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The implications of using multiple resources for consumer density dependence

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ABSTRACT

Questions: What is the relationship between the population size and per capita growth for a consumer species experiencing resource limitation? How is this relationship influenced by the presence of multiple resources that differ in their vulnerability to the consumer? How well do traditional models of density dependence represent these relationships?

Methods: Simple differential equation models of one-consumer/multiple-resource systems are used to determine the relationship between the per capita mortality of the consumer and the equilibrium (or average) consumer density, as well as the associated relationship between per capita growth and population size. Most models have either two or very many resources.

Key assumptions: Resources are nutritionally substitutable and different resources do not interact with each other.

Predictions: If total mortality is low, use of multiple resources is likely to produce a decelerating decrease in consumer population size with an increase in imposed mortality. Deceleration is caused by relaxed apparent competition between resources as consumer mortality increases. This represents a relaxation of the conditions for persistence in a game played between the strategies represented by different prey species. Because most functional responses saturate at high resource densities, the density–mortality relationship becomes accelerating at high mortalities. As a consequence, generalist consumers often have different curvature of density dependence at high and low population sizes (unlike the widely used 'theta-logistic' model of density dependence).

Keywords: apparent competition, consumer–resource interaction, density dependence, exclusion, growth–defence trade-offs, harvesting populations, logistic model.

INTRODUCTION

The relationship between population size and per capita population growth rate defines simple models of density dependence in which per capita population growth is expressed as a decreasing function of population density. By far the most commonly used continuous-time models of density dependence are the logistic equation, and its generalization, Gilpin and Ayala's (1973) θ-logistic. The latter model allows per capita growth to decrease with

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density at an accelerating or decelerating rate. These simple models have informed many ideas about resource management and conservation, and have formed a component of almost all predator–prey and food web models in community and evolutionary ecology. However, relatively little is known about the likely range of shapes of density dependence in natural populations, or whether these two simple models can adequately represent that range of shapes. This gap in our knowledge has arisen because direct measurements are generally not feasible (see following paragraph). In addition, inferring the shape of density dependence from time-series analysis is often inconclusive due to lack of data, measurement errors, and difficulties in incorporating delayed effects. The commentary on Sibly and colleagues' (2005, 2006) set of time-series analyses (Doncaster, 2006; Freckleton *et al.*, 2006; Getz and Lloyd Smith, 2006; Peacock and Garshelis, 2006; Ross, 2006) provides some insight into problems associated with this approach. Although other time-series analyses have avoided some of the problematic features in Sibly and colleagues' study (e.g. Saether *et al.*, 2002; Coulson *et al.*, 2008; Eberhardt *et al.*, 2008), it remains true that time-series have difficulty dealing with time delays in density effects (Doncaster, 2008), and the difficulties are exacerbated by the multiple non-linear distributed delays that result from resource depletion. Available time-series often do not cover the full range of densities that the population experiences, and frequently are not long enough to draw meaningful conclusions. For example, Brook and Bradshaw (2006) noted that even the existence of density dependence often could not be established from a large fraction of the more than 1100 time-series that they analysed.

A direct approach to measuring the shape of density dependence would be to maintain population size at a fixed level and measure the number of individuals removed (i.e. the population growth). However, combining continuous and highly accurate monitoring of population size and continuous removal is generally impossible. Fortunately, the same measurements are possible, at least in laboratory systems, if the dependent and independent variables are reversed. If a constant per capita or absolute harvest is applied to a species and its community is allowed to reach equilibrium, the per capita removal rate corresponds to the per capita population growth rate at that equilibrium population size (Abrams, in press). This simply switches the dependent and independent variables in the relationship. When the density dependence is due to resource exploitation, the consumer population is in fact an independent variable in the dynamic consumer–resource system, and keeping it constant could produce spurious results. Unfortunately, this harvesting technique has seldom been used in empirical work (but see Fryxell *et al.*, 2005), and is impractical for most natural systems.

Given the difficulties reviewed above, and the importance of a quantitative understanding of density dependence to many aspects of applied ecology, it seems appropriate to develop tools for deducing the shape of density dependence from knowledge of the mechanisms that underlie the process. Such tools are particularly important because qualitative changes in the estimated shape of density dependence under different environmental conditions have been observed in some species (Miller, 2007). Density dependence can be caused by several mechanisms, including direct antagonistic interactions between individuals. However, resource limitation is often regarded as the most important mechanism underlying density dependence (Krebs, 2002; Begon *et al.*, 2006), and it is the mechanism assumed here. Schoener's (1983) review of inter-specific competition showed that 'consumptive' competition was by far the most common of the mechanisms he identified, and there is no *a priori* reason to expect this to be different for intra-specific competition (i.e. density dependence). A generally applicable model of density dependence should be at least qualitatively consistent with density dependence arising from resource limitation. Previous theory has attempted to

relate general features of the shape of density dependence to whether competition is contest or scramble (Royama, 1992; Sutherland, 1996) or whether life histories are relative fast or slow (Fowler, 1981, 1988). However, the theory has remained largely non-mechanistic, and has largely ignored the dynamics of resources.

Abrams (in press) analysed density dependence using models of specialist consumer–resource systems, and showed that the curvature of the relationship between the equilibrium consumer density ($N_{\mathbf{eq}}$) and the per capita mortality rate of the consumer reflects the curvature of the resource's density dependence and the curvature of the consumer's functional and numerical responses. One of the main results of that study is that, at low consumer population densities, density dependence is almost always accelerating (convex; negative $\partial^2 N_{\mathbf{eq}}/\partial d^2$) because functional and numerical responses are close to saturation. The acceleration applies to both the relationship between consumer population size and per capita growth rate, and the inverse relationship between per capita mortality and equilibrium consumer population size. However, at high population densities, a variety of influences on density dependence (the shapes of the consumer's functional and numerical responses and the shape of the resource growth function) could produce either accelerating or decelerating (concave; positive $\partial^2 N_{\mathbf{eq}}/\partial d^2$) relationships. The presence of accelerating and decelerating sections of the same relationship occurred for several classes of models. In addition, there are many cases in which population density increases with mortality (Abrams, 2002, 2009, in press; Matsuda and Abrams, 2004; Abrams and Matsuda, 2005; Abrams and Quince, 2005; Schreiber and Rudolf, 2008).

Because most consumers are not specialists on a single resource, it is important to have similar deductive results for the shape of density dependence in generalist consumers. Differences between the dynamics of systems with specialist and generalist consumers continue to be of great interest (Murdoch *et al.*, 2002, 2003). However, the possibility of systematic differences in the shape of density dependence between specialist and generalist consumers does not appear to have been considered before. A key process entailed by multiple resources is apparent competition (Holt, 1977) between resources due to their mutual effects on the consumer species' population density. The presence of distinct resources (prey) that differ in their vulnerability to the consumer (predator) sets up a frequency-dependent interaction between the resources; resources that reproduce quickly or are less vulnerable to the predator are likely to dominate when predation pressure is high. However, predation pressure itself is a function of the characteristics of the prey that persist. Consumer–resource models have been widely used to study inter-specific competition in multiple-resource systems (MacArthur, 1970, 1972; Schoener, 1973, 1986; Chesson, 1990, 2000; Abrams *et al.*, 2008), and they can be equally valuable in understanding intra-specific competition (i.e. density dependence) in those cases. In the present article, I analyse one-consumer/multiple-resource models to determine the resulting shape of density dependence in the consumer species. I quantify density dependence by determining equilibrium population size as a function of imposed mortality. The results allow an assessment of the adequacy of the commonly used θ-logistic model (Gilpin and Ayala, 1973), provide guidance for preserving or exploiting consumer species, and help explain differences in the dynamics of specialists and generalists.

MODELS

The consumer–resource system explored here has a single consumer species, with population size N, and $i_{\mathbf{max}}$ nutritionally substitutable resources, each with population size R_i. The dynamics are described by:

$$\frac{dR_i}{dt} = z_i + R_i f_i(R_i, R_j, R_k \ldots) - C_i R_i g_i(R_i, R_j, \ldots, N)N$$

$$\frac{dN}{dt} = b\left(\sum_{i=1}^{i\max} e_i C_i R_i g_i(R_i, R_j, \ldots, N)\right) - dN \qquad \text{(1a, b)}$$

Here, f_i is the per capita growth rate of resource i; f_i is assumed to decrease with increasing R_i. In principle, f_i may also decrease with the densities of other resources due to direct competition, but this possibility is not analysed in the current article. The term z_i represents the immigration rate of resource of type i from outside the system; here it is generally assumed to be at least two orders of magnitude smaller than the maximum growth rate of the within-system resource population. Immigration reflects the fact that most systems have some degree of openness, and its main effect here is to prevent complete extinction of any resource. The term $C_i R_i g_i$ is the consumer's functional response to resource i, where the mass action term, $C_i R_i$, is modified by a 'foraging intensity' function, g_i, which reflects all processes modifying the basic mass action term. Foraging intensity is affected by satiation, handling time, adaptive adjustment of relative and absolute effort, and by resource defensive behaviour in response to consumers. If the consumer has a multi-species Holling (1959) type-2 response, g is the same for all resources, and is given by $1/(1 + \Sigma C_i h_i R_i)$, where h_i is the handling time for an item of resource i and the summation is over all resource types consumed. The function b is the consumer's numerical response, which converts the summed, weighted intake of resources into a per capita rate of increase of the consumer. The function b includes the per capita birth rate (which always depends on resource intake) minus the component of the per capita death rate that depends on resource intake. The constants e_i are the nutritional values of each of the resources. The parameter d is the density-independent death rate of the consumer; it includes natural density-independent mortality and may also include an imposed per capita harvest rate. At equilibrium, the per capita harvest rate is equal to the natural per capita growth rate (which includes the natural density-independent mortality).

Two types of systems are analysed here. The first consists of systems with an effectively infinite number of resources, where each reproduces independently, and all can be ordered along a one-dimensional axis that measures some property that affects the interaction (in most cases, their vulnerability to the consumer). The second type of model assumes that the consumer uses two resources. The two-resource system allows some analytical results to be obtained, and it corresponds to the mean number of prey per predator in natural food webs (Schoener, 1989). Some simulations of systems having a moderate number of resources are used to gain insight into the stability of multi-resource models. Within each of the two main classes, models are distinguished by the nature of resource dynamics and the shape of the consumer's functional response. The analysis assumes that the consumer has a linear numerical response to food intake. Most of the analysis assumes that resources do not compete with each other, although the impact of competition is explored briefly. Alternative forms of the model are reviewed in the section that precedes the Discussion.

Models with many resources and linear functional responses

The models in this section assume a very large number of resources that can be arrayed along an axis. In this section, the models assume an effectively infinite number of

resources, a common approximation in analogous models of inter-specific competition (e.g. May, 1973).

Logistic resources

The first model is the consumer–resource system introduced by MacArthur (1970) to study inter-specific competition; this model forms the foundation of much consumer–resource theory (Chesson, 1990, 2000; Haygood, 2002; Abrams *et al.*, 2008; Chesson and Kuang, 2008). MacArthur's model incorporates linear functional and numerical responses. It assumes a large array of independent, logistically growing resources that can be arranged along a linear axis; here the axis measures relative vulnerability to capture by the consumer. The consumer's attack rate parameters, C, for different resources can be described by an increasing curve along the resource axis, which measures the vulnerability rank x ($0 \le x \le 1$). The relationship $C(x)$ is referred to as the consumer's utilization curve. In models with a finite numbers of resources, the continuous curve may be replaced by a set of attack rates, C_i, where C increases with the index i. The energetic value of a resource with vulnerability x is given by $e(x)$. Logistic growth is parameterized as $dR(x)/dt = R(x)(r(x) - R(x))$, so that the single growth parameter, $r(x)$, gives the maximum per capita population growth rate as well as the equilibrium population size. The growth parameter, r, may also be a function of position on the vulnerability axis, x. To keep total consumption abilities of different consumer species constant, the integral of $C(x)$ from 0 to 1 is assumed to be constant (= 1). Similarly, when either e or r is a function of x, the mean value of each of those parameters over the resource axis is assumed to equal 1. The equilibrium resource density at position x, given logistic growth (and assuming $z = 0$ for all resources), is given by:

$$R(x) = \left\{ \begin{array}{ll} r(x) - C(x)N & \textit{if this is non-negative} \\ 0 & \textit{if the above is negative} \end{array} \right\} \tag{2}$$

In the first set of models below, all of the resources have identical r-values; in this case, r may be set to 1 without loss of generality. The consumer density is determined by the condition that the integral of $e(x)C(x)R(x)$ over the range of extant resources must be equal to the per capita density-independent mortality, d. If d is small enough, a range of resources characterized by the largest $C(x)$ will become extinct. The range of vulnerability ranks, x, where apparent competition causes resource exclusion can be determined analytically for some cases (see Appendix 1).

The baseline case in which $r(x)$ is constant (here $r = 1$) and $C(x)$ is constant ($C = 1$) has equal equilibrium densities of all resources; those densities are positive for all consumer death rates, d. MacArthur's (1970) work implies that the equilibrium consumer density is $\hat{N} = 1 - (d/\bar{e})$. Here we assume that the mean value of the resources, $\bar{e}$, is unity. However, regardless of the function $e(x)$, the equilibrium consumer population size decreases linearly with its per capita mortality rate, implying linear density dependence in the consumer's growth (i.e. logistic growth). However, Holt (1977) showed that in MacArthur's model, differences between resources in their values of C or r could lead to exclusion of some resources at low values of d. This leads to non-linearity in the consumer's density dependence.

First, consider a system where $e = 1$ for all resources, but $C(x)$ varies between resources. In the absence of resource extinction, the presence of multiple resources characterized by different $C(x)$ does not affect the linearity of the relationship between the equilibrium consumer population, $N_{\mathbf{eq}}$, and mortality, d, although it can affect the slope. Figure 1

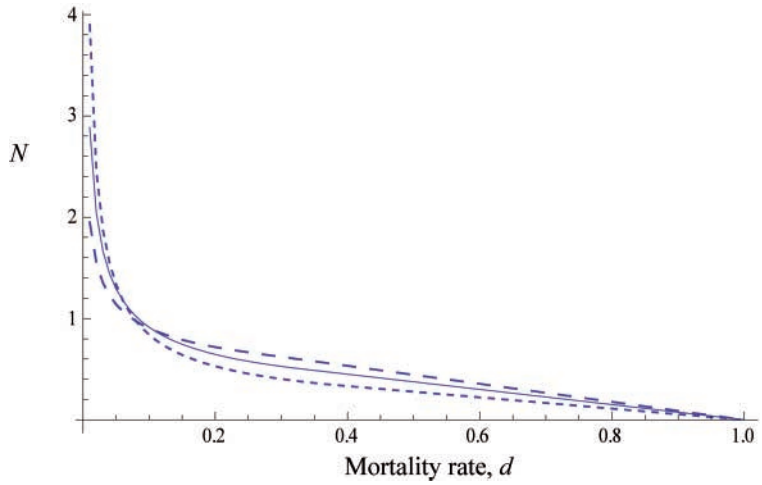

Fig. 1. Consumer population size as a function of mortality in a model having a uniform resource spectrum ($r = 1$ for all), and three different distributions of the attack rate parameter, $C(x)$. The energetic value of all resources is equal, and this value has been set to 1 in the present analysis. The resource axis parameter, x, measures the vulnerability of the resource to capture, where $x = 0$ corresponds to $C = 0$, and where $x = 1$ corresponds to the most rapidly caught resource. Differently shaped $C(x)$ functions all correspond to the same total consumption ability. The three functions explored in the figure are: $C(x) = 2x$, given by the solid line; $C(x) = 3x^2$, given by the short-dashed line; and $C(x) = (3/2)\sqrt{x}$, given by the long-dashed line. The population size decreases linearly with d for a large enough value of d because all resources are present (see text).

illustrates the relationship for cases when the range of $C(x)$ is wide enough and consumer mortality is low enough for apparent competition to cause resource exclusion. ('Exclusion' here means exclusion in the absence of immigration; having a small rate of immigration of resource from outside the system prevents zero densities in the numerical analyses, but has a minimal numerical impact on the results.) The range of excluded resources can be determined analytically in many cases; the technique is presented in Appendix 1. To translate the graphs in Fig. 1 into relationships between population density and per capita growth rate, it is only necessary to reverse the axes. As noted before, the mortality, d, includes both natural and imposed mortality. The relationships of N_{eq} to imposed mortality are identical to those shown except for being truncated at the N_{eq} corresponding to the natural mortality alone.

Figure 1 considers three different utilization curves. In all cases, if mortality rate is initially very low, population size falls rapidly with mortality at first, but then drops at a decreasing rate until the population size becomes a linear function of mortality once all resources are present. The three $C(x)$ relationships explored in Fig. 1 assume linear, quadratic, and square root $C(x)$ functions respectively. The technique in Appendix 1 shows that some resources are excluded for $d < 1/3$ for the linear curve, $d < 2/5$ for the quadratic curve, and $d < 1/8$ for the square root curve. The quadratic curve, $C(x) = 3x^2$ (short dashed line), implies the highest maximum population size (at very low d) and the lowest population size at high mortalities. The relatively broad range of low C-values implied by the quadratic function results in a larger number of extant resources at low mortalities than do the other two curves. However, at higher mortalities, the relatively small proportion of

vulnerable resources is over-exploited, and the relatively large fraction of resources characterized by low C-values no longer provides sufficient intake relative to the high requirements implied by a large d. Among the curves illustrated, the quadratic utilization curve makes the equilibrium consumer density decrease non-linearly over the broadest range of mortalities. The minimum C (at $x = 0$) is assumed to be zero in these examples; increasing that minimum while maintaining the average C would reduce the range of mortalities producing resource exclusion, thus reducing the range of mortalities over which this relationship is non-linear.

It may seem counter-intuitive that population size is very large when only one or a few low vulnerability resources are present. However, the low vulnerability prevents over-exploitation, which allows a high consumer population density. The equilibrium consumer population decreases most rapidly with mortality when its only available resource(s) is (are) caught slowly (low C); this reduces the compensatory increase in resource intake with higher consumer mortality. As d increases, more resource types return to the system, and the average C over all extant resources increases. The increase in mean C buffers the consumer to further increases in mortality, resulting in deceleration in the decrease of N_{eq} with d. The qualitative shape of this relationship is basically independent of the shape of the utilization curve; it is characterized by a decelerating decrease at low d, and a linear decrease at high d. These relationships imply that, if the consumer–resource system is represented as a model without explicit resources, per capita growth rate should decrease linearly at low population sizes, but then may decrease at a decelerating rate (and with a lower slope) at high population sizes. The minimum d is likely to vary considerably across systems, but empirical studies have found values consistent with many resources being excluded by apparent competition (Abrams *et al.*, 2008). Thus it is likely that the left-hand side of Fig. 1 is applicable to many natural systems.

Figure 2 explores cases in which energetic value, e, and resource growth rate, r, are functions of relative vulnerability to consumption, which is again indexed by x. Figure 2A shows that the non-linearity of density dependence at low mortality rates increases when the energy content of a resource decreases as its vulnerability increases. The non-linearity again arises from resource exclusion. When well-defended (low C) resources have high energy contents, they produce higher consumer population sizes at low mortalities, which allows exclusion of other resources over a wider range of mortalities. The opposite occurs when low vulnerability resources have low e-values; here the decelerating part of the N_{eq} vs. d relationship is restricted to the lowest range of mortalities. Figure 2B shows the impact of different functional relationships between r and x on the N_{eq} vs. d relationship. If $r(x)$ is proportional to $C(x)$, resource exclusion does not occur at any value of d, and, because of the linearity assumptions in MacArthur's model, the equilibrium consumer population decreases linearly with its own mortality. If r increases with x according to a different functional relationship than does C, the N_{eq} vs. d relationship becomes decelerating, with the degree of curvature increasing when a range of low-C resources have relatively large r-values. This combination promotes exclusion of other resources.

Cases in which r decreases with x were not considered in Fig. 2; r is usually expected to be positively correlated with C due to the commonly observed trade-offs between growth and defence (Lima, 1998). However, if it occurs, a negative relationship between r and C will greatly increase resource exclusion and thereby increase non-linearity (and this has been confirmed by numerical results). The low-C/high-r resources have a huge advantage in apparent competition, and produce exclusion of other resources even at moderate mortality rates.

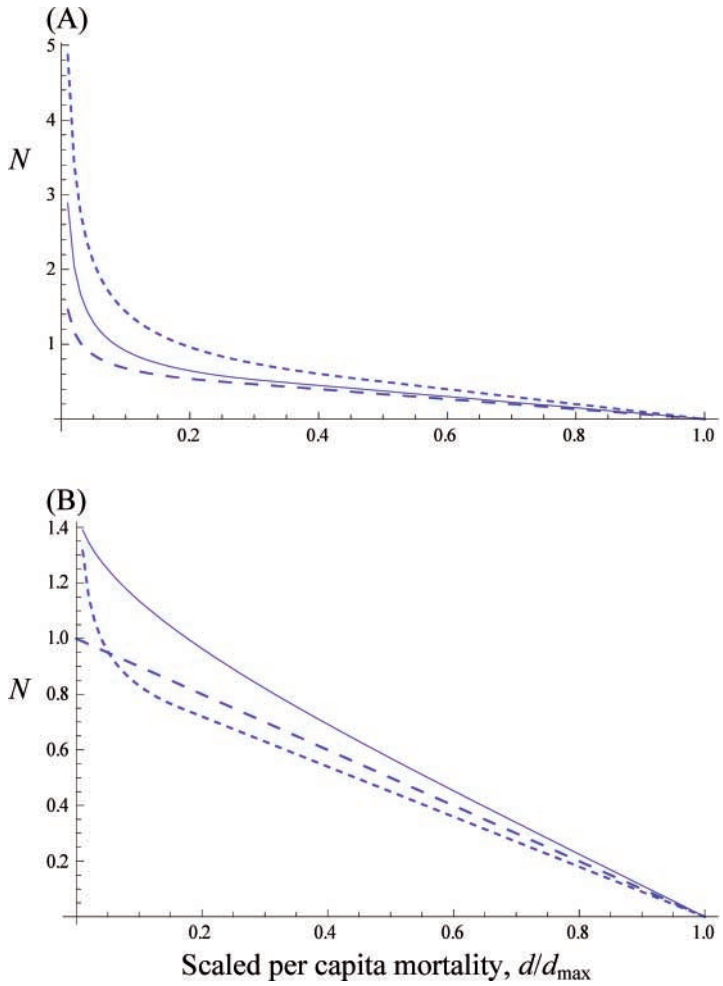

Fig. 2. (A) Consumer population size as a function of its scaled mortality for the continuous resource spectrum MacArthur model with different correlations between the consumer parameters C and e ($r(x) = 1$ for all x). $C(x)$ is represented by the linear function $C(x) = 2x$. The solid line represents a case where $e(x) = 1$ for all resources. The short-dashed line assumes $e(x) = 2(1 - x)$, and the long-dashed line assumes $e(x) = 2x$. Non-linearity is greatest and is present over the widest range of mortalities when e is negatively related to C (poorly caught resources are more valuable). The maximum mortality, d_{max}, is 1 for the solid line, 2/3 for the short-dashed line, and 4/3 for the long-dashed line. (B) Consumer population size as a function of scaled mortality when the maximum resource growth rate, r, varies with vulnerability. The vulnerability function is $C(x) = 2x$. The cases illustrated assume that: (1) r increases with x at the same rate as does C ($r(x) = 2x$; long-dashed line); (2) r increases at an accelerating rate ($r(x) = 3x^2$; solid line); and (3) r increases at a decelerating rate ($(3/2)\sqrt{x}$; short-dashed line). In all cases, $e(x) = 1$. The decelerating relationship for $r(x)$ given by the short-dashed line is characterized by resource exclusion over the broadest range of mortalities.

Non-logistic resources

One way to relax the several assumptions of linearity in MacArthur's model is to allow resource dynamics to be described by one of the following two models:

$$\frac{dR}{dt} = rR\left(1 - \left(\frac{R}{K}\right)^{\theta}\right)$$
$$\frac{dR}{dt} = I - ER \qquad \text{(3a, b)}$$

where equation (3a) is Gilpin and Ayala's (1973) θ-logistic model, which allows decelerating ($\theta < 1$) or accelerating ($\theta > 1$) density dependence in a self-reproducing resource. This model is almost universally used to represent non-linear density dependence in continuous-time models (e.g. Saether *et al.*, 1998; Abrams *et al.*, 2008; Filin *et al.*, 2008). Abrams (in press) shows that, in single-resource systems with linear functional responses, consumer density dependence is decelerating when $\theta < 1$ for the resource and accelerating when $\theta > 1$. Equation (3b) represents abiotic or chemostat growth for a renewing, but not self-reproducing, resource (MacArthur, 1972). Abrams (in press) shows that, in single-resource systems with linear functional responses, consumer density dependence is always decelerating when resource dynamics are given by equation (3b).

I first consider multiple resources whose growth is described by equation (3a) and which differ in vulnerability to the consumer. The range of mortalities producing resource exclusion increases relative to that shown in Fig. 1 if the resource dynamics are characterized by equation (3a) with $\theta > 1$. Figure 3 illustrates the N_{eq} vs. d relationships for $\theta = 2$ (dashed line) and $\theta = 4$ (solid line) for three different utilization functions (assuming $r = e = 1$). Figure 3C shows the special case with a flat utilization curve, which is equivalent in shape to the case of a single resource. Here, N_{eq} decreases at an accelerating rate across all values of d [as predicted by single-resource models (Abrams, in press)]. Figures 3A and 3B have higher maximum consumer population sizes than in Fig. 3C, and have an extended range of mortalities over which N_{eq} decreases with d at a decelerating rate (roughly $0 < d < 0.4$). Figures 3A and 3B exhibit an accelerating decrease in N_{eq} at the highest mortalities; this shape is predicted for models having a single resource which itself exhibits accelerating density dependence (Abrams, in press). The decelerating range in Figs. 3A and 3B corresponds to mortalities that are low enough to produce some resource exclusion. The range of mortalities with accelerating decreases in N_{eq} has less curvature in Figs. 3A and 3B than in Fig. 3C, due to increased vulnerability with increased d in the first two panels. If $\theta < 1$, single-resource models with linear consumer responses are characterized by a decelerating decrease in N_{eq} as d increases (Abrams, in press); the same is true of the many-resource models considered here, although the curvature is more pronounced at low mortalities. If the resources are described by the abiotic model (equation 3b), the N_{eq} vs. d curve is decelerating at all mortalities in single-resource models (Abrams, in press), but the presence of multiple resources only increases the curvature of this relationship by a small amount (results not shown).

These results show that the presence of multiple resources is likely either to produce or increase deceleration in the N_{eq} vs. d relationship at low mortalities. This relationship implies that per capita growth rate is a decelerating function of population size at high abundances.

Models with many resources and type-2 functional responses

In single-resource systems, a type-2 functional response often produces an accelerating decrease in equilibrium density with mortality when the interaction is stable (Abrams, 2002, in press). Thus, it is of interest to combine the type-2 response with multiple resources. The

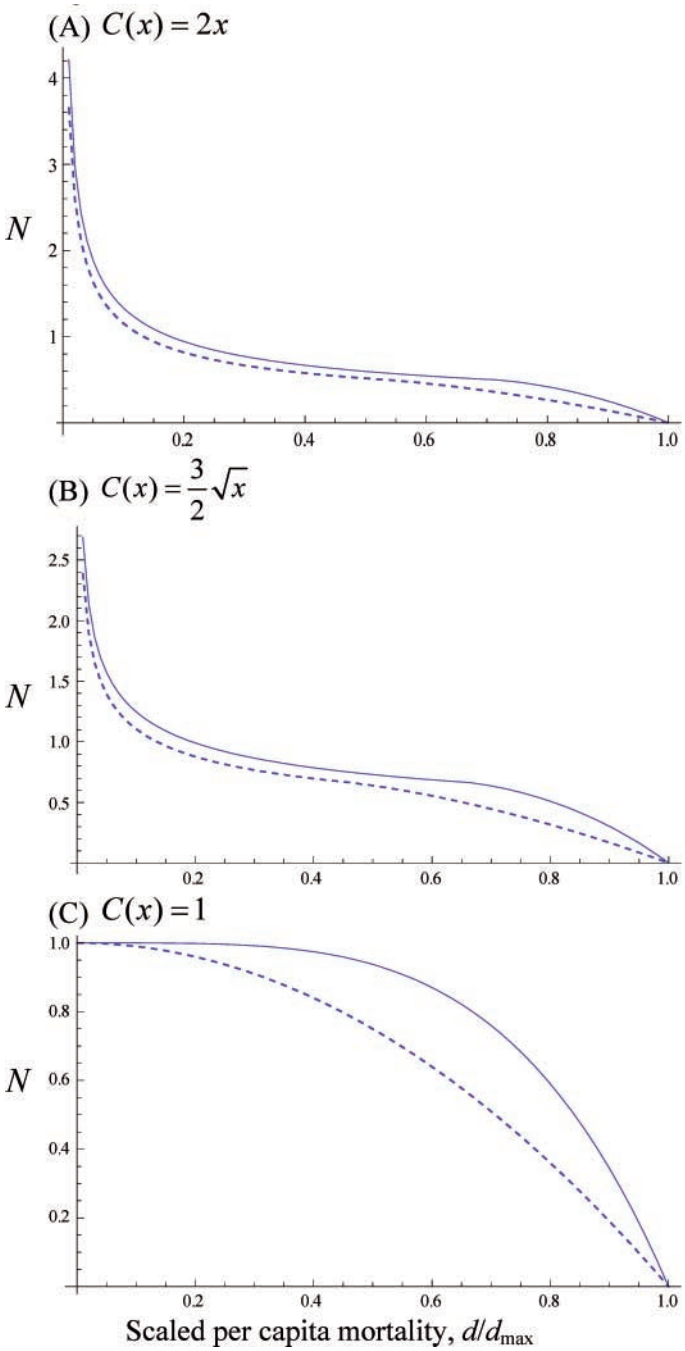

Fig. 3. Consumer population size as a function of mortality when resources are characterized by independent θ-logistic growth functions with $\theta = 4$ (solid line) or $\theta = 2$ (dashed line). Resources have identical growth parameters ($r(x) = e(x) = 1$). Panels (A)–(C) illustrate the relationships for the different utilization curves given. Note that the y-axis scales differ. Panel (C) represents a case where all resources are equally vulnerable to the consumer.

type-2 response produces frequency-dependent resource fitness because the predator's level of satiation depends on the mean vulnerability of all resources. Figure 4 shows three typical N_{eq} vs. d relationships for this type of system. All panels in Fig. 4 assume that each resource in the infinite array has an independent and identical logistic growth function. The consumer has a relatively large handling time, which is identical for all resources; nutritional value is also identical across resources. In Fig. 4A, the consumer has a linear utilization function, $C(x) = 2x$; in Fig. 4B, $C(x) = (3/2)\sqrt{x}$; and in Fig. 4C, $C(x) = 1$. In Figs. 4A and 4B, the lower range of mortality rates is characterized by a strongly decelerating decrease in N_{eq} within increasing d. The upper range of mortalities is characterized by an accelerating decrease in N_{eq}. The decelerating portion at low d is caused by resources returning from exclusion, resulting in an increase in the mean C.

In Figs. 4A and 4B, N_{eq} increases slightly with increasing mortality over an intermediate range of mortalities. Such an increase was termed a 'hydra effect' by Abrams and Matsuda (2005), and is usually associated with cyclic dynamics in models with a single resource (Abrams, 2002, 2009). The assumption of an effectively infinite number of resources in the present model makes it impossible to determine the exact dynamics in unstable cases. A similar model with eight resources was used to determine the stability of a system with parameters defined by the same $C(x)$ functions used in Figs. 4A and 4B. For the eight-resource model corresponding to Fig. 4A, the equilibrium was stable for all but a relatively small range of mortalities (roughly $d = 0.123$–0.130). The cycles that occurred within this range were small enough in amplitude that they did not greatly alter the mean consumer density. In the eight-resource system corresponding to Fig. 4B, the intermediate range of d producing instability was wider, but again the difference between mean and equilibrium densities was quite small. Cases with increasing N_{eq} vs. d relationships correspond to systems in which there would be alternative equilibria in the resource community if the consumer population was maintained at a constant size.

Figures 4A and 4B contrast markedly with Fig. 4C, which assumes that all resources have identical vulnerabilities, so no exclusion occurs at any mortality. Here the equilibrium population density increases over most of the range of consumer mortalities, and cycles occur over much of this range. The mean and equilibrium populations often differ significantly when single-resource systems (as in Fig. 4C) cycle. Low per capita mortalities do not produce the high consumer densities that occur when resource vulnerabilities differ significantly. Figure 4C has an identical N_{eq} vs. d relationship to a comparable single-resource model (Abrams, 2002, 2009).

Many other utilization functions could be explored in the context of type-2 responses. A range of numerical calculations suggests that the minimum value of $C(x)$ (i.e. $C(0)$) has the largest impact on the shape of the relationship between N_{eq} and d. The minimum $C(x)$ also has a significant impact on stability. A larger $C(0)$ reduces the range of low mortality values over which there is a decelerating decrease in N_{eq} with C, and increases the range of mortality rates over which N_{eq} is nearly constant or increases with C. The mortalities where N_{eq} increases with d usually have unstable equilibria. The effect of the minimum C is illustrated in Appendix 2.

The type-2 functional response also affects the N_{eq} vs. d relationship when resources vary in their maximum per capita growth rate, r, rather than vulnerability, C. Low-r resources are eliminated by apparent competition at low but not at high consumer mortality rates. As noted for linear response models, variation in r, by itself, has less of a qualitative effect on the relationship between consumer mortality and density than does variation in C.

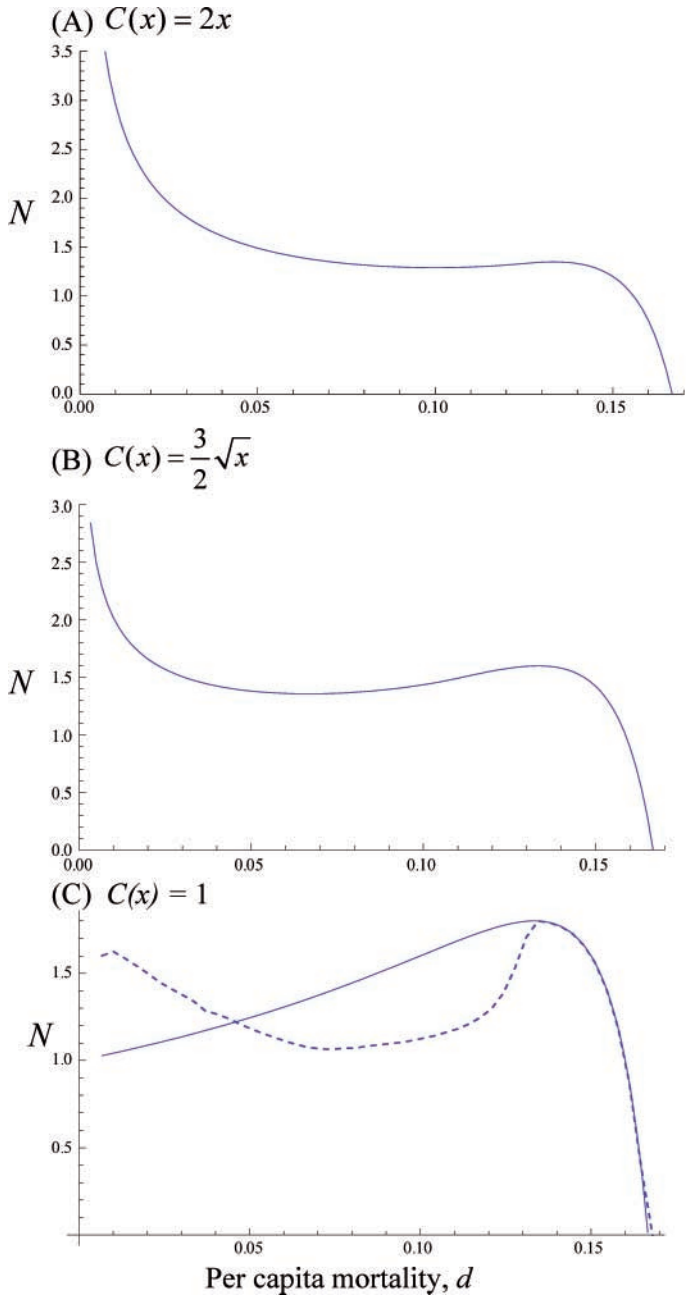

Fig. 4. Consumer population size as a function of mortality, given a type-2 functional response of the consumer (with handling time $h = 5$) and an infinite array of resources having identical logistic growth with $r = 1$. In (A), the consumer's utilization function is linear, as in Fig. 3A, while in (B), it has the square root formula assumed in Fig. 3B. In (C), all resources have $C(x) = 1$, and mean density (dashed line) differs significantly from the equilibrium density (solid line) in most cases with unstable dynamics. Mean density is sensitive to the resource immigration rate, which is $z = 10^{-7}$ in (C).

Appendix 3 presents an example of a system with variation in r rather than C for a consumer with a type-2 functional response identical to the response assumed in Fig. 4. In all cases illustrated in Appendix 3, equilibrium consumer density increases with mortality over most of the range of mortalities, but this increase is steepest when there is least variation in r between resources. A wider range of resource growth rates leads to more resources being excluded at low death rates, but the variation in r increases the size of the consumer population compared with cases with little variation in r. Greater population size is again a consequence of the extant resources experiencing less over-exploitation.

Models with two resources and non-linear functional responses

In assessing the impact of apparent competition, it is also important to consider systems with two resources. Not only is this the simplest possible multiple-resource system, but it may be the most common system in natural communities (Schoener, 1989). In such systems, the more resistant prey (resource) type may exclude the less resistant one at low consumer mortality rates; at high mortality rates, both prey (resources) will be present, but the consumer's dynamics is often dominated by the more vulnerable one. The resulting N_{eq} vs. d relationship is often characterized by several distinct segments. Figure 5 presents three examples, all of which assume that prey 1 has a much lower capture rate than prey 2 ($C_1 \ll C_2$). In Fig. 5A, the better-defended prey has a larger growth rate ($r_1 > r_2$). In Fig. 5B, the better-defended prey has an equal growth rate ($r_1 = r_2$). Finally, in Fig. 5C, the better-defended prey has a lower growth rate ($r_1 < r_2$). In all three cases, C_1 is large enough that the predator can persist on resource 1 alone over a significant range of low mortality rates. If r_1 is very small, the low-r/low-C species is a small part of the consumer's diet at all mortalities, so the system behaves similarly to one with a single resource. All panels in Fig. 5 are characterized by the near-exclusion of the less-defended resource 2 for a range of low mortalities, followed by an intermediate range of mortalities over which the relative density of the more vulnerable resource increases while that of the less vulnerable resource decreases. For this intermediate range of mortalities, the system is often unstable, and the mean consumer density is relatively insensitive to mortality. At the highest mortality levels, both resources increase in density with d, while the consumer decreases rapidly. The consumer functional response is nearly saturated in this zone, and the system has a stable equilibrium point. In all figures, stabilization of the dynamics (denoted by the dashed arrow) corresponds to a local maximum in population size. The increase in density with stabilization is particularly pronounced in Fig. 5C, in which the more vulnerable resource has a relatively large growth rate.

Figure 6 shows the yields corresponding to various harvest rates for the examples shown in Fig. 5, assuming a relatively low value of the natural mortality. The most notable feature here is the bimodality in Figs. 5A and 5B. In these cases, there is a local minimum in harvest, corresponding to the point where the more vulnerable resource returns to the system. The minimum is typically at a harvest rate close to 1/2 of the maximum rate allowing persistence. This is opposite to the pattern produced by logistic density dependence in which yield is maximized at 1/2 the maximum harvest rate.

The final example of a two-resource system is one in which the resources have different growth functions, logistic and abiotic. The presence of both types in the diet of a consumer is likely to be common. A variety of cases in which resources make transitions from invulnerable to vulnerable classes within a population result in approximately abiotic

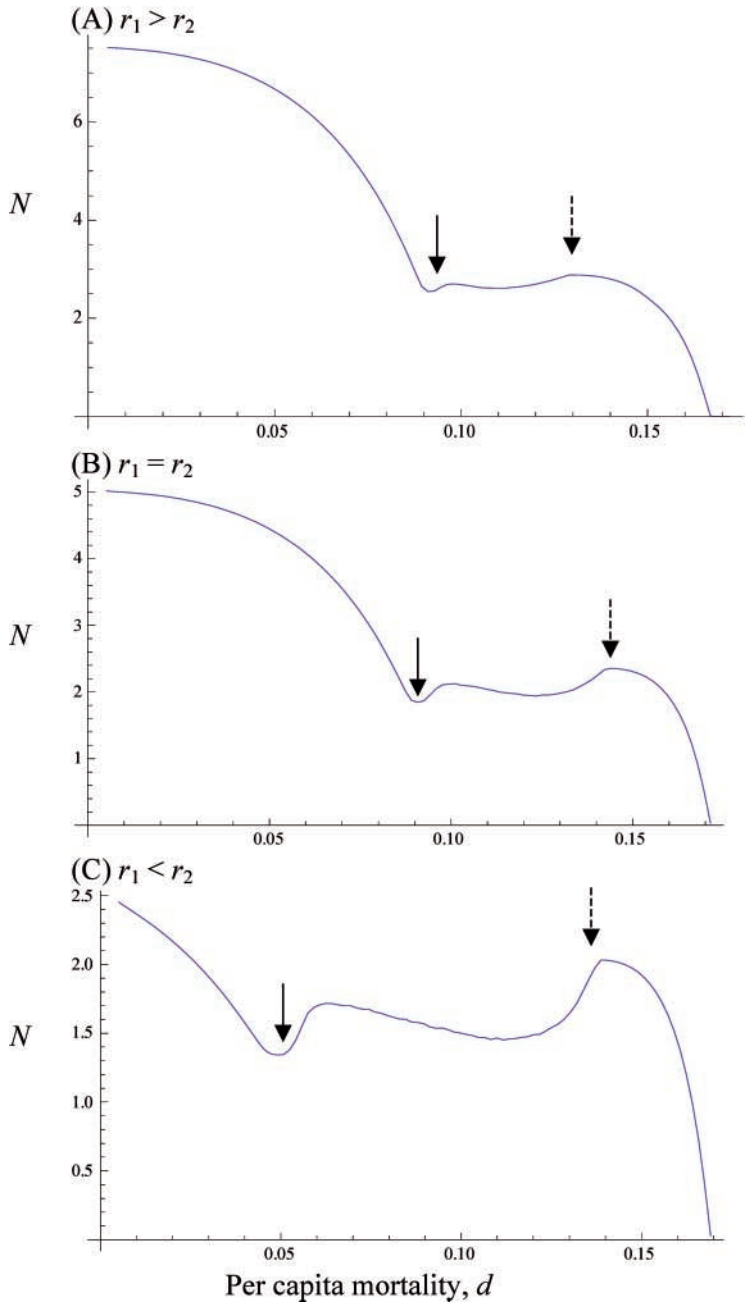

Fig. 5. Consumer population size (averaged over the course of a cycle for unstable systems) as a function of consumer per capita mortality rate, for systems with two logistic resources. The parameters that are common to all panels are: $b = 1$; $z = 0.0001$; $C_1 = 0.2$; $C_2 = 1$; $h = 5$; $r_2 = 1$. In (A) $r_1 = 1.5$, in (B) $r_1 = 1$ ($= r_2$), and in (C) $r_1 = 0.5$. The solid arrows show the point at which the more vulnerable resource (resource 2) is able to achieve significant densities, and the dashed arrows denote points at which the system becomes stable.

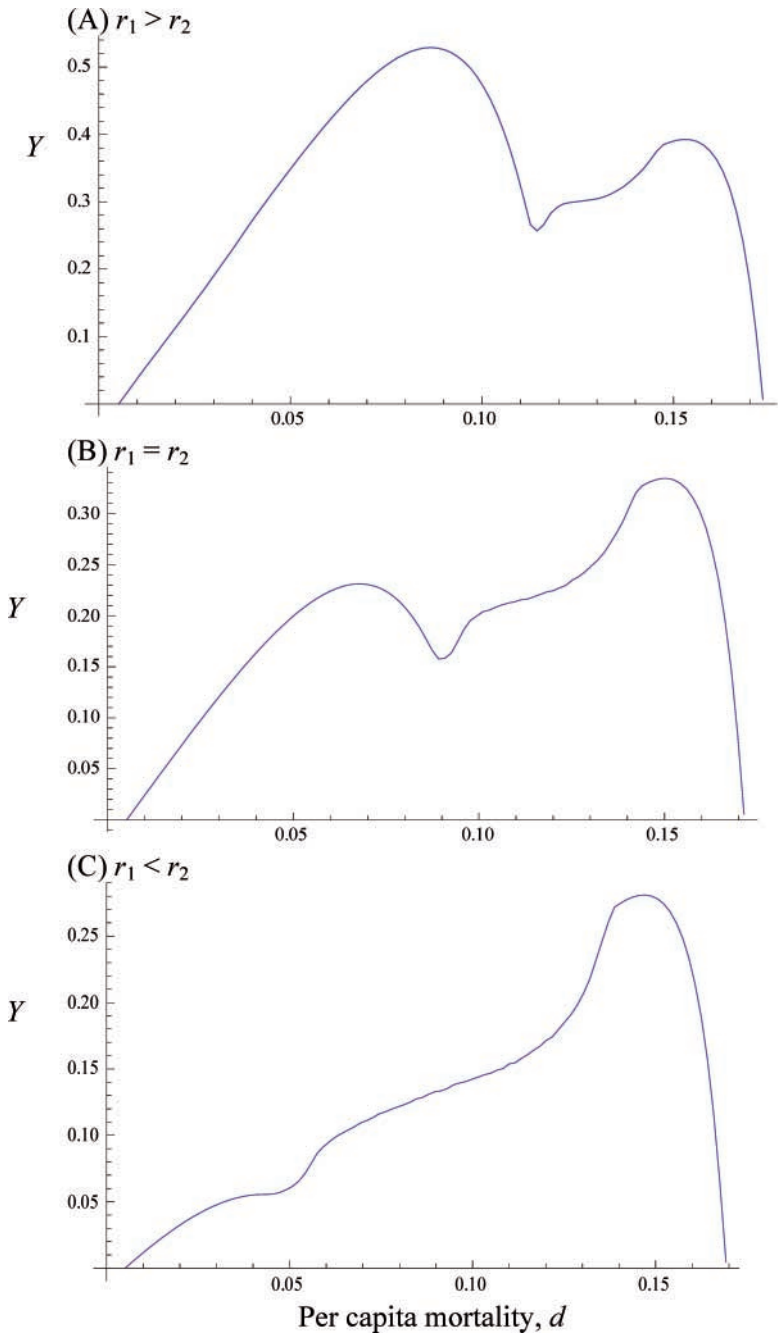

Fig. 6. The equilibrium yields (total harvest per unit time), Y_{eq}, as a function of mortality for the three systems illustrated in Fig. 5, assuming that natural mortality represents 3% of the maximum mortality that allows the consumer to exist.

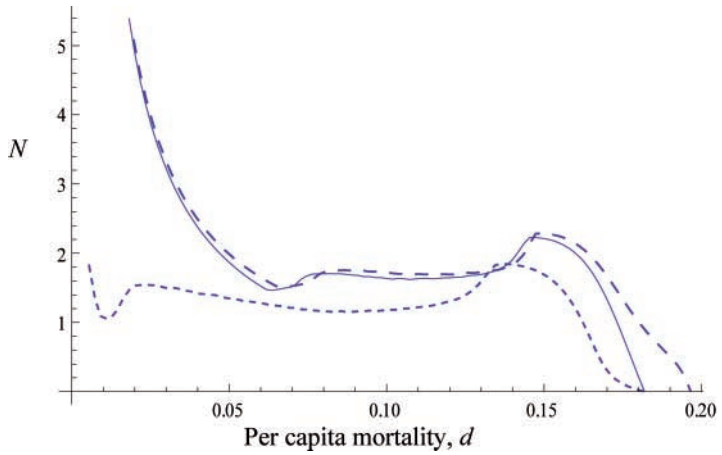

Fig. 7. Mean consumer population size as a function of mortality in a two-resource system in which resource 2 is abiotic (equation 3b) and resource 1 is logistic. The three lines correspond to different parameters of the abiotic growth model. Parameters common to all three lines are: $r_1 = 1$, $C_1 = C_2 = 1$, $h = 5$, $b = 1$, $z = 10^{-6}$. The solid line assumes $I = 0.1$ and $E = 0.1$; the short-dashed line assumes $I = 0.01$ and $E = 0.01$; and the long-dashed line assumes $I = 0.1$ and $E = 0.01$. The abiotic resource has the same equilibrium density as the biotic resource (= 1) for the first two pairs of parameters, but is ten times that of the biotic resource for the third (long-dashed line).

growth of the vulnerable class (Abrams and Walters, 1996). Figure 7 shows how population size changes with mortality for three different pairs of growth parameters for the abiotic resource. Except when the abiotic resource has an input rate much lower than the maximum growth rate of the abiotic model, the system is characterized by a decelerating decrease in N_{eq} with increasing mortality when the mortality rate is low. Abiotic resources in single-resource systems produce such decelerating decreases (Schoener, 1973; Abrams, in press), and the abiotic resource usually forms by far the largest part of the consumer's diet when consumer mortality is low. Because abiotic resources are renewed at a rate that is independent of their population size, they are better able to withstand the heavy predation that occurs when consumer mortality is low. When consumer mortality is high enough that the logistic resource contributes significantly to its diet, consumer population size becomes virtually independent of its mortality over a significant range of mortalities, but N_{eq} ultimately decreases at an accelerating rate at still higher mortalities.

Additional variations on the model

The models above suggest that changes in concavity with population density should characterize density dependence in most systems with multiple resources, and that apparent competition often results in decelerating density dependence at high population size. However, several factors have been left out of the above analysis, including nutritional interactions between the resources, non-linear numerical responses, real competition between resource species, and the presence of various types of adaptive behaviour in the consumer (e.g. switching and diet choice) or in the resource (e.g. flexible defence). All of these have been examined numerically for particular models, and will be the subjects of future articles. However, preliminary results suggest that the patterns shown here are at least

possible with all of these modifications. Predator-dependent functional responses (Abrams and Ginzburg, 2000; Skalski and Gilliam, 2001) may moderate the acceleration at high mortality in single-resource models (Abrams, in press), but little is known of the nature of predator-dependent responses in multiple-resource models. Non-linear numerical response functions (b in equations (1)) seem most likely to be saturating, which may increase the range of densities over which density dependence is accelerating, but is less likely to change the decelerating pattern at low consumer mortalities.

Allee Effects were not considered here. Such effects represent a reversal of the density dependence in which higher density increases the per capita growth rate. Allee Effects in the resource can produce increases in equilibrium consumer with increasing consumer mortality at low resource density in single-resource systems, even with linear consumer functional responses (Abrams, 2002). Apparent competition between two or more resources with Allee Effects is particularly likely to produce exclusion of low-growth or high-vulnerability resources at low consumer mortalities, so it is likely that many of the effects observed here would also be observed in such a system.

It is also important to extend the simple consumer–resource theory to help understand density dependence in structured populations. Lande *et al.* (2002a, 2002b, 2006), Coulson *et al.* (2008), and others have shown that the time lags due to life history are important in determining the dynamics of density-dependent populations. These models have lacked explicit resources. Recent work on *Daphnia* population cycles (McCauley *et al.*, 2008) suggests the possibility that lags due to the time required for resource re-growth and lags due to the consumer's life history may interact in complicated ways. Thus, although more work needs to be done, it is unlikely that a wider range of models will alter the general findings that changes in the sign of the curvature between different segments of the $N_{\mathbf{eq}}$ vs. d relationship are often more common than is a uniform curvature, and that apparent competition often generates decelerating density dependence at high consumer densities (low consumer mortalities).

DISCUSSION

I begin with some general remarks on the consumer–resource approach to density dependence, and some practical implications of the preceding results. This is followed by a comparison of the dynamics of generalist and specialist predator–prey systems. The discussion ends with a review of previous work related to the shape of density dependence.

The scarcity of consumer–resource models of density dependence (intra-specific competition) is fundamentally inconsistent with the prevalence of such models in studies of inter-specific competition (MacArthur, 1970, 1972; Schoener, 1986; Abrams *et al.*, 2008). This inconsistency has resulted in a less mechanistic approach to studies of density dependence. Models that include resources call attention to the fact that stochastic fluctuations in the population growth of a species may arise from impacts of environmental variation on parameters that are independent of resources, parameters that determine resource growth dynamics, and parameters that affect the interaction of resources and consumers. Thus, a meaningful statistical separation of the effects of environmental variation and density dependence – as has often been attempted (e.g. Saether *et al.*, 2002; Turchin, 2003) – is frequently impossible without knowledge of the type of stochasticity. Models that simply add a stochastic term to a fixed density-dependent growth function (e.g. Saether *et al.*, 2002) are not likely to make reliable predictions about the impact of environmental variation that directly affects resource dynamics.

Earlier work has tried to relate the form of density dependence to whether competition is contest or scramble (Royama, 1992; Sutherland, 1996) and whether organisms are large (or K selected) or small (r selected) (Fowler, 1981). Although there are some elements of mechanism in both approaches, neither provides an adequate general framework for understanding density dependence. Both 'contest' and 'scramble' competition assume division of a fixed amount of resources, which does not characterize competition for most renewing resources. The life-history distinctions are best represented in the simple unstructured models used here by differences in the shape of the numerical responses of the species, with convex responses being associated with larger or more K-selected species. As shown in Abrams (in press), convex numerical responses are likely to have an impact on density dependence similar to that of saturating functional responses.

The functional form of density dependence is important for many aspects of pure and applied population biology. If density dependence was uniformly decelerating (concave), it would mean that very small populations with per capita growth rates near zero would be buffered from extinction by the sharp rise in per capita growth rate expected at lower densities. Populations experiencing a variable environment will exhibit less variation in population size if their density dependence is decelerating. In fisheries, uniformly decelerating density dependence would mean that an exploited population currently at a small fraction of its unharvested density is more likely to withstand a significant increase in harvesting without extinction. The different views of Hilborn (2007) and of Hutchings and Reynolds (2004) on whether populations at 20% of their unharvested abundance are at risk of collapse (Hutchings and Reynolds) or simply optimally exploited (Hilborn) could be resolved (in Hilborn's favour) if density dependence was known to be strongly decelerating. The current results suggest that populations near 20% of their unharvested abundance are likely to be on the sharply accelerating part of the most common N vs. d relationship, and therefore to be at risk of extinction. This is true even though density dependence is likely to be concave at higher population densities.

Density dependence has a large impact on the range limits of species and on local adaptation of species in a spatially heterogeneous environment; Filin *et al*. (2008) show that local adaptation is much more likely when density dependence is decelerating. Deceleration magnifies the impact of gene flow in these models. In all of these cases, an accelerating relationship has effects that are opposite to those of decelerating relationships.

The two-resource models analysed here suggest that the yield versus harvesting effort relationship often has a local minimum when harvesting is close to half of its maximum level. This result is not confined to cases with exactly two resources, but is likely to apply to many systems in which resources have a bimodal distribution of vulnerability. An intermediate minimum is the opposite of standard theory in the fisheries literature, which typically assumes a parabolic relationship between yield and harvesting effort (e.g. Reynolds and Peres, 2006).

Thinking about density dependence in terms of consumer–resource relationships is likely to be essential in population viability analysis. The models presented here suggest that low population densities are often associated with saturated functional responses, implying a high sensitivity of the equilibrium population size to changes in any demographic parameter. However, before this result is applied to a small population, it is important to determine whether it is small because of high mortality or because environmental changes have reduced resource populations or altered their dynamics. The latter situations may imply a very different form of density dependence.

The models examined here predict that there often exists a range of intermediate mortality rates over which the consumer's equilibrium population is relatively insensitive to mortality. Population size may even increase with mortality. Both outcomes occur because increases in the average vulnerability and abundance of the resources present in the system, combined with the lower consumer attack rates entailed by a saturating functional response, compensate (or more than compensate) for the increased mortality. The potential for greater mortality to increase consumer population size has been noted in several previous articles (reviewed in Abrams, 2009). Abrams and Matsuda (2005) suggested that this phenomenon be called the 'hydra effect'. The present work has revealed several cases where hydra effects of small magnitude occur. However, it also suggests some potential reasons why this counterintuitive outcome may occur less often and/or be smaller in magnitude than previous models (with one or two resources) have suggested. The fact that highly defended resources are likely to dominate when consumer mortality is low means that the functional response is likely to be close to linear over all resource densities for these mortality rates, which prevents hydra effects. Appendix 2 shows that the magnitude of the hydra effect (the difference between the maximum population size and the unharvested population size) decreases steeply as the relative attack rate on the least vulnerable resource decreases. Comparing Fig. 4C with Figs. 4A and B also shows the reduction in the hydra effect caused by resources that differ in vulnerability to the consumer.

Stability in simple one-predator/one-prey models usually represents a balance between the stabilizing effect of prey density dependence, and the destabilizing effect of predator satiation. In these models, decreasing mortality can only destabilize a system; if limit cycles occur they will be observed at low, but not high, predator mortality rates. The same result follows from Rosenzweig and MacArthur's (1963) more general graphical analysis of predator–prey stability. However, the presence of many prey species that differ in vulnerability to the predator produces an additional stabilizing force that alters the relationship between mortality and stability. This force is the reduction in the average vulnerability of prey due to apparent competition, which becomes more intense as predator (consumer) mortality is reduced. This enhances stability relative to a situation in which all prey are characterized by the same vulnerability. Apparent competition also means that, when cycles occur, they are most likely to occur at intermediate mortality rates. Murdoch *et al*. (2002, 2003) speculated that generalist consumers are more stable than specialists because a predator with many prey would not be tightly coupled to any one. The models of generalists presented here suggest a different explanation for the stability of generalists. Generalists may often have tight coupling with some prey, but these prey are likely to be depleted or excluded by apparent competition when predator mortality is low.

The nature of density dependence in prey species has received relatively little attention in models of evolution or co-evolution in predator–prey systems. The usual assumption is that prey have logistic growth, and that one of the logistic growth parameters is reduced when vulnerability to the predator decreases (e.g. Brown and Vincent, 1987, 1992; Abrams and Matsuda, 1997). The results presented here suggest that the nature of density dependence in the prey will change as a function of the mortality imposed by the predator. It will require considerable additional work to determine how evolutionarily stable states (Vincent and Brown, 2005) differ between traditional predator–prey models, and models in which the prey are themselves consumers of multiple resources.

The apparent competition between resources (prey) that underlies the consumer (predator) density dependence is essentially a 'game' played between prey types in which the

vulnerability of a particular prey type influences the predator population size, and thereby the fitness of other prey types with different vulnerabilities. The difference between these models and traditional models of prey evolution in a predator–prey system is simply that the different prey types were assumed not to compete directly in the current analysis, while they are usually assumed to be complete competitors in most evolutionary models (Abrams and Matsuda, 1997; Vincent and Brown, 2005). This difference in assumptions is likely to have little impact on the relationship between predator mortality and predator population size because the average level of defence of the set of prey types will decrease with increasing predator mortality in both cases. The similarities between purely ecological multi-species models and analogous 'multi-genotype' models in evolutionary ecology deserves more detailed study.

Currently, density dependence in continuous-time models is usually represented by the logistic or θ-logistic (Gilpin and Ayala, 1973) function. These can neither produce hydra effects (which are possible in most consumer–resource models) nor represent cases where the curvature of the per capita growth rate changes with population size. Because the presence of multiple resources that differ in vulnerability usually produces a decelerating $N_{\mathbf{eq}}$ vs. d relationship at low d, and saturating functional responses produce an accelerating relationship at high d, a change in curvature is likely to be the most common form of density dependence in generalist species. Models with a small number of resources (e.g. two) produce an even wider variety of forms of density dependence than do the models with a continuous array of resources. All of this argues against basing management decisions on the logistic or theta-logistic model.

Most previous work has attempted to deduce the shape of density dependence using time-series analysis of natural population fluctuations (Diserud and Engen, 2000; Saether *et al.*, 2002; Sibly *et al.*, 2005). Problems with this approach were mentioned in the Introduction. Saether *et al.* (2002) and Sibly *et al.* (2005) found that a majority of species were characterized by decelerating (concave) density dependence. This is consistent with the present analysis, because most measurements are likely to have been made on species at moderate or high densities, where the present models predict a concave relationship. However, the present models also suggest that that relationship will change to convex at low densities for any species with saturating functional (or numerical) responses. The limitations of time-series analysis and the lack of such data for most species suggests that deductive approaches, similar to those employed here, will be needed to determine the likely shape of density dependence.

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APPENDIX 1

Range of resources excluded by apparent competition, given a continuous resource spectrum

The range of resources excluded by apparent competition may be determined by jointly solving two equations. The case illustrated here assumes linear functional responses and that r is identical for all resources. The consumer population reaches equilibrium when

$$\int_0^y e(x)C(x)(r - C(x)N)dx = d \tag{A1}$$

where y is the value of the vulnerability parameter above which resources are excluded and N is the equilibrium consumer population size. By definition, the value of y must satisfy the equation $r - C(y)N = 0$, and this equation may be solved to give $N_{eq} = r/C(y)$. Substituting $r/C(y)$ for N in equation (A1) yields an integral equation for y in terms of d, and (because the range of x is from 0 to 1) $1 - y$ gives the fraction of resources that are excluded by apparent competition. If the equation does not have a solution for $y < 1$, then no resources are excluded. For example, if $e(x) = 1$, $r = 1$, and $C(x) = 2x$ (as for the solid line in Fig. 1), the solution is $y = \sqrt{(3d)}$. This means that some resources are excluded at equilibrium for $d < 1/3$, and that, at $d = 0.05$ (the short dashed line in Fig. 1), approximately 61% of the resources are excluded.

APPENDIX 2

The impact of the range of $C(x)$-values in the utilization curve on the shape of consumer density dependence can be explored by changing the example used in Fig. 4A so that $C(x) = C(0) + 2(1 - C(0))x$, where $C(0)$ is the minimum value of $C(x)$. Figure 4A represents the case of $C(0) = 0$. All other parameters are identical to Fig. 4A, which assumes a type-2 functional response with $h = 5$.

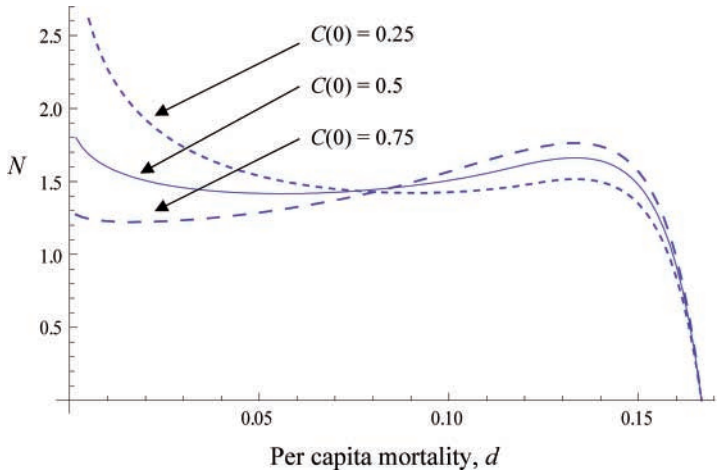

Fig. A2

APPENDIX 3

The impact of the range of $r(x)$-values on the mortality versus consumer population size relationship in a system where $C(x) = 1$ for all consumers. The different functions describing r as a function of position, x on the resource axis ($0 < x < 1$), are given in Fig. A3. All other parameters are identical to Fig. 4C, which assumes a type-2 functional response with $h = 5$; the $r(x) = 1$ curve is identical to the curve in Fig. 4C

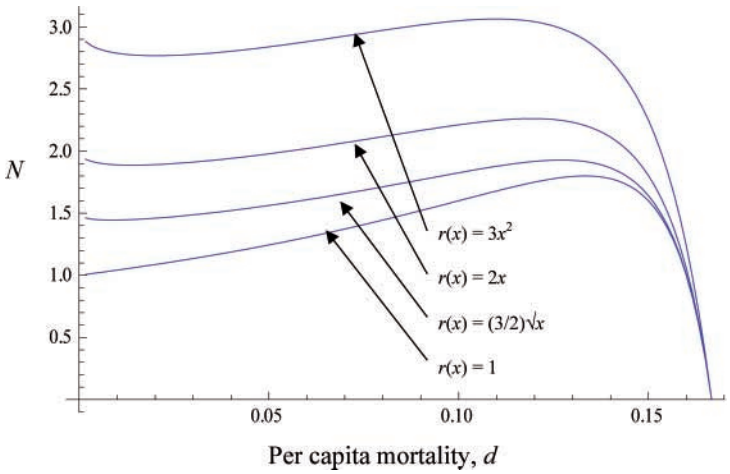

Fig. A3