Theoretical Population Biology **62**, 281–295 (2002)
doi:10.1006/tpbi.2002.1614

TPB

The Impact of Consumer–Resource Cycles on the Coexistence of Competing Consumers

Peter A. Abrams[1]
Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 3G5

and

Robert D. Holt
Department of Zoology, 111 Bartram Hall, University of Florida, P.O. Box 118525, Gainesville, Florida 32611-8525

Received September 19, 2001

This article seeks to determine the extent to which endogenous consumer–resource cycles can contribute to the coexistence of competing consumer species. It begins with a numerical analysis of a simple model proposed by Armstrong and McGehee. This model has a single resource and two consumers, one with a linear functional response and one with a saturating response. Coexistence of the two consumer species can occur when the species with a saturating response generates population cycles of the resource, and also has a lower resource requirement for zero population growth. Coexistence can be achieved over a wide range of relative efficiencies of the two consumers provided that the functional response of the saturating consumer reaches its half-saturation value when the resource population is a small fraction of its carrying capacity. In this case, the range of efficiencies allowing coexistence is comparable to that when two competitors have stable dynamics and a high degree of resource partitioning. A variety of modifications of this basic model are analyzed to investigate the consequences for coexistence of different resource growth equations, different functional and numerical response shapes, and other factors. Large differences in functional response shape appear to be the most important factor in producing robust coexistence via resource cycles. If the unstable species has a concave numerical response, this greatly expands the conditions allowing coexistence. If the stable consumer species has a convex (accelerating) functional and/or numerical response, the range of conditions allowing coexistence is also expanded. We argue that large between-species differences in functional response form can often be produced by between-consumer differences in the adaptive adjustments of foraging effort to food density. Consumer–resource cycles can also expand the conditions allowing coexistence when there is resource partitioning, but do so primarily when resource partitioning is relatively slight; this makes the ease of coexistence relatively independent of consumer similarity.

INTRODUCTION

A substantial body of theoretical literature has shown that temporal variability can allow the coexistence of competing species that would not coexist under constant conditions (Armstrong and McGehee, 1976a, b, 1980; Chesson and Warner, 1981; Abrams, 1984; Chesson, 1986, 1994). Recently, attention has focused mainly on the "storage effect" mechanism identified by Chesson and Warner (1981). In this mechanism, environmental variation acting at one life history stage in effect results in temporal partitioning of resources. Chesson and

---

[1] To whom correspondence should be addressed. E-mail: abrams@zoo.utoronto.ca.

0040-5809/02 $35.00

Huntly (1997) have argued that this contributes significantly to the coexistence of desert plants. By contrast, a mechanism of coexistence based on endogenous rather than exogenous variation, first described by Armstrong and McGehee (1976a), has received far less attention. A brief sketch of the Armstrong–McGehee (A–M) mechanism of coexistence for two competing species is as follows.

One consumer species (here referred to as the "unstable" consumer) has a saturating functional response that is sufficient to generate consumer–resource cycles when alone with the resource. The other "stable" consumer does not induce cycles (or produces cycles of significantly lower amplitude) but requires a higher resource density to increase when rare. The unstable species cannot fully exploit periods of high resource abundance during the cycles (because of its saturating responses), whereas the stable species can make greater use of pulses of resource abundance and so benefits from the resource cycles generated by the unstable species. However, the stable species cannot exclude the unstable species; when the stable species becomes dominant, its higher resource requirement leads to higher resource levels, permitting the more efficient unstable species to increase. In turn, cycles generated by the unstable consumer result in a time-averaged resource density that is greater than the equilibrium density (Armstrong and McGehee, 1980; Abrams and Roth, 1994); this resource enhancement allows the stable species to increase when rare. The difference between equilibrium and time-averaged densities increases as cycle amplitude increases. Thus, the A–M mechanism is most likely to operate when the cycles created by the unstable species are of large amplitude. Under this mechanism one species is superior at low resource levels, and the other at high levels, and the dependence of cycle amplitude on the relative abundances of the consumers ensures periods when each species enjoys an advantage over the other.

This basic scenario was described independently by several investigators during the 1970s (Koch, 1974; Armstrong and McGehee, 1976a, b, 1980; Hsu *et al.*, 1978). Chesson (1994) refers to the scenario sketched above as a special case of coexistence due to "relative nonlinearity". During the past two decades, no empirical demonstrations of coexistence due to this mechanism have appeared, and the impact of consumer–resource cycles on competing consumers is seldom mentioned (but see Vandermeer, 1993; Chesson, 1994, 2000). Indeed, the consensus seems to be that deterministic consumer–resource cycles are a very weak coexistence-promoting mechanism (e.g., Hsu, 1980; Chesson, 1994; Anderies and Beisner, 2000). Yet, the demise of this idea may be premature. It is very difficult to identify the mechanisms underlying competitive coexistence, and only recently have efforts been made to quantify the roles of different mechanisms in the field (Chesson and Huntly, 1997). Because a degree of resource partitioning is likely to exist between any pair of species, there is a tendency to regard partitioning as a sufficient explanation for coexistence, and to neglect the potential role of unstable dynamics. Consumer–resource cycles may occur in many natural systems (Ellner and Turchin, 1995; Kendall *et al.*, 1998). For instance, Kendall *et al.* (1998) argue that roughly 30% of 694 long-term time-series of Northern hemisphere animal populations show cycles. Cycles are conspicuous in some systems with coexisting consumers (e.g., bank and field voles in Fennoscandia (Hansson, 1983)), although the cause of the cycles and their impact on coexistence is unknown. Coexistence of many insect herbivores in systems where one or more species have periodic outbreaks (e.g., Myers, 1988) provides other potential examples where unstable dynamics could facilitate coexistence.

The purpose of this article is to argue that endogenously generated consumer–resource cycles may, in fact, play an important, if under-appreciated, role in resource competition and coexistence. We begin by showing that the simplest model of the A–M mechanism is quantitatively comparable to resource partitioning in its ability to produce coexistence. We then show that robust coexistence of two species is possible in a broad range of related models with a large-amplitude cycles in resource density. We argue that the biological prerequisites for coexistence due to endogenous cycles should be satisfied frequently, particularly for competition between organisms with dissimilar adaptive responses to changes in resource density. Elsewhere (Abrams *et al.*, under review) we explore in more detail the range of population dynamics produced by this model, and responses of average abundances to changes in environmental conditions. These differ considerably from the dynamics and responses of species coexisting via resource partitioning.

MEASURING THE RANGE OF CONDITIONS ALLOWING COEXISTENCE

A robust mechanism of coexistence allows persistence of two (or more) species over a substantial range of species' traits. Exact quantification of the volume of parameter space permitting coexistence is often difficult in models with even a moderate number of parameters. Our approach here is to determine the range of relative resource requirements of consumer species consistent with coexistence. The resource density required for population growth is likely to vary between species, and within species across space or through time, because it is affected by climatic conditions (which determine metabolic demands) and by mortality factors (and thus the resources required to replenish losses). The resource requirement also determines the outcome of competition for a single resource in the absence of cycles (Volterra, 1926; Armstrong and McGehee, 1980). Thus, the resource requirement for population growth is arguably the most important composite parameter determining coexistence in many models of resource competition. If only a narrow range of resource requirements permits coexistence, coexistence is unlikely to be observed in natural systems; environmental variation in resource requirements is then likely to destroy the delicate balance needed for coexistence. Our approach of using the range of parameters allowing coexistence to gauge the likelihood that species in fact coexist was employed by MacArthur and Levins (1967), May (1973), Abrams (1975) and Armstrong (1976) in early deterministic theories of limiting similarity. Armstrong (1976) coined the term, "coexistence bandwidth", to denote ranges of critical parameters permitting coexistence. We will demonstrate that coexistence bandwidth is often relatively broad for systems with the A–M mechanism.

THE ROBUSTNESS OF COEXISTENCE IN CONSUMER–RESOURCE SYSTEMS WITH RESOURCE PARTITIONING AND A STABLE EQUILIBRIUM

To judge the contribution of the Armstrong–Mc Gehee mechanism to coexistence, it is necessary to have a standard of comparison. Here we use MacArthur's (1970, 1972) well-known consumer–resource model as a standard for comparison of coexistence bandwidths. The model is described in Appendix 1 (see also MacArthur, 1972; Hsu and Hubbell, 1979; Chesson, 1990; Abrams, 1998). We adopt a symmetric 2-consumer–2-resource version of the model, in which the two consumers have consumption rates that are mirror images, and both resources have identical growth parameters. In particular, if C_{ij} is the per capita consumption rate of resource j by consumer i, we assume that $C_{12} = C_{21}$, and $C_{11} = C_{22} = C$. We further assume the per capita capture rates of a given consumer sum to one, so overlap in resource use can be summarized in a single parameter, C. The resource requirements, denoted as d_1 and d_2, are scaled relative to the resource-carrying capacities. These assumptions mean that the range of d_i allowing existence in the absence of the competitor is $0 < d_i < 1$. The coexistence bandwidth is the range of d_i allowing coexistence with d_j; this bandwidth is automatically scaled relative to the range of d_i allowing existence without competition (i.e., 1).

