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Co-adaptations of feeding behaviours and gut modulation as a mechanism of co-existence

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ABSTRACT

Question: How do foods differing in bulk, energy content, and ease of digestion influence diet choice, gut characteristics, community organization, and species co-existence?

Mathematical method: Application of evolutionary game theory to a consumer–resource model. We let the consumer species choose their optimal diets, and we seek the ESS values for each species' gut volume and gut throughput time.

Key assumptions: Gut physiology of consumers influences diet through differences in gut size and throughput time, and both of these gut characteristics can adjust evolutionarily to differences in food properties. Foods differ in key properties, including energetic reward, handling time, ease of absorption, and bulk. Consumer species encounter two food types simultaneously and may choose to forage selectively or partially selectively on one food type or opportunistically on both food types.

Conclusions: Evolutionary co-adaptation of behaviour and gut physiology results in different communities of consumers depending upon properties of the available foods. Foods can differ along a quantitative or a qualitative niche axis, although most changes in food properties result in quantitative niche axes. When foods possess similar digestive properties, a single generalist species foraging opportunistically forms the ESS. Along a quantitative niche axis (with all consumers ranking food similarly), sufficiently different foods produce communities of a selective specialist on the rich resource and an opportunistic or partially selective generalist feeding on both resources. The specialist will evolve a smaller gut size than the generalist. The relative throughput times of these strategies will depend on the nature of the food. Simultaneously, increasing the bulk and the absorption rate between two foods produces a qualitative niche axis. Such foods can select for an ESS community of two selective specialists. The specialist on the bulkier resource evolves a shorter throughput time than the specialist on the less bulky resource.

Keywords: consumer–resource game, generalist, *G*-function, gut modulation, opportunist, selective, specialist.

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INTRODUCTION

Heterogeneous foods appear to promote species diversity among consumers: frugivores, granivores, insectivores, herbivores, and more. There are often diet subdivisions among co-existing species within each of these broad diet categories. Between and within these categories, mechanisms of co-existence often seem to combine differences among the foods in nutritional composition with digestion trade-offs. For instance, fruits offer simple, relatively easily digestible carbohydrates in a bulky medium, and guts can be small with short throughput times. Insects offer a more nutritious but complex set of nutrients, and as such guts may be larger and throughput times longer, with numerous specialized enzymes. Seeds, leaves, grasses, lichens, earthworms, and so on all represent foods that may select for particular guts that may create niches for the co-existence of more or less specialized consumer species.

Foods can vary in energy reward, ease of handling, and in their bulk. When foods differ in these properties they can influence: (1) which food types to eat or not to eat (diet choice); (2) the size of the digestive tract and digestion rates (gut modulation with respect to gut volume and gut retention or throughput time); and (3) opportunities for the co-existence of different species selecting for, or specializing on, different foods. Here, we first use evolutionary game theory within a consumer–resource framework to examine the co-adaptations between diet choice, gut volume, and throughput time through the gut. Second, we examine how the interplay between these co-adaptations and the properties of two different foods influences the evolution and co-existence of two consumer species on two food types.

In the absence of digestion limitations, a forager should rank food items based on energy to handling time ratio (e/h); indeed, most feeding animals have been shown to prefer foods with high e/h to those with low e/h (Stephens and Krebs, 1986; Stephens *et al.*, 2007). In fact, when e/h is sufficiently small a food ceases to be profitable and should not be included in the diet. When focusing on gut limitations, diet is also influenced by the bulk of the food and its digestible energy content (e/b). Either because of a 'digestive pause' (Holling, 1965) or because of gut filling (Jeschke *et al.*, 2002), foods with higher energy to bulk ratios may be favoured over those with lower ratios (Whelan and Brown, 2005). The rate at which food clears the gut also becomes important for determining the extent to which gut capacity will limit or influence diets. By fermenting cellulose, ruminants such as deer, antelope, and cows have much longer throughput times than horses or other perrisodactyls that pass large volumes of food quickly through the gut.

Recently, Whelan and Brown (2005) combined both the 'external' and 'internal' aspects of feeding into a model of optimal diet choice. By external, the forager had to search for and handle food items from its environment. By internal, the animal had capacity limitations of gut volume and passage rate that influenced time available for gathering food via gut fullness. Food preference in the form of e/h created the traditional boundary between whether a food should be rejected or accepted for consumption. Food richness (e/b) created a second boundary determining when some but not all of a particularly bulky food should be included in the diet, resulting in partially selective diets. While feeding behaviour was flexible, the gut volume and passage time were not. Yet, many studies show how animals modulate these internal aspects of digestion in response to changes in diet (Starck and Wang, 2005; Karasov and Martínez del Rio, 2007).

Changes in diet substrate induce changes in gut structure and function. Whelan *et al.* (2007) modelled this by considering the optimal gut size and throughput time for a given food type that possessed properties of *e*/*h* and *e*/*b*. A larger gut, while more costly, reduced the length of the digestive pause associated with gut filling. A longer throughput time increased the food's digestibility at the expense of gut filling. The modelling considered foragers feeding on just one food type at a time [similar to many laboratory studies of gut modulation, such as that of Levey and Karasov (1992)]. With two foods there is the opportunity for a co-adaptation among behaviour (diet choice), gut volume, and throughput time; and the opportunity for the evolution and co-existence of different consumer species with different suites of co-adaptations.

Here we generalize and extend prior models by using a consumer–resource approach to predict the co-adaptations between diet choice, gut volume, and throughput time for a forager facing two different foods. When the two foods select for similar responses, the forager should be able to accommodate both foods easily. When the foods select for very different gut volumes and/or throughput times, the abundances and characteristics of the two foods may challenge the forager to adopt a generalist gut. But, a forager with a generalist gut feeding opportunistically on both foods may not be evolutionarily stable, and may permit the invasion of species that have specialized guts and forage selectively on just one of the foods. Foods that place divergent demands on the gut may promote the co-existence of diet selectors. Following the extension of the model, we will determine which combinations of foods are likely to promote single generalist species, or two more specialized species. And when there are two co-existing species, when will these be selective specialists, or when can we expect the co-existence of an opportunistic generalist with a selective specialist? (Rosenzweig, 1987; Brown, 1990).

THE MODEL

The model presented here combines previous work on diet selection with gut constraints (Whelan and Brown, 2005) and the evolution of gut modulation (Whelan *et al.*, 2000). We consider a consumer–resource game including *n*-consumers and 2-resources, where consumers evolve strategies that impact their efficiency of resource use through diet selection and gut modulation. The game-theoretic component emerges because the consumers' strategies influence the abundance of resources, and the abundance of resources determines a consumer's fitness-maximizing strategy of behaviours and gut modulation.

In developing a consumer *G*-function [fitness-generating function (Vincent and Brown, 2005)], we start with a consumer–resource model where salient parameters for the consumer include resource conversion efficiency, resource harvest rate, and consumer maintenance costs. Resource conversion efficiency for each resource is modelled using Michaelis-Menton kinetics:

$$e_i = \alpha_i e_{\mathrm{max},i}\, u_2/(\chi_i + \alpha_i u_2).$$

Here, α_i is the rate (time^{-1}) that food *i* is digested (hydrolysed) and then absorbed from the lumen of the small intestine (hereafter referred to simply as absorption rate), $e_{\mathrm{max},i}$ is the maximum resource conversion efficiency (reproductive biomass produced/unit resource consumed) for food *i*, u_2 is the time resources are processed within the gut (throughput time), and χ_i is the half saturation constant for food *i*. Note that longer throughput times result in a higher assimilation of the potential nutrients contained in a food item. As throughput time gets very long, *e* approaches e_{max}.

