

Linking consumer–resource theory and digestive physiology: Application to diet shifts

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ABSTRACT

We develop mathematical and graphical models of diet selection incorporating recent advances in digestive physiology – that is, the adaptive modulation of active nutrient transport and gut retention time in response to changes in diet composition – into an explicitly ecological context based on consumer–resource dynamics and optimal foraging theory. The models indicate that gut modulation causes the consumer to treat two resources that are perfectly substitutable (the benefit derived from consumption of one resource is a constant fraction of the benefit derived from consumption of the second resource) as if they are antagonistic resources (the benefit derived from consumption of either resource alone is greater than the benefit derived from joint consumption of both resources). This will tend to favour diet switching and specialization, and also suggests a definitive (laboratory or field) test of the models. The models also suggest that modulation ultimately leads to more efficient use of resources, although it incurs an initial cost. We further cast gut modulation in three ecological scenarios. In the first, the consumer species does not deplete its resources and the optimal modulation strategy is determined by the standing crop of resources. In the second, a fixed population size of consumers results in resource depletion and the standing crop of resources results from a dynamic equilibrium between resource renewal and resource consumption. Under this scenario, the optimal gut-modulation strategy is determined by this dynamic equilibrium between renewal and consumption. In the third, we let resource renewal, depletion and consumer population sizes equilibrate. In this last scenario, the optimal gut modulation strategy emerges from the combined effects of resource renewal and the intersection of the depletion trajectory with the consumer's zero net growth isocline. We conclude that forging tighter links between gut physiology and foraging ecology will lead to greater understanding and predictability of diet selection and its ecological consequences.

Keywords: active nutrient transport, consumer–resource dynamics, digestive physiology, frugivory, gut modulation, insectivory, modulation isoleg, optimal foraging theory, passive nutrient absorption.

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INTRODUCTION

Understanding of animal diets has progressed recently through two contrasting and largely separate, but complementary, research approaches. On the one hand, theoretical development and empirical testing of optimal foraging models have advanced our understanding of many ecological factors, such as resource distribution, predation risk, vigilance and group size, which influence diet selection. On the other, the development of sophisticated laboratory techniques has greatly increased our understanding of digestive physiology and the processing of food post-consumption. Although physiological investigations demonstrate that ultimately diet is constrained (ecologically) by what the gut is capable of processing (i.e. by gut capacity and digestive physiology), they also reveal considerable gut adjustment, or modulation, of both morphology and physiology as a consequence of consuming different food types (e.g. sugar-rich/lipid-poor *vs* lipid-rich/sugar-poor; see reviews in Karasov, 1996; Karasov and Hume, 1997). This, in turn, suggests considerable diet plasticity in relation to gut morphology and physiology in ecological time. Linking such digestive processing capabilities with consumer–resource dynamics and optimal foraging models may clarify understanding of diet selection, particularly the often drastic shifts in diet composition that some foragers experience seasonally. Moreover, the development of foraging models incorporating digestive physiology can help clarify the adaptive significance of gut modulation strategies in relation to ecological characteristics (ecological garnering traits; see Vincent *et al.*, 1996) of different foragers.

Here we propose a modelling framework for incorporating modulation of digestive physiology into an explicitly ecological context using consumer–resource dynamics and optimal foraging as an initiative for new theory. In this, we follow the lead of Belovsky (1997, and references therein), who first incorporated physiological characteristics of foragers into an optimal foraging framework. Our approach differs from Belovsky's in that we do not treat digestive processing or gut capacity as a constraint on foraging. Instead, our model examines diet selection when resource abundances fluctuate spatially, temporally or through consumption, and it incorporates gut modulation as an adaptive feeding strategy (Karasov and Diamond, 1983, 1988; Ferraris and Diamond, 1989; Karasov, 1990, 1996; Karasov and Levey, 1992; Moyle *et al.*, 1995; Piersma and Lindström, 1997; Derting and Austin, 1998; Sabat *et al.*, 1998; Witmer and Van Soest, 1998; Young Owl and Batzli, 1998).

