

Functional responses of adaptive consumers and community stability with emphasis on the dynamics of plant–herbivore systems

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Summary

A comparatively recent focus in consumer–resource theory has been the examination of whether adaptive foraging by consumers, manifested through the functional response, can stabilize consumer–resource dynamics. We offer a brief synthesis of progress on this body of theory and identify the conditions likely to lead to stability. We also fill a gap in our understanding by analysing the potential for adaptively foraging herbivores, which are constrained by time available to feed and digestive capacity, to stabilize dynamics in a single-herbivore/two-plant resource system. Because foraging parameters of the adaptive functional response scale allometrically with herbivore body size, we parameterized our model system using published foraging data for an insect, a small mammal and a large mammal spanning four orders of magnitude in body size, and examined numerically the potential for herbivores to stabilize the consumer–resource interactions. We found in general that the herbivore–plant equilibrium will be unstable for all biologically realistic herbivore population densities. The instability arose for two reasons. First, each herbivore exhibited destabilizing adaptive consumer functional responses (i.e. density-independent or inversely density-dependent) whenever they selected a mixed diet. Secondly, the numerical response of herbivores, based on our assumption of density-independent herbivore population growth, results in herbivores reaching densities that enable them to exploit their resource populations to extinction. Our results and those of studies we reviewed indicate that, in general, adaptive consumers are unlikely to stabilize the dynamics of consumer–resource systems solely through the functional response. The implications of this for future work on consumer–resource theory are discussed.

Keywords: adaptive behaviour; community dynamics; functional response; regulation; stability

Introduction

A primary motivation for developing mechanistic theory in ecology was to create a framework for modelling the dynamics of natural systems that incorporates considerable relevant natural history detail (MacArthur, 1972). Predator–prey theory or, more generally, consumer–resource theory, has been extremely successful in this regard throughout the history of its development. Fundamentally, predator–prey interactions impart a sense of action. So, the linkage between predators and their prey is easily conceived as the behavioural act of subduing and consuming prey. Historically, much of the work in predator–prey theory has focused on characterizing the functional nature of this behavioural act (e.g. Holling, 1959; Emlen, 1966; MacArthur and Pianka, 1966; Oaten and Murdoch, 1975a,b; Hassell, 1978) and evaluating its consequences for the stability of predator and prey

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communities (e.g. Rosenzweig and MacArthur, 1963; Rosenzweig, 1971, 1973; Murdoch and Oaten, 1975; Noy-Meir, 1975; Oaten and Murdoch, 1975a,b; Hassell, 1978; May, 1981; Kuno 1987).

Consumer behaviour can have an important bearing on the stability of consumer–resource interactions because it determines the functional relationship between the consumption rate of resources and resource density; for example, Holling-type functional responses (Holling, 1959; Noy-Meir, 1975; Real, 1977, 1979; May 1981; Abrams, 1990b) or alternative formulations (e.g. Arditi and Ginzburg, 1989). The form of the functional relationship may differ in single and multiple resource systems simply due to the presence of alternative resources (e.g. Murdoch and Oaten, 1975; Oaten and Murdoch, 1975a,b; Abrams, 1987; Kuno, 1987). For example, the functional response on a specific resource may change from being inversely density-dependent, and hence destabilizing, in consumer-single resource systems, to being positively density-dependent, and stabilizing, in consumer-multiple resource systems (Murdoch and Oaten, 1975).

Early analyses of stability in consumer-multiple resource systems began to embody a specific form of consumer foraging behaviour known as prey switching (Oaten and Murdoch, 1975b). In this case, a consumer uses the single resource with the highest relative abundance and switches to an alternative resource when the relative abundance of the alternative resource exceeds the relative abundance of the resource being consumed. In many real-world systems, resource selection by consumers is somewhat more involved because consumers may use several resources simultaneously rather than always switch to the one with highest relative abundance. Moreover, resource choice is often based on the nutritional quality of resources as well as their abundance in space and time. Most importantly, many consumers select resources in ways that are consistent with the predictions of models of optimal foraging (Stephens and Krebs, 1986; Belovsky and Schmitz, 1991, 1994) and hence exhibit adaptive responses to resource abundances (Abrams, 1987, 1990a; Fryxell and Lundberg, 1994).

