Body size and species coexistence in consumer–resource interactions: A comparison of two alternative theoretical frameworks

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Abstract Species coexistence involving trophic interactions has been investigated under two theoretical frameworks—partitioning shared resources and accessing exclusive resources. The influence of body size on coexistence is well studied under the exclusive resources framework, but has received less attention under the shared-resources framework. We investigate body-size-dependent allometric extensions of a classical MacArthur-type model where two consumers compete for two shared resources. The equilibrium coexistence criteria are compared against the general predictions of the alternative framework over exclusive resources. From the asymmetry in body size allometry of resource encounter versus demand our model shows, counterintuitively, and contrary to the exclusive resource framework, that a smaller consumer should be competitively superior across a wide range of supplies of the two resource types. Experimental studies are reviewed to resolve this difference among the two frameworks that arise from their respective assumptions over resource distribution. Another prediction is that the smaller consumer may have relatively stronger control over equilibrium resource abundance, and the loss of smaller consumers from a community may induce relatively stronger trophic cascades. Finally, from satiating consumers' functional response, our model predicts that greater difference among resource sizes can allow a broader range of consumer body sizes to coexist, and this is consistent with the predictions of the alternative framework over exclusive resources. Overall, this analysis provides an objective comparison of the two alternative approaches to understand species coexistence that have heretofore developed in relative isolation. It advances classical consumer–resource theory to show how body size can be an important factor in resource competition and coexistence.

Keywords Coevolution · Coexistence · Foraging · Predator prey · Plant herbivore · Resource partitioning · Niche

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Introduction

Species coexistence in natural communities has been extensively investigated through observational studies, manipulative experiments and modeling. Theoretical approaches based on the phenomenological Lotka–Volterra models suggest that coexistence of competitors is likely

only under very restrictive conditions (Strobeck 1972); and the principle of competitive exclusion states that only a single species will dominate a community and cause competitive exclusion of others, when they compete for a shared resource (Armstrong and McGehee 1980). Reviews of the empirical evidence (Schoener 1983; Connell 1983), however, found that while competition occurs frequently in nature, competitive exclusions are rare. Subsequently, more mechanistic models of resource competition (MacArthur 1969; 1970) have provided additional insights into species coexistence. Among the proposed determinants of multi-species coexistence are external forcing and fluctuations, intrinsic non-equilibrium dynamics including chaos (Huisman and Weissing 1999), and the availability of exclusive resources (Schoener 1976).

Following MacArthur (1969; 1970), mechanistic models for two consumers that share two resources have received much attention (León and Tumpson 1975; Case and Casten 1979; Hsu and Hubbell 1979; Chesson 1990). Higher-dimensional extrapolations do exist but are more difficult to visualize and are mathematically less tractable (Yodzis 1989) and require numerical analyses (Huisman and Weissing 1999). A distinct emphasis in previous investigations into models of two-consumer and two-resources has been that each consumer has a primary preferred resource and a secondary non-preferred resource, such that the two sub-systems are connected via the occasional consumption of non-preferred resources. Abrams and Shen (1989) investigated a scenario where each consumer follows a foraging strategy of consuming a fixed ratio of the preferred and non-preferred resource. Vandermeer (1993) further investigated the consequences of such coupling between the two sub-systems due to occasional consumption of the non-preferred resource. Depending on the degree of coupling, a variety of oscillatory dynamics were observed, ranging from independent oscillations, entrainment, and chaos.

These studies, however, have not accounted for an important observation that coexisting species often differ substantially in body size (e.g., Case et al. 1983; Kiltie 1988; Prins and Olff 1998; Dayan and Simberloff 1998). Body size influences a suite of species' traits via allometric and metabolic constraints that have important ecological manifestations (Peters 1983; Calder 1984; Brown et al. 2004). Even though a possible role of body size differences over the outcome of competition has been recognized for decades (Huxley 1942; Hutchinson 1959), most theoretical studies have not explicitly addressed its relevance in niche determination and species coexistence in natural communities. Instead, size-dependent physiological and metabolic constraints have been incorporated into models to investigate the periodicity of oscillatory

behaviors (Yodzis and Innes 1992). Wilson (1975) predicted that larger consumers are more efficient and can exploit a wider range of prey sizes than smaller ones, and Schoener (1983) advanced a similar view in favor of the larger competitor. But, Persson (1985) argued how such asymmetric competitive interactions may not always benefit the larger competitor because it may be superior in interference competition, but, not in exploitative competition. More recently, Basset and DeAngelis (2007) have suggested that smaller consumers can counter the competitive advantage of a larger competitor by their ability to reduce resource densities to a low level by virtue of their lower resource requirements. However, these studies have not explicitly connected body size to mechanisms of competitive coexistence of the consumers, and uncertainties persist over how the widely documented patterns of size-related niche partitioning might yield competitive coexistence.

Very few theoretical studies have directly incorporated body size into consumer–resource interactions, and these are closely related to the Schoener's (1976) concept of exclusive resources. The Ritchie–Olff framework (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010) links body size to the availability of exclusive resources (Schoener 1976) based on the perceived differences in scale-dependent heterogeneity of resource distribution. Recently, Yoshiyama and Klausmeier (2008) have also investigated a body-size-based model tailored to unicellular organisms. But, unlike the Ritchie–Olff model, instead of consumers searching for resources in their environment, they considered the resources to arrive at the cells through fluid movement in well-mixed environments.