Consumer–resource theory

Consumer–resource theory provides a mechanistic approach to interactions between consumers and their resources (Tilman, 1982; Abrams, 1987, 1988; Vincent *et al.*, 1996). There are two constraints on diet (*sensu* Tilman, 1980, 1982). First, the consumption constraint determines the maximum amount of two or more resources that can be consumed in some unit of time. Second, the nutritional constraint determines the energy balance, growth rate or fitness that results from consumption of some amount of two (or more) resources. For two resources, the constraints are depicted graphically as isoclines within axes (the state space) representing the amount of the two resources consumed. These constraints need not be static. For example, nutritional constraints may vary during the annual cycle as the activities of the organism vary (e.g. reproduction, lactation, moulting, fat deposition, etc.; Robbins, 1981, 1993; Murphy, 1994), which in turn may substantially vary the optimal diet

as the constraints vary. Karasov (1982, 1985) examined such issues for the antelope ground squirrel, *Ammospermophilus leucurus*.

Tilman (1980, 1982, 1988) developed a graphical approach for combining the consumption and nutritional constraints into the zero net growth isocline (ZNGI), the minimal equal consumption rate isocline (hereafter, consumption isocline) at which a consumer can profitably harvest two resources. To this Tilman added the resource supply point, or the carrying capacity of resources in the absence of consumption, and the consumption vector, which depicts joint consumption of resources by a forager, to predict optimal selection of resources. Vincent *et al.* (1996) developed Tilman's graphical approach mathematically, combining the theoretical bodies of optimal foraging theory, density-dependent habitat selection and consumer–resource theory. Specifically, they derived a mathematical expression for the ZNGI based on Holling's (1959) disc equation and, in combination with the trajectory by which resources are depleted (similar to Tilman's consumption vector), they determined equilibrium outcomes of exploitative competition and conditions for co-existence.

Here we follow and build upon the treatment of Vincent *et al.* But we consider a single consumer species living in an environment in which resource abundances fluctuate either seasonally or due to consumption. And we incorporate into the model modulation of digestive physiology in response to a diet that shifts seasonally or in response to consumer–resource dynamics. We consider three scenarios:

- The consumer species does not deplete its resources.
- A fixed population size of consumers results in (1) resource depletion and (2) a standing crop of resources at a dynamic equilibrium between resource renewal and resource consumption. Here, the interaction between resource renewal and depletion determines the optimal gut-modulation strategy.
- Resource renewal, depletion and consumer population sizes equilibrate. Here, the gut modulation strategy emerges from the combined effects of resource renewal and the intersection of the depletion trajectory with the consumer's ZNGI.

Digestive physiology

Intestinal nutrient absorption is influenced both by the particular make-up of food items included in the diet as well as their rate of consumption (Karasov and Diamond, 1985; Karasov, 1992). Absorption of hexoses and amino acids from the lumen of the intestine to surrounding capillaries seems to occur transcellularly via mediation by transport (or carrier) proteins in the apical and basolateral membranes of intestinal epithelial cells (Diamond, 1991; Pappenheimer, 1993). We will refer to this active mechanism alternatively as active nutrient transport or nutrient uptake, and we will distinguish this mechanism from passive absorption (see below).

The adaptive modulation hypothesis (Karasov and Diamond, 1985; Ferraris and Diamond, 1986) states that a nutrient 'transporter should be repressed when its biosynthetic and other costs (of maintenance) exceed the benefits it provides' (Karasov, 1992, p. R496). Although it has long been known that nutrient uptake in the alimentary canal varies in relation to diet composition and other factors, such as fasting or starvation (e.g. Campbell and Fell, 1965; Leese and Mansford, 1971; Debnam and Levin, 1975; Hopper, 1975; Kotler *et al.*, 1980), only recently has this physiological response to changing diet composition

been examined from an ecological perspective. Recent studies of nutrient assimilation in birds show that much of glucose and amino acid absorption occurs passively via paracellular solvent drag (Pappenheimer, 1993; Karasov and Cork, 1994; Levey and Cipollini, 1996). Although controversial (Diamond, 1991), passive absorption via solvent drag (Pappenheimer, 1993) allows for more rapid adjustment of nutrient uptake than modulation of transporters (Levey and Cipollini, 1996). Even if passive absorption is paramount in some bird species (Karasov, 1992, 1996; Levey and Cipollini, 1996; Afik *et al.*, 1997a,b), adaptive modulation of active nutrient transporters does seem to be the rule in mammals and other vertebrates.