Adaptive foraging behaviour of consumers can influence the shape of the consumer functional response and, accordingly, influence the dynamics of consumer–resource systems (Holt, 1983, 1984; Gleeson and Wilson, 1986; Abrams, 1989, 1990a; Abrams and Shen, 1989; Fryxell and Lundberg, 1994; Schmitz, 1995; Krivan, 1996). We offer here a synthesis of the tremendous progress that has been made in assessing how adaptive foraging influences the dynamics of consumer–resource systems. Also, to fill what we believe to be an important gap in our understanding, we present a detailed examination of the implications of adaptive herbivore foraging on consumer–resource dynamics. Virtually all analyses to date have explored the dynamics of a ‘generic’ adaptive consumer and resources as described by the classic prey model (Stephens and Krebs, 1986; also known as the contingency model: Schoener, 1971) of diet selection (Holt, 1983; Gleeson and Wilson, 1986; Fryxell and Lundberg, 1994). This form of diet selection, and the associated functional response, assumes that consumers are limited only by time to search and handle resources, and that resources are encountered in a fine-grained (*sensu* MacArthur and Pianka, 1966) or random manner (Stephens and Krebs, 1986; Belovsky *et al.*, 1989). Most herbivores, however, are limited by both time and digestive constraints and they often encounter resources in a very coarse-grained or non-random manner (Belovsky *et al.*, 1989; Belovsky and Schmitz, 1994). The consequence of this is that we may observe a variety of functional response forms not represented by the classic model of optimal foraging (Abrams, 1989, 1990a; Schmitz, 1995).

Consumer–resource models with adaptive consumer behaviour

Previous examinations of adaptive foraging and dynamics of consumer–resource systems have involved a single optimal, or adaptive, consumer feeding on two resource populations. The prognosis for the stabilizing effects of adaptive behaviour were mixed and depended on assump-

tions about the resource selection behaviour of the consumer. The studies, their assumptions and conclusions are summarized in Table 1.

The first study to explore the effects of optimal foraging on a single-consumer/two-resource system was that of Holt (1984), who assumed that each prey population was spatially distributed in unique patches – that is, predators encountered prey in a coarse-grained or non-random manner. This amounted to optimal patch selection in which predators were free to select patches containing a specific prey species. It was assumed that predators would become resident in a

Table 1. Summary of analyses examining the stability of consumer–resource systems involving adaptive consumer behaviour

Assumptions			
Prey population growth	Predator functional response	System stability	Reference
Prey resources linearly substitutable			
Density-dependent	Non-random prey encounter Coarse-grained (patchy) prey distributions Consumer limited by feeding time only	Stable equilibrium as predator patch selection offers prey refuges	Holt (1984)
Lotka-Volterra competition	Random prey encounter Fine-grained prey distribution Consumer limited by feeding time only	Stable equilibrium when inferior competitor excluded from diet due to low profitability, or included only when predator was starving	Gleeson and Wilson (1986)
Logistic	Random prey encounter Fine-grained prey distribution Consumer limited by feeding time only	Generally unstable, stable equilibrium when net energy return of less profitable prey too low for predators to live on that prey alone	Fryxell and Lundberg (1994)
Logistic	Random prey encounter Fine-grained prey distribution Consumer limited by feeding time only	Generally unstable; stable in the sense that optimal foraging dampens predator–prey oscillations	Krivan (1996)
Prey resources non-substitutable			
Logistic	Random prey encounter Constant ratio of intake of two prey	Multiple equilibria, locally stable if equilibrium resource density $> 1/2 K$	Abrams and Shen (1989)

specific, chosen patch because the prey population in the patch could support the predator population. Such spatial structure promoted stability of the system because optimal patch selection by a predator (i.e. not selecting certain patches) could effectively provide a spatial refuge for prey.

Gleeson and Wilson (1986) examined the effect of a predator, behaving according to the classical model of optimal diet selection (Stephens and Krebs, 1986), on the dynamics of two competing prey species, where the superior competitor was also the most profitable prey species. The model incorporated both intra- and interspecific competition in the prey populations. Co-existence of all three species in this system tended to occur only when the profitability of the inferior competitor was so low that it was excluded from the diet. If the three species equilibrium was locally unstable due to decreasing abundances of the most profitable prey species, global stability could arise if the consumer broadened its diet to include the less profitable prey in the diet when it was on the verge of starvation. It was concluded that adaptive behaviour only stabilized consumer–resource dynamics under restricted conditions by shifting prey losses from the declining profitable prey population to the less profitable prey which was increasing.

Fryxell and Lundberg (1994) used a model virtually identical to that of Gleeson and Wilson (1986) except that the assumption of interspecific competition between prey populations was relaxed. This study contrasted the effects of an adaptive consumer foraging according to the classical model of optimal foraging with a consumer that exhibited suboptimal, partial preferences. Fryxell and Lundberg concluded that adaptive foraging behaviour only had a stabilizing effect when the net energetic return of the less profitable prey species was too low for predators to sustain themselves indefinitely on that species; this was only found for a narrow range of parameter values. In general, Fryxell and Lundberg suggested that adaptive behaviour was less likely to stabilize consumer–resource interactions than suboptimal behaviour where predators exhibited partial preferences. Recently, Krivan (1996) drew similar conclusions using the same type of system explored by Fryxell and Lundberg (1994) but using a different mathematical analysis.

All of the above studies assumed that resources were linearly substitutable, where the nutritional value of one resource is a constant proportion of another. This is a reasonable assumption in most cases of optimal foraging. However, this is one of many possible assumptions about resources (Tilman, 1982). Abrams and Shen (1989) considered a single-consumer/two-resource system in which resources were non-substitutable because their nutritional value was complementary. In this case, the optimal strategy was to select a constant ratio of the two resources. It was shown that such an apparently simple consumer–resource system could result in a wide range of dynamics involving multiple equilibria. The stability of the various equilibria was sensitive to assumptions about population parameters of resources and consumers.

In summary, most analyses have shown that optimal foraging tends not to be a stabilizing factor in consumer–resource systems. This is because the functional responses generated by the particular foraging models tend to be inversely density-dependent (e.g. the classical diet model; see Gleeson and Wilson, 1986; Fryxell and Lundberg, 1994) or negatively frequency-dependent (e.g. foraging for non-substitutable resources; see Abrams and Shen, 1989).

We now consider an adaptive consumer–resource system in which consumers have the theoretical potential to exhibit a positively density-dependent functional response (Schmitz, 1995). We direct our assessment towards the interaction between a generalist herbivore and two plant resources. Generalist herbivores exhibit adaptive behaviour when selecting their diets (Belovsky and Schmitz, 1991, 1994) and they have additional constraints limiting resource intake, which causes the functional responses to differ substantially from Holling-type or those that emerge from classical optimal foraging models (Abrams, 1989, 1990a; Schmitz, 1995).

Consumer–resource system with adaptive herbivore foraging

We consider a simple model system comprised of a single herbivore (H) and two plant populations (V_1 and V_2). We begin by constructing a hypothetical consumer–resource system, using functional notation, that couples the dynamics of plants and herbivores. We then make the system biologically more realistic by substituting appropriate growth and consumption functions.

We assume that the population growth rate of plants (dV_i/dt) is a function of plant density, $f_i(V_i)$, minus consumption by herbivores (H). Herbivore population growth rate (dH/dt) is assumed to be an increasing function of nutrient intake from plants minus requirements for maintenance and replacement reproduction. The basic framework describing interactions in the plant–herbivore system becomes:

$$dH/dt = H\rho(e_1X_1 + e_2X_2 - m) \quad (1a)$$

$$dV_1/dt = f_1(V_1) - X_1H \quad (1b)$$

$$dV_2/dt = f_2(V_2) - X_2H \quad (1c)$$

where ρ is a constant converting nutrient intake into offspring production; e_i is the nutrient content per unit mass of plant resource i ; m is energy requirements for maintenance and replacement reproduction; and X_i is the consumption of plant resource i by the adaptive herbivore, hereafter called the adaptive consumer functional response.

Defining growth and consumption functions

As a first step towards isolating the effects of consumption, we assume that each plant population exhibits only intraspecific competition and that plants grow logistically. The choice of logistic growth is to allow comparison of our results with previous analyses of optimal consumer–resource dynamics (Table 1). Given this assumption, plant population dynamics, in the absence of herbivores, can be approximated by the equation:

$$f_i(V_i) = r_iV_i[1 - V_i/K_i] \quad (2)$$

where V_i , r_i and K_i are the density, intrinsic growth rate and carrying capacity of plant species i , respectively.