The harvest rate of a single resource is modelled using a modified Holling's disk equation (Holling, 1959) that includes both external handling and internal processing of food:

$$H_i = (a_i y_i)/\{1 + a_i y_i[h_i + g_i m(B_i)]\}, \tag{1}$$

where H_i is harvest rate, a_i is encounter probability, and y_i is resource abundance or density for resource i. External handling, h_i, is identical to that in the original disc equation. Internal handling consists of two variables. The first, g_i, represents processing of food within the gut, and the second, $m(B_i)$, represents the proportion of gut handling time that is exclusive of alternative foraging activities. External handling, h, and internal handling, g, have units of (time × item^{-1}).

Internal food processing, g, is determined by the quotient of food bulk per item, b (ml × item^{-1}), and the volumetric flow rate of food through the gut, Vo (ml × item^{-1}): $g = b/Vo$. But Vo = gut capacity, u_1 (ml), divided by retention or throughput time, u_2 (time) (see Jumars and Martinez del Rio, 1999). Thus passage time per item is given by $g = (bu_2)/u_1$. Exclusive internal handling time, $m(B)$, increases monotonically with gut fullness. For simplicity, we let $m(B) = B$ (a linear function), the proportion of gut volume occupied by food. Gut fullness, B, is given by the sum of the bulk intake rate of both resources (bulk of the resource, b_i, multiplied by its ingestion or harvest rate, H_i) and the retention time of food in the gut (the quotient of throughput time, u_2, and gut volume, u_1): $B = (b_1H_1 + b_2H_2)\ (u_2/u_1)$. This definition of $m(B)$ allows the exclusivity of internal handling to be a continuous, sliding scale that reflects the extent to which gut volume is filled from food consumption. Now let the probabilities of accepting resources 1 and 2 be given by u_3 and u_4 respectively. Substituting g_i and B into (1), while allowing for a second resource, and simplifying yields

$$H_1 = (a_1 y_1 u_3)/[1 + a_1 y_1 u_3(h_1 + b_1(u_2^2/u_1^2)(b_1H_1 + b_2H_2)) + a_2 y_2 u_4(h_2 + b_2(u_2^2/u_1^2)(b_1H_1 + b_2H_2))]$$

$$\tag{2}$$

$$H_2 = (a_2 y_2 u_4)/[1 + a_1 y_1 u_3(h_1 + b_1(u_2^2/u_1^2)(b_1H_1 + b_2H_2)) + a_2 y_2 u_4(h_2 + b_2(u_2^2/u_1^2)\ (b_1H_1 + b_2H_2))].$$

The harvest rates (H_1 and H_2) can be explicitly solved using the quadratic formula (see Whelan and Brown, 2005).

Finally, the cost function (γ) includes both a fixed cost (for maintenance of all tissues including the gut) and a variable cost, which increases linearly with gut volume (u_1). The ease of resource harvest associated with large gut sizes is offset by the cost of maintaining a large gut:

$$\gamma = c + \beta u_1.$$

Here c is the fixed maintenance cost (time^{-1}), and β is the variable cost of gut size (time^{-1} × gut size^{-1}).

Putting these components of fitness together we can construct the G-function for a consumer:

$$G = e_1H_1 + e_2H_2 - \gamma.$$

The fitness-generating function is equivalent to the per capita growth rate of the consumer, so the change in population growth rate is given by:

$$dx_j/dt = x_j G_j.$$

For simplicity, we assume a linear relationship between net profit from foraging and per capita growth rate. Here x_j is the population size of species j.

Resource population dynamics are given by a density-dependent renewal process minus the consumption by the consumer:

$$dy_i/dt = r_i(K_i - y_i) - x_i H_i.$$

Here, r_i is the maximum rate of resource renewal (time^{-1}), K_i is the resource supply point, and y_i is the population size of resource i.

ZERO NET GROWTH ISOCLINES AND DIET SELECTION ISOLEGS

The consumer's effect on the equilibrium abundance of resources and its diet selection can be displayed graphically with the use of zero net growth isoclines (ZNGI) and isolegs, respectively. Zero net growth isoclines are lines in the state space of resource abundances that give all combinations of y_1 and y_2 for which the consumer species' population growth rate is zero (Tilman, 1982). The ZNGI is solved for by setting the consumer growth rate equal to zero and solving for y_2. The shapes of ZNGIs are influenced by the consumer's diet selection behaviour and the attributes of the resources. Both determine the subsistence levels of resources. Isolegs also exist in this resource state space; they are curves that separate regions of resource abundances where the consumer has a different optimal feeding behaviour [for isoleg solutions to this model, see Whelan and Brown (2005)].

The feature that separates this model from the classical model of diet selection is the internal handling time in the gut. In the absence of internal handling times, the model collapses to the classical diet selection model. In this situation, e_i/h_i solely determines food preferences, and only the Pulliam Isoleg (*sensu* Mitchell and Brown, 1990) exists as a straight line (vertical or horizontal). It separates a region of complete selectivity on the better resource from a region of opportunism. The ZNGI is a negatively sloped straight line in areas of opportunism, and a vertical straight line in areas of selectivity (assuming $e_1/h_1 > e_2/h_2$).

Resources will differ in internal handling times when they differ in richness (e_i/b_i). Now, if we assume that resource 1 has greater richness and greater energy per external handling time, then the model produces a second isoleg. This isoleg, the Mitchell Isoleg (*sensu* Whelan and Brown, 2005), separates a region of partial selectivity from a region of opportunism. The Pulliam Isoleg still exists but it now separates a region of complete selectivity from one of partial selectivity. Here, the ZNGI is bowed towards the origin (in a manner that produces slight complementarity between the two resources) in regions of opportunism, and a vertical straight line in regions of both partial and full selectivity (Fig. 1). The complementarity results from resource interactions via gut processing. When both foods 1 and 2 occur at low abundance, and the ratio of food 2 to food 1 ($y_2 : y_1$) is low, the gut is mostly empty and the less rich resource, food 2, is valuable. As $y_2 : y_1$ increases, the gut starts to become full from consuming food 2, and its value declines as its processing time-cost increases.