In addition to modulating nutrient uptake, various species modulate the rate of food transport through the gut (gut retention time), gut volume and enzyme activities (Campbell and Fell, 1965; Steiner *et al.*, 1968; Levey and Karasov, 1989; Brugger, 1991; Foley and Cork, 1992; Martínez del Río *et al.*, 1995; Piersma and Lindström, 1997; Witmer and Van Soest, 1998; Young Owl and Batzli, 1998) in relation to diet composition. In this paper, we consider the ability to modulate the gut as an adaptation to the species' natural diet (Karasov *et al.*, 1985a,b).

THE MODELS

As discussed at length by Tilman (1980, 1982), resources can vary in their relative contribution to meeting the energetic or nutritional needs of consumers. For instance, two or more resources are perfect substitutes when their joint consumption results in benefits equal to that predicted by consumption of a linearly weighted sum of the resources. Resources are complementary when their joint consumption results in greater benefits than would be predicted from consumption of a linearly weighted sum of the resources. Finally, resources are antagonistic when their joint consumption results in less benefits than would be predicted from consumption of a linearly weighted sum of the resources.

We consider two perfectly substitutable resources denoted 1 and 2, although the same arguments should also hold for resources that are complementary or antagonistic. Let the forager's per capita growth rate be a monotonically increasing function of its feeding rate, f . Let feeding rate be described by Holling's (1959) disc equation for an opportunistic forager seeking two co-occurring foods:

$$f = (e_1 a_1 R_1 + e_2 a_2 R_2) / (1 + a_1 h_1 R_1 + a_2 h_2 R_2) \quad (1)$$

where e is net assimilated energy from consuming a food item (metabolizable energy content, $MEC = 1 - [\text{excreta energy}/\text{food energy}]$; Karasov, 1990), a is the encounter probability for a resource, h is the handling time for a resource and R represents the density of a resource (see Royama, 1971, for a derivation).

Let a consumption isocline be defined as all of the combinations of resource abundances, R_1 and R_2 , such that a forager has a constant feeding rate, k (Holt, 1983; Brown and Mitchell, 1989). We can solve for the consumption isocline by setting equation (1) equal to k and solving for R_2 in terms of R_1 :

$$R_1 = k/a_2(e_2 - h_2 k) - [a_1(e_1 - h_1 k)/a_2(e_2 - h_2 k)]R_2 \quad (2)$$

In the state space of resource abundances 1 and 2, this equation describes a straight line that has a negative slope when $e_i/h_i > k$. Combinations of R_1 and R_2 that lie outside this isocline

yield harvest rates greater than k ; combinations inside the isocline yield feeding rates less than k . When k represents the subsistence level of resource consumption by the forager, the corresponding consumption isocline is the zero net growth isocline, ZNGI, at which the forager's per capita growth rate is zero (Vincent *et al.*, 1996).

Gut modulation

Gut modulation in relation to changing diet composition is likely to occur on a seasonal basis (e.g. Dykstra and Karasov, 1992), as when a bird's diet changes from insects to fruit or vice versa (Martin *et al.*, 1951; Levey and Stiles, 1991); or energy demands increase or decrease because of, for example, changing temperatures (Gross *et al.*, 1985; Dykstra and Karasov, 1992), migration (Piersma and Lindström, 1997; Piersma, 1998) or lactation (Derting and Austin, 1998). Gut modulation leading to different rates of nutrient uptake via modulation of active nutrient transporters can be modelled by assuming that the terms representing assimilation of resources 1 and 2, e_1 and e_2 , increase or decrease in relation to a changing diet composition. Similarly, gut modulation leading to different rates of food transport through the gut (gut retention time) can be modelled by assuming that h_1 and h_2 implicitly include both pre- and post-consumption handling of food, and thus change in response to changing diets.

By incorporating gut modulation in e , we assume that resource assimilation is independent of gut retention time (i.e. that e and h are independent). But this is certainly not the case (Sibly, 1981). Note, however, that net resource assimilation, e , can be assumed to occur both by active nutrient transport as well as by passive absorption via solvent drag. In the latter case, high rates of absorption seem to be achieved when luminal concentrations of the nutrient are high. Rates decrease as the nutrient is absorbed and luminal concentration declines (Karasov, 1996). This, in turn, appears to be facilitated by modulation of gut retention time. Therefore, we propose three gut modulation scenarios:

- Active nutrient uptake, e_1 and e_2 , is modulated independently of food retention time (e.g. by change in active transporters/cm² intestine).
- Gut retention time, h_1 and h_2 , is modulated independently of active nutrient transporters. Different resources may move at different rates through the gut and thus be differentially exposed to membrane-bound hydrolytic enzymes, fermenting bacteria or active transport mechanisms. Related to this, we assume that the movement of nutrients from the lumen of the intestine into the bloodstream may also occur by passive absorption via solvent drag, which, in turn, is affected by modulation of gut retention time and its effect on luminal concentrations of nutrients.
- Modulation of both gut retention time, h_1 and h_2 , and active nutrient uptake, e_1 and e_2 , occurs simultaneously.

Allowing the e and/or h terms to vary results in two gut modulation modes, which we will designate A and B, respectively. Each modulation mode has its own respective consumption isocline (see below). These isoclines can have three possible relationships to each other, depending on the direction and magnitude of the altered (modulated) terms. In two relationships, one isocline always lies inside the other. Then, that isocline corresponds to a gut-modulation mode that is always the more efficient. This pair of outcomes is uninteresting from the perspective of gut modulation. However, under other circumstances

(specified below for each model), the isoclines will intersect in such a way that one modulation mode is more efficient at certain resource abundances, while the other modulation mode is more efficient at other resource abundances. In this case, you expect the organism to evolve the ability to modulate its gut. The optimal diet that will maximize the forager's fitness reduces to $G = \max\{f_A, f_B\}$. This objective function is general for a family of fitness functions that can be found in Brown (1992) and Brown *et al.* (1992).

Modulation of active nutrient uptake

Assume that a forager can modulate between two gut physiological modes or strategies. Let modulation strategy A increase the rate of assimilation of resource 1 via an increase of active 1 transporters, e_1 , coupled with a decreased rate of assimilation of resource 2 via a decrease of active 2 transporters, e_2 . Let the opposite be true for gut modulation strategy B. These different rates of resource assimilation can be represented by e_{1A} and e_{1B} for resource 1 where A and B represent the two gut modulation strategies, with equivalent terms for resource 2. For any given feeding rate k , we now have two consumption isoclines, one for each gut modulation strategy, A and B:

$$R_2 = k/a_2(e_{2A} - h_2k) - [a_1(e_{1A} - h_1k)/a_2(e_{2A} - h_2k)]R_1 \quad (3a)$$

$$R_2 = k/a_2(e_{2B} - h_2k) - [a_1(e_{1B} - h_1k)/a_2(e_{2B} - h_2k)]R_1 \quad (3b)$$

Each of these equations is a straight line with negative slope. When $e_{1A} > e_{1B}$ and $e_{2A} < e_{2B}$, then the two lines must cross at positive values for resource abundances. This indicates that each digestive strategy yields a higher feeding rate (in terms of assimilated energy per unit time) at some combinations of resource abundances. At the point of intersection, both gut modulation strategies yield the same feeding rate.

All combinations of resource abundances for which the two gut modulation strategies yield the same feeding rate define the modulation isoleg (*sensu* Rosenzweig, 1981). The modulation isoleg can be found by setting the feeding rate with modulation strategy A equal to that with modulation strategy B, $f_A = f_B$, and solving for R_2 as a function of R_1 :

$$R_2 = [a_1/a_2][(e_{1A} - e_{1B})/(e_{2B} - e_{2A})]R_1 \quad (4)$$

This modulation isoleg is a straight line with positive slope. Successive points along this isoleg away from the origin represent higher feeding rates, k (Fig. 1). Above the isoleg, a forager will have a higher feeding rate using gut modