-mass constraints on other foraging parameters such as attack rates, Hill and predator interference coefficients remained unexplored. Generally, increasing Hill and predator interference coefficients can strongly stabilize population dynamics and food-web persistence (Williams & Martinez 2004; Rall, Guill & Brose 2008, Williams 2008). However, a lack of knowledge how these parameters are related to consumer and resource body masses prevents merging these findings with those of allometric food-web models (e.g. Brose, Williams & Martinez 2006b; Otto, Rall & Brose 2007; Brose 2008), and future studies will need to close this lingering gap.

Conclusions

Allometric relationships affect the biological rates and species traits affecting foraging interactions. Combining trophic information (who eats whom) with the body-mass structure of natural communities yields allometric-trophic network models that define a biological plausible parameter space for population dynamics. Improving these models requires (i) extending the generality of hump-shaped attack rates across different ecosystem types, (ii) documenting optimum body-mass ratios (leading to maximum attack rates and interaction strengths) for different consumer groups, and (iii) addressing allometric scaling relationships of the Hill exponent and the predator-interference coefficient. Ultimately, allometric models of foraging interactions could bridge the gap between the classic Eltonian ecology describing patterns across species and ecosystems and the more process oriented foraging ecology addressing interactions and quantitative population dynamics. This allow broadening the perspective of mechanistic foraging ecology to predict patterns across species

(Beckerman, Petchey & Warren 2006; Otto, Rall & Brose 2007; Petchey *et al.* 2008) and ecosystems (Brose, Williams & Martinez 2006b; Brose *et al.* 2006a). Considering that mobility is also closely related to body mass (Peters 1983) this approach may enable a mechanistic understanding of patterns and dynamics of populations in space (Brose *et al.* 2004; McCann, Rasmussen & Umbanhowar 2005) and food-web constraints on ecosystem functioning (Thebault & Loreau 2003; Duffy *et al.* 2007).

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