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Grazers and Diggers: Exploitation Competition and Coexistence among Foragers with Different Feeding Strategies on a Single Resource

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ABSTRACT: A mathematical model is presented that describes a system where two consumer species compete exploitatively for a single renewable resource. The resource is distributed in a patchy but homogeneous environment; that is, all patches are intrinsically identical. The two consumer species are referred to as diggers and grazers, where diggers deplete the resource within a patch to lower densities than grazers. We show that the two distinct feeding strategies can produce a heterogeneous resource distribution that enables their coexistence. Coexistence requires that grazers must either move faster than diggers between patches or convert the resources to population growth much more efficiently than diggers. The model shows that the functional form of resource renewal within a patch is also important for coexistence. These results contrast with theory that considers exploitation competition for a single resource when the resource is assumed to be well mixed throughout the system.

Keywords: exploitation competition, foraging, coexistence, invasion analysis.

Understanding the mechanisms that allow species coexistence remains a key topic in community ecology. The mathematical model of Volterra (1926) was the first to suggest that the indefinite coexistence of more than one species on the same resource was impossible. This result was then expanded, and the competitive exclusion principle (Hardin 1960) was proposed, which stated that n species could not coexist on $<n$ resources. In order to apply this principle, a clear way in which to identify distinct resources and consumers is required (Haigh and Maynard Smith 1972; Schoener 1974; Levins 1979), as well as a clear definition of coexistence (Koch 1974; Hsu et al. 1978; Armstrong and McGehee 1980; Smith and Waltman 1995). There have been numerous theoretical studies where models have apparently violated the competitive exclusion principle. Competing species can coexist if mechanisms are present that effectively increase the number of resources present and/or allow populations to exhibit stable cyclic behavior. Examples include resource partitioning of the same prey item (Haigh and Maynard Smith 1972; Schoener 1974), interspecific variation during the resource's life cycle (Briggs 1993; Briggs et al. 1993), life-history variation among the consumers (McCann 1998), temporal fluctuations in environmental conditions (Koch 1974; Levins 1979; Turelli 1981; Abrams 1984; Chesson 1990), disturbance (Hastings 1980), interference competition (Vance 1985; Fishman 1997), and spatial structuring of the habitat (Tilman 1994).

In this article we investigate whether two species (or phenotypes) that differ in their strategies for resource exploitation can coexist in a system where they both utilize the same resource. We assume the resource is distributed in a patchy but homogeneous environment; that is, all patches are intrinsically identical. The two species differ in the degree to which they deplete resources within a patch and hence differ in their feeding strategy. The species that depletes the resource to lower levels is termed the "digger" species; the other is termed the "grazer" species. An important assumption we make is that the two species interact only through exploitation competition (Milinski and Parker 1991). There is no direct interference between individuals, all interactions occur through each species' influence on a shared food resource. Schmitt (1996) has studied an example of such a system, where two species

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of benthic marine snails, *Tegula aureotincta* and *Tegula eiseni*, compete for microalgae. Differences in the foraging morphologies of the two snails have been shown to have different effects on the distribution of the algal resource. *Tegula eiseni* was found to be capable of reducing algal densities to lower levels than *T. aureotincta.* Nectarivores are another example of a group of consumers that often appear to interact through exploitation competition. Laverty and Plowright (1985) studied a system where two species of bumblebee and a hummingbird compete for nectar in jewelweed. In this example the consumer species were found to differ in the depth to which they could drain the nectar spur and also the rate at which they visited flowers (Laverty and Plowright 1985).

Possingham (1987) constructed a mathematical model of nectarivore competition (which was assumed to be exploitative) and showed that two consumer species, which differed in their ability to deplete nectar from a flower, could coexist on a single flower species. Coexistence was dependent on the competitive ability of both species, which was defined as the mean net energy gained per calorie extracted from a flower, divided by the cost of using each flower. Wilson et al. (1999) fitted a similar mathematical model, which described the dynamics of two benthic grazers competing for algae, to data collected by Schmitt (1996). Although the model required a number of parameters, the data were sufficient to give estimates to all parameters but one. The best fit was found to lie very close to a region of coexistence. Given the uncertainty in the fitted parameters, the model predictions were not inconsistent with observed coexistence in the field (Schmitt 1996). In this article we have reviewed, generalized, and extended the work of Possingham (1987) and Wilson et al. (1999) by investigating how the model of resource renewal affects coexistence.

We present a mathematical model that describes the dynamics of the two consumer species and the shared resource. The habitat is assumed to be made up of a large number of identical patches, each containing a renewing resource. Each patch is sufficiently small so that its resource drops rapidly whenever a consumer visits and then recovers relatively slowly between visits. Both consumer species visit patches in a random manner. This form of consumer-resource interaction has been shown in previous work to have a stabilizing effect on consumer-resource dynamics (Nisbet et al. 1997, 1998). We use invasibility analyses to identify the outcome of exploitation competition. In most cases one of the two species is predicted to displace the other; however, coexistence can occur over a relatively small range of parameter values. It is important to note that coexistence in our model does not occur because of any intrinsic patch heterogeneity. Differences in the resource abundance among patches are created by the contrasting feeding strategies of the two competing species and the dynamics of resource renewal. Coexistence can occur because each consumer does not encounter a fixed amount of resource when it visits a patch but an amount that depends on the time since the last consumer's visit and its type. Hence, consumers encounter resource levels described by a probability density function, which effectively increases the number of resource types. The digger species can often persist because it can exploit resources that the grazer species cannot reach. The grazer species can also persist if it moves faster among patches than the digger species and encounters patches that have not been recently visited by diggers. In doing so the grazer species can often reduce the mean resource abundance within the system so that it stops the diggers from taking over. We also find that the dynamics of resource renewal play an important role in determining the outcome of exploitation competition.

The Model

We consider a habitat that contains a large number of identical small patches each containing a resource of density x. There are two species of consumers, which we refer to as diggers and grazers. Grazers (G) can only consume resources on a patch whose density exceeds x_G, and when a grazer visits such a patch, its density drops to x_G. Diggers (D) consume resources in a similar manner, reducing the resources in a patch to level x_D. They may eat resources on patches that have a lower density than that accessible to the grazers so that $x_D < x_G$. We assume that patch size is sufficiently small so the timescale at which patches are depleted of resources is fast compared with the timescale of resource renewal (Possingham 1988). A patch can be in one of two states, depending on the amount of resource it contains. The state of a patch is dependent on the time since it was last visited by a consumer and the species of the last visitor. Patches that have a resource density $>x_D$ and $< x_G$ are referred to as low-density patches (L-patches), and patches that have a resource density $>x_G$ are referred to as high-density patches (H-patches). Consumers are assumed to move randomly among patches. The resource in a patch renews according to the following equation:

$$\frac{dx}{dt} = r(x). \tag{1}$$

Hence, renewal is a continuous process that depends on the current resource density within the patch. Renewal may be due to local processes (e.g., regrowth or resource production) or resource immigration from sources that are external to the habitat.

As well as their state, patches are also characterized by their age, a. The age of an L-patch is the time that has elapsed since the patch was last visited by a digger. The age of an H-patch is the time since its density was x_G. This density occurs either when the patch is visited by a grazer or when the density on an L-patch renews and reaches x_G. Denote by τ the time it takes for the resource on an L-patch to renew from x_D to x_G. This time interval is obtained by solving

$$\int_0^{\tau} r(x(a))da = x_G - x_D. \tag{2}$$

Note that $x(0) = x_D$, $x(\tau) = x_G$, and all L-patches have an age $<\tau$.

In order to describe resource and consumer dynamics, we keep track of the age distribution of patches. The fraction of the L-patches at time t that are aged between a and $a + da$, is $n_L(a, t)\,da$. Similar notation is used to represent the age distribution of the H-patches. The fraction of all patches that are L-patches and the fraction of all patches that are H-patches at time t are denoted $N_L(t)$ and $N_H(t)$, respectively. These fractions can be calculated using

$$N_L(t) = \int_0^{\tau} n_L(a, t)da, \tag{3}$$

$$N_H(t) = \int_0^{\infty} n_H(a, t)da. \tag{4}$$

Note that $N_L(t) + N_H(t) = 1$ for all time t.

The resource density within L-patches and H-patches, which are of age a, are denoted $x_L(a)$ and $x_H(a)$, respectively. The average resource density within L-patches and H-patches at time t can be calculated from the following equations:

$$X_L(t) = \int_0^{\tau} n_L(a, t)x_L(a)da/N_L(t), \tag{5}$$

$$X_H(t) = \int_0^{\infty} n_H(a, t)x_H(a)da/N_H(t). \tag{6}$$

Resource dynamics are governed by the following equations:

$$\frac{\partial n_L}{\partial t} + \frac{\partial n_L}{\partial a} = -\mu(t)n_L, \tag{7}$$

$$\frac{\partial n_H}{\partial t} + \frac{\partial n_H}{\partial a} = -(\mu(t) + \nu(t))n_H, \tag{8}$$

$$\frac{dx_L}{dt} = r(x_L), \tag{9}$$

$$\frac{dx_H}{dt} = r(x_H), \tag{10}$$

where $\mu(t)$ and $\nu(t)$ are the rates that all patches are visited by the digger and grazer populations at time t, respectively. These four equations are associated with the following boundary conditions:

$$n_L(0, t) = \mu(t), \tag{11}$$

$$n_H(0, t) = n_L(\tau, t) + \nu(t)N_H(t), \tag{12}$$

$$x_L(0) = x_D, \tag{13}$$

$$x_H(0) = x_G. \tag{14}$$

Equation (11) expresses the fact that the rate of creation of age-0 L-patches at any time is equal to the rate that all patches are visited by diggers. Equation (12) arises because the rate of creation of age-0 H-patches is equal to the rate that L-patches change their state (which occurs when they have survived to age τ) plus the rate that grazers visit H-patches.

The variables $D(t)$ and $G(t)$ represent the density of diggers and grazers, respectively. Because all individuals in the system move randomly from patch to patch and movements are independent of the presence of other individuals, patches are visited by the consumers at a rate that is proportional to the number of consumers. When individual diggers and grazers are searching for patches, they encounter them at rates σ_D and σ_G, respectively. Both species exhibit a Holling Type II functional response when seeking and handling the resource. The parameter h is the average time a consumer takes to handle a unit of resource, which we assume is the same for both consumer species. If the number of patches is large compared to the number of consumers, then the patch-encounter rates exerted by the digger and grazer populations can be approximated by the following (Nisbet et al. 1997, 1998):

$$\mu(t) = \frac{\sigma_D D(t)}{1 + \sigma_D h[N_L(t)X_L(t) + N_H(t)X_H(t) - x_D]}, \tag{15}$$

$$\nu(t) = \frac{\sigma_G G(t)}{1 + \sigma_G h N_H(t)[X_H(t) - x_G]}. \tag{16}$$

Note that in this model grazers may visit patches that contain a resource density too low for them to consume.

We assume constant conversion efficiencies of resource to consumer numbers, ε_D and ε_G. Both species have constant per capita death rates, δ_D and δ_G. Consumer dynamics come from the two ordinary differential equations (ODEs),

$$\frac{dD}{dt} = \left[\frac{\varepsilon_D\sigma_D(N_LX_L + N_HX_H - x_D)}{1 + \sigma_D h(N_LX_L + N_HX_H - x_D)} - \delta_D\right]D, \quad (17)$$

$$\frac{dG}{dt} = \left[\frac{\varepsilon_G\sigma_G N_H(X_H - x_G)}{1 + \sigma_G h N_H(X_H - x_G)} - \delta_G\right]G. \quad (18)$$

Note that we have assumed there is no direct intraspecific or interspecific competition for the resource in these equations. Consumer growth rates are only directly regulated by the distribution of the resource, which is regulated by the two populations.

Invasion Analysis

In this section we examine under what conditions, if any, the two consumer species can coexist. To do this we use the technique termed "invasion analysis" (MacArthur and Levins 1967; Turelli 1981). We first let one species establish itself within the environment and come to equilibrium. We next examine whether the population size of the second species will increase when it is placed within the environment at low densities (i.e., we see whether it can invade). We then repeat this with the role of both species reversed. Coexistence occurs when both species can invade each other when the resident is well established.

To show coexistence is possible, we need to show that both species can become well established in the absence of the other (Turelli 1981). To show this is indeed true for the model presented here, we rewrite the model in terms of coupled time-dependent ODEs and use this formulation to show that there exists a unique globally stable nontrivial equilibrium population size and resource distribution (see app. A). Stability of the equilibrium with only one consumer present is assumed in the analysis to follow.

Grazers Invading Diggers

First, we assume that only diggers are present and the system is at equilibrium. We can calculate resource densities within patches using $x_L(a) = x(a)$ and $x_H(a) = x(a + \tau)$, where $x(a)$ is the solution to $dx/da = r(x)$ subject to $x(0) = x_D$. Because movement among patches is random, all patches, irrespective of their age or state, experience the same risk of a visit from a digger. As a result, the distribution of patch ages is described by an exponential density function (Nisbet et al. 1997). The associated steady state distributions for $n_L(a, t)$ and $n_H(a, t)$ are defined and given by

$$n_L^*(a) = \mu^* \exp(-\mu^* a) \qquad 0 \le a \le \tau, \quad (19)$$

$$n_H^*(a) = \mu^* \exp[-\mu^*(a + \tau)] \qquad a \ge 0, \quad (20)$$

where μ^* is the equilibrium patch visitation rate of the digger population. Later we will show how this rate can be calculated.

The average resource density in patches at steady state, which we denote X_D^*, can be calculated from the above steady state distributions:

$$X_D^* = \int_0^\tau n_L^*(a)x_L(a)da + \int_0^\infty n_H^*(a)x_H(a)da, \quad (21)$$

$$= \int_0^\infty \mu^* \exp(-\mu^* a)x(a)da. \quad (22)$$

We also know from equation (17) that at steady state,

$$N_L^*X_L^* + N_H^*X_H^* = Q_D + x_D, \quad (23)$$

where $Q_D = \delta_D/[\sigma_D(\varepsilon_D - h\delta_D)]$ and the star notation indicates steady state values. The left-hand side of equation (23) is simply the average resource density among all patches, X_D^*. This density must be $>x_D$, which means Q_D must be positive or equivalently $\varepsilon_D > h\delta_D$. If this condition is not true, the digger population cannot persist. When we combine equation (22) with equation (23) we get an implicit formula for calculating μ^*, namely,

$$\int_0^\infty \mu^* \exp(-\mu^* a)x(a)da = Q_D + x_D. \quad (24)$$

Equation (23) tells us that the average density of resource among all patches, when only diggers are in the system, is independent of the assumptions on resource renewal. However, the fraction of patches that are L-patches and the fraction that are H-patches, at equilibrium, is dependent on the assumption about resource renewal. This dependence can be seen by noting that the patch-visiting rate of the diggers, μ^*, is dependent on $x(a)$ in equation (24).

Grazers can invade if, in equation (18), $dG/dt > 0$, when the resource is in the steady state distribution associated with the digger-only state. This is true when

$$Q_G < N_H^*(X_H^* - x_G), \quad (25)$$

where $Q_G = \delta_G/[\sigma_G(\varepsilon_G - h\delta_G)]$. We can expand the previous equation to give the following condition for invasion:

$$Q_G < \int_{\tau}^{\infty} \mu^* \exp(-\mu^* a)(x(a) - x_G)da. \tag{26}$$

In order to determine whether the grazer species can invade the digger species when resources renew according to some function r, we first evaluate the steady state patch-visitation rate of the digger population, μ^*, using equation (24). Next, we use this visitation rate in equation (26) and see whether the invasion condition is satisfied.

Diggers Invading Grazers

When only grazers are present and the population has reached steady state, all patches have a resource density of at least x_G, so $N_L^* = 0$ and $N_H^* = 1$. From equation (18), we know that $N_H^*(X_H^* - x_G) = Q_G$; hence,

$$X_H^* = Q_G + x_G \tag{27}$$

is the average resource density among patches. Diggers can invade the system if

$$Q_D < N_L^* X_L^* + N_H^* X_H^* - x_D. \tag{28}$$

Substituting equation (27) into equation (28) gives the following invasion condition:

$$Q_D < Q_G + x_G - x_D, \tag{29}$$

which is independent of the assumption on resource renewal. The important feature for invasion is the difference in the depletion levels of the two competitors.

Results

In this section we investigate three models that describe resource renewal. For each of these models, we determine whether coexistence of the grazer and digger species is possible using the invasion conditions derived in the previous section.

Linear Renewal

The simplest assumption about resource renewal is that it occurs at some constant rate, r_0, and resources remain viable until they are consumed. The renewal function is

$$r(x) = r_0. \tag{30}$$

Suppose there are only diggers present, then the resource density on a patch of age a is

$$x(a) = x_D + r_0 a. \tag{31}$$

The time for the resource on a patch to renew from level x_D to level x_G is $\tau = (x_G - x_D)/r_0$. Substituting the above renewal function into equation (24) gives $\mu^* = r_0/Q_D$. When this rate is then substituted into equation (26), we get the following condition for grazers to invade diggers,

$$Q_G < Q_D \exp[-(x_G - x_D)/Q_D]. \tag{32}$$

Note that this condition is independent of the renewal rate, r_0. The condition for diggers to invade grazers is given by equation (29). It can be easily shown that for all $x_G > x_D$, there exist pairs (Q_D, Q_G) that satisfy both invasion conditions. Hence, if resource renewal is linear and unbounded, then diggers and grazers may coexist. An example of this model is presented in figure 1*A*, which shows when coexistence occurs and when either the digger or the grazer excludes the other. We have confirmed the locations of the boundaries in figure 1*A* using an explicit numerical solution to the dynamic equations.

Free-Space Renewal

An alternative formulation for the rate of renewal is

$$r(x) = r_0\left(1 - \frac{x}{K}\right). \tag{33}$$

This can describe a number of situations where, in the absence of consumers, the resource density approaches some density, K. One example of such a situation is when resources renew at a constant rate, as in the previous model, but now resources become nonviable at some constant rate. An example of this process is aerial insects that have fallen onto water being washed up along a riverbank at a constant rate and then washed away at some constant per capita rate (Davies and Houston 1981). Alternatively, this model can be used to describe the process where resource particles enter a patch at a fixed rate but only establish within the patch if they happen to land on a section of the patch that is not currently occupied by another resource particle. This process is often referred to as free-space recruitment and has been applied to models that describe population dynamics of benthic marine invertebrates (e.g., Roughgarden 1997 and references within). In this case the parameter K is often referred to as the patch-carrying capacity.

This renewal model gives the following:

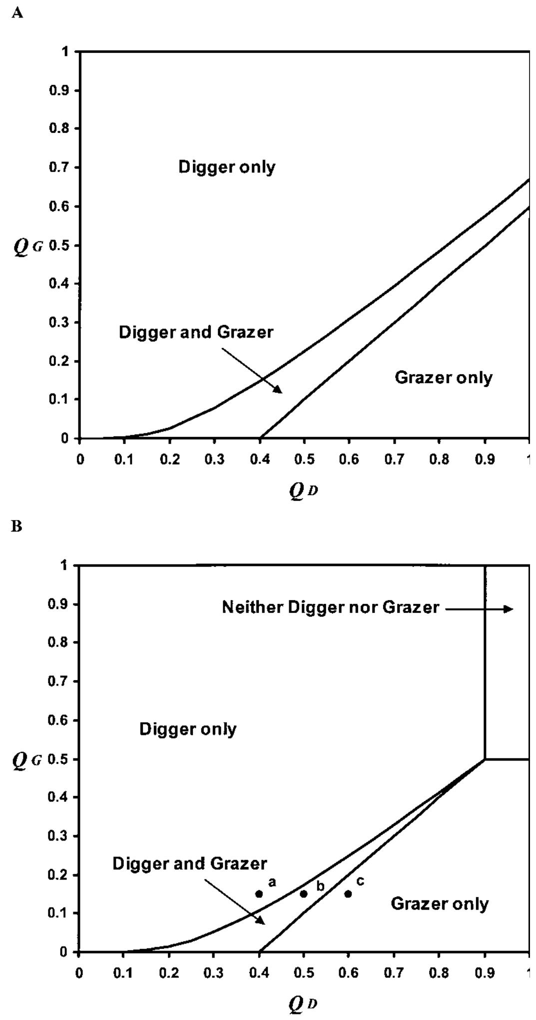

Figure 1: Coexistence regions when resource renewal is (*A*) linear and (*B*) free space (carrying capacity, $K = 1$). In both examples, the digger and grazer resource thresholds are given by $x_D = 0.1$ and $x_G = 0.5$.

$$x(a) = K - (K - x_D)\exp(-r_0 a/K), \tag{34}$$

$$\tau = \frac{K}{r_0}\ln\left(\frac{K - x_D}{K - x_G}\right), \tag{35}$$

$$\mu^* = \frac{r_0}{Q_D K}(K - x_D - Q_D). \tag{36}$$

The condition for grazers to invade diggers can be shown to be

$$Q_G < Q_D\left(\frac{K - x_D}{K - x_G}\right)^{-(K-x_D)/Q_D}. \tag{37}$$

Again, note that this condition is independent of the parameter r_0. The rate at which the resource approaches the carrying capacity has no influence on whether the digger population will be invaded; however, the success of invasion is influenced by the carrying capacity. The presence of a carrying capacity means we have extra conditions about when the grazers and diggers can persist in the system. From equation (17) it can be shown that the growth rate of the digger population is never positive and, hence, cannot persist if $Q_D > K - x_D$. Similarly, the grazer population cannot persist if $Q_G > K - x_G$. Thus, for any given K, there now exists a region in the (Q_D, Q_G) plane where neither the digger nor the grazer can persist. As with the previous model on resource renewal, it can be shown that for this model, pairs (Q_D, Q_G) exist that satisfy both invasion conditions; therefore, coexistence is possible. An example of the coexistence region for this model is presented in figure 1*B*.

Three examples of consumer-resource dynamics are presented in figure 2. The grazer species is characterized by the same parameter values in each example (table 1) and is associated with a Q value of $Q_G = 0.15$. Grazers encounter patches twice as fast as diggers, and both diggers and grazers live, on average, one time unit (table 1). The three examples differ in the Q value associated with the diggers: (*A*) $Q_D = 0.4$, (*B*) $Q_D = 0.5$, and (*C*) $Q_D = 0.6$. In all three examples, the grazer species is assumed to be well established before an inoculum of diggers is introduced. The dynamics are qualitatively different in each of the three examples, and they match the predictions (fig. 1*B*). The steady state resource density when only grazers are present is $X_G^* = 0.65$ resource units. The steady state resource densities for the three examples, when only diggers are present, are (*A*) $X_D^* = 0.5$, (*B*) $X_D^* = 0.6$, and (*C*) $X_D^* = 0.7$ resource units. Although $X_G^* > X_D^*$ in figure 2*B*, the grazers clearly coexist with the diggers. The dynamics presented in figure 2 were generated by numerically solving a set of six coupled delay differential equations (app. B).

Logistic-Type Renewal

A more general model that can be used to describe resource renewal is

$$r(x) = r_0 x^i\left(1 - \frac{x}{K}\right)^j, \tag{38}$$

where i and j are nonnegative constants. The linear renewal model is recovered when $i = j = 0$, and the free-space model is recovered when $i = 0$ and $j = 1$. When $i = j = 1$, resource renewal is logistic, which is a commonly adopted model to describe the growth of a wide range of prey

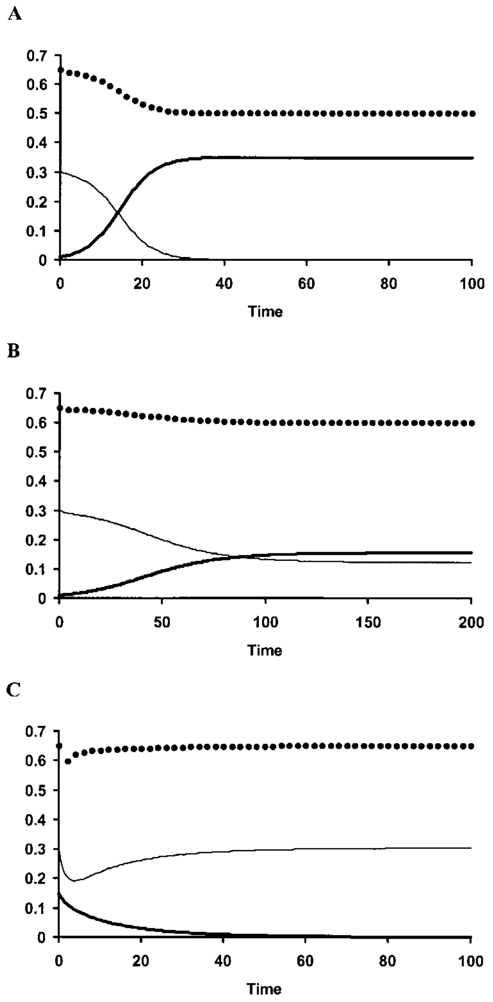

Figure 2: Consumer-resource dynamics for the three cases presented in figure 1*B* (*solid circles*). In all examples $K = 1$, $x_D = 0.1$, $x_G = 0.5$, and $Q_G = 0.15$. The *Q*-values associated with the digger species are (*A*) $Q_D = 0.4$, (*B*) $Q_D = 0.5$, and (*C*) $Q_D = 0.6$. Each example shows the mean resource level, $N_LX_L + N_HX_H$ (*dotted line*); digger density, *D* (*solid thick line*); and grazer density, *G* (*solid thin line*).

organisms. There are two important properties of this model. When $j > 0$ the resource density within a patch will tend toward a carrying capacity K, and when $i > 0$ the resource does not renew after it has been completely depleted from a patch. From the previous model, we have seen that the presence of a carrying capacity means that species characterized by high Q values cannot persist in the system regardless of the presence or absence of other species. The second property is particularly important if consumers deplete all resources from a patch because eventually they will drive themselves to extinction.

An analytic solution to the invasion condition, equation (26), is generally not possible for this model and so must be evaluated numerically. Figure 3 shows four examples of the renewal function, equation (38), and the form of the age-dependent change in resource density that results. In figure 4 we present the coexistence regions associated with the renewal functions presented in figure 3. Coexistence is possible for all resource-renewal functions presented, and the region of coexistence varies depending on the assumption of resource renewal. The region is smallest when renewal is described by the free-space model and is largest when renewal is described by the third model. Numerical results again show that the condition for grazers to invade diggers is independent of the renewal parameter, r_0.

Discussion

In this article we have shown that in some situations it is possible that species that compete exploitatively for a common resource may coexist. This result is in contrast to previous studies of exploitation competition that assume the resource is well mixed within the habitat (e.g., Fishman 1997). The fact that we found the possibility of coexistence in our model is not all that surprising. Our model is a subtle example of resource partitioning, which, as was noted in our introduction, has been shown to promote coexistence. The two consumers are essentially competing within a system that contains two types of resources, namely L-patches and H-patches. An important result from our model is that spatial and temporal changes in the resource distribution and, hence, the two types of patch are created by the foraging behaviors of the consumers and not from any intrinsic differences among resource patches. Although the abundance of L-patches and H-patches are correlated at any time, knowledge of the abundance of one does not necessarily specify the abundance of the other; hence, coexistence may occur in this system (Haigh and Maynard Smith 1972).

The situation presented here corresponds to the idea of an included niche (Miller 1964, 1967), where in this case

Table 1: Parameter values used in all the simulations presented

Parameter	Description	Value
K	Patch carrying capacity	1
r_0	Maximum renewal rate	20
h	Resource handling time	.01
x_D	Digger resource threshold	.1
x_G	Grazer resource threshold	.5
δ_D	Digger mortality rate	1
δ_G	Grazer mortality rate	1
σ_D	Digger patch encounter rate	100
σ_G	Grazer patch encounter rate	200

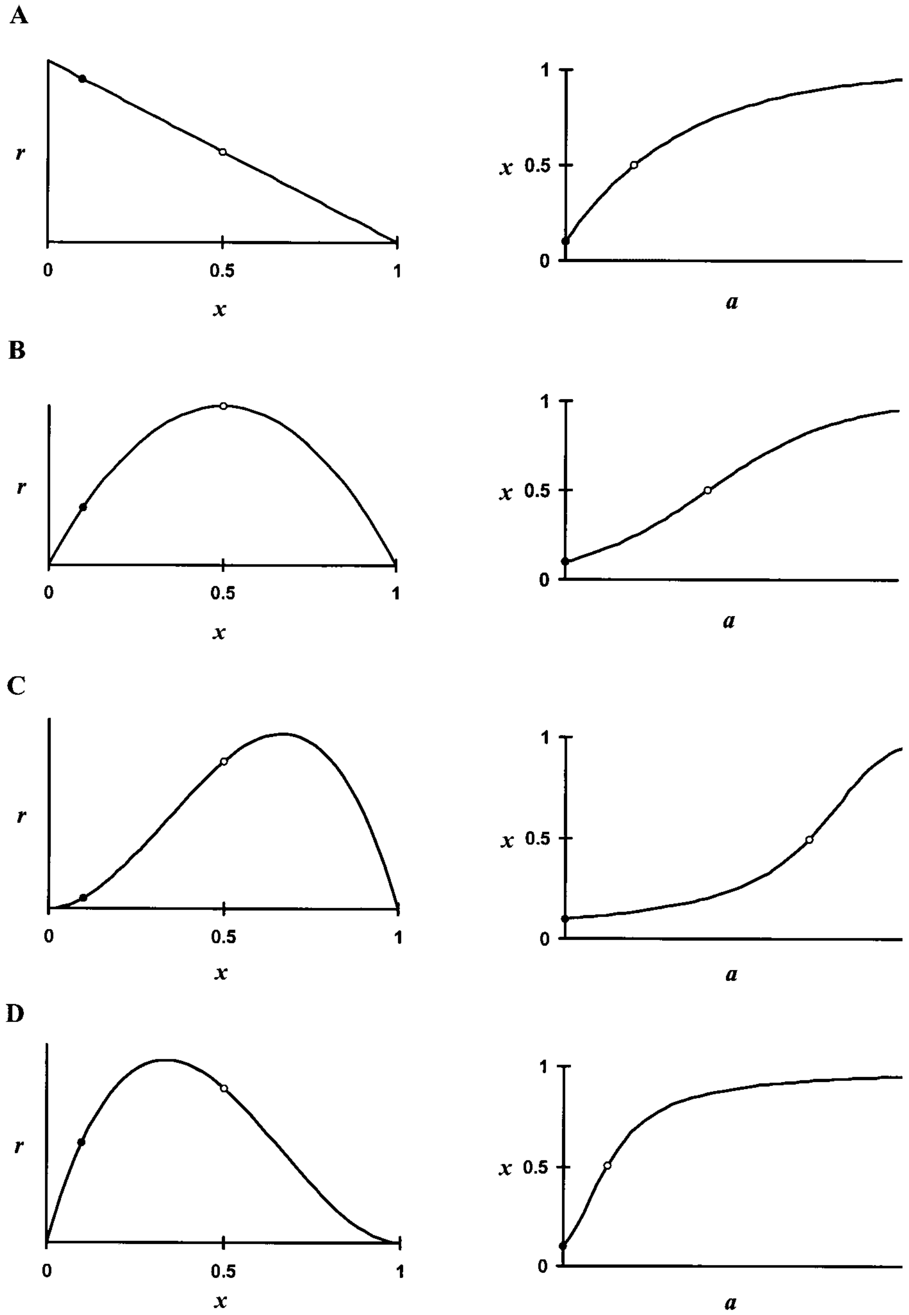

Figure 3: Examples of the logistic-type resource-renewal model as described by equation (38). Also shown are the associated renewal trajectories, $x(a)$. Parameter values for each example are as follows: (*A*) $i = 0$, $j = 1$; (*B*) $i = 1$, $j = 1$; (*C*) $i = 2$, $j = 1$; and (*D*) $i = 1$, $j = 2$. In all examples, the digger and grazer resource thresholds are given by $x_D = 0.1$ (*filled dots*) and $x_G = 0.5$ (*open dots*), and the carrying capacity $K = 1$.

the niche of the grazer (i.e., the densities of resource that can be accessed) is a subset of the niche of the digger. Coexistence may be possible, provided the grazer species is more efficient than the digger species at utilizing high-density resource patches (i.e., it is a better competitor within its restricted niche). We have shown that if the consumer with the restricted niche is sufficiently efficient, then it can exclude the consumer that has the greater niche.

The parameter r_0 that appears in all three renewal models considered in this article has no influence on the region

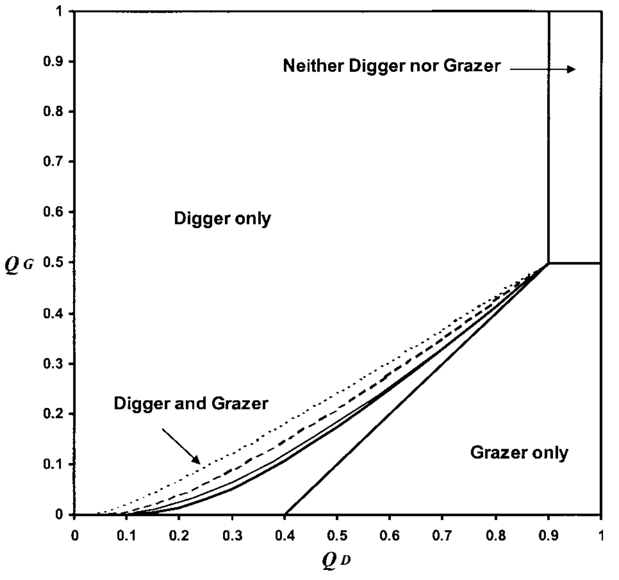

Figure 4: Coexistence regions when resource renewal is described by the logistic-type functional form. The *Digger only* and *Digger and Grazer* boundary correspond to the four cases presented in figure 3: (*A*) *solid thick line*, (*B*) *long-dashed line*, (*C*) *short-dashed line*, and (*D*) *solid thin line*.

of coexistence. The effect of r_0 is to alter the timescale of resource renewal, which affects population sizes but not the essential qualities of the dynamics that influence coexistence. Thus, the rate at which a resource renews has no bearing on which species are expected to persist in a habitat. What is important for determining species composition is the manner in which the resource renews within patches. The functional form of resource renewal defines the conditions under which the grazer is able to persist in a habitat that is occupied by diggers. The region of coexistence is increased when the relative rate of renewal in the H-patches compared to the L-patches is increased. When a free-space renewal function is assumed, the resource increases much faster in the L-patches compared to the H-patches, and in this case the region of coexistence is small. However, if the rate of renewal is high in H-patches (e.g., fig. 3*C*), then the region of coexistence is significantly increased (fig. 4). Although in this case it may take some time for patches to become accessible to grazers after they have been visited by a digger, if diggers move slowly or have a low population size, then grazers can persist if they are sufficiently efficient (i.e., they make better use of the high resource-renewal rates of the H-patches). By either moving quickly through the habitat or having high population growth rates, the grazers persist even though they may encounter patches that they cannot utilize. However, if diggers are not efficient consumers, then their persistence depends on the presence of high-density patches, which may become sufficiently rare in the presence of grazers such that diggers are driven to extinction.

A similar mechanism that shares many features with ours was studied by Briggs (1993) in the context of insect parasitoids. In her system two parasitoid species attack different developmental stages of a single host species. Briggs (1993) presents an age-structured model of the system and shows that the two parasitoids could coexist if the parasitoid that utilizes the later host stage could successfully attack hosts that had been attacked earlier by the other parasitoid. Like the results presented here, it was found that the outcome of competition was dependent on the consumer efficiency of both parasitoid species, which was defined in a similar manner as the *Q* value of the diggers and grazers in this article.

In this article we have shown that the consumer's effect on the distribution of resources, and not necessarily the mean abundance of resources, is important for coexistence. This result was also shown by Mittler (1997), who investigated a model of predator-prey dynamics that overlaps to some extent with the model presented in this article. Predators did not necessarily consume prey in their entirety, leaving smaller prey items that may be more efficiently consumed by other predators. Mittler (1997) showed that a rich range of dynamics could occur in a two-predator system. In some cases, depending on certain competitive trade-offs, frequency-dependent dynamics occurred, where the first predator species to occupy a habitat could exclude the other predator species. In other cases coexistence of the two predator species was predicted. Resources, which may vary in size, were assumed to enter the habitat at some deterministic rate. Once a prey item entered the habitat it did not change its size until it was attacked by a predator. Our work differs from Mittler (1997) because we assume the state of the resource changes as it ages.

One important issue in models of coexisting consumers is how the density of the resource compares with the situation when only one consumer is present. This question is of course important in biological control, where the resource is the item that we wish to regulate. W. W. Murdoch (private communication) noted that in the simple models of coexistence discussed in our introduction, the addition of a second coexisting consumer (e.g., predator, herbivore, parasite) to a system never decreases the resource level below that which would arise with the most "effective" consumer present alone. The dynamics of the current model are consistent with this pattern. When coexistence occurs the digger is always the most effective consumer, and in these circumstances the mean equilibrium resource density among patches with both diggers and consumers present is the same as when only diggers are present (fig. 2). This minimum density is simply $X_D^* = x_D + Q_D$.

Previous theoretical studies have shown that when multiple species compete exploitatively for the same limiting resource, it is the species with the lowest equilibrium resource requirement that eventually displaces all other species (Armstrong and McGehee 1980; Tilman 1982). An important result from our model is that one cannot predict which species will persist by only looking at the equilibrium resource level when each species is in isolation. We have shown that grazers that have a higher equilibrium than the diggers may still coexist with the diggers (fig. 2*B*).

In order to allow analytic tractability for much of our analysis, we have had to make a number of simplifying assumptions with regards to consumer and resource dynamics. An important assumption we have made that needs further investigation is a lack of resource-dependent consumer behavior. Consumers are assumed to move randomly through the habitat; they do not make systematic movements or modify their movements based on recent resource encounters. When visits to resource patches are not random the distribution of resources that a forager encounters is not necessarily the same as the overall distribution of resources (Possingham 1989; Abrams 1999). This may affect the region of coexistence. Because we have assumed random movements, both consumer species will be scattered within the habitat at any time, but systematic foraging may partition the distributions of the two species. Laverty and Plowright (1985) observed that hummingbirds (diggers) and bumblebees (grazers) partition the resource distribution in both space and time. Part of the spatial segregation may be explained by differences in each species' ability to access the flowers (the inner flowers of a patch were protected from hummingbirds by vegetative cover). Temporal segregation may be due to differences in the metabolic cost of foraging. Here we have assumed that consumers are always foraging and renewal is a continuous process. Despite our simple assumptions on foraging behavior, the model does suggest that multiple species that exhibit little or no apparent systematic foraging may still coexist even if they consume the same resource.

Another potentially important assumption we have made is that the habitat is homogeneous. In a real system we would expect variability among patches with regard to renewal rates and their carrying capacity (Possingham 1988, 1989). We have also assumed that the population growth of the consumer is related to the mean intake rate, but variability in the resources encountered may be particularly important for risk-sensitive foragers (Bulmer 1994). Consumers may be expected to alter their foraging behavior depending on whether they are risk averse or risk prone. This work could be extended and applied to risk-sensitive foragers by incorporating the variance of the encountered resource in the equation that describes consumer growth.

A final assumption that needs further investigation is that age-0 H-patches renew at the same rate regardless of whether they were just attacked by a grazer or whether they were an L-patch that reached the age τ. We may expect for some resource types that renewal may differ depending on whether it was just attacked by a grazer (e.g., vegetative regrowth). The rate at which a patch is grazed may be important for modeling how a resource renews. This is certainly true for resource depression where the resource itself may exhibit predator avoiding behavior (e.g., insect prey). Resource responses could potentially alter the model's predictions.

The model presented in this article has shown that two species, which compete exploitatively, can coexist on a single resource in a homogeneous environment, given that they satisfy certain conditions with regard to the level at which they deplete resources (x) and their associated character value (Q). However, this model does not tell us whether another species could invade and exclusively take over the system and not be invadable by any other potential species. If there exists some trade-off between x and Q (Schmitt 1996), then future work could use the model to investigate whether selection would favor some intermediate species or allow coexistence of a suite of species.

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APPENDIX A

Stability Analysis of the Single Consumer–Single Resource Model

Here we present an alternative way to describe resource and consumer dynamics when only one consumer species is present. Suppose only the grazer species is present. It can be shown that the dynamics of the mean patch density (X_H) and the grazer population size (G) are governed by the following coupled ODEs:

$$\frac{dX_H}{dt} = F_H(t) - \frac{\sigma_G(X_H(t) - x_G)G(t)}{1 + \sigma_G h(X_H(t) - x_G)},$$

$$\frac{dG}{dt} = \left[\frac{\varepsilon_G\sigma_G(X_H(t) - x_G)}{1 + \sigma_G h(X_H(t) - x_G)} - \delta_G\right]G(t),$$

where

$$F_H(t) = \int_0^\infty n_H(a, t)r(x_H(a, t))da.$$

This formulation requires that the renewal function r is such that $x(a)$ is not exponential for large a. When resource renewal is linear, $F_H(t) = r_0$; when resource renewal obeys the free-space model, $F_H(t) = r_0(1 - X_H(t)/K)$. A simple analytic form for $F_H(t)$ is not possible for logistic-type renewal because the function $r(x)$ is nonlinear. Note that the age distribution of patches may not need to be explicitly modeled in this system.

Now we examine the stability of this model formulation. The associated Jacobian is

$$\mathbf{J} = \begin{bmatrix} -\sigma_G G^*/(1 + \sigma_G hQ_G)^2 + \partial F_H/\partial X_H|_{X_H^*} & -\sigma_G Q_G/(1 + \sigma_G hQ_G) \\ \varepsilon_G\sigma_G G^*/(1 + \sigma_G hQ_G)^2 & 0 \end{bmatrix},$$

where G^* and X_H^* are equilibrium values for the system. There exist two equilibrium points for this model. One is the trivial solution where there are no consumers at all, $G^* = 0$, and X_H^* is the carrying capacity (this is infinite for the linear renewal model). There also exists a nontrivial equilibrium point, $X_H^* = Q_G + x_G$ and $G^* = F_H^*(1 + h\sigma_G Q_G)/(\sigma_G Q_G)$. If we let D and T denote the determinant and trace of the Jacobian matrix $\mathbf{J}$, then an equilibrium point (G^*, X_H^*) is locally stable if $D > 0$ and $T < 0$; otherwise, it is unstable (Bulmer 1994). Using these criteria, it can be easily shown that for both the linear and the free-space renewal models, the trivial equilibrium point is unstable and the nontrivial point is stable. Hence, the grazer will always become well established when introduced into the system when it is free of the digger. The same reasoning can be applied to the digger-only situation. Although we cannot prove analytically that consumers can become well established when resources renew according to the more general logistic-type model, numerical simulations suggest this is true also (see Nisbet et al. 1998).

APPENDIX B

Resource Dynamics Expressed as Ordinary Differential Equations

When one wishes to generate numerical approximations to partial differential equations (PDEs), it is sometimes easier to convert them to ODEs and approximate the solutions to the ODEs instead. Here we transform equations (7)–(10), which describe the dynamics of $n_L(a, t)$, $n_H(a, t)$, $x_L(a)$, and $x_H(a)$, into equivalent equations that describe the dynamics of $N_L(t)$ and the products $N_L(t)X_L(t)$ and $N_H(t)X_H(t)$. Hence, we show that resource dynamics can be described by equations that do not explicitly keep track of the age distribution of patches.

First, we integrate equation (7) over the duration it takes an L-patch to become an H-patch,

$$\int_0^\tau \frac{\partial n_L}{\partial t} + \frac{\partial n_L}{\partial a} da = -\mu(t) \int_0^\tau n_L(a, t) da,$$

which reduces to the following:

$$\frac{dN_L}{dt} = -\mu(t)N_L(t) - n_L(\tau, t) + n_L(0, t). \tag{B1}$$

The last term is simply $\mu(t)$ (see eq. [11]). The second to last term represents the fraction of patches that were last visited by a digger at time $t - \tau$. The probability a patch is not visited by a digger from time $t - \tau$ to time t is given by

$$S(t) = \exp\left(-\int_{t-\tau}^t \mu(\xi) d\xi\right). \tag{B2}$$

Hence,

$$n_L(\tau, t) = S(t) n_L(0, t - \tau) = S(t)\mu(t - \tau). \tag{B3}$$

Substituting equations (11) and (B3) into (B1) gives the following delay differential equation (DDE) for N_L:

$$\frac{dN_L}{dt} = \mu(t)(1 - N_L(t)) - S(t)\mu(t - \tau). \tag{B4}$$

Differentiating equation (5) with respect to t gives

$$\begin{aligned}
\frac{d}{dt}(N_L(t)X_L(t)) &= \int_0^\tau \frac{\partial n_L}{\partial t} x_L da, \\
&= \int_0^\tau \left(-\frac{\partial n_L}{\partial a} - \mu(t) n_L\right) x_L da, \\
&= -\int_0^\tau \left(\frac{\partial n_L}{\partial a} x_L + n_L \frac{dx_L}{da}\right) da + \int_0^\tau n_L \frac{dx_L}{da} da - \mu(t) \int_0^\tau n_L x_L da, \\
&= -\int_0^\tau \frac{\partial}{\partial a}(n_L x_L) da + \int_0^\tau n_L r(x_L) da - \mu(t) N_L(t) X_L(t), \\
&= n_L(0, t) x_L(0, t) - n_L(\tau, t) x_L(\tau, t) + F_L(t) - \mu(t) N_L(t) X_L(t), \\
&= \mu(t) x_D - S(t)\mu(t - \tau) x_G + F_L(t) - \mu(t) N_L(t) X_L(t),
\end{aligned} \tag{B5}$$

where

$$F_L(t) = \int_0^\tau n_L(a, t) r(x_L(a)) da.$$

When resource renewal is described by the free-space model (eq. [33]),

$$F_L(t) = r_0(N_L(t) - N_L(t)X_L(t)/K).$$

Similarly, we can differentiate equation (6) with respect to t, which, after a little algebra, gives

$$\frac{d}{dt}(N_H(t)X_H(t)) = [S(t)\mu(t-\tau) + \nu(t)(1 - X_L(t))]x_G + F_H(t) - (\mu(t) + \nu(t))N_H(t)X_H(t), \tag{B6}$$

where

$$F_H(t) = \int_0^\infty n_H(a, t)r(x_H(a))da.$$

For the case of free-space renewal,

$$F_H(t) = r_0(1 - N_L(t) - N_H(t)X_H(t)/K).$$

Differentiating equation (B2) with respect to t gives the final DDE that closes the system:

$$\frac{dS}{dt} = [\mu(t-\tau) - \mu(t)]S(t). \tag{B7}$$

Consumer-resource dynamics can be generated by numerically approximating solutions to the following sets of coupled equations: (B4)–(B7), (17), and (18). Subtleties related to initializing DDEs are discussed by Nisbet (1997).

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