Clearly, it still remains to be fully investigated whether and how species coexistence in classical consumer–resource interactions over shared resources, is influenced by body-size-related allometric constraints and how the predictions from a general, allometric extension of classical consumer–resource model compare with those from the alternative framework based on exclusive resources (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010). In this article, we incorporate size-related allometric and metabolic constraints into a classical consumer–resource model for two-consumer species that share two resource types. We explore the equilibrium criteria for competitive coexistence, and investigate a limiting similarity in the relative use of two resource types that is dictated by the difference in body size of the coexisting consumers. We first analyze a simplistic model with linear consumer functional responses and subsequently incorporate satiating consumer functional responses. Finally, we compare this classical model's predictions with those of the alternative framework (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010).

Model with linear functional response

The model of MacArthur (1969; 1970) for the dynamics of the abundance of different consumer and resource types is:
   Resource dynamics are given by

$$\frac{dP_i}{dt} = P_i \left[\frac{r_i}{K_i}(K_i - P_i) - \sum_j c_{ij}H_j \right] \quad (1)$$

Consumer dynamics are given by

$$\frac{dH_j}{dt} = b_j H_j \left(\sum_i w_i c_{ij} P_i - D_j \right) \quad (2)$$

where P_i and H_j are densities of resource type i and consumer species j; r_i = intrinsic growth rate of resource i; K_i = carrying capacity of resource i; c_{ij} is the rate at which consumer j encounters and captures resource i; w_i is the nutritional value such as mass of resource i; D_j = zero-growth resource requirement of consumer j; and b_j is mass-specific conversion efficiency of consumer j of captured resources.

Equilibrium conditions for the two-dimensional system can be obtained analytically using zero net growth isoclines (ZNGI). These ZNGI are illustrated as a phase-diagram in Fig. 1a. Solving the ZNGI for consumers gives the following equilibrium densities for resources:

$$P_1^* = \frac{D_1 c_{22} - D_2 c_{21}}{w_1(c_{11}c_{22} - c_{21}c_{12})}, \text{ and } P_2^* = \frac{D_2 c_{11} - D_1 c_{12}}{w_2(c_{11}c_{22} - c_{21}c_{12})} \quad (3)$$

For a feasible equilibrium, the numerators and denominators in Eq. 6 must have the same sign. From this, it follows that the coexistence of all species involves the following three conditions (or their converse):

$$c_{11}c_{22} > c_{21}c_{12} \quad (4a)$$

$$D_1 c_{22} > D_2 c_{21} \quad (4b)$$

$$D_2 c_{11} > D_1 c_{12} \quad (4c)$$

Clearly, the coexistence of resource types, and thereby the potential coexistence of the consumers, depends on diet choice of the two resource types represented in the c_{ij} constants and consumers' metabolic demands represented by D_j. The inequalities depicted in Eqs. 4a–4c are in compliance with Abrams and Holt (2002) because D_j, and c_{ij} are key resource partitioning parameters that allow coexistence, and emphasize the top-down control inherent in classical theory.

In a manner similar to the study by Wilson (1975), we now distinguish between the rate at which consumers encounter and capture resources. The parameter c_{ij} is the product of two components—the rate at which consumer j searches for food (a_j), and the probability that it will consume resource species i once encountered (s_{ij}). In this way $c_{ij} = a_j s_{ij}$, where a_j is determined by searching behavior, while s_{ij} is an outcome of diet choice (Owen-Smith and Novellie 1982). Following this, Eq. 4 is modified to:

$$s_{11}s_{22} > s_{21}s_{12} \quad (5a)$$

$$D_1 a_2 s_{22} > D_2 a_1 s_{21} \quad (5b)$$

$$D_2 a_1 s_{11} > D_1 a_2 s_{12} \quad (5c)$$

Fig. 1 Zero net growth isoclines of two consumers (H_1 and H_2) over a range of abundance of two resources (P_1 and P_2). Results from linear consumer functional response (Eqs. 1–2) are shown in (a), while results from satiating consumer functional response (Eqs. 7–8) are shown in (b)
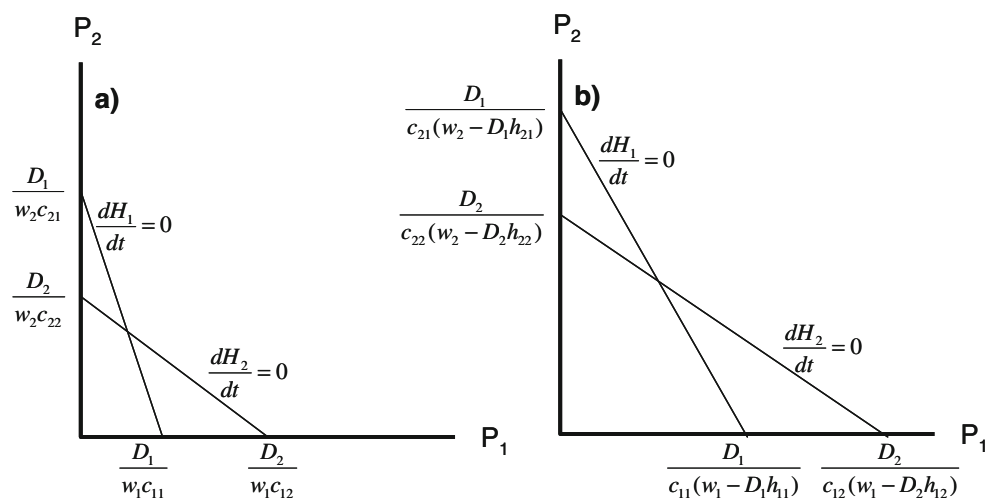
When these criteria are satisfied, the system attains a stable equilibrium (Case and Casten 1979; Hsu and Hubbell 1979).

Body-size-based allometric constraints

We shall now invoke allometric constraints over foraging and basal resource requirements. The parameters a_j and D_j scale with body size (M_j) as $a_j \propto M_j^{\theta}$ and $D_j \propto M_j^{\kappa}$. Empirical evidence suggests $\theta \approx 1/4$ and $\kappa \approx 3/4$ (Peters 1983; Calder 1984; Brown et al. 2004) and almost certainly $\kappa > \theta$. This implies that the rate at which consumers search their habitat increases more slowly with body size than the rate at which metabolism increases. In other words, the rate at which resources are required generally increases more rapidly with size than the rate at which they are encountered, and this difference is sufficient to derive the major conclusions that follow. Following the general body size allometry literature (Peters 1983; Calder 1984; Brown et al. 2004), we substitute $\theta = 1/4$ and $\kappa = 3/4$ in (5a–5c), and this reduces the coexistence criteria to

$$\frac{s_{21}}{s_{22}}\sqrt{\frac{M_1}{M_2}}, \text{ and } \frac{s_{12}}{s_{11}}\sqrt{\frac{M_2}{M_1}} \tag{6}$$

Inspection of Eq. 6 shows that consumer preference for one resource species over another (i.e., $s_{11} \neq s_{21}$; $s_{12} \neq s_{22}$) imposes strong constraints over what body sizes may

coexist. Therefore, the degree of coupling between the two sub-systems represented by the s_{ij} determines what body sizes may coexist. This result provides additional insights into previous studies (Abrams and Shen 1989; Vandermeer 1993) and suggests that when the consumers are similar in body size, the two sub-systems are tightly coupled, whereas, a large difference in body size can allow loose coupling between the two sub-systems. These criteria can be used to further evaluate how selectivity influences coexistence, given that it is linked to body size. We consider actual selectivities as required deviations from boundary conditions of Eq. 6 that ensure coexistence: $s_{22} = \delta s_{21}\sqrt{\frac{M_2}{M_1}}$, and $s_{12} = \gamma s_{11}\sqrt{\frac{M_2}{M_1}}$; where the constants $\delta > 1$ and $\gamma < 1$ determine the extent to which coexisting species will deviate from the boundary conditions. In a graphical representation (Fig. 2), these boundary conditions depict the equation of a straight line that separates the domains of diet selectivity of the two consumers over a particular resource. Any point in this s_{i1} and s_{i2} plane represents a possible combination of consumer selectivity of the two resources, and Eq. 6 separates the choices available to one consumer from those available to the other; as the slope of the line separating these two compartments depends on $\left(\frac{M_2}{M_1}\right)^{1/2}$; or, in more general terms, $\left(\frac{M_2}{M_1}\right)^{\kappa-\theta}$, with $\kappa > \theta$. For coexistence, even for similar-sized consumers, diet selectivity or the potential mix of the two resources incorporated in the diet, of both consumer species cannot lie on the same side of the line, and must fall on either side (i.e., stippled region and clear region,
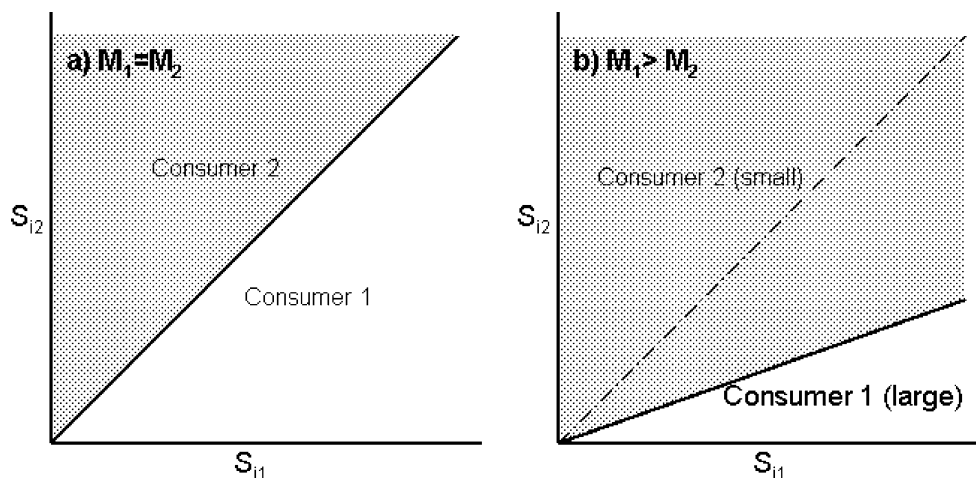

Fig. 2 Graphical representation of the relationship between diet selectivity (s_{1j} and s_{2j}) and consumer body sizes (M_1 and M_2). Any point in this graph represents a combination of consumer diet selectivities over two alternative resource species. Eq. 6 defines the combinations of diet selectivity that allow coexistence of the two consumers and the options available to the different consumers are separated by a line whose slope depends on $(M_2/M_1)^{1/2}$. In (a), the two consumers are similar in body size, and the respective domains of diet selectivity are separated by a *straight line* with slope=1. Note that the area under *stippled region* is matched by area under *clear region*.

However, as the size difference between the two consumers increases, the slope of the line becomes shallower (b). This leads to increase in area under the *stippled region* (smaller consumer), and a decrease in the area under *clear region* (larger consumer). The *dotted line* in (b) is for reference to the situation described in (a). Some relevant predictions emerge from this graphical representation. From (a), it is predicted that smaller consumers are likely to have a more even mix of both resource items in their diet (high diet diversity) compared to the larger, where diets will be dominated by a single resource (low diet diversity)

Fig. 2a). The influence of increasing body size difference is depicted in Fig. 2b. Considering a situation with different sized consumers (e.g., $M_1 > M_2$); diet selectivity of the smaller consumer must fall above the line (i.e., stippled region, Fig. 2b), and that of the larger consumer fall below the line (i.e., clear region, Fig. 2b). As the difference in their body sizes increase, the slope of the line becomes shallower and the options of diet selectivity available to the larger consumer become more limited while the dietary options available to the smaller consumer increase. This asymmetrical interaction between competitive consumers arises, as mentioned above, simply from the differences in allometries of search rate and metabolic requirements.

The constraints described by Eq. 6 will also influence a consumer's diet profile, and the proportion of resource species i among k items in the diet of consumer species j is given by $d_{ij} = \frac{w_i a_j s_{ij} P_i^*}{\sum_k w_i a_j s_{ij} P_i^*}$. After algebra, the relative proportions of the two resources in the diet of a consumer are given by the ratios $F_1 = \frac{d_{11}}{d_{21}} = \frac{s_{11} w_1 P_1^*}{s_{21} w_2 P_2^*}$ for consumer species H_1, and $F_2 = \frac{d_{12}}{d_{22}} = \frac{s_{12} w_1 P_1^*}{s_{22} w_2 P_2^*}$ for consumer species H_2. These ratios, F_1 and F_2, indicate whether the diets are comprised of an even mix of both resource items, or, are they dominated by any single item. In the former case, under an even mix of both items, these ratios approach 1. In the latter case, when diet is dominated by one item (preferred resource type) with relatively lower representation of the other (non-preferred resource type), these ratios deviate from 1 (either $F_j \ll 1$ or $F_j \gg 1$, depending on which item is over-represented). From the analysis leading to Fig. 2a–b, this outcome predicts that the diet of smaller consumers may comprise a relatively even mix of both resources, while the larger consumer will strongly prefer one resource item over the other. Or, in other words, the degree of coupling between the two sub-systems is largely determined by the smaller consumer and only minimally by the larger consumer, and this is an additional insight into previous studies (Abrams and Shen 1989; Vandermeer 1993).

The boundary conditions described in Fig. 2, also lead to an analysis of patterns of dominance and relative abundance among the resource species at equilibrium. From Eq. 3, we can write $\frac{P_1^*}{P_2^*} = \frac{w_2}{w_1} \left(\frac{s_{22}\sqrt{M_1} - s_{21}\sqrt{M_2}}{s_{11}\sqrt{M_2} - s_{12}\sqrt{M_1}} \right)$. Substituting $s_{22} = \delta s_{21} \sqrt{\frac{M_2}{M_1}}$, and $s_{12} = \gamma s_{11} \sqrt{\frac{M_2}{M_1}}$ from Eq. 6, reduces the above to $\frac{P_1^*}{P_2^*} = \frac{w_2}{w_1} \frac{s_{21}(\delta-1)}{s_{11}(1-\gamma)} = \frac{w_2}{w_1} \frac{s_{22}(1-\gamma)}{s_{12}(\delta-1)}$.

This expression can be used to determine the boundary conditions at which $P_1^* = P_2^*$. After substitutions, it leads to the expression of a second straight line that separates the domains of diet selectivities, $s_{22} = \gamma \frac{(\delta-1)^2}{(1-\gamma)^2} \sqrt{\frac{M_2}{M_1}} s_{21}$ (and likewise, $s_{12} = \delta \frac{(1-\gamma)^2}{(\delta-1)^2} \sqrt{\frac{M_2}{M_1}} s_{11}$). Revisiting the previous scenario where $M_1 > M_2$ note that the slope of this second line (Fig. 3) must be steeper than the slope of the first line (Fig. 2b). From this, it follows that if diet selectivity of the
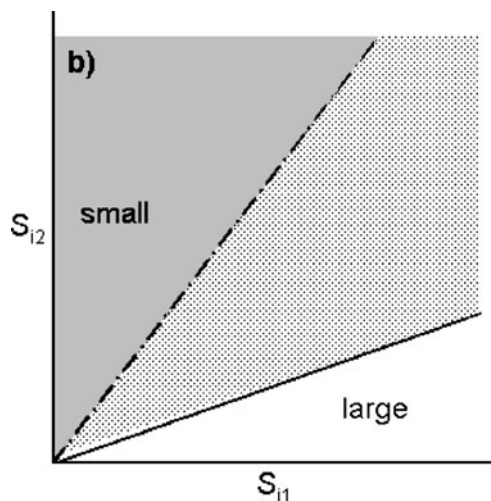

Fig. 3 Further exploration of the arguments presented in Fig. 2 that depict the relationship between consumer body size and relative abundance of resources at equilibrium. As in Fig. 2b, the *solid line* represents the criteria of coexistence as determined by Eqs. 5a–5c and 6. The *dotted line* represents the boundary condition where abundances of both resource types are maximized. If diet selectivity of the smaller consumer falls above the *dotted line* (shaded portion), then resource species 1 dominates in abundance. If it falls below the *dotted line* (stippled region), then resource species 2 dominates. This suggests that the smaller consumer has greater dynamical control over equilibrium resource densities

smaller consumer falls above this line (shaded region, Fig. 3), then resource species P_1 will dominate. If it falls in between the two lines (stippled region, Fig. 3), then resource species P_2 will dominate. Thus, the asymmetry imposed on consumer diet selectivity for competitive coexistence is also linked with dominance patterns among the resource species, as it can determine which resource species may attain higher abundance at equilibrium. As earlier, this result emphasizes the top-down nature of classical theory and provides new insights into how body size of competing consumers may lead to community-wide patterns of equilibrium resource abundance.

Satiation in consumers' functional response

The model with linear functional response is simplistic, as consumers are likely to encounter satiation with increasing resource density. This aspect is incorporated by revising Eq. 1 and 2 to introduce h_{ij} as the handling time for resource i by consumer j. An appropriate formulation of consumers' satiating functional response would be one where the handling times are non-independent. Krivan and colleagues have investigated such optimal foraging con-

straints imposed by non-independent handling times (Krivan 1996; Krivan and Sikder 1999). This requires that Eqs. 1 and 2 be modified to the following form:

$$\frac{dP_i}{dt} = \frac{r_i P_i}{K_i}(K_i - P_i) - \frac{\sum_j c_{ij} P_i H_j}{1 + \sum_i c_{ij} h_{ij} P_i} \qquad (7)$$

$$\frac{dH_j}{dt} = b_j H_j \left(\frac{\sum_i w_i c_{ij} P_i}{1 + \sum_i c_{ij} h_{ij} P_i} - D_j \right) \qquad (8)$$

Continuing with the ZNGI approach implemented above, we can now derive new isoclines in a phase-diagram (Fig. 1b). For this, we get new equilibrium resource densities as:

$$P_1^* = \frac{w_2 c_{21} P_2^* - D_1 - D_1 c_{21} h_{21} P_2^*}{c_{11}(D_1 h_{11} - w_1)} \text{ and}$$

$$P_2^* = \frac{w_1 c_{11} P_1^* - D_1 - D_1 c_{11} h_{11} P_1^*}{c_{21}(D_1 h_{21} - w_2)}$$

For brevity, the equilibrium solutions are not shown in terms of parameters alone and can be obtained by using algebraic substitutions in the above expressions. Note that although the equilibrium resource densities have changed by incorporating satiation (optimal foraging through non-independence of handling times), and are now greater than in the previous case, the qualitative attributes of isoclines remain comparable with the linear model (Fig. 1a–b).

Now, for stable coexistence, the isoclines must intersect, which requires,

$$\frac{D_1}{c_{21}(w_2 - D_1 h_{21})} > \frac{D_2}{c_{22}(w_2 - D_2 h_{22})}$$

$$> 0 \text{ and } \frac{D_2}{c_{12}(w_1 - D_2 h_{12})} > \frac{D_1}{c_{11}(w_1 - D_1 h_{11})} > 0$$

Rearranging the above, we get

$$\frac{D_1 c_{22}}{D_2 c_{21}} > \frac{w_2 - D_1 h_{21}}{w_2 - D_2 h_{22}} > 0 \text{ and } \frac{D_2 c_{11}}{D_1 c_{12}} > \frac{w_1 - D_2 h_{12}}{w_1 - D_1 h_{11}} > 0$$

Now, the numerator and denominator must have the same sign to give a positive and meaningful solution. If the numerator is positive, then $w_2 > D_1 h_{21}$ and $w_2 > D_2 h_{22}$ (or, the converse). Similarly, $w_1 > D_2 h_{12}$ and $w_1 > D_1 h_{11}$ (or, the converse). These paired inequalities can be expressed as paired equations using new constants of proportionality. After algebra, we obtain $\frac{D_1}{D_2} = \mu \frac{w_1 h_{22}}{w_2 h_{11}}$ and $\frac{D_2}{D_1} = \mu' \frac{w_1 h_{21}}{w_2 h_{12}}$ where μ and μ' are positive constants of proportionality.

After substituting the above, we get $\mu \frac{w_1 h_{22} c_{22}}{w_2 h_{11} c_{21}} > 0$ and $\mu' \frac{w_1 h_{21} c_{11}}{w_2 h_{12} c_{12}} > 0$ and we can now introduce allometric constraints as before: $c_{ij} = a_j s_{ij}$, $a_j \propto M_j^\theta$, $D_j \propto M_j^\kappa$ and

$h_{ij} \propto w_i^\lambda M_j^{-\varepsilon}$. These allometric substitutions modify the coexistence criteria to:

$$\left(\frac{w_1}{w_2}\right)^{1-\lambda}\left(\frac{M_2}{M_1}\right)^{\theta-\varepsilon}\frac{s_{22}}{s_{12}} > 0 \quad \text{and} \quad \left(\frac{w_1}{w_2}\right)^{1-\lambda}\left(\frac{M_1}{M_2}\right)^{\theta-\varepsilon}\frac{s_{11}}{s_{21}} > 0.$$

The perceptive reader will notice that unlike the coexistence criteria for the linear model (Fig. 2a–b), coexistence is now dependent on not only consumer's body size $\left(\frac{M_2}{M_1}\right)$ and diet choice (s_{ij}), but also on size of the resources (w_i). For any given condition of resource sizes, it is evident that the coexistence criteria link M_j with s_{ij} in the same manner that is depicted in Fig. 2a–b. So, below, we investigate the effect of variable conditions of resource sizes and consumer body size for any given condition of s_{ij}.

After rearranging, the new coexistence criteria represent equations that relate $\left(\frac{M_1}{M_2}\right)$ and $\left(\frac{w_2}{w_1}\right)$ in the following manner: $\left(\frac{M_1}{M_2}\right)^{(\theta-\varepsilon)} = \alpha \left(\frac{s_{12}}{s_{22}}\right)\left(\frac{w_2}{w_1}\right)^{(1-\lambda)}$, and $\left(\frac{M_1}{M_2}\right)^{(\theta-\varepsilon)} = \alpha'\left(\frac{s_{21}}{s_{11}}\right)\left(\frac{w_2}{w_1}\right)^{(1-\lambda)}$, where $\alpha > 1$ and $\alpha' < 1$ are positive constants of proportionality. These relationships can be represented by a pair of curved lines whose intercepts depend on s_{ij} and slopes are determined by λ (Fig. 4a). The zone of coexistence is delineated by the region in between the curved lines.

This result now allows us to investigate the effects of increasing body size differences among the resources on coexistence of consumers (Fig. 4b). This suggests that, for any given combination of s_{ij}, only a narrow range of consumer body sizes can coexist under low resource heterogeneity when $w_1 \approx w_2$. However, for the same criterion of s_{ij}, a much larger range of consumer body sizes can coexist at greater levels of resource heterogeneity when $w_1 \gg w_2$ (Fig. 4b). This result parallels the predictions of the alternative models for exclusive resources (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010).

Discussion

Several practical interpretations of these results emerge in the form of model predictions. It is beyond the scope of this article to attempt a comprehensive quantitative review and formal meta-analysis of the empirical evidence around these predictions. Below, we highlight the major predictions and provide instances known to us that are in agreement with these predictions. We also discuss some cases that do not conform to these predictions.

(I) *Diet choice of the smaller consumers influence the degree of coupling more strongly than the larger consumer.* When two consumers differ in body sizes, the larger must prefer one resource type more strongly than the other (Fig. 2b). Thus, while both species may consume either resource types, the smaller competitor can consume a more even mix of both resource items
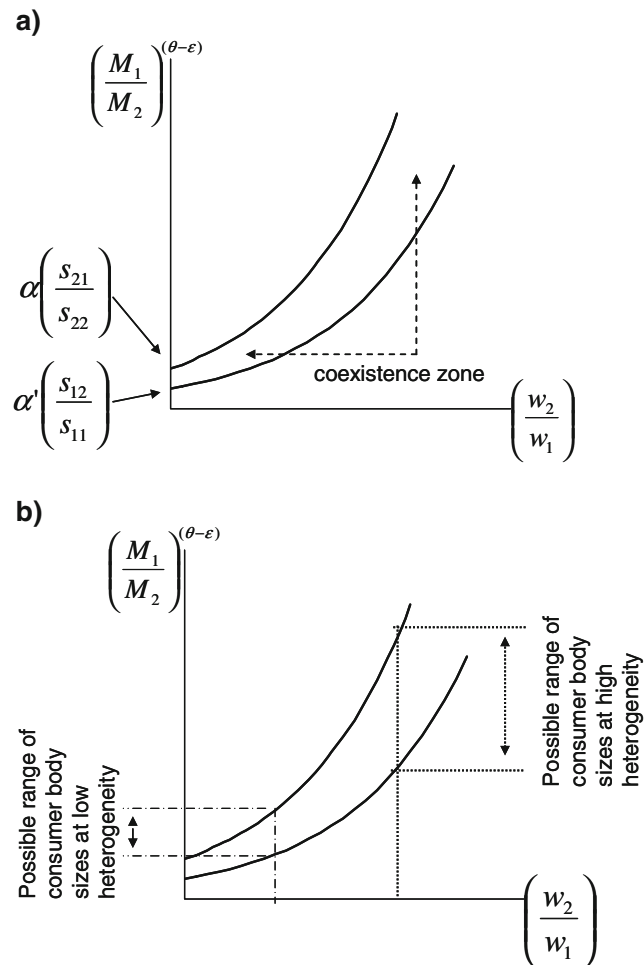
a)

b)

Fig. 4 Diagrammatic representation of coexistence conditions over conceptual space defined by ratio of consumers' body size $\left(\frac{M_i}{M_j}\right)^{(\theta-\varepsilon)}$ on y-axis and ratio of resources' size $\left(\frac{w_j}{w_i}\right)$ on x-axis. In **a**, the zone of coexistence is the region between two curved lines, whose intercepts depend on s_{ij} and slope depends on λ which is the allometric exponent of handling time for a given resource size, and is described in the text based on Eqs. 7–8. In **b**, the range of consumer body sizes that can coexist at low- and high-level of resource heterogeneity (i.e., size ratio among the resources) are compared. For any given difference in ratio of s_{ij} among the consumers, the range of consumer body size that can coexist increases with the size difference among the resources

while the larger strongly prefers one resource item. When species are relatively similar in size, and thereby, in their search rate and resource requirements; relatively small difference in the selectivity of resource types will allow coexistence. In contrast, when two species differ greatly in size, the two species must differ much more in diet, which will be manifested as greater specialization over one resource type by the larger consumer. In Table 1, we list empirical studies where smaller competitors were found to have relatively more even consumption of resource items, compared to the larger consumers. Statistical relationship between diets and body size in these studies are

described in further detail in the Appendix. Exceptions to this pattern were found in a group of livestock species that has been historically assembled by humans, and may lack diet differentiation that exists in assemblages of native species (Bagchi et al. 2004; Bagchi and Ritchie 2010). Among these livestock, diet patterns were not related to body size. Other notable exceptions were among Galapagos finches (Grant 1999) and Caribbean lizards (Schoener 1968). The Galapagos finches are very similar in their body size, and instead show remarkable morphological adaptations in their beaks, and Grant (1999) discusses how body- and beak-size may have evolved independently in these species. Similarly, among Caribbean lizards, coexistence is achieved primarily through behavioral interference competition and spatial segregation (Schoener 1968). Evidently, body-size-based competitive interactions appear less important when alternative mechanisms determine coexistence.

(II) As a corollary to prediction (I) above, *the smaller among a species pair will compete more strongly and this asymmetric advantage will increase as their size difference increases*. As the size differences between a pair of consumer species increases, the smaller species has a greater relative per capita effect on the larger species, because, the potential advantage in a faster search rate for the larger species is masked by the lower resource requirements of the smaller species, and this is the mechanistic manifestation of the previous observation that $\kappa > \theta$ (Peters 1983; Calder 1984; Brown et al. 2004). This counterintuitive prediction contrasts with the alternative framework of size-related coexistence over exclusive resources (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010). The Ritchie–Olff framework predicts that a larger size difference leads to less intense competition and more likely coexistence. This difference between these two modeling frameworks may arise from their assumptions about resource distribution. Classical MacArthur-type models assume that resources are randomly or uniformly distributed, and that they are consumed at different rates depending on selectivity and search rate. On the other hand, the Ritchie–Olff model assumes that resources are packaged within material (e.g., nutrients within food items) that are heterogeneously distributed as fractals, which lead to exclusive sets of resources for species of different sizes (Schoener 1976; Ritchie 2010). These differences in assumptions may directly lead to the differences in model predictions.

Relatively few studies have examined competitive interactions simultaneously with diets, and impacts on

Table 1 Description of different studies which provide qualitative support to our model prediction that the smaller competitor's diet can consist of a relatively even mix of resource items, while the larger should strongly favor one item

Guild type	No. of species	Body size range	Reference
Montana grasshoppers	4	2.04×10^{-4} to 1.6×10^{-3} kg	Belovsky (1986)
Amazonian fishes	9	1.5 to 9 kg	de Merona and Rankin-de Merona (2004)
Mbuna fishes, Lake Malawi	7	11 to 18 cm	Reinthal (1990)
Serengeti mammals	9	21 to 650 kg	Hansen et al. (1985)
Montana mammals	10	0.035 to 636 kg	Belovsky (1986)
Tibetan plateau mammals	7	15 to 410 kg	Harris and Miller (1995)
African rainforest carnivores	8	1.2 to 40 kg	Ray and Sunquist (2001)

Trends in these data are summarized statistically in the Appendix

abundances of different resource types. One set of studies where this was done for grasshoppers (Orthoptera: Acrididae) in successional old field plants (Ritchie and Tilman 1992, 1993), yielded mixed support for our model predictions, but help clarify the counterintuitive nature of the predictions. When plant nutrients were judged to be relatively homogeneously distributed within juvenile plant tissue early in the growth season, the smaller of two grasshopper species (*Arphia pseudonietana*) was less specialized in diet, exhibited less diet shift under competition, reduced shared grass species to a lower biomass and competitively excluded a larger grasshopper species (*Pardalophora apiculata*). This pattern is consistent with our predictions. However, when plant nutrients were judged to be more heterogeneously distributed among mature and senescent stems, leaves, and flowers late in the growth season, the converse was true. Now, the smallest of three grasshopper species (*Phoetaliotes nebrascensis*) exhibited the most specialized diet, had the strongest impact on grass biomass, and suffered the greater increase in mortality rate when competing with the largest grasshopper (*Spharagemon collare*). This late-season trend is consistent with the alternative Ritchie–Olff framework. Thus, experimental studies with grasshoppers and plants (Ritchie and Tilman 1992; 1993) suggest that the outcome of competition and the relative advantages of large versus small body size can be reversed when resources are more heterogeneously distributed. Or, depending on whether there are qualitative differences between the resources (e.g., leaf quality at the beginning or the end of the growing season), empirical trends may switch between the predictions of these alternative frameworks.

Similar counterintuitive patterns have also been observed in bivoltine lepidopterans (Teder et al. 2010). In bivoltine moths (two life cycles a year), the first instar larve (early season birth during high food quality) were found to be smaller than the second instar larvae (late-season birth during low food quality). So, as in the study with small and large grasshoppers, competitive advantage of larger body

size may manifest only when resource distribution or quality becomes heterogeneous.

(III) *Selectivity of resource types by the smaller, and not the larger consumer, drives the equilibrial relative abundance of the resource types.* The asymmetry in competitive advantage translates into stronger dynamical control of resource abundance by the smaller species (Fig. 3). This also implies that loss of the smaller consumer may lead to stronger trophic cascades. While trophic cascades have been widely studied over the last few decades (Shurin et al. 2002), the role of consumer diversity and identity (and hence, their body size) in determining stability of ecosystems and food webs is a relatively new frontier of research (Duffy and Harvilicz 2001; Duffy et al. 2003), and data are scarce to further explore this prediction at present.

(IV) *Introduction of, or invasion by, a smaller consumer can either drive the larger consumer to extinction, or cause strong diet shifts in the larger consumer.* In the absence of a smaller competitor, the larger species' diet will likely include relatively larger proportions of the resource type preferred by the smaller species. Upon invasion by, or the introduction of, a smaller species, the larger species will likely be competitively excluded or will shift its diet to specialize on one resource type. We are aware of a few case studies where introductions of exotic species into new habitats provide qualitative support for this idea. The interaction between large sized native whitefish (*Coregonus lavaretus*, 10 kg) and the invasive vendance (*Coregonus albula*, 1 kg) in subarctic European lakes supports this idea (Bøhn and Amundsen 2001). Further, experimental manipulations of such interactions between a smaller invasive and a larger native species in the North American Great Lakes region (e.g., ruffe *Gymnocephalus*

cernuus, 0.4 kg; and yellow perch *Perca flavescens*, 1.8 kg), also suggest that the smaller invading species has the competitive edge (Savino and Kolar 1996). Among mammals, there is evidence to suggest that small-sized introduced species such as sheep (30 kg) can strongly negatively affect larger native species (e.g., guanacos *Lama guanicoe* 100 kg). Following sheep introduction in Patagonia at the end of the nineteenth century, guanaco densities are now negatively related to sheep abundance, and the diets of guanacos more restricted (Baldi et al. 2004).

Curiously, the reverse interaction where a larger species invades a community with a smaller species seems to occur less frequently. And when it does, the larger species relies upon alternative strategies such as intra-guild predation. Obrycki et al. (1998) provide an interesting insight into such a complementary scenario where an introduced beetle interacts with a much smaller species that is native to North America. Under laboratory conditions, they found that a larger beetle (*Coccinella septumpunctata*) introduced into North America suffers 60% larval mortality compared to 27% suffered by a smaller native species (*Coleomegilla maculata*) when the two interact competitively. Similar results were found in an experimental setup with large and small poeciliid fishes (Schröder et al. 2009), where the large-bodied species had higher invasion success due to alternative mechanisms such as intra-guild predation. Thus, invasion success of large competitors may not always be attributed to superiority in exploitative competition per se, but, to alternative strategies such as intra-guild predation and other interference behaviors as stressed by Persson (1985).

(V) *With increasing heterogeneity in resource size, a wider range of consumer body sizes can coexist.* This result parallels the predictions of the alternative framework over exclusive resources (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010) as well as models for unicellular organisms (Yoshiyama and Klausmeier 2008). As in the case of unicellular organisms suspended in fluid environments, our analysis of classical MacArthur-type consumer–resource dynamics also suggests the same trend for organisms that actively search for resources. Together, these lend credence to the idea that body size may provide a unified framework to view competitive coexistence when there are distinct quantitative differences among the resources (e.g., resource size, Ritchie 2010).

A key assumption of MacArthur-type consumer resource models is that the two resource types can themselves coexist in absence of consumers, and in the presence of consumers the resources experience apparent competition (Holt 1977). An alternative scenario that might apply in nature is that one consumer species reduces a dominant resource type, stimulates the growth of the other resource, and yields a positive effect on the density of a competing consumer species (Farnsworth et al. 2002). We did not explore that scenario here, but qualitatively, we would predict that a smaller consumer species might reduce the dominant resource type to a lower level than the larger, and thus, produce a greater stimulating effect. Indeed, such an influence of body size did occur in the grasshopper–plant system studied by Ritchie and Tilman (1992; 1993) where the smaller grass-feeder *P. nebrascensis* decreased biomass of the dominant grasses, stimulated production of forbs and increased the density and reduced the mortality of a forb-feeding grasshopper *Melanoplus sanguinipes* more strongly than the larger grass-feeding *S. collare*. If the smaller consumer has greater control over equilibrium resource densities, then is it likely that strength of trophic cascades is linked to consumer body sizes? Or, are keystone consumers more likely to be small? Such consequences of body size through indirect effects remain a rich area of exploration for consumer–resource theory. Since this will merge biodiversity research with food-web theory, it promises to be an exciting frontier for future research on the pressing challenges facing biodiversity conservation (Worm and Duffy 2003).

In summary, our understanding of species coexistence stems from two families of models that have developed in relative isolation. The first emphasizes partitioning of shared resources (MacArthur and Levins 1967), and the other is based on access to exclusive resources (Schoener 1976). The role of body size has been recently investigated using the Ritchie–Olff framework (Ritchie and Olff 1999; Ritchie 2002; Ritchie 2010), building upon Schoener's (1976) concept of exclusive resources. But, the influence of body size on the classical MacArthur-type models has received less attention. We show that when allometric relationships are incorporated into a simple and classical model of consumer–resource dynamics, body size has a strong influence on the limiting similarity in diets that allow competitive coexistence in ways that can be compared and contrasted against the predictions of the alternative model. The differences in predictions among these alternative frameworks appear to arise from their assumptions over resource distribution. Our model predictions on diet choice receive good support from observed body size differences in a variety of guilds including insect and mammalian herbivores, fishes and mammalian carnivores (Table 1). The model predicts several additional implications for the effects of consumers on resource diversity and relative abundance, as well as the success of invasion by species of different body size.

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