The conditions for coexistence in MacArthur's system (derived in Hsu and Hubbell, 1979; Abrams, 1998) were used to generate Fig. 1. Figure 1A shows the maximum and minimum values of d_2 permitting coexistence, as a function of similarity in resource capture rates of the two consumer species; these quantities are shown for three possible resource requirements, d_1, of competitor 1. In Fig. 1B, the range of d_2 yielding coexistence is shown as a function of d_1, for two levels of resource partitioning. Resource partitioning ranges from non-existent ($C = 0.5$) to complete (when $C = 0$). Figure 1 shows that the coexistence bandwidth is greatest when resource partitioning is greatest; for a given level of partitioning, bandwidth is greatest for intermediate resource requirements of the focal species (d_1). These two features arise in many related models, given symmetrical differences in resource use. For instance, numerical results were obtained with the same system, but with type-2 functional responses (as in Eq. (1a)). This change narrowed the coexistence bandwidth for systems with a small amount of partitioning, but did not change these two basic features: coexistence bandwidth increased with resource partitioning and, for a given degree of partitioning, was maximal for intermediate resource requirements. The latter feature arises because at high d, existence is precarious even in the absence of competition, so adding competition can easily push a species over the edge; at low d, consumers can cause exclusion of a resource population, reducing the diversity of available resources.

The above results provide a scale for measuring the robustness of coexistence under the A–M mechanism. Given a resource requirement, d, of one species and the range of d (or N^*) of the other species that allows coexistence in a model with the A–M mechanism, the formulas used to generate Fig. 1 yield a value of C (i.e., an amount of resource partitioning) that produces the same range of permissible resource requirements, were partitioning alone to produce coexistence.

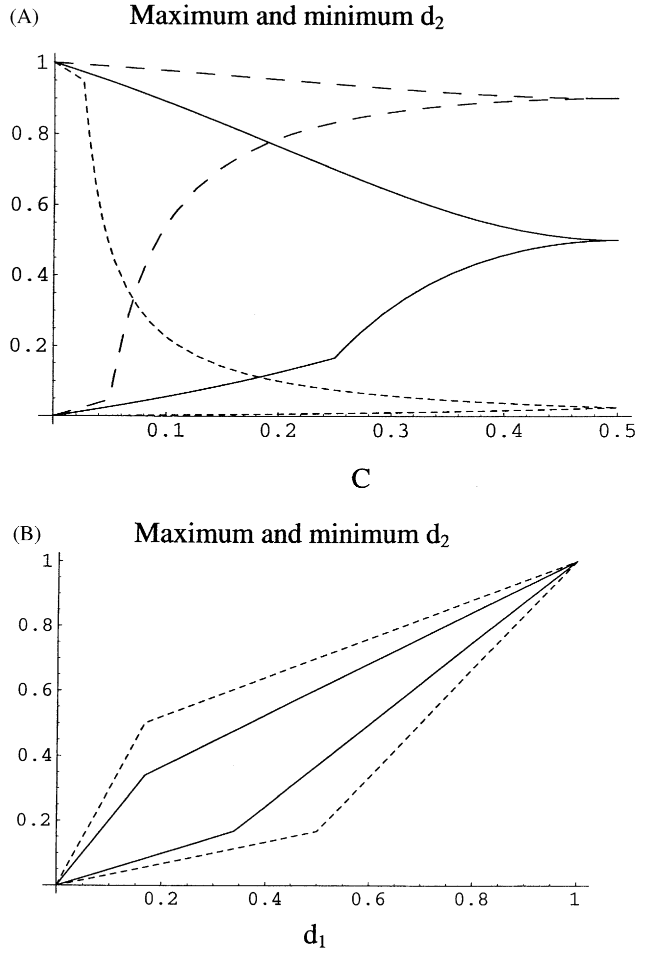

FIG. 1. (A) shows the upper and lower bounds of resource requirements (measured by d_2) needed for coexistence in MacArthur's consumer–resource model (Eqs. (A1) and (A2)) as a function of the degree of similarity in resource use. $C = 0$ means both consumer species are complete specialists on different resources, while $C = 0.5$ means that both consumers are identical generalists. The three line styles give the upper and lower boundaries of d_2 for three different values of d_1; $d_1 = 0.025$ for the short dashed line; $d = 0.5$ for the solid line; $d = 0.9$ for the long dashed line. In each case, in parameter regions above the top line, species 1 wins, whereas for parameters below the bottom line, species 2 wins. (B) shows the upper and lower bounds of d_2 as a function of d_1 for two levels of resource partitioning. The dashed line represents a system where $C = 0.25$ (resulting in a value of 0.5 for Schoener's overlap formula), while the solid line assumes $C = 0.33$ (overlap of 0.66).

ROBUSTNESS OF TWO-SPECIES COEXISTENCE UNDER THE ARMSTRONG–McGEHEE MODEL

We assume consumer species 2 is the stable species, with a linear functional response. Consumer species 1 (the unstable species) has a nonlinear (Holling, 1959, type-2) functional response. The range of conditions allowing coexistence is found by determining parameters that permit each species to invade a system in which the other consumer and resource have reached their limiting dynamics. Although invasion analyses do not always guarantee coexistence in models with different structures (e.g., Armstrong and McGehee, 1980; Abrams and Shen, 1989; Case, 1995), it does so for Eqs. (1) (Armstrong and McGehee, 1976, a, b, 1980; McGehee and Armstrong, 1977). Numerical explorations of the related models considered in later sections of this article have not revealed cases where it fails for those models.

If the resource (prey) has logistic growth, the description above corresponds exactly to the example in Armstrong and McGehee (1980). The dynamics of the two consumers (predators), P_1 and P_2, and the resource (prey), N, are given by

$$\frac{dP_1}{dt} = P_1\left(\frac{B_1C_1N}{1 + hC_1N} - D_1\right),$$
$$\frac{dP_2}{dt} = P_2(B_2C_2N - D_2),$$
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{C_1NP_1}{1 + hC_1N} - C_2NP_2. \qquad \text{(1a–c)}$$

Here B_i is the conversion efficiency of food into offspring for consumer i; h is the handling time for a resource item eaten by consumer 1; D_i is the resource intake rate required for population growth; C_i is a searching consumer's attack rate; and, r and K are logistic growth parameters. After scaling to reduce the number of parameters (substituting $t' = rt$; $N' = N/K$; $P_1' = P_1/(B_1K)$; and $P_2' = P_2/(B_2K)$, and then dropping the primes), the system is

$$\frac{dP_1}{dt} = P_1\left(\frac{a_1N}{1 + bN} - d_1\right),$$
$$\frac{dP_2}{dt} = P_2(a_2N - d_2),$$
$$\frac{dN}{dt} = N(1 - N) - \frac{a_1NP_1}{1 + bN} - a_2NP_2. \qquad \text{(2a–c)}$$

The new parameters are $a_1 = KB_1C_1/r$; $a_2 = KB_2C_2/r$; $b = KC_1h$; $d_1 = D_1/r$; $d_2 = D_2/r$. The minimal resource requirement for consumer species i, denoted N_i^*, is found by solving $(1/P_i)(dP_i/dt) = 0$; hence, $N_i^* = d_1/(a_1 - bd_1)$, and $N_2^* = d_2/a_2$.

A necessary condition for coexistence is that consumer species 1 undergoes limit cycles when it interacts with the resource in the absence of species two. Such cycles occur if and only if $d_1 < a_1(b - 1)/(b(b + 1))$. Given that this requirement is satisfied, coexistence occurs if and only if each consumer can invade a system consisting of the other consumer and resource undergoing their limiting dynamics (McGehee and Armstrong, 1977; Armstrong and McGehee, 1980). These mutual invasion conditions are: (1) for invasion of species 1 into the stable system consisting of species 2 and the resource, $d_1/(a_1 - bd_1) < d_2/a_2$, which is equivalent to $N_1^* < N_2^*$; and (2) for invasion of species 2 into the cycling system consisting of species 1 and the resource, $\langle N \rangle_1 > d_2/a_2$, where $\langle N \rangle_1$ denotes the average resource density over a limit cycle of consumer 1 and the resource. This average density must be determined numerically. Putting the two invasion conditions together, coexistence requires

$$N_1^* < N_2^* < \langle N \rangle_1. \qquad (3)$$

Because we are interested in comparing the range of conditions that allows coexistence in the A–M model with the comparable range for the MacArthur model, we will concentrate on species 2. The linear functional response of this species makes its interaction with resources comparable to a consumer in the MacArthur model. We will use the term "coexistence bandwidth for species *i*" to refer to the range of N_i^* that permits species *i* to coexist with species *j*. The bandwidth for species 2 clearly depends on the growth parameters of species 1, because both N_1^* and $\langle N \rangle_1$ depend on those parameters (d_1, a_1 and *b*). Because $N_2^* = d_2/a_2$ in inequality (3), the coexistence bandwidth for species 2 is directly proportional to the range of the per capita mortality rate, d_2 that allows coexistence. In the special case when $a_2 = 1$, these two ranges are equal. Because carrying capacity has been scaled to unity in Eqs. (2), the coexistence bandwidth is also scaled relative to *K*.

We begin by exploring the dependence of coexistence bandwidth on the three growth parameters of the cycling consumer species (species 1). The range of N_2^* allowing coexistence is shown as a function of d_1 for three values of *b* in Fig. 2. Because $a_2 = 1$, this figure also gives the range of d_2 that allows coexistence. In each panel of the figure, the bandwidth is given by the distance between the solid and dotted line. As in the MacArthur model, the largest coexistence bandwidths for the A–M model occur for intermediate levels of efficiency of the other consumer (measured either by d_1 or N_1^*). Figure 2 reveals that the largest coexistence bandwidths occur when *b* is large (coexistence is impossible when $b < 1$, because this condition guarantees stability). It is clear that a strongly saturating functional response (e.g., $b = 5$ or $b = 10$) is required for a moderately large coexistence bandwidth. The remaining growth parameter that can influence bandwidth is the maximum per capita resource capture rate of that species, a_1. For a given value of *b* and N_1^*, a change in a_1 implies a proportional change in d_1. Proportional changes in both a_1 and d_1 do affect $\langle N \rangle_1$, and therefore have an effect the coexistence bandwidth for species 2. In all cases, increases in a_1 and d_1 decrease the coexistence bandwidth; decreases in the parameters

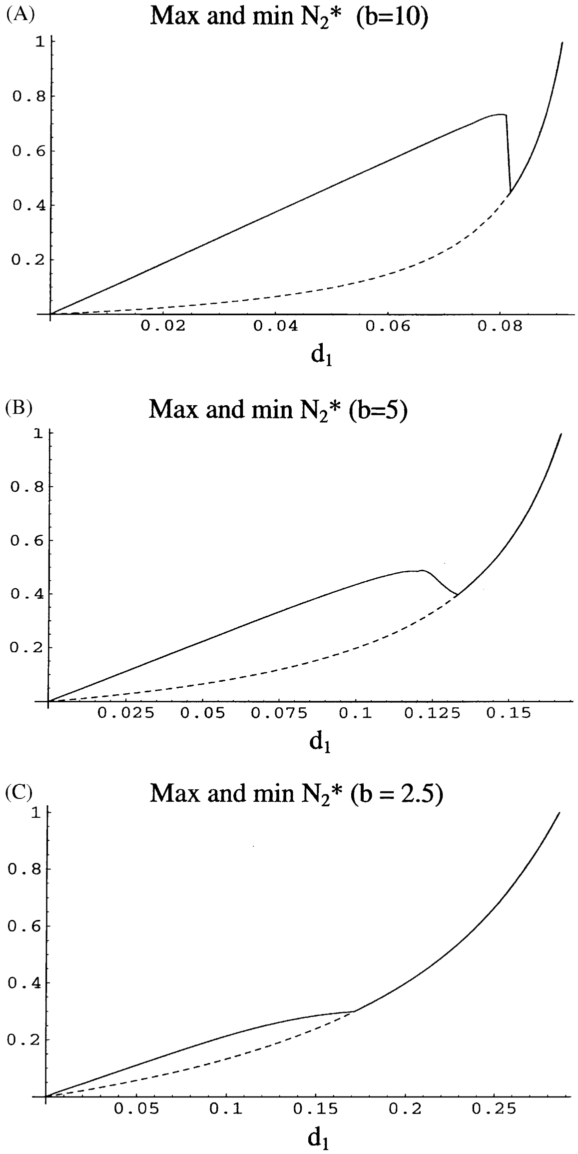

FIG. 2. Maximum (solid line) and minimum (dotted line) values of d_2 (here equal to N_2^*) for coexistence in Eqs. (2) when $a_i = 1$ and when d_1 has the value given on the *x*-axis. The abrupt drop in the maximum (at $d_1 = 0.081818$ in panel (A)) occurs when the system becomes stable. Coexistence is impossible for values of d_1 larger than this. (B) shows the same relationship for $b = 5$, and (C) shows the same relationship for $b = 2.5$.

increase bandwidth. A slower predator response increases the amplitude of the prey cycles in a single-predator–single-prey system. However, this effect tends to be rather small. The mean density $\langle N \rangle_1$ is usually changed by less than 10% by changes of less than an order of magnitude in the magnitudes of a_1 and d_1. Larger changes in $\langle N \rangle_1$ with a_1 and d_1 can occur when N_1^* is very close to the value at which the system becomes stable. Proportional changes in a_2 and d_2 have no effect on coexistence bandwidth for species 1.

Figure 2 alone does not allow us to say how the coexistence bandwidths for the A–M model compare with those for more widely accepted coexistence mechanisms. Here, we use the coexistence boundaries for the standardized 2-resource MacArthur model as a yardstick to compare the efficacy of coexistence by resource partitioning to that produced by the A–M mechanism. We ask, what level of resource partitioning in a "comparable" MacArthur model yields the same range of d_2 (equivalently N_2^*) that allows coexistence in the A–M system? The "comparable" MacArthur model is one in which the other consumer species is equally efficient. We therefore select a MacArthur system that is characterized by the same equilibrium resource intake requirement that characterizes the cycling consumer species in the A–M model. The level of resource overlap in the MacArthur system can be measured by Schoener's (1970) formula, here given by $2C$. Thus, we seek the value of $2C$ that generates the same bandwidth in the MacArthur system, as does an equally efficient non-linear consumer species in the A–M system. Table I shows the range of N_2^* $(= d_2)$ that allows coexistence, given several different efficiencies of the cycling consumer in the A–M system. These ranges are paired with the measure of resource overlap in the comparable MacArthur system that is characterized by the same range of N^* allowing coexistence. For example, in the lower rightmost cell ($b = 10$ and $d_1 = 0.2d_{1stab}$), an overlap of 0.2493 in the comparable MacArthur model is required to allow species with as broad a range of efficiencies to coexist as in the A–M model. This overlap corresponds to a case in which the two species have different preferred resources, and each consumes its preferred resource at a per capita rate over seven times greater than the rate at which it consumes the non-preferred resource. More generally, Table I and other numerical results show that, when b is large and predators are efficient, the A–M mechanism produces a coexistence bandwidth comparable to a high degree of partitioning in a system that lacks the A–M mechanism. The coexistence bandwidth of species 2, measured by the range of d_2 or N_2^*, often decreases as d_1 decreases, but the bandwidth in the corresponding MacArthur model often decreases more rapidly with a decreasing per capita death rate of the competitor.

TABLE I

Coexistence Bandwidths for Consumer Species 2 (the Linear Consumer) Based on Eqs. (2)

d_1	$0.8d_{1stab}$	$0.5d_{1stab}$	$0.2d_{1stab}$
(A) $b = 1.25$; $d_{1stab} = 0.08888$			
Range of d_2 allowing coexistence	0.00391	0.00559	0.00340
Equivalent overlap, $2C$	0.9674	0.96177	0.9534
(B) $b = 2.5$; $d_{1stab} = 0.17143$			
Range of d_2 allowing coexistence	0.06367	0.07734	0.03933
Equivalent overlap, $2C$	0.8582	0.8280	0.7537
(C) $b = 5$; $d_{1stab} = 0.13333$			
Range of d_2 allowing coexistence	0.2324	0.1990	0.09976
Equivalent overlap, $2C$	0.7005	0.5872	0.4419
(D) $b = 10$; $d_{1stab} = 0.081818$			
Range of d_2 allowing coexistence	0.4296	0.3173	0.1346
Equivalent overlap, $2C$	0.5174	0.3435	0.2493

Note: The range of mortality rates, d_2 yielding coexistence is identical to the range of equilibrium resource densities (N_2^*) producing coexistence, given our assumption that $a_2 = 1$. Also shown is the amount of resource overlap (measured by Schoener's (1970) formula $= 2C$) required to produce the same coexistence bandwidth for the 2-resource MacArthur system given in Appendix 1. Calculations assume $a_1 = 1$.

The scaled parameter b equals ChK, which is the ratio of total handling time to total search time for a consumer individual (of species 1) when the resource is at carrying capacity. More generally, $1/b$ may be interpreted as the fraction of resource carrying capacity at which the consumer functional response reaches half saturation. The scarcity of measurements of functional responses in natural or semi-natural conditions makes it difficult to assess the biological probabilities of the different values in Table I. However, there are measurements in natural or semi-natural conditions with an estimated b of 5 or greater (Abrams *et al.*, 1990; Gross *et al.*, 1993; Messier, 1994; Eby *et al.*, 1995; Ruesink, 1997). A small half-saturation value can result from adaptive variation in foraging effort, given costs to searching for resources; it need not reflect long times to subdue and ingest resources, nor imply that consumer guts are usually full (Abrams, 1990).

The range of either d_1 or N_1^* that allows coexistence can also be determined when species 2, the linear consumer, has fixed values of its growth parameters. These results will not be detailed here, but the same general patterns emerge. A low half-saturation point of the functional response of species 1 results in relatively large coexistence bandwidths. Our general conclusion is that the A–M mechanism embodied in model (1) permits coexistence of species with a wide range of efficiencies of resource use, provided that the consumer species differ sufficiently in the shapes of their functional responses.

ROBUSTNESS OF TWO-SPECIES COEXISTENCE DUE TO RELATIVE NONLINEARITY

Equations (1) describe a highly specific, simplified representation of a consumer–resource system. It is important to confirm that special properties of this particular model are not responsible for the relatively wide range of parameter values that permit species to coexist via the A–M mechanism. This section assesses the contribution of the A–M mechanism to the coexistence of two species in a variety of related models.

One concern is that unstable consumer–resource systems with a logistic resource and a consumer with a type-2 functional response with a low half-saturation point (high b) have very high-amplitude oscillations. Cycle amplitude grows very rapidly as N^* decreases below the stability threshold, and minimum resource densities quickly become many orders of magnitude less than resource carrying capacity. Persistence of species undergoing such extreme cycles is probably not biologically reasonable (Gilpin, 1975). It is useful to assess if our results are substantially altered by factors preventing low minimum resource densities. Two such factors are resource immigration or type-3 functional responses. These modifications of Eqs. (1) or (2) are considered below.

Even if the cycle amplitude required for the A–M mechanism is not extreme, other questions about robustness remain. For instance, does the breadth of conditions allowing coexistence under the A–M mechanism depend strongly on the assumption of exact linearity of the functional response for the stable species, or on the exact form of the response of the unstable consumer species? Because the nature of density dependence in the resource species has a major impact on the nature of population cycles, the functional form of resource density dependence represents another factor that may affect coexistence. We consider all these factors below.

I. Type-3 (sigmoid) functional response: First consider an "unstable" species (species 1) with a type-3 functional response. A flexible model for this response (Abrams and Roth, 1994) is: $\frac{CN^2}{\gamma+N+ChN^2}$. When γ is small, this approaches a type-2 response, while a large γ implies that the response increases at an accelerating rate with N over a broad range of N. The scaling of variables is identical to Eqs. (2); this divides the parameter γ by K, yielding a shape parameter denoted η. Thus, Eqs. (2) are altered by substituting the following expression for the functional response of species 1:

$$\frac{aN^2}{\eta + N + bN^2}. \tag{4}$$

The change to a type-3 functional response affects both equilibrium densities and stability. When N^* is less than the inflection point of the functional response, the system is stable, because the equilibrium occurs at a resource density where the response is accelerating (Murdoch and Oaten, 1975). However, if $\eta \ll 1/b$, the response is accelerating only at very low resource levels. Here, the behavior of the model away from very low N^* is similar to that of the analogous model with a type-2 response, with the exception that minimum resource densities in cycling systems are much higher than with pure type-2 response. Generally, minimum resource densities in the scaled model are on the order of η. When $\eta \gg 1/b$, instability occurs over at most a narrow range of parameter values, and the two consumers are correspondingly unlikely to coexist. When $\eta \approx 1/b$, the inflection point of the functional response occurs near its half saturation point. In this case the range of parameters yielding cycles is significantly reduced relative to model (2), but there is still a nontrivial range of values of the other parameters that yield cycles. Table II recalculates the results in Table I for the case of $b = 10$, given two different values of η; i.e., $\eta = 0.01$ ($= 1/(10b)$), and $\eta = 0.1$ ($= 1/b$). It is clear that the type-3 response does reduce the coexistence potential of the A–M mechanism. However, when b is large relative to one, and η is significantly less than $1/b$, the A–M mechanism produces a coexistence bandwidth equivalent to a substantial degree of resource partitioning. For most of the range of possible N^* values of the potentially unstable consumer species, the range of N^* of its

TABLE II

Coexistence When the Unstable Species in an Armstrong–McGehee System Has a Type-3 Functional Response with $a = 1$ and $b = 10$ in Eq. (4)

(A) *Results for* $\eta = 0.01$

d_1	0.025	0.0409	0.05	0.06545	0.07	0.08
Range of $d_2 = N_2^*$	0.06549	0.17568	0.22953	0.29427	0.29797	0.22673
Equivalent overlap, $2C$	0.65225	0.550892	0.571042	0.635424	0.64391	0.691514

(B) *Results for* $\eta = 0.1$

d_1	0.04	0.05	0.05727	0.06545	0.07	0.08
Range of $d_2 = N_2^*$	0	0.07606	0.11224	0.13280	0.12887	0
Equivalent overlap, $2C$	1.0	0.849422	0.812742	0.788144	0.784326	1.0

Note: Calculations assume that the comparable MacArthur model has the same N^* implied by the value of d_1.

competitor allowing coexistence matches that of a 2-resource MacArthur system with overlap values (Schoener's (1970) formula) on the order of 0.6, when $\eta = 0.01$.

2. *Immigration of resources*: A second way to prevent extremely low resource densities in cycling consumer–resource systems is to have a constant, small trickle of resource into the system. This could reflect actual immigration, or input from a physical refuge or from an invulnerable age/size class. This modifies Eqs. (1) or (2) by the addition of a constant term I to the expression for dN/dt. This influences dynamics in ways similar to those produced by the type-3 functional response; high enough immigration eliminates cycling entirely, while very low immigration has little effect on dynamics, aside from bounding the resource away from very low population densities. We again restrict attention to the case where the A–M mechanism generates robust coexistence in Eqs. (2), (i.e., $b = 10$), and examine two immigration rates, equal to 10% and 1% of the maximum resource growth rate ($I = 0.025$ and 0.0025; these rates are significant percentages of the equilibrium resource growth rates for the parameter values analyzed below). If scenarios equivalent to Table II are recalculated for this model with immigration, we obtain the results in Table III. Immigration prevents cycles of extreme amplitude, and thus reduces the range of relative efficiencies of the two consumers that allow coexistence. However, the A–M mechanism may still be as robust a means of achieving coexistence as is a very substantial degree of resource partitioning. When $b = 10$, the coexistence bandwidth matches that of resource overlap values ranging from 0.44 to 0.76 in the examples given in Table III.

TABLE III

Coexistence with Prey Immigration Added to the Basic Armstrong–McGehee System (Immigration Rate I Added to Eq. (2c))

(A) *Results for* $I = 0.025$ ($b = 10$; $a_i = 1$)

d_1	0.03	0.04	0.05	0.06	0.07	0.08
Range of $d_2 = N_2^*$	0	0.07421	0.15481	0.21159	0.24048	0.18581
Equivalent overlap, $2C$	1.0	0.76444	0.65819	0.68283	0.69414	0.72258

(B) *Results for* $I = 0.0025$ ($b = 10$; $a_i = 1$)

d_1	0.02	0.03	0.04	0.05	0.06	0.07	0.08
Range of $d_2 = N_2^*$	0.07119	0.13821	0.20252	0.26267	0.31153	0.33185	0.26343
Equivalent overlap, $2C$	0.48013	0.44348	0.46110	0.50453	0.57470	0.61326	0.63159

3. Type-2 functional responses with nonzero resource handling times for both consumers: In general, if both species have significant handling times, the range of other parameters allowing coexistence is considerably reduced. For example, reconsider the example from Table IIIB with immigration at $I = 0.0025$, $b_1 = 10$, $a_1 = a_2 = 1$, and $d_1 = 0.05$, but assume that consumer 2 has a handling time, yielding, $dP_2/dt = P_2(a_2N/(1 + b_2N)d_2)$. The range of N_2^* that allows coexistence decreases rapidly as b_2 increases. The coexistence range of N_2^* is approximately 0.26 when $b_2 = 0$; 0.11 when $b_2 = 1$; 0.05 when $b_2 = 2$; and 0.03 when $b_2 = 3$. Even this last value of b_2 represents a very different functional response from that of species 1; the handling time differs by a factor of 3.33, and the capture rate of resource at carrying capacity by species 2 is 2.75 times larger than that of species 1. Thus, it appears that very significant differences in the functional response parameter are needed to achieve coexistence by the A–M mechanism over significant ranges of relative efficiencies when both consumers have type-2 responses. (Hsu *et al.*, 1978, present additional results for this model.)