ONE RESOURCE: EVOLUTION OF SPECIALIZED GUTS

Whelan *et al.* (2007) explored the adaptation of guts specialized for particular food types. They considered a single consumer species depleting its single resource to a subsistence level [R^* of Tilman (1980)]. Whelan and colleagues' (2007) Figure 7 and Appendix Table 1 show how foods with different properties influence gut strategies (size and throughput time). We begin

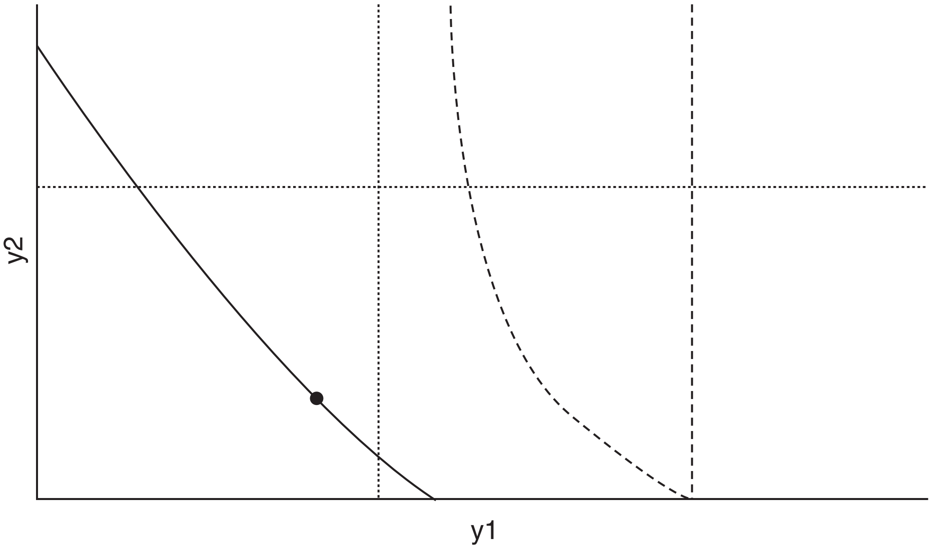

Fig. 1. The effect of co-adaptations of foraging behaviour and gut physiology on the ZNGIs and behavioural isolegs of consumers feeding on two foods that differ only slightly in bulk. The resource state space of abundance of food 2 (y_2) versus the abundance of food 1 (y_1) contains three behavioural regions. To the right of the vertical dashed line, the Pulliam Isoleg, the consumer is selective on food 1. Between the Pulliam Isoleg and the curved dashed line, the Mitchell Isoleg, the consumer is partially selective on food 1, meaning it consumes some but not all of the encountered items of food 2. To the left of the Mitchell Isoleg, the consumer harvests all encountered items of both foods opportunistically. The vertical and horizontal dotted lines represent the ZNGIs of specialist consumers that feed selectively on food 1 or food 2, respectively. The solid line with negative slope represents the ZNGI of the optimal strategy, a consumer with a generalist gut physiology. The dot represents the equilibrium abundances of foods 1 and 2 resulting from the consumption by the generalist species. Parameter values are: $a_1 = a_2 = 0.1$; $h_1 = h_2 = 1.0$; $\alpha_1 = \alpha_2 = 0.1$; $e_{\mathrm{max1}} = e_{\mathrm{max2}} = 10$; $\chi_1 = \chi_2 = 1$; $b_1 = 1.3$, $b_2 = 2.7$; $c = 0.1$; $\beta = 0.1$; $r_1 = r_2 = 0.001$; $K_1 = K_2 = 100$.

our analyses by using our model to re-analyse that of Whelan *et al.* (2007). We found some discrepancies, which we have corrected in this paper's Table 1 and Fig. 2. Numerical convergence to the optimum can be quite slow for some food types, and Whelan *et al.* (2007) appear to have stopped numerical analyses at strategies that performed close to optimal, but were still some distance from their ESS values.

The evolutionarily stable strategy (ESS) of the consumer appears to balance the minimization of gut fullness with the maximization of resource conversion efficiency. For instance, a bulky food requires a large gut and a short throughput time. A food with a low absorption rate requires a large gut and a long throughput time. Intriguingly, most foods selected for strategies that left consumers with relatively empty guts and with throughput times far shorter than would confer maximum resource conversion efficiency (Table 1). Of interest is how external handling time, h, has little or no influence on the optimal gut strategies.

When inspecting Fig. 2, imagine three straight lines radiating from the origin in the state space of optimal gut size and throughput time. Each line represents a constant richness ($e_{\mathrm{max},i}/b_i$) of the resources. The line with the steepest slope represents resources with

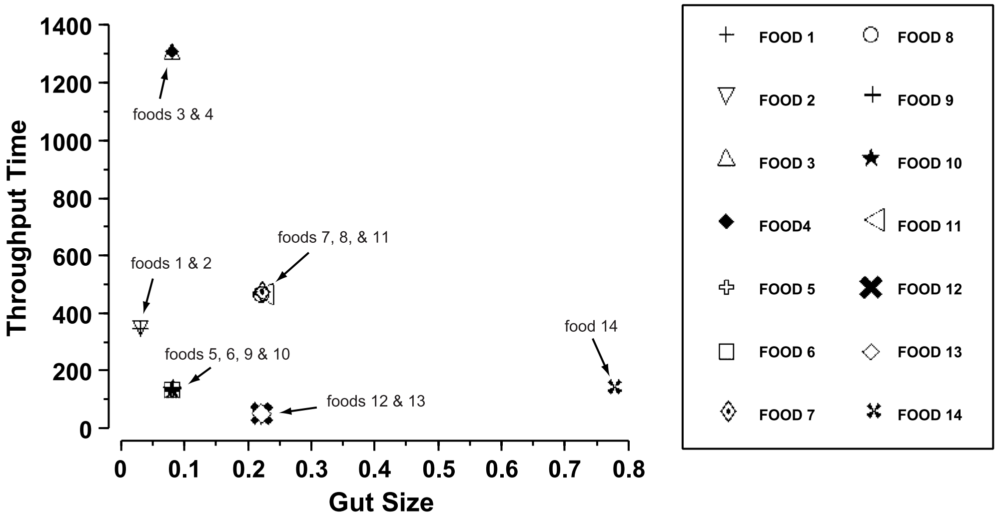

Fig. 2. The effect of 14 different foods on optimal gut size and throughput time. Foods differ in energetic reward, bulk, ease of absorption, and external handling (see Table 1). Joint adjustment or modulation of gut size and throughput time results in six apparent digestive physiological syndromes. Increasing food richness (energy-to-bulk ratio) leads to smaller gut volumes and little change in throughput times. Higher absorption rates favour shorter throughput times with smaller effects on gut volume.

high richness (foods 1–4), the line with intermediate slope represents resources with intermediate richness (foods 5–11), and the line with the least steep slope represents resources with low richness (foods 12–14). Moving along each one of these equal richness lines away from the origin represents a decline in resource absorption rate (α). Therefore, Fig. 2 depicts the effect of the interaction between resource richness and absorption rate on consumer gut evolution. We can see that as absorption rate, α, decreases, both gut volume and throughput time increase, but the relative changes in the two gut characteristics are set by the degree of resource richness. For example, when richness is high, lowering absorption rate increases gut volume slightly, but greatly increases throughput time. Since the resource is rich, by definition it is efficiently converted to new biomass and/or takes up minimal room in the gut. Therefore, decreasing absorption rate selects for a longer throughput time while only slightly increasing gut size.

The reverse is true when richness is low. Resources with low richness by definition have low conversion efficiencies and/or high bulk. As absorption rate declines, the consumer responds by dramatically increasing gut size and slightly increasing throughput time. Resources low in absolute richness and absorption rate tend to quickly fill the gut as the optimal throughput time increases slightly. To accommodate all of this bulk, the optimal gut volume increases significantly.

To take a further step, we can analyse the subsistence level of resources, y^*'s, and gut evolution together (Table 1). Intuitively, resources with high absolute richness and absorption rate result in the lowest y^*'s, as consumers require only a low standing crop to subsist. Resources with the lowest richness and absorption rate cause the highest y^*'s. The most efficiently used resources drive consumer evolution to the smallest gut sizes and intermediate throughput times, whereas the least efficient resources drive consumer

Table 1. Sixteen foods that differ in energetic value, $e_{\max}$, bulk, b, rate of absorption, α, and external handling time, h, and the optimal gut volume, u_1^*, throughput time, u_2^*, and minimal level of resource density, y^*, that result. The effective rate of absorption ('e') and gut fullness are also shown when the forager has reached optimal adjustment of gut volume and throughput time at y^*

Food	$e_{\max}$	b	Richness (e/b)	α	h	u_1^* (ml)	u_2^* (time)	y^*	'e' (%)	Fullness (%)
1	10	0.1	100	0.1	1	0.03	340	0.0011	97	12
2	10	0.1	100	0.1	10	0.03	340	0.0011	93	12
3	10	0.1	100	0.01	1	0.08	1300	0.0012	93	19
4	10	0.1	100	0.01	10	0.08	1300	0.0012	93	19
5	10	1	10	0.1	1	0.08	130	0.0012	93	19
6	10	1	10	0.1	10	0.08	130	0.0012	93	19
7	10	1	10	0.01	1	0.22	460	0.0016	82	31
8	10	1	10	0.01	10	0.22	460	0.0016	82	3
9	1	0.1	10	0.1	1	0.08	130	0.012	93	19
10	1	0.1	10	0.1	10	0.08	130	0.012	93	19
11	1	0.1	10	0.01	1	0.22	460	0.017	82	31
12	1	1	1	0.1	1	0.22	46	0.017	82	31
13	1	1	1	0.1	10	0.22	46	0.017	82	31
14	1	1	1	0.01	1	0.77	130	0.044	57	52
15	1	0.1	10	0.01	10	23.0	0	—	—	—
16	1	1	1	0.01	10	27.0	0	—	—	—

Note: Foods are roughly arrayed from most favourable (top) to least favourable (bottom). Note that two foods (15 and 16) will not sustain the forager. Note also that for each of the first 14 foods, the forager is food limited, but typically operates below peak rate of absorption (effective $e < 100\%$) with a mostly empty gut.

evolution to large gut sizes and low throughput times. As examples, contrast foods 1 and 2 versus food 14 in Table 1.

In a more explicit example, we can focus on the instances where different foods (foods 5, 6, 9, and 10 vs. food 14) select for the same throughput times but very different gut volumes (Fig. 2 and Table 1). The food selecting for the greater gut size, food 14, causes a greater y^*. Therefore, when throughput time remains the same, differences in the gut sizes of consumers specialized for different foods implies quantitative differences in these foods' properties.

When foods vary in absorption rate or richness and they select for different throughput times, we need to clarify the definitions of reward and richness within an explicitly evolutionary context (Table 2). This is because throughput time and absorption rate combine to determine the effective amount of nutrients assimilated from a given food item. Whereas $e_{\max}$ and $e_{\max}/b$ are absolute rewards and absolute richness, respectively, they give rise to effective reward, e, and richness, e/b, when adjusted for the actual amount of nutrients assimilated by the gut. In Table 2, we also define and distinguish between absorption reward, $\alpha e_{\max}$, and absorption richness, $\alpha e_{\max}/b$, to make clear the value of a food item in terms of absorption per unit passage time. This gives us a new evolutionary perspective of how resources may be ranked by both reward and richness. Looking at the formula for effective richness, it is clear that changing gut volume alone will not alter the ranking of food preferences based on richness. Thus, when foods select for significantly different gut sizes (but not throughput times), we know that they lie along a quantitative niche axis.

Table 2. Evolutionary definitions for reward and richness

	Reward	Richness
Absolute	$e_{\mathrm{max},i}/h_i$	$e_{\mathrm{max},i}/b_i$
Absorption	$\alpha_i e_{\mathrm{max},i}/h_i$	$\alpha_i e_{\mathrm{max},i}/b_i$
Effective	$\alpha_i u_2 e_{\mathrm{max},i}/h_i(\chi_i + \alpha_i^* u_2)$	$\alpha_i u_2 e_{\mathrm{max},i}/b_i(\chi_i + \alpha_i^* u_2)$

Note: In an evolutionary setting, resources acquire effective rewards and richnesses due to the effect of changing throughput time (u_2) on conversion efficiency (e_i).

We can now look at the reverse situation, where two foods require different throughput times but the same gut sizes. Combinations of these foods lie vertically in state space of optimal gut strategies. There are two examples of such foods in Fig. 2, and upon examination of y^*'s (Table 1) we see that each pair has an equal y^*. Referring back to effective richness, we can confirm that the rank ordering of such foods depends upon the forager's throughput time. Each specialist would see its food as having a higher effective richness than the other food. Therefore, foods that require different throughput times and equal gut sizes lie along a purely qualitative niche axis. The distinction between whether pairs of foods create quantitative versus qualitative niche axes becomes critical for the evolution of consumer communities driven by co-adapations of behaviour and gut characteristics.

TWO RESOURCES: NUMERICAL AND GRAPHICAL ANALYSIS

As our next step, we used Fig. 2 to select pairs of different foods that favour either similar or disparate gut strategies. We can then determine ESS solutions for the resulting two-resource system and see whether the ESS contains a single or two co-existing consumer species. We do this by examining both the adaptive landscapes (reveals evolutionary stability) and ZNGIs (reveals ecological stability of consumer–resource population dynamics). Ecologically, it is possible to have three consumer species that co-exist (one generalist species with two specialist species), but we never found these to be evolutionarily stable. The ESS communities possessed either a single generalist species, a generalist co-existing with a specialist species, or two co-existing specialist species. We used Matlab to simultaneously solve for the ecological and evolutionary equilibria of the model. From the viewpoint of two co-evolving specialists, resources can differ along a quantitative or a qualitative niche axis. In the following, we present examples of each and discuss how they determine community evolution.

Quantitative differences in the food

When foods vary in bulk, b, energy reward, e, and/or absorption rate, α, most will create quantitative differences between foods (Table 3). All pairs of foods that vary quantitatively produce similar results and community organizations. For example, consider two foods that differ only in bulk. We assume $b_1 < b_2$. Evolutionarily, food 1 is the better food, and this represents a quantitative niche axis in the sense that no matter what gut strategy a species possesses, food 1 will always be preferred. The specialist on food 1 (the less bulky resource)

Table 3. Combinations of parameters that affect digestion and simple relationships between them

	$e_{\max,i}$	α_i	b_i
$e_{\max,i}$	**Quantitative** $e_{\max1} > e_{\max2}$	**Quantitative** $\alpha_i e_{\max,i} = k$ $\alpha_2 > \alpha_1$ $e_{\max1} > e_{\max2}$	**Quantitative** $e_{\max,i}\, b_i = k$ $e_{\max1} > e_{\max2}$ $b_2 > b_1$
α_i	**Quantitative** $\alpha_i / e_{\max,i} = k$ $\alpha_1 > \alpha_2$ $e_{\max1} > e_{\max2}$	**Quantitative** $\alpha_1 > \alpha_2$	**Quantitative** $\alpha_i b_i = k$
b_i	**Quantitative** $e_{\max,i}/b_i = k$ $e_{\max1} > e_{\max2}$ $b_1 > b_2$	**Qualitative** $\alpha_i / b_i = k$ $\alpha_2 > \alpha_1$ $b_2 > b_1$	**Quantitative** $b_2 > b_1$

Note: k is a constant. Food combinations diverge along either a qualitative or quantitative niche axis.

evolves a small gut and long throughput time. The specialist on food 2 (the more bulky resource) evolves a large gut and short throughput time. The optimal strategy for an opportunistic species is a generalist strategy that approximates some averaging of the extreme specialist strategies. A strategy of selectively feeding on food 2 and adopting the corresponding food 2 specialist gut is never an ESS. Because food 1 remains preferred, it is always optimal to accept all encountered items of food 1.

When the two foods differ only slightly in bulk, the ESS community is the generalist species (Fig. 1), the generalist gut does not compromise the forager's digestive aptitudes on the two foods, and it has the advantage of offering the consumer considerably more food items to harvest. The food specialist that selectively feeds on food 1 cannot invade this community, as the generalist species depresses the abundance of food 1 to below the specialist's subsistence level (ZNGI).

As the bulk properties of the two foods diverge further, the ESS shifts from a single generalist species to an ESS with two species: a specialist on food 1 that feeds only on food 1, and a generalist species that feeds either opportunistically or partially selectively on food 1 (rejects some items of food 2 for harvest). These ESS strategies come about because a single species with the optimal compromise strategy of the generalist can no longer depress the level of food 1 sufficiently. A species that specializes and feeds selectively on food 1 can invade (Fig. 3). In fact, this specialist will out-compete the resident generalist species.

There are two ways to achieve the ESS of two species: (1) one can start with the specialist species and let the appropriate generalist invade, or (2) one can start with the single generalist species at its optimal (pre-invasion by the specialist) gut strategy. The specialist then invades, causing a decline in the generalist's population size, an increase in the abundance of food 2, and a shift in its adaptive landscape towards a larger gut and shorter throughput time. If acclimation or adaptation along this landscape occurs fast enough, the generalist species can evolve into a region of its adaptive landscape where it can maintain a positive

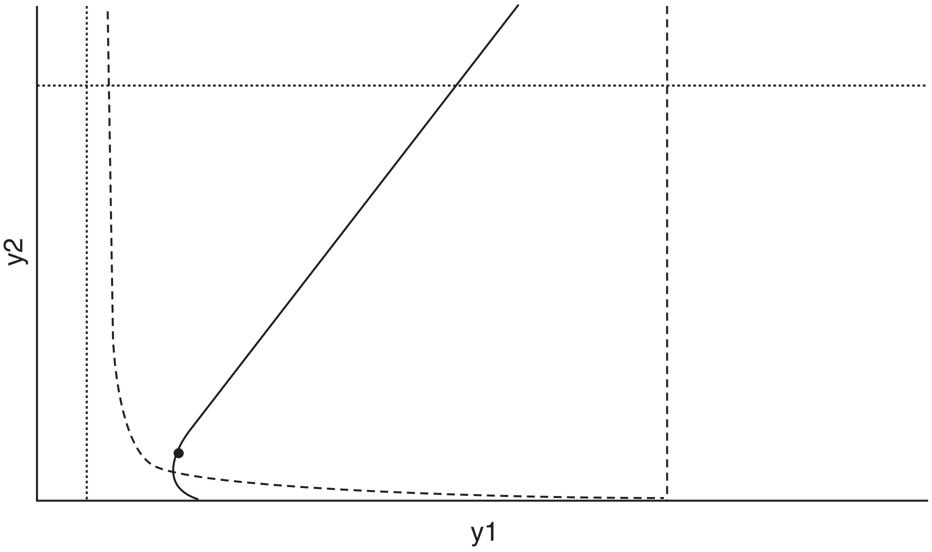

Fig. 3. The effect of co-adaptations of foraging behaviour and gut physiology on the ZNGIs and behavioural isolegs of consumers feeding on two foods that differ greatly in bulk. The state space, and all lines except the solid line, are the same as in Fig. 1. The solid line that switches from negative to positive slope represents the ZNGI of the optimal strategy, a consumer with a generalist gut physiology. The dot represents the equilibrium abundances of foods 1 and 2 resulting from consumption by the generalist strategy. In this figure, a specialist strategy on food 1 will out-compete the generalist strategy. Parameter values are: $a_1 = a_2 = 0.1$; $h_1 = h_2 = 1.0$; $\alpha_1 = \alpha_2 = 0.1$; $e_{\max 1} = e_{\max 2} = 10$; $\chi_1 = \chi_2 = 1$; $b_1 = 0.1$, $b_2 = 3.9$; $c = 0.1$; $\beta = 0.1$; $r_1 = r_2 = 0.001$; $K_1 = K_2 = 100$.

population size. At this point, the generalist continues to evolve towards the two-species ESS, even as this species continues to consume food 1 and bulk up on food 2. Regardless of how the community gets to its ESS, the ESS remains the same.

The specialist species is evolutionarily unaffected by the generalist. The generalist does not influence the specialist's gut strategy or its subsistence level of food 1. The generalist does influence the specialist's equilibrium population size, but not by as much as the specialist influences the generalist's population size. The presence of the specialist strongly influences the generalist species and its evolution towards a larger gut and shorter passage rate.

A special case

A special case of the quantitative niche axis is when foods differ only in their sizes (Table 3, combination in lower left-hand corner). This can be represented by foods that have the same absolute richness, but differ in their magnitudes of $e_{\max}$ and b. If the energy per volume of the two foods is the same, then as their total volume changes (b), so does $e_{\max}$. Since these two foods have the exact same absorption efficiency, they produce specialists with the same gut characteristics. The foods thus have the same effective richness, but different effective rewards. The larger food also has a larger reward, which gives it a lower y^* and makes it the preferred food of the consumer. Since these foods produce identical gut characteristics, foods differing only in size can never create co-existence solely based on gut physiology.

Depending on the magnitudes of the foods' difference in sizes (i.e. differences in effective reward) and their abundances at equilibrium, the generalist consumer may either be behaviourally opportunistic or partially selective.

Key predictions

First, when two foods differ only in their absorption richness, small differences in richness will be insufficient to produce species co-existence via species-specific differences in gut volume and throughput time.

Second, when the two foods have sufficiently different richnesses as to promote co-existence, one species will specialize on the rich food, while the other species will feed more opportunistically on both foods 1 and 2. The generalist species will possess a larger gut and a shorter throughput time. (This prediction may have to be adjusted allometrically for body size and metabolic rates.)

Finally, in the special case that foods differ only in size, co-existence cannot be a consequence of species' differences in gut physiology, and in fact foods that differ only in size should produce similar gut physiologies.

Qualitative differences in the food

In our model, a purely qualitative niche axis can be achieved in only one way (Table 3). It requires two foods that differ in bulk (b) and absorption rate (α), while holding the ratio of the two constant. We assume that $b_1 > b_2$ and that $\alpha_1 > \alpha_2$. Hence, food 1 is bulkier but is absorbed more quickly, while food 2 is less bulky but digests more slowly. The specialist on food 1 and the specialist on food 2 both have the same optimal gut size. However, the specialist on food 1 evolves a short throughput time, and the specialist on food 2 evolves a long throughput time. This creates a qualitative niche axis where the specialist on food 1 prefers its food. Its rapid throughput time makes food 2 less rewarding. The specialist on food 2 prefers its food. Food 1 is too bulky and fills its gut.

When the two foods differ only slightly in b and α, a compromised generalist strategy will use both resources most efficiently, and this single species is the ESS (Fig. 4).

As foods diverge in their magnitudes of α and b, the generalist's strategy shifts towards that of a specialist on food 1. This is because eating an item of the bulky food 1 with a gut adapted for food 2 (long throughput time) severely decreases overall resource use efficiency by filling the gut. On the other hand, a specialist on food 1 that consumes an item of food 2 can increase its resource use efficiency. In this case, consuming food 2 does not add much to fitness, because food 2 has such a low absorption rate. Because of this, there is a threshold in the differences between b and α beyond which the ZNGI of the opportunistic generalist is to the right of its Pulliam Isoleg. This means that the generalist cannot be at a behavioural and gut strategy equilibrium with its resources – this point cannot be an ESS. The ESS community will be two specialist species (Fig. 5). The two specialists do not have to have exactly the same resource conversion efficiencies, e_i's (or gut sizes), on the two different foods to produce a two-species specialist community, but the efficiencies must be relatively close in value.

Key predictions

First, when two foods diverge along a qualitative niche axis, an ESS of one generalist species arises when foods are relatively similar.

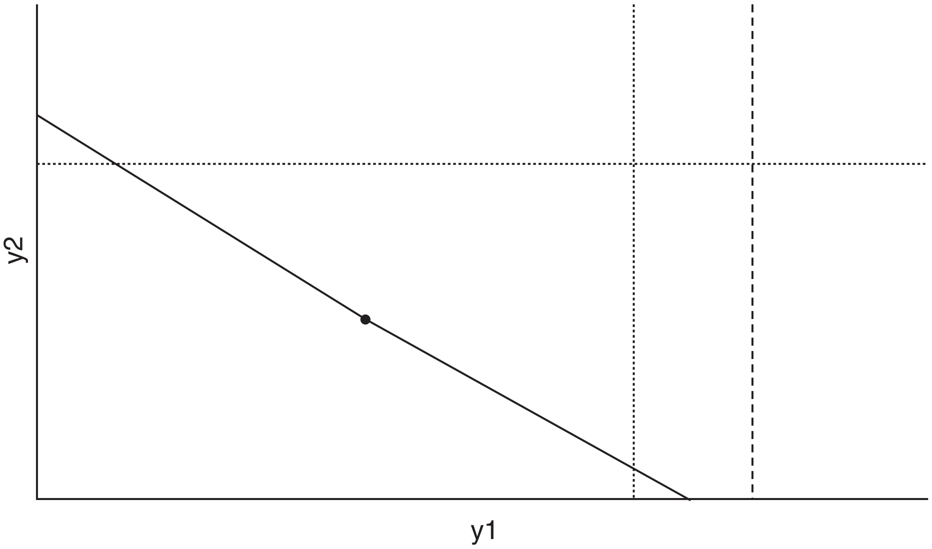

Fig. 4. The effect of co-adaptations of foraging behaviour and gut physiology on the ZNGIs and behavioural isolegs of consumers feeding on two foods that differ moderately in both absorption rate and bulk. The state space and all lines are the same as in Fig. 1. The dot represents the equilibrium abundances of foods 1 and 2 resulting from consumption by the generalist strategy. Parameter values are: $a_1 = a_2 = 0.1$; $h_1 = h_2 = 1.0$; $\alpha_1 = 1.6$, $\alpha_2 = 0.4$; $e_{\max 1} = e_{\max 2} = 10$; $\chi_1 = \chi_2 = 1$; $b_1 = 1.6$, $b_2 = 0.4$; $c = 0.1$; $\beta = 0.1$; $r_1 = r_2 = 0.001$; $K_1 = K_2 = 100$.

Second, when foods are sufficiently different along the qualitative niche axis, the ESS community will consist of two specialist species, one on each resource. The specialist species will have relatively similar gut sizes. The specialist on the bulkier but more easily digestible resource will have a much smaller throughput time than the specialist on the less bulky but less easily digestible resource.

In summary, differences in $e_{\max}$, b, and α will each select for different co-adaptations of gut size and throughput time, and represent quantitative niche axes. In contrast, only differences in the magnitudes of α and b, while holding their ratio constant, will result in a qualitative niche axis.

In Figs. 6 and 7 we depict the adaptive landscapes and evolutionary dynamics of the generalist and the specialist strategy, respectively. The ecological dynamics of these two strategies are those of Fig. 3. The landscapes in Fig. 6 are not evolutionarily stable, as the consumer's fitness is greatly reduced by accepting any food 2. This provides strong selection for behavioural and physiological specialization on food 1. Once the consumer has completely specialized on food 1, the landscapes will correspond to Fig. 7.

DISCUSSION

The resources found within a consumer's environment often vary in properties that influence digestive processing; as such, they provide opportunities for different communities of consumers based on co-adaptations of consumer behaviour and gut physiology. Our mechanistic model provides a framework for this problem, and predicts the ESS

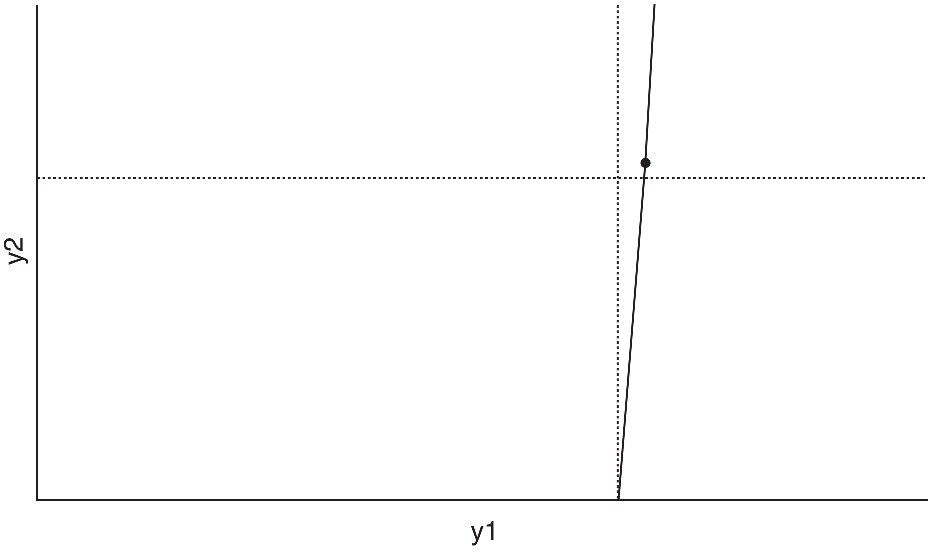

Fig. 5. The effect of co-adaptations of foraging behaviour and gut physiology on the ZNGIs and behavioural isolegs of consumers feeding on two foods that differ greatly in both absorption rate and bulk. The state space and all lines are the same as in Fig. 1. The dot represents the equilibrium abundances of foods 1 and 2 resulting from consumption by the generalist strategy. Parameter values are: $a_1 = a_2 = 0.1$; $h_1 = h_2 = 1.0$; $\alpha_1 = 10$, $\alpha_2 = 0.01$; $e_{\mathbf{max1}} = e_{\mathbf{max2}} = 10$; $\chi_1 = \chi_2 = 1$; $b_1 = 10$, $b_2 = 0.01$; $c = 0.1$; $\beta = 0.1$; $r_1 = r_2 = 0.001$; $K_1 = K_2 = 100$.

communities resulting from the co-adaptation of behaviour and physiology to pairs of foods differing in reward (energy/handling time) and richness (energy/bulk).

Different foods select for different specialized gut physiologies. Animals optimize their harvest rate by balancing conversion efficiency, gut fullness, and costs. Our model indicates that large guts signify specialization on poor resources. It can be the optimal strategy in response to bulky resources (low absolute richness), poor absorption rate, or high costs. This agrees with results from physiological studies of gut plasticity where gut size increased in response to poor quality foods in grasshoppers (Yang and Joern, 1994) and migratory birds (McWilliams and Karasov, 2001). In comparing specialists, most conceivable differences in food properties result in changes in gut size and throughput time. Most of these differences promote a quantitative niche axis. In contrast, when two specialists differ only in their throughput times, food qualities are equal, but foods differ in the time required for digestion. These qualitative food combinations require specific differences, such as simultaneous differences in bulk and absorption rates.

When two food types occur together, they can select for different ESS communities, depending on the differences in the foods. Quantitative differences in foods, if great enough, can lead to a community of one specialist on the richer resource and one partially selective or opportunistic generalist. Once a specialist evolves to feed on the richer resource, then a generalist will evolve to use both resources; it is always optimal to accept the richer resource. Specialists on rich resources are common in nature – carnivores and insectivores. In the presence of these predators, we find opportunistic generalists. For example, periodical

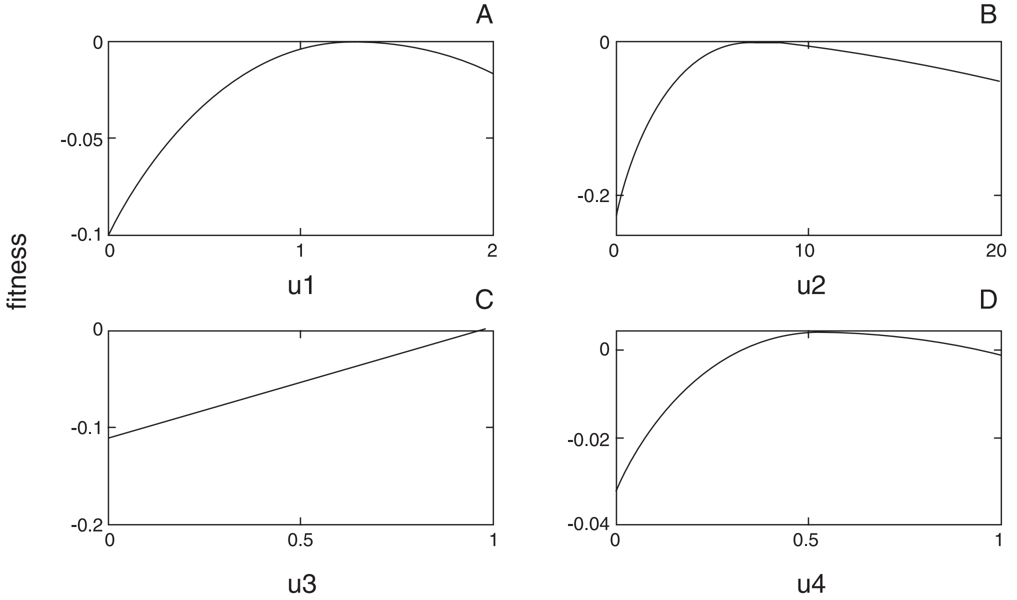

Fig. 6. Adaptive landscapes of the four control variables: u_1 = gut size, u_2 = throughput time, u_3 = probability of accepting food 1, and u_4 = probability of accepting food 2. These adaptive landscapes correspond to isolegs and ZNGIs of Fig. 3. These landscapes are not evolutionarily stable and selection will drive the landscapes to those depicted in Fig. 7.

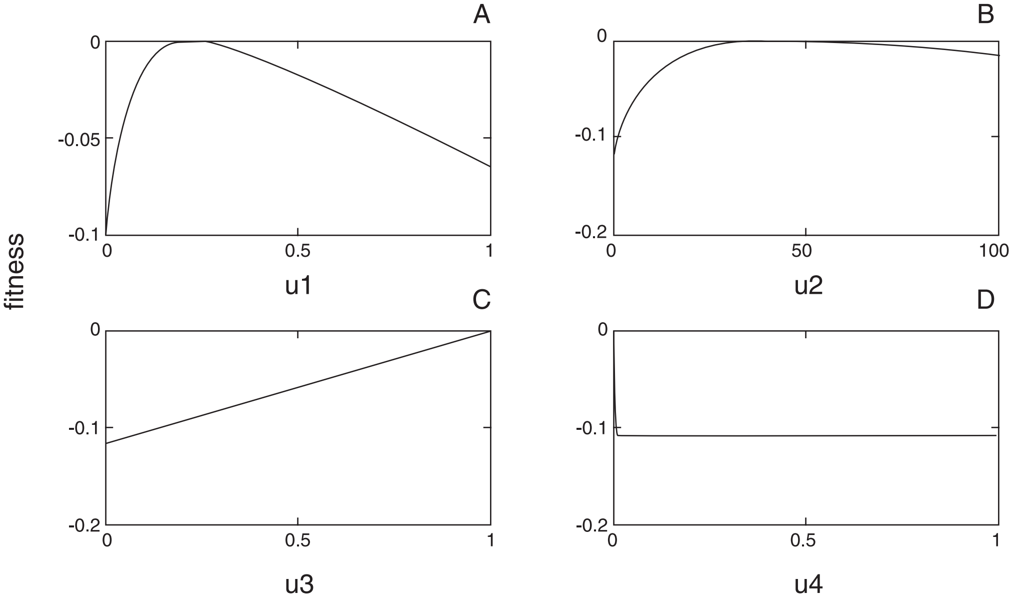

Fig. 7. Adaptive landscapes of the four control variables: u_1 = gut size, u_2 = throughput time, u_3 = probability of accepting food 1, and u_4 = probability of accepting food 2. These adaptive landscapes correspond to isolegs and ZNGIs of Fig. 3. These landscapes depict the evolution of the specialist on food 1 that comprises one species of the ESS.

cicada emergences provide a pulse of food that is utilized by many animals, including ducks and squirrels (Williams, 1995). In an extreme example, white tailed deer have been known to eat bird nestlings from nests (Pietz and Granfors 2000). Specialists on poor resources, such as grazers, are not predicted to evolve in the presence of richer resources. Including additional co-adaptations in the model can explain their evolution. This is discussed further in the following sections.

In our model, a positive covariance between bulk and absorption rate provides the easiest means for creating qualitative differences between foods. Such differences can produce an ESS with two specialist species. More compact but less easily digestible foods versus bulkier yet easily digestible foods will create such differences. For this to happen in nature, there likely are trade-offs in the gut relating to gut configurations that directly influence absorption rates. This may require additional gut physiological strategies that we have not included in our model.

In the following, we apply the predictions of our model to the East African ruminant community, then we compare and contrast our modelling approach to those of others, and finally we discuss the implications of introducing additional co-adaptations into our model.

Application to the East African ruminants

Hofmann (1973, 1989) proposed a classification of ruminants based on their morpho-physiological adaptation to different diet types (high-quality browse vs. low-quality grass and roughage). Hofmann (1989) recognized (1) concentrate selectors (CS), which feed selectively on dicot leaves and utilize plant cell contents (e.g. non-structural carbohydrates), (2) grazers (GR), which feed on grass and roughage and utilize plant cell wall and fibre, and (3) intermediate types (IM), which switch between feeding as concentrate selectors and grazers, depending upon season. The results of our models appear to fit Hofmann's classification of feeding types based on the co-adaptation of behaviour and gut structure/function.

According to Hofmann (1989), about 25% of the 150 or so extant ruminant species fall into the GR group, feeding on foods rich in cell wall (structural carbohydrates like cellulose). Grazers rely on microflora within the reticulo-rumen to provision cellulolytic enzymes that make such 'low-quality' foods sufficiently rich for subsistence. Grazers have relatively large reticulo-rumen and long throughput times.

About 40% of the species fall into the CS group. The gut and associated microflora of these species are less capable of digesting cell walls, and instead CS species select plants rich in soluble (non-structural) plant cell contents. These nutrients are easier to digest and absorb. The remaining 35% of species fall into the IM group. These species possess guts that are intermediate in structure and function between those of the GR and CS species. Intermediate species forage selectively and avoid fibrous foods when possible, but they often eat a mixed diet. Intermediate species are capable of adjusting gut structure and function to seasonal changes in forage quality. Like CS species, the guts and microflora of IM species are poor at processing fibrous forage. Both CS and IM species have guts with relatively small reticulo-rumen, fast absorption and short throughput times.

In our analysis, several foods appeared to produce guts typical of CS and IM ruminants. These are those foods with intermediate richness, and either high (foods 5, 6, 9, 10) or low (foods 7, 8, 11) absorption rates, α. Foods with high absorption rates possess guts that appear similar to those of CS species, whereas those with low absorption rates may be more similar to IM species. Given the values of the parameters we used in our analyses, we do not see foods that select for both large guts and long throughput times. Additional numerical analysis, however, confirms that such guts do result if we reduce absorption rates to even lower values than we used to generate Table 1 and Fig. 2, while holding richness constant at the intermediate value used in the original analysis.

Only one food (food 14) selected for a gut with large size and short throughput time. This food, with low richness and low α, may represent the gut strategy utilized by African and Asian elephants, which are non-selective browsers. These very large non-ruminants consume foods very high in structural carbohydrates. For their body size, they possess very large guts with short throughput times (Van Soest, 1996). Equids (horses) also possess large guts and short throughput times (Boyd and Houpt, 1994).

Strategies for modelling digestive function

Until the pioneering work of Penry and Jumars (1986, 1987), most models of digestion were compartment models. In these models, the different parts of the gastrointestinal tract (e.g. stomach, small and large intestine) represent distinct and homogeneous compartments, each with specific dynamic or static properties. Penry and Jumars (1986, 1987) introduced chemical reactor theory as an alternative paradigm for modelling gut structure and function. They identified the similarity of digestive structures like the reticulo-rumen to that of an industrial batch reactor. Similarly, small intestines appear analogous to plug-flow reactors.

Models based on chemical reactor theory provided a useful conceptual framework for examining digestive processes with respect to gut structure/function and the chemical properties of foods. These models assume that all features of the reactor represent a matched set of properties (Karasov, 1996). They do not consider the simultaneous changes and adaptations of gut (reactor) traits like size and throughput time. In contrast, the evolutionary game theory model we develop using the fitness-generating approach allows for such adjustments, while the forager simultaneously reaches an ecological equilibrium of consumption and renewal with its resource base.

Our model paradigm demonstrates that in response to some foods (e.g. foods with identical richness but different absorption rates, α's), gut size and throughput times co-vary positively, while in response to other foods (e.g. foods with identical α's but different richness), they co-vary negatively. Another difference in our model from those based on the chemical reaction paradigm is that we combine the rates of digestion (hydrolysis) and the rate of absorption into a single parameter, α. This probably faithfully reflects situations in which the gut is processing simple sugars that require no digestion prior to absorption. For substrates that require both hydrolysis and absorption, it can be considered a mathematical convenience. These processes are generally incorporated into reactor-based models as separate parameters, and they can be in our modelling approach if deemed necessary.

Additional co-adaptations

Our model assumes that the food characteristics of bulk, absorption rate, and maximum conversion efficiency are fixed and equal for all competing consumers. More realistically, these characteristics are properties of both the foods and the consumers themselves. For instance, the evolution and modulation of digestive enzymes can affect both $e_{\max}$ and α.

Starlings, Mimids, and Thrushes all lack the enzyme sucrase. When fed sucrase, these birds suffer from osmotic diarrhoea (Malcarney *et al.*, 1994). Many birds outside this phylogentic grouping are equipped with sucrase enzymes. Thus, for the Starlings, Mimids, and Thrushes, fruits high in sucrose content potentially represent zero or negative maximum conversion efficiency and zero absorption rate. But, for bird species with sucrase, these fruits represent valuable resources with positive values of $e_{\mathbf{max}}$ and α.

A consideration of gut chemistry and gut ecology (microflora communities) can provide strong trade-offs in digestive efficiency for different food types, through the additional co-adaptations of maximum conversion efficiency and absorption rate. In our model, most foods differ quantitatively – that is, a single food is richer and becomes the preferred food item in a community of consumers. Trade-offs in the presence/absence or relative concentrations of digestive enzymes may transform foods that otherwise would represent a quantitative niche axis into foods that now lie on a qualitative axis. With this consideration, there is the potential that foods differing in their nutritional constituents may create evolutionary minima in adaptive landscapes (Brown and Pavlovic, 1992, Abrams *et al.*, 1993). Thus, trade-offs in gut physiology and their co-adaptations with behaviour may provide an important mechanism of adaptive speciation (Geritz *et al.*, 1997; Doebeli and Dieckmann, 2000). Diversification along dietary niche axes is common within many groups of animals.

Prey preparation is another possible co-adaptation. Animals frequently modify food items before ingestion. For example, Kaspari (1990) studied Grasshopper Sparrows that often remove the wings and legs of grasshoppers before swallowing them. He showed that prey preparation was an increasing function of both gut fullness and prey abundance. Essentially, prey preparation is a mechanism by which animals decrease the bulk of food at the expense of increased external handling time. In relation to our model, this is expected to evolve when equilibrium abundances of foods are relatively high and consumer guts are relatively full (at equilibrium). Increases in fixed (e.g. predation) and/or variable costs (i.e. gut expensive to maintain) create these conditions. From a consumer's point of view, the co-adaptation of prey preparation can change both the richness and rewards of foods. This, in turn, can result in changes of how a consumer ranks resources relative to one another.

CONCLUSIONS

We contribute a modelling paradigm integrating gut physiology and consumer–resource theory, and we provide testable predictions of how gut physiology and foraging behaviours should co-adapt and contribute to community organization. We predict that foods that are sufficiently different quantitatively will produce communities of a selective specialist on the richer resource and a generalist that is either partially selective on the poor resource or opportunistically feeds on both resources. The resource-rich specialists will have smaller guts than the generalists that maintain larger guts to feed on the poor resource. The relative throughput times of these co-existing consumers will depend on the exact nature of the foods. We also predict that foods that are sufficiently different qualitatively will lead to communities of two selective specialist species. Both specialists will have similar gut sizes. The specialist on the bulky resource will have a shorter throughput time. These predictions can be tested with behavioural assays, comparative studies of gut physiology, and studies of community organization. The model also invites extensions via additional traits, such as prey preparation, chemistry or digestion, and gut uptake kinetics.

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