The adaptive consumer functional response for herbivores feeding on plant species i (X_i) will depend on assumptions about the spatial distribution and nutritional quality of the two plants, operative foraging constraints, and the herbivores' foraging goal (Abrams, 1990a; Schmitz, 1995). We make the following specific assumptions based on evidence from empirical studies of herbivore optimal foraging (Belovsky and Schmitz, 1991, 1994; Forchhammer and Boomsma, 1995; Grantham *et al.*, 1995). First, the two plants are assumed to be patchily distributed in space (i.e. coarse-grained *sensu* MacArthur and Pianka, 1966), such that searching for and handling one plant resource precludes searching for and handling the other plant resource. We next assume that plant 1 (V_1) represents a higher-quality resource for herbivores than plant 2 (V_2) because of a higher level of nutrients important to herbivore fitness (e.g. higher digestible energy). Our third assumption is that energy intake (as opposed to time) is the most important currency for fitness, such that the herbivores have a goal of energy maximization rather than time minimization (*sensu* Schoener, 1971). Our fourth assumption is that herbivores are potentially limited by two foraging constraints when attempting to maximize energy intake: time and digestive capacity.

We derive the functional form for each adaptive consumer response, X_i , by finding solutions to an optimal foraging model that maximizes energy intake per unit feeding time given the two operative constraints. The procedure for deriving the adaptive consumer response is detailed in Abrams (1990a) and Schmitz (1995). The predicted diet from the optimal foraging model will depend on (1) whether the nutritional value of plant resource 1 and 2 are similar or whether

resource 1 is far more nutritious than resource 2, and (2) whether the consumption of the more nutritious plant resource is limited by time or digestive capacity (Schmitz, 1995). This leads to three scenarios that must be considered, two of which result in the forager selecting a single diet composed of the most nutritious resource; the third is a mixed diet of both resources.

First, the optimal solution could be to consume only the most nutritious plant resource when its consumption is limited by feeding time. Schmitz (1995) has shown that, in this case, the adaptive consumer response becomes identical to the Holling functional response, the exact form (e.g. Type I, II or III) depending on the consumption rate of plant resource in relation to resource density for the particular herbivore species being examined. In most cases, herbivores exhibit Type I or Type II functional responses when single resources are considered (Batzli *et al.*, 1981; Wickstrom *et al.*, 1984; Hudson and Watkins, 1986; Hudson and Frank, 1987; Lundberg, 1988; Lundberg and Astrom, 1990; Lundberg and Danell, 1990; Fryxell and Doucet, 1993; Gross *et al.*, 1993). In this scenario, resource 2 will not be included in the diet and the simple system involving the consumer and resource 1 will not be stabilized because of the lack of positive density-dependence in Type I or Type II functional responses.

The optimal solution could be to consume only the most nutritious plant resource when its consumption is limited by digestive capacity. Schmitz (1995) has shown that, in this case, the adaptive consumer response is a constant, independent of plant density; that is, D/b_1 , where D is digestive capacity (wet mass/time) and b_1 is the wet mass bulkiness of resource 1 (wet mass/dry mass). In this scenario, resource 2 again will not be included in the diet. The consumer will be unable to stabilize resource dynamics through its functional response because of its density-independent form.

The third and most interesting case in the context of community dynamics occurs when herbivores are limited by both time and digestive constraints and the optimal diet is a mixture of resources 1 and 2. The adaptive consumer functional responses for resource 1 (X_1) and resource 2 (X_2) are determined by solving for the optimal diet determined by the intersection of the time and digestive constraints. This gives rise to the following expressions describing the rate of intake of resources 1 and 2 as a function of foraging parameters in the time and digestive constraints, and the densities of resources 1 and 2 (Abrams, 1990a; Schmitz, 1995):

$$X_1 = \frac{C_1(V_1)[C_2(V_2)b_2T - D]}{C_1(V_1)b_1 - C_2(V_2)b_2} \quad (3a)$$

$$X_2 = \frac{C_2(V_2)[D - C_1(V_1)b_1T]}{C_1(V_1)b_1 - C_2(V_2)b_2} \quad (3b)$$

where $C_i(V_i)$ is the cropping rate of resource i (mass/time) as a function of resource density, b_i is the wet mass bulkiness of resource i (wet mass/dry mass), T is maximum available feeding time (time/time) and D is maximum digestive capacity (wet mass/time).

Given the above assumptions, we substitute Equations (2) and (3) into Equations (1) to generate a complete set of equations to describe a single-herbivore/two-plant resource system with herbivore adaptive foraging.

The quantitative shape of the adaptive consumer response over a specified range of resource density may vary with the species of herbivore being considered. This is because the foraging parameters (e.g. feeding time, digestive capacity, cropping rate; see Equation 3) all scale allometrically with herbivore body size (Belovsky, this issue). We therefore parameterized our model system using foraging data representative of an insect, a small mammal and a large mammal from Belovsky (1986). We examined numerically the potential for herbivores of different body size to stabilize the consumer–resource interactions through the adaptive consumer functional response.

Parameterization

In our model, there are six foraging parameters in the functional response, X_i , and four non-foraging parameters related to survival and reproduction of the consumer and resource populations. We used data on the foraging ecology of three co-existing herbivore species whose body sizes span four orders of magnitude (Belovsky, 1986), a small grasshopper (*Melanoplus sanguinipes*), a meadow vole (*Microtus pennsylvanicus*) and a deer (*Odocoileus virginianus*). Values of parameters for which data were absent (e.g. ρ) were selected to yield biologically 'plausible' densities of consumers. Table 2 presents the species-specific parameter values used in our numerical analyses.

Herbivore adaptive response shapes

The adaptive consumer response curves cannot be generalized for i resources as it can with the classical model of optimal foraging. This is because there is asymmetry in Equations (3a) and (3b). The shapes of the adaptive consumer response curves can be illustrated by examining the consumption of resource 1 while holding the density of resource 2 constant and vice versa.

We examined the shapes of the adaptive consumer response curves for each herbivore species by programming Equations (3a–c) in Mathematica (Wolfram, 1991) and parameterizing the equations with values from Table 2. The shapes were examined over the range of plant densities (mean \pm 2 s.e.) reported in Belovsky (1986). Figure 1 presents a numerical example for the grasshopper *M. sanguinipes*; the qualitative shapes of the curves for the other two species were similar to those for the grasshopper.

The adaptive consumer functional response in Fig. 1a is derived using Equation (3a). This equation specifies that the consumption of resource 1 is limited more by time than by digestive capacity. In such a case, the consumer response curve increases exponentially (in a positively

Table 2. Parameter values used in the numerical analyses of herbivore adaptive functional responses

Parameter ^a	Units	Species		
		<i>Melanoplus sanguinipes</i>	<i>Microtus pennsylvanicus</i>	<i>Odocoileus virginianus</i>
e_1	KJ g ⁻¹ dry mass	7.04	8.84	9.63
e_2	KJ g ⁻¹ dry mass	9.67	9.63	10.05
b_1	wet mass/dry mass (g)	1.64	1.64	1.64
b_2	wet mass/dry mass (g)	2.67	2.67	2.67
$C_1(V_1)^b$	dry mass min ⁻¹ (g)	0.00014 + 1.2 × 10 ⁻⁶ V_1	0.042 + 5.5 × 10 ⁻⁵ V_1	5.15 + 3.5 × 10 ⁻⁴ V_1
$C_2(V_2)^b$	dry mass min ⁻¹ (g)	0.00012 + 3.5 × 10 ⁻⁷ V_2	0.039 + 1.5 × 10 ⁻⁴ V_2	9.30 + 1.4 × 10 ⁻² V_2
T	min day ⁻¹	239	231	230
D	wet mass day ⁻¹ (g)	0.0812	31.2	4788
m	KJ day ⁻¹	0.279	70.6	9853
r_1	fraction/time	0.10	0.10	0.10
r_2	fraction/time	0.10	0.10	0.10
K_1	biomass m ⁻²	185	185	185
K_2	biomass m ⁻²	100	100	100

^aData are average values from Belovsky (1986).

^bThe functions were derived by calculating a range of cropping rates and plant densities using the mean \pm 2 s.e. of values reported in Belovsky (1986) and regressing the range end-points and average cropping rate on the range end-points and average plant density.

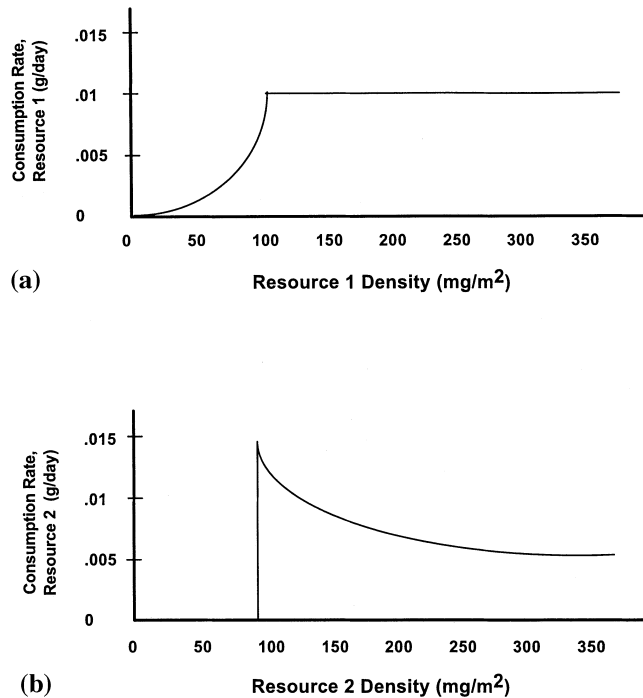


Figure 1. Numerical example of adaptive consumer responses for grasshoppers feeding on two resources. (a) Consumption rate of resource 1 as a function of variable resource 1 density at fixed resource 2 density. We assume that the intake of resource 1 is limited more by time than by digestive capacity. The consumption rate increases exponentially until the consumer is limited by time and digestive constraints, after which intake of resource 1 becomes constant. (b) Consumption rate of resource 2 as a function of variable resource 2 density at fixed resource 1 density. We assume that resource 2 is more limited by digestive capacity than by time. The threshold represents the resource density at which the digestive and time constraints become binding and resource 2 is included in the diet.

density-dependent manner) over low densities of resource 1, given a low fixed density of resource 2 (Fig. 1). Over such low abundance of resource 1, the forager does not fill its gut to capacity and hence consumption of resource 1 is only limited by feeding time. The intake rate of resource 1 will saturate once the density of resource 1 is sufficient to allow the consumer to fill its gut to capacity. Once that capacity is reached, the intake of resource 1 will be limited by time and digestive capacity. This combination of constraints now restricts intake of resources to an optimal diet specified by time and digestive limits. This leads to a fixed intake rate of resource 1, regardless of increases in resource 1 density, given a fixed density of resource 2.

Equation (3b) describes the adaptive consumer response for resource 2. The consumer should only eat resource 2 beyond a threshold density of that resource (Fig. 1). Below this threshold density, resource 2 is not sufficiently profitable to be included in the diet. This assumes that the consumer is not expected to select a mixed diet, since time and digestive constraints will not be binding over the low density range, and that resource 1 is the most nutritious. Once the threshold density of resource 2 is reached, the consumer will be limited by both time and digestive constraints. In this case, the adaptive consumer response on resource 2 decreases asymptotically with increasing density of resource 2 and fixed density of resource 1. This is the decreasing functional response shape first described by Abrams (1989, 1990a).

The quantitative range of plant density over which the adaptive consumer response was increasing or decreasing varied with herbivore body size. However, in all cases, the consumer responses for each resource saturated at densities that were at least an order of magnitude smaller than the mean density present in the field site. In other words, there is a very small range of resource densities over which any of the herbivores we examined had the potential to regulate resource dynamics. Indeed, the joint adaptive consumer responses for each of the three herbivore species, obtained by plotting consumption rate of resource i as a function of *variable* densities of both resources, saturate rapidly and converge on a fixed intake rate of resources 1 and 2, defined by the time and digestive constraints, beyond densities of 200–400 mg m⁻². Hence, the optimal diet should remain fairly constant over most resource densities (i.e. from 400 mg m⁻² to 185 g m⁻²) observed in Belovsky's (1986) field system.

Adaptive herbivore–plant dynamics

The stability of the herbivore–plant system described by Equation (1) was examined using a standard eigenvalue analysis (Edelstein-Keshett, 1988) of the parameterized equations in Mathematica. We discovered the potential for multiple states in our system. However, inspection of those states revealed only one biologically plausible state, given that Equation (3) requires that the consumers select a mixed diet. We found in general that the biologically plausible equilibrium would be stable only if $e_1X_1 + e_2X_2 < m$. This condition requires that the herbivore populations always have negative densities because of a failure to meet maintenance requirements. This is biologically implausible, and hence the equilibrium will be unstable for all biologically realistic herbivore population densities.

The instability of the adaptive herbivore–plant systems arose for two reasons. First, each herbivore exhibited destabilizing adaptive consumer functional responses (i.e. density-independent or inversely density-dependent; Fig. 1) whenever it selected a mixed diet; that is, the potential to regulate dynamics does not happen when a mixed diet is selected. Secondly, the numerical response of herbivores, based on our assumption of density-independent herbivore population growth, results in herbivores reaching densities that enable them to exploit their resource populations to extinction.

None of the eigenvalues had imaginary parts indicating that we should not expect oscillatory behaviour in this particular herbivore–plant system. This observation differs from other analyses of adaptive consumer–resource systems (e.g. Fryxell and Lundberg, 1994; Krivan, 1996).

Discussion

Adaptive consumer behaviour based on models of diet optimization is understood today as much more than the original classical prey models first posited. Coarse- as well as fine-grained resource distributions (MacArthur and Pianka, 1966) have been formalized as a variety of search modes for consumers (Belovsky *et al.*, 1989). Furthermore, digestive capacity has emerged as a constraint on foraging, especially in herbivores (Belovsky and Schmitz, 1994), that is equally as important as time. We have attempted here to assimilate much of this understanding of foraging ecology into community ecological theory.

Our analysis indicates that adaptive foraging by herbivores, when time and digestive constraints are limiting resource intake, results in density-independent or inversely density-dependent adaptive functional responses. Such herbivores will be incapable of stabilizing the dynamics of the consumer–resource system solely through the consumption of their resources. This pattern was consistent for three herbivore species spanning four orders of magnitude in body size.

Curiously, our assumptions about the spatial dispersion of resources and the consumer foraging goal (i.e. energy maximization) match those of Holt (1984). Yet, Holt arrived at the opposite

conclusion about the stability of the consumer–resource system (Table 1). In the model system examined by Holt, resource uptake by consumers was only limited by feeding time and it was further assumed that both resources were consumed by the forager. Technically, an optimal diet composed of both resources, given the form of time constraint assumed by Holt, is only possible under very restrictive conditions (Belovsky *et al.*, 1989): when the slope of the objective function of an optimality model (i.e. the energy intake objective function) is identical to the slope of the time constraint. In optimality jargon, this would result in a degenerate solution in which any diet combination falling along the time constraint is a plausible solution. Essentially, consumers would, on average, select the different resources in proportion to their availability in the environment – simple frequency-dependent resource selection. The addition of a digestive constraint in our model also leads to a mixed diet, but the consumption of resources becomes inversely density-dependent or density-independent. This illustrates how slight changes in assumptions at the physiological or behavioural ecological level can have a tremendous effect on the interpretation of dynamics at the population and community level.

Our analysis also shows that, unlike many previous models (Table 1), the shapes of the adaptive functional response may differ for different resources included in the diet. This arises because the consumption of each resource is constrained differently by time and digestive limitations; that is, there is asymmetry in the way herbivores are constrained in their consumption of each resource. The consequence is that one gets mixed responses (*sensu* Abrams, 1990c) to changes in resource densities.

A persistent issue in studies of consumer–resource systems is whether consumers regulate (stabilize) the dynamics through their functional responses. Currently, there is very limited empirical evidence that consumers can (Kuno, 1987; Schmitz, 1995), primarily because of the preponderance of consumers exhibiting destabilizing functional responses (i.e. Type I or II forms for single-consumer/single-resource systems). In multiple-resource systems, switching behaviour has the potential to produce stabilizing, density-dependent functional responses (Oaten and Murdoch, 1975b). However, switching behaviour tends to be suboptimal (Holt, 1983). Curiously, many consumers exhibit optimal behaviour when selecting their resources (Stephens and Krebs, 1986; Belovsky and Schmitz, 1994), yet optimal foraging tends largely to produce destabilizing functional response shapes (this study and Table 1). Stabilizing effects were examined when consumers exhibited suboptimal, partial preferences (see Fryxell and Lundberg, 1994), or in a special case of frequency-dependent foraging (Holt, 1984).

The emerging insight seems to be that adaptive consumer behaviour in multiple-resource communities is largely unlikely to stabilize the dynamics of the consumer–resource system. It should be recognized, however, that individual level adaptive foraging behaviour is not only connected to consumptive behaviour (functional response) but also to life-history characteristics (e.g. numerical response). The functional connection between foraging behaviour and the numerical responses of consumers has largely been ignored in consumer–resource theory (but see Holling, 1959; Hassell, 1978; Kuno, 1987). It is perhaps time to refocus by considering the interplay between foraging behaviour and life-history when examining factors contributing to community stability (Mangel and Clark, 1986)

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