4. Accelerating functional responses of the stable species: If handling time is sufficiently small relative to resource carrying capacity, a type-3 response can be approximated by a function that increases at an accelerating rate over the relevant range of resource densities. Such responses are predicted by models of adaptive adjustment of foraging effort (Abrams, 1982, 1991). If the stable species (species 2) has such a response, it benefits more from cycles than would a species with a linear functional response, thus widening the coexistence bandwidth under the A–M mechanism. We investigated a system with Eqs. (2) modified so that species 2 had a functional response of a_2N^2. This response arises when foraging costs increase quadratically with time spent foraging, there is adaptive adjustment of foraging time, and the functional response while foraging is linear (Abrams, 1982). Figure 3 shows approximate ranges of N_2^* values allowing coexistence for a range of values of d_1, given that $a_1 = a_2 = 1$, and $b_1 = 10$. For a large slice of the possible range of d_1, the bandwidth of N_2^* giving coexistence represents 40–50% of the possible range of N_2^* in the absence of competition from consumer 1. Because neither species in this model has dynamics matching the consumers in MacArthur's model, detailed comparisons with coexistence bandwidths due to resource partitioning cannot be presented without additional analyses. However, comparison with Fig. 2 makes it clear that, when the stable species has an accelerating functional response, coexistence bandwidths are increased compared to similar systems in which the stable species has a linear functional response.

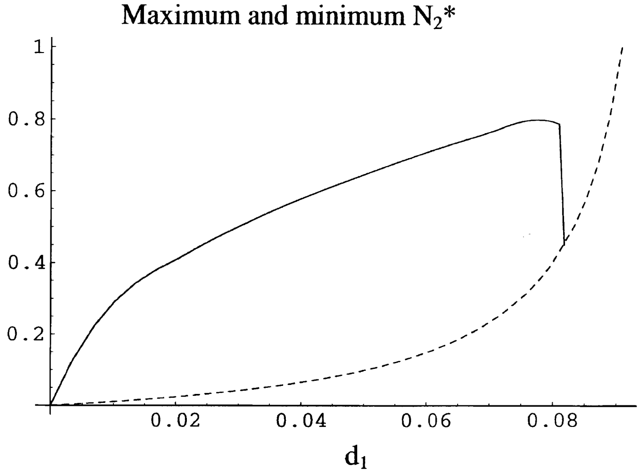

FIG. 3. Coexistence boundaries (maximum and minimum N_2^*) for a range of values of the intake requirement of species 1 (d_1) for a model like that in Fig. 2A, except that the stable species (2) has an accelerating functional response of the form aN^2.

5. Other forms of resource density dependence: In the theta-logistic model (Gilpin and Ayala, 1973), the resource per capita growth rate is described by $dN/dt = rN(1 - (N/K)^{\theta})$, where a larger θ implies the effects of density dependence are more concentrated at densities near carrying capacity. The value of θ has a modest effect on the invasion conditions for the consumer with a linear functional response, because mean resource density in a cycling 1-consumer–1-resource model increases with θ. Thus, mutual invasion occurs over a wider range of parameter values at large θ. However, unless the value of θ is extreme, this effect on invasion is moderate. Conditions for invasion of a resident linear species by the nonlinear species are not affected by this parameter. If we consider Eqs. (2) with $P_2 = 0$, theta-logistic resource growth, and parameters $a_1 = 1$, $b = 10$, $d_1 = 0.05$, mean resource density in a cycling system increases from 0.4004 when $\theta = 0.5$ to 0.5194, when $\theta = 4$. These mean densities also represent the maximal values of N_2^* ($= d_2/a_2$) that allow invasion of species 2. Thus, the form of resource density dependence has only a modest effect on the parameter ranges allowing coexistence in the A–M mechanism.

6. The contribution of the numerical response of the consumer species to coexistence via the A–M mechanism: The A–M mechanism rests on the fact that mean resource density in a system with the unstable consumer exceeds its equilibrium density. This difference between mean and equilibrium resource densities is amplified if the unstable consumer also has a numerical response that increases at a decreasing rate with increasing resource intake rate (Abrams and Roth, 1994). To assess the impact of this effect, we calculated the range of N_2^* that allows coexistence when species 1 has a numerical response with the following form: $B_1 - \chi_1/(\text{f.r.})$, where f.r. is the functional response, B_1 is the maximum per capita growth rate, and χ_1 determines the rate of approach to maximal growth. At equilibrium, the resource intake rate of species 1 is χ_1/B_1, equivalent to d_1 in the linear numerical response model illustrated in Fig. 2. Comparing the coexistence bandwidths shown in Fig. 4 with the corresponding ones in Fig. 2 shows that the nonlinear numerical response leads to coexistence over a significantly wider range of values of N_2^*. In addition, this model produces a wide coexistence bandwidth even when there is a moderate value of the handling time (i.e., a moderate half-saturation constant); compare Fig. 4B with Fig. 2C.

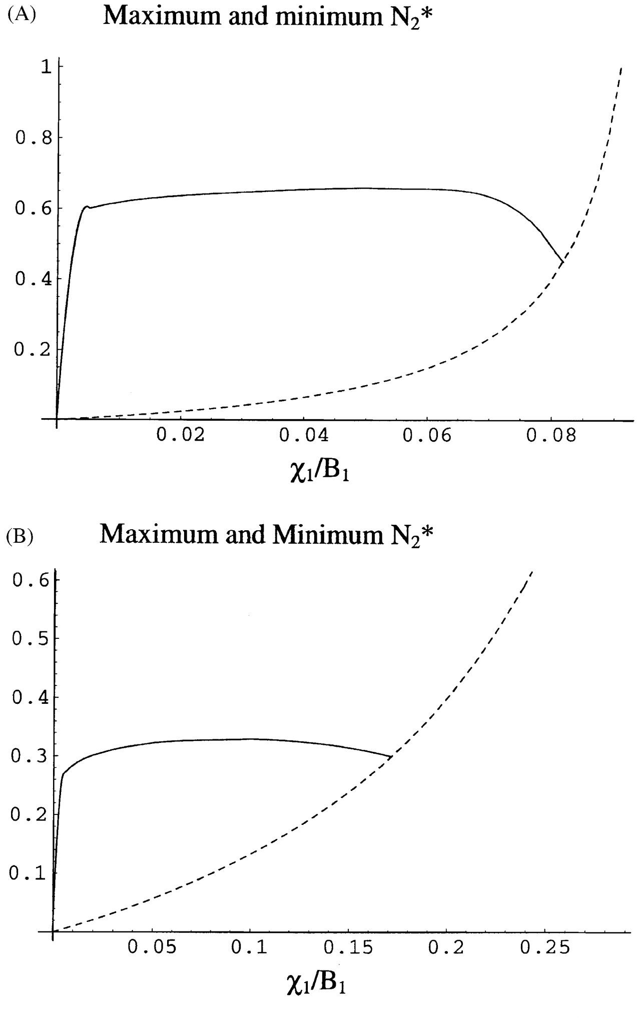

FIG. 4. Coexistence boundaries (maximum and minimum N_2^*) for a range of values of the resource intake requirement of species 1 (χ_1/B_1) for a model like that illustrated in Fig. 2, except that the unstable species (2) has a numerical response given by $B_1 - \chi_1/(\text{f.r.})$, where B_1 and χ_1 are constants, and "f.r." denotes the rate of resource intake. Here $B_1 = 1$ and the x-axis gives the value of χ_1 (see text for a more complete description). (A) assumes $h = 10$, while (B) assumes $h = 2.5$.

Nonlinearity in the numerical response of the stable consumer also affects the coexistence bandwidth. Here, an accelerating numerical response benefits the stable species when there are resources cycles. An accelerating numerical response can arise if the consumer has an adaptive behavioral tradeoff based on an accelerating relationship between its efficiency of conversion of resource intake into offspring and its death rate. For example, if the parameters B_2 and D_2 in Eq. (1b) are functions of a behavioral trait, x, such that $B_2 = z_2x$, and $D_2 = q_{02} + q_{22}x^2$, then the optimal x is $z_2C_2N/(2q_{22})$. The per capita growth rate of consumer 2 is then $(z_2C_2N)^2/(2q_{22}) - q_{02}$, and N_2^* is $\sqrt{2q_{22}q_{02}}/(z_2C_2)$. The coexistence bandwidths for species 2 are significantly greater than the comparable values on the bottom row of Table I, which assumes a linear functional response for species 2. The three overlap values (2C) on that row of Table I shrink from 0.5174 to 0.418, when $d_1 = 0.8d_{1\text{stab}}$; from 0.3453 to 0.2328, when $d_1 = 0.5d_{1\text{stab}}$; and from 0.2493 to 0.1704, when $d_1 = 0.2d_{1\text{stab}}$. The corresponding bandwidths of N_2^* for the accelerating numerical response are 0.5495, 0.5164, and 0.1741. Thus, an accelerating numerical response of the stable species greatly expands the coexistence bandwidth.

MULTI-RESOURCE EXTENSIONS OF THE ARMSTRONG–McGEHEE MODEL WITH RESOURCE PARTITIONING AND CYCLES

We have so far considered competition for a single limiting resource. Resource partitioning and the Armstrong–McGehee mechanism are likely to operate simultaneously in any system with more than one resource, which includes the vast majority of natural systems. However, there is no reason to expect that combining mechanisms has a simple additive effect on the range of resource requirements that allows coexistence. Thus, we briefly explore a model with two resources and two consumers. The two consumers potentially differ in their relative capture rates of the two resources, and in addition, one of the consumer species has a nonlinear functional response while the other has a linear response. The model has the following form:

$$\frac{dP_1}{dt} = P_1\left(\frac{B_{11}C_{11}N_1 + B_{12}C_{12}N_2}{1 + h_{11}C_{11}N_1 + h_{12}C_{12}N_2} - D_1\right),$$

$$\frac{dP_2}{dt} = P_2(B_{21}C_{21}N_1 + B_{22}C_{22}N_2 - D_2),$$

$$\begin{aligned}\frac{dN_1}{dt} &= I_1 + rN_1\left(1 - \frac{N_1}{K}\right)\\ &\quad - \frac{C_{11}N_1P_1}{1 + h_1C_{11}N_1 + h_{12}C_{12}N_2} - C_{21}N_1P_2,\\ \frac{dN_2}{dt} &= I_2 + rN_2\left(1 - \frac{N_2}{K}\right)\\ &\quad - \frac{C_{12}N_2P_1}{1 + h_1C_{11}N_1 + h_{12}C_{12}N_2}\\ &\quad - C_{22}N_2P_2. \qquad (5a-d)\end{aligned}$$

For simplicity, the two resources are assumed to have identical growth parameters. To avoid cases where a resource should be avoided under energy maximizing foraging rules, both resources are given identical handling times, and energy contents for consumer 1 ($h_{11} = h_{12} = h; B_{11} = B_{12} = B$). Resource immigration (at rates I_i) is included to prevent unrealistically low densities. We assess the contribution of the A–M mechanism to coexistence bandwidth by comparing the bandwidth for Eqs. (5), given nonzero h, to the same system with $h = 0$. In the latter case, Eqs. (5) reduce to the MacArthur model, and only resource partitioning contributes to coexistence. This comparison was made for a range of consumer efficiencies at two different levels of resource partitioning.

As in the 2-resource MacArthur system, we assume that, for each consumer species, $C_{i1} + C_{i2} = 1$, that $r = 1$ and $K = 1$, and that the two consumers have opposite resource consumption specializations (i.e., $C_{11} = C_{22}$ and $C_{12} = C_{21}$). These assumptions make D_2 in Eq. (5b) equivalent to either d_i in Eqs. (2). For the numerical results presented here, we assume that the handling time of prey for consumer 1 is $h = 10$. This corresponds to $b = 10$ in the single-resource model. The stability of the subsystem that lacks consumer species 2 depends in a rather complicated manner on the consumer's resource requirement and the level of partitioning. In general, values of C relatively close to (but still significantly different from) 0 or 1 favor stability. It is also common for there to be two unconnected ranges of the resource requirement, D, that produce limit cycles in systems with a single consumer species. We therefore present results for cases with relatively low ($C = 0.4$) and high ($C = 0.25$) levels of resource partitioning. When $h = 0$, Eqs. (5) reduce to the two-resource MacArthur model. The coexistence bandwidths for $h = 0$ and 10 are shown in Fig. 5. In each panel, the lower of the two solid lines gives the upper bound of N_2^* when $h = 0$ (i.e., no contribution from the A–M mechanism); the upper of the two solid lines gives the upper bound of N_2^* when $h = 10$. The dashed line gives the lower bound of N_2^* that allows species 1 to persist; this is independent of h. This figure suggests that the A–M mechanism contributes relatively little towards expanding the coexistence bandwidth when partitioning is high (Fig. 5A), but does contribute significantly when partitioning is low and there are cycles (i.e., Fig. 5B for low N_1^*).

There are two reasons why the A–M mechanism makes a more limited contribution to coexistence with high partitioning. First, the system is stable for a large fraction of the total range of N^*, precluding operation of the A–M mechanism. When parameters produce limit cycles, the difference in the consumption rates of the two resources greatly reduces the amplitude of the oscillations produced by the potentially unstable consumer species. Low consumption rates of alternative resources have been shown to stabilize predator–prey interactions in related models (McCann *et al.*, 1998). A second constraint on the contribution of the A–M mechanism towards coexistence is that, when the coexistence bandwidth is large simply due to partitioning, the maximum potential increase in bandwidth is limited. With less pronounced partitioning (Fig. 5B), single consumer systems with consumer 1 are unstable over much of the possible range of D_1. Here, the A–M mechanism contributes more to the coexistence bandwidth than does partitioning, over almost the entire range of N_1^* that produce cycles. Because of the differential contribution of cycling to coexistence depending on the level of partitioning, coexistence bandwidth is much less sensitive to the degree of partitioning than in the 2-resource MacArthur model.

DISCUSSION

The Armstrong–McGehee mechanism represents a robust scenario for achieving coexistence of pairs of species, provided: (1) one competitor produces large-amplitude fluctuations in resources; (2) the functional and/or numerical responses of the unstable species saturate rapidly with increasing resources; (3) the functional and numerical responses of the stable

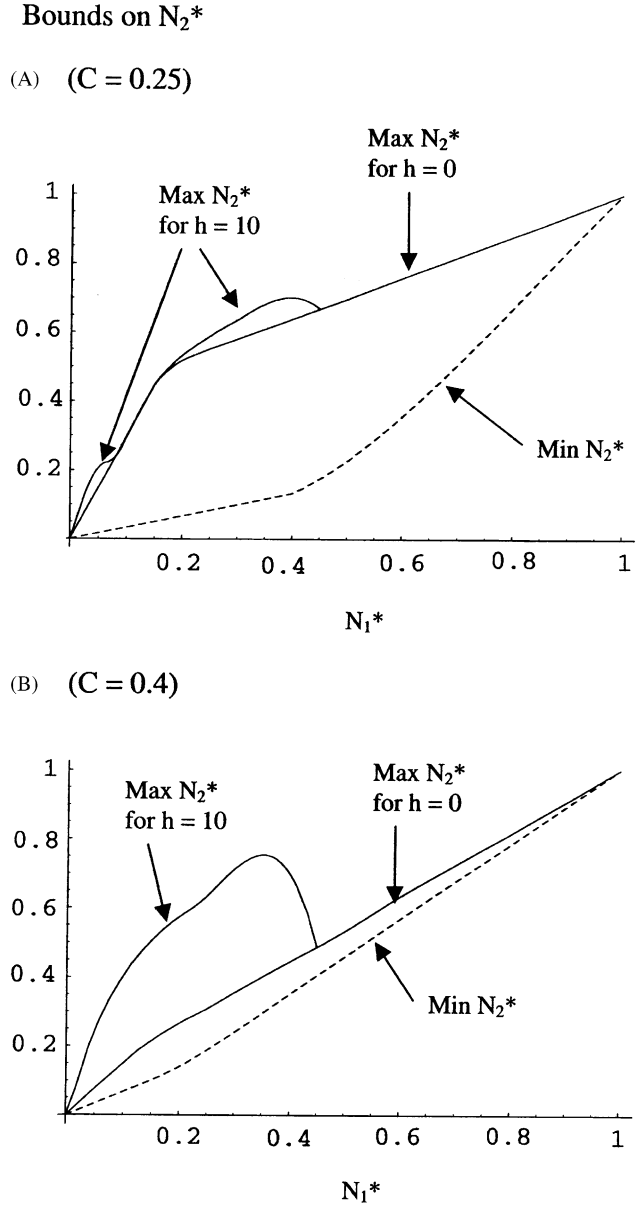

FIG. 5. The coexistence boundaries (maximum and minimum N_2^*) for a range of N_1^* in models with resource partitioning based on different relative consumption rates of two resources (Eq. (5)). In (A), the consumption rates are $C_{11} = C_{22} = 0.25$ and $C_{12} = C_{21} = 0.75$. The dashed line gives the lowest N_2^* that allows persistence of consumer species 1. The two solid lines give the greatest N_2^* that allows persistence of consumer 2; the higher of the two (sometimes overlapping) lines corresponds to a case where consumer 1 has a handling time of 10; the lower line assumes that consumer 1 has a zero handling time. In (B), the consumption rates are $C_{11} = C_{22} = 0.4$ and $C_{12} = C_{21} = 0.6$.

consumer species are linear or accelerating. Thus, the key question about the potential importance of this mechanism is the plausibility of the joint occurrence of these three requisites. Biologists have disagreed about the rarity of large-amplitude cycles, but there are now numerous examples of large-amplitude cycles (Ellner and Turchin, 1995; Kendall *et al.*, 1998). The half-saturation point of functional responses has usually been measured in the laboratory, where parameter estimates may differ greatly from those in nature. Given the paucity of field estimates of functional responses, it is difficult to judge the likelihood of satisfying the second and third of the above requirements (Abrams and Ginzburg, 2000). Several studies of functional responses have measured half-saturation densities roughly an order of magnitude less than the resource carrying capacity (e.g. Abrams *et al.*, 1990; Gross *et al.*, 1993; Messier, 1994; Eby *et al.*, 1995; Ruesink, 1997). Theory suggests that small differences in the shapes of functions describing the costs and benefits of foraging can lead to large differences in functional response shapes of adaptive consumers (Abrams, 1982, 1993). Adaptive adjustment of foraging time or effort can lead to both increasing and decreasing relationships between effort and food availability, in both models and experiments (Abrams, 1991). Increasing food–effort relationships produce accelerating (type-3) responses; decreasing food–effort relationships imply decelerating responses. Numerical responses are seldom measured, but there is no reason to believe they are usually linear, and Getz (1993) argues for the prevalence of nonlinear relationships.

Large differences in functional response shape are also most likely to occur when the two species differ significantly in feeding morphology or physiology. This seems most probable when competing species are taxonomically distant. Competition between distantly related species has been documented repeatedly (Hochberg and Lawton, 1990), but has received less experimental attention than has competition between closely related species; even fewer attempts have been made to develop or parameterize models for competition specifically tailored to such systems.

We suggest that in the light of our results, it is plausible that the A–M mechanism could operate in a variety of biological communities. The first steps in looking for this mechanism are to identify systems with cycles, to show that consumer–resource interactions are the cause of the cycles, and to identify potentially competing species in these cycling systems. It is then important to determine whether the functional or numerical responses of the species are such that cycles confer differential benefits to the species with greater resource requirements. Suggestive evidence of the mechanism may be obtained from responses of population densities to environmental parameters, which are considered in Abrams *et al.* (under review).

The A–M mechanism requires that the resource cycles be generated by the most efficient consumer. It is known that coexistence of two or more consumer species is also possible in systems with one resource that fluctuates in density due to external environmental drivers (e.g., Stewart and Levin, 1973; Armstrong and McGehee, 1976b; Nisbet *et al.*, 1997). However, the range of parameters permitting such coexistence appears to be restrictive even in the two-species case, unless species have time-dependent (Abrams, 1984), as well as resource-dependent, functional responses. This is why it is difficult to achieve coexistence of three or more species in the models with endogenous cycles considered here. The cycles are generated by the most efficient species, whose dynamics are relatively unaffected by the presence of the other species. Thus, for those species, the cycles in effect are generated by exogenous environmental factors, and so it is difficult for two or more subordinate competitors to coexist. Although in theory any number of species may coexist on a cycling biotic resource (Zicarelli, 1975), numerical results for the models considered here suggest that differences in functional response shape alone are unlikely to allow coexistence of more than three species.

Nevertheless, the difficulty of achieving coexistence of three or more species on a single resource need not imply that the A–M mechanism is a minor influence on species diversity. We suspect that overlaying the A–M mechanism with other mechanisms reflecting environment variation (e.g., the storage effect) may at times greatly facilitate species coexistence. For instance, the environment may consist of a variety of habitat patches in which different species pairs coexist. This form of spatially variable two-species coexistence has been used by Tilman (1982,1986) and Leibold (1996) to explain species diversity gradients in multi-species communities. There are limitations on the ability of such spatial variation to explain regional coexistence of very high global diversity (Abrams, 1988, 1995). Nevertheless, spatial variation in the identity of the dominant species pairs can certainly increase the role of the A–M mechanism in maintaining global diversity. Immigration can maintain significant densities of many species locally, even when only two would persist in an isolated population. These points suggest that more study of the implications of consumer–resource cycles for species coexistence in metapopulations should be worthwhile.

If it operates frequently, the A–M mechanism is likely to influence patterns of species richness as a function of environmental factors (e.g., along gradients). There is still uncertainty about how often it does so. The instability required for the mechanism to work is less likely to occur if density-independent mortality is high or resource carrying capacity is low. Thus, if the mechanism is moderately common, species richness may be lowered by high chronic mortality or low resource availability, because these conditions preclude unstable consumer–resource dynamics. Consumption by higher-order predators can also, in some circumstances, prevent unstable consumer–resource dynamics. If such predators are more likely to occur when underlying resource carrying capacities are high, or chronic consumer mortality is low, then gradients of diversity with these factors may have a variety of forms. In any event, studies of species diversity along gradients may help provide insights into the operation of the mechanism. The increasing knowledge of population fluctuations in a wide range of systems (Inchausti and Halley, 2001) argues that it is time for ecologists to seriously reconsider the potential importance of the Armstrong–McGehee mechanism for the coexistence of competing consumer species.

APPENDIX 1. MACARTHUR'S CONSUMER–RESOURCE MODEL

MacArthur's (1970, 1972) model has the following form:

$$\frac{dP_i}{dt} = P_i\left(\sum_j B_{ij}C_{ij}N_j - D_i\right),$$

$$\frac{dN_j}{dt} = r_jN_j\left(1 - \left(\frac{N_j}{K_j}\right)\right) - \sum_i C_{ij}P_iN_j, \qquad \text{(A1a, b)}$$

where each consumer species i, with population density P_i, has a per capita consumption rate C_{ij} of resource species j, with density N_j. The conversion efficiency of food into offspring is B_{ij} for consumer i and resource j, and the per capita resource requirement is D_i. The resources grow logistically with intrinsic growth rates r and carrying capacity K. Conditions for coexistence in this model were first discussed by MacArthur (1970), and a corrected analysis of the 2-consumer–2-resource version has recently appeared (Abrams, 1998). In the example considered here, both resources are assumed to have identical growth parameters, which allows the resource intrinsic growth rates and carrying capacities, r and K, to be scaled to one. The resources are assumed to be equally rewarding to the consumer, which allows all

B_{ij} to be scaled to 1. It is assumed that the total per capita consumption rate is the same for both consumers; i.e., for a given consumer species $i, C_{i1} + C_{i2} = C_m$. The consumers are assumed to have identical levels of specialization on a different resource; $C_{11} = C_{22} = CC_m$ and $C_{12} = C_{21} = (1 - C)C_m$. This symmetry allows C_m to be scaled to 1, and leads to the following set of four equations, that was used to generate Fig. 1:

$$\begin{aligned}
\frac{dP_1}{dt} &= P_1(CN_1 + (1 - C)N_2 - d_1), \\
\frac{dP_2}{dt} &= P_2((1 - C)N_1 + CN_2 - d_2), \\
\frac{dN_1}{dt} &= N_1(1 - N_1) - CN_1P_1 - (1 - C)N_1P_2, \\
\frac{dN_2}{dt} &= N_2(1 - N_2) - CN_2P_2 - (1 - C)N_2P_1. \qquad \text{(A2a-d)}
\end{aligned}$$

Three parameters determine coexistence; the scaled death rates d_1 and d_2, and the resource partitioning parameter C. In terms of the original parameters, $d_i = D_i/(BC_mK)$.

ACKNOWLEDGMENTS

We thank Michael Barfield, Troy Day, and Erik Noonburg for comments on a previous draft of the manuscript. An operating grant from the Natural Sciences and Engineering Research Council of Canada provided financial support to PAA, and RDH acknowledges support from the National Science Foundation (USA) and the Florida Foundation. We are greatly indebted to the National Center for Ecological Analysis and Synthesis for sponsoring the working group on competition theory, which provided the intellectual impetus for this work. NCEAS is supported by NSF (Grant DEB-0072909), the University of California, and UC Santa Barbara.

REFERENCES

Abrams, P. A. 1975. Limiting similarity and the form of the competition coefficient, *Theor. Popul. Biol.* **8**, 356–375.

Abrams, P. A. 1982. Functional responses of optimal foragers, *Am. Nat.* **120**, 382–390.

Abrams, P. A. 1983. The theory of limiting similarity, *Ann. Rev. Ecol. Syst.* **14**, 359–376.

Abrams, P. A. 1984. Variability in resource consumption rates and the coexistence of competing species, *Theor. Popul. Biol.* **25**, 106–124.

Abrams, P. A. 1988. Resource productivity–consumer species diversity: Simple models of competition in spatially heterogeneous environments, *Ecology* **69**, 1418–1433.

Abrams, P. A. 1990. The effects of adaptive behavior on the type-2 functional response, *Ecology* **71**, 877–885.

Abrams, P. A. 1991. Life history and the relationship between food availability and foraging effort, *Ecology* **72**, 1242–1252.

Abrams, P. A. 1993. Indirect effects arising from optimal foraging, *in* "Mutualism and Community Organization: Behavioral, Theoretical and Food Web Approaches" (H. Kawanabe, J. Cohen, and K. Iwasaki, Eds.), pp. 255–279, Oxford Univ. Press, Oxford, UK.

Abrams, P. A. 1995. Monotonic vs. unimodal diversity vs. productivity gradients; What is predicted by competition theory?, *Ecology* **76**, 2019–2027.

Abrams, P. A. 1998. High competition with low similarity and low competition with high similarity: The interaction of exploitative and apparent competition in consumer–resource systems, *Am. Nat.* **152**, 114–128.

Abrams, P. A., and Ginzburg, L. R. 2000. Models of predation: Prey dependent, ratio dependent or neither? *TREE* **15**, 337–341.

Abrams, P. A., Brassil, C. E., and Holt, R. D. Dynamics and responses to mortality rates of competing predators undergoing predator–prey cycles. *Theor. Popul. Biol.*, under review.

Abrams, P. A., Hill, C., and Elmgren, R. 1990. The functional response of the predatory polychaete, *Harmothoe sarsi* to the amphipod, *Pontoporeia affinis*, *Oikos* **59**, 261–269.

Abrams, P. A., Namba, T., Mimura, M., and Roth, J. D. 1997. Comment on Abrams and Roth: The relationship between productivity and population densities in cycling predator–prey systems, *Evol. Ecol.* **11**, 371–373.

Abrams, P. A., and Roth, J. 1994. The responses of unstable food chains to enrichment, *Evol. Ecol.* **8**, 150–171.

Abrams, P. A., and Shen, L. 1989. Population dynamics of systems with consumers that maintain a constant ratio of intake rates of two resources, *Theor. Popul. Biol.* **35**, 51–89.

Anderies, J. M., and Beisner, B. E. 2000. Fluctuating environments and phytoplankton community structure: A stochastic model, *Am. Nat.* **155**, 556–569.

Armstrong, R. A. 1976. Fugitive species: Experiments with fungi and some theoretical considerations, *Ecology* **57**, 953–963.

Armstrong, R. A., and McGehee, R. 1976a. Coexistence of two competitors on one resource, *Theor. Biol.* **56**, 499–502.

Armstrong, R. A., and McGehee, R. 1976b. Coexistence of species competing for shared resources, *Theor. Popul. Biol.* **9**, 317–328.

Armstrong, R. A., and McGehee, R. 1980. Competitive exclusion, *Am. Nat.* **115**, 151–170.

Case, T. J. 1995. Surprising behavior from a familiar model and implications for competition theory, *Am. Nat.* **146**, 961–966.

Chesson, P. 1986. Environmental variation and the coexistence of species, *in* "Community ecology" (J. M. Diamond and T. J. Case, Eds.), pp. 240–256, Harper and Row, New York.

Chesson, P. 1990. MacArthur's consumer-resource model, *Theor. Popul. Biol.* **37** 26–38.

Chesson, P. 1994. Multispecies competition in variable environments, *Theor. Popul. Biol.* **45**, 227–276.

Chesson, P. 2000. Mechanisms of maintenance of species diversity, *Ann. Rev. Ecol. Syst.* **31**, 343–366.

Chesson, P., and Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities, *Am. Nat.* **150**, 519–553.

Chesson, P. L., and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems, *Am. Nat.* **117**, 923–943.

Eby, L. A., Rudstam, L. G., and Kitchell, J. F. 1995. Predator responses to prey population dynamics—an empirical analysis based on lake trout growth rates, *Can. J. Fish. Aquat. Sci.* **52**, 1564–1571.

Ellner, S., and Turchin, P. 1995. Chaos in a noisy world; New methods and evidence from time-series analysis, *Am. Nat.* **145**, 343–375.

Getz, W. M. 1993. Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources: r-K, selection revisited, *Evol. Ecol.* **7**, 287–305.

Gilpin, M. E. 1975. "Group Selection in Predator–Prey Communities", Princeton Univ. Press, Princeton, NJ.

Gilpin, M. E., and Ayala, F. J. 1973. Global models of growth and competition, *Proc. Natl. Acad. Sci.* (*USA*) **70**, 3590–3593.

Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E., and Wunder, B. A. 1993. Functional response of herbivores in food-concentrated patches: Tests of a mechanistic model, *Ecology* **74**, 778–791.

Hansson, L. 1983. Competition between rodents in successional stages of taiga forests: *Microtus agrestis* vs. *Clethrionomys glareolus*, *Oikos* **40**, 258–266.

Hochberg, M. E., and Lawton, J. H. 1990. Competition between kingdoms, *TREE* **5**, 367–371.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly, *Can. Ent.* **91**, 293–320.

Hsu, S. B. 1980. A competition model for a seasonally fluctuating nutrient, *J. Math. Biol.* **9**, 115–132.

Hsu, S. B., Hubbell, S. P., and Waltman, P. 1978. A contribution to the theory of competing predators, *Ecol. Monog.* **48**, 337–349.

Hsu, S. B., and Hubbell, S. P. 1979. Two predators competing for two prey species: An analysis of MacArthur's model, *Math. Biosci.* **47**, 143–171.

Inchausti, P., and Halley, J. 2001. Investigating long-term ecological variability using the global population dynamics database, *Science* **293**, 655–657.

Kendall, B. E., Predergast, J., and Bjørnstad, O. 1998. The macroecology of population dynamics: Taxonomic and biogeographic patterns of population cycles, *Ecol. Letts.* **1**, 160–164.

Koch, A. L. 1974. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions, *J. Theor. Biol.* **44**, 387–395.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence and diversity patterns in communities, *Am. Nat.* **147**, 784–812.

MacArthur, R. H. 1970. Species packing and competitive equilibria for many species, *Theor. Popul. Biol.* **1**, 1–11.

MacArthur, R. H. 1972. "Geographical Ecology", Princeton Univ. Press, Princeton, NJ.

MacArthur, R. H., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385.

May, R. M. 1973. "Stability and Complexity in Model Ecosystems", Princeton Univ. Press, Princeton, NJ.

McCann, K., Hastings, A., and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature, *Nature* (*London*) **395**, 794–798.

McGehee, R., and Armstrong, R. A. 1977. Some mathematical problems concerning the ecological principle of competitive exclusion, *J. Differential Equations* **29**, 214–234.

Messier, F. 1994. Ungulate population models with predation: A case study with the North American moose, *Ecology* **75**, 478–488.

Murdoch, W. W., and Oaten, A. 1975. Predation and population stability. *Adv. Ecol. Res.* **9**, 1–131.

Myers, J. 1988. Can a general hypothesis explain population cycles of forest Lepidoptera?, *Adv. Ecol. Res.* **18**, 179–242.

Nisbet, R. M., McCauley, E., Gurney, W. S. C., Murdoch, W. W., de Roos, A. M. 1997. Simple representations of biomass dynamics in structured populations, *in* "Case Studies in Mathematical Modeling: Ecology, Physiology, and Cell Biology" (H. G. Othmer, F. R. Adler, M. A. Lewis, and J. C. Dallon, Eds.), pp. 60–78, Prentice-Hall, Englewood Cliffs, NJ.

Ruesink, J. L. 1997. Variation in per capita interaction strength: Thresholds due to nonlinear dynamics and nonequilibrium conditions, *Proc. Natl. Acad. Sci.* (*USA*) **95**, 6843–6847.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats, *Ecology* **51**, 408–418.

Stewart, F. M., and Levin, B. R. 1973. Partitioning of resources and the outcome of interspecific competition: A model and some general considerations, *Am. Nat.* **107**, 171–198.

Tilman, D. 1982. "Resource Competition and Community Structure," Princeton Univ. Press, Princeton, NJ.

Tilman, D. 1986. Evolution and differentiation in terrestrial plant communities: The importance of the soil resource: Light gradient, *in* "Community Ecology" (J. M. Diamond and T. J. Case, Eds.), pp. 359–380, Harper and Row, New York.

Vandermeer, J. H. 1993. Loose coupling of predator–prey cycles: Entrainment, chaos, and intermittency in the classic MacArthur consumer–resource equations, *Am. Nat.* **141**, 687–716.

Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together, Reprinted 1931 in R. N. Chapman, "*Animal Ecology*," McGraw–Hill, New York.

Zicarelli, J. 1975. "Mathematical Analysis of a Population Model with Several Predators on a Single Prey," Ph.D. Thesis, University of Minnesota, Minneapolis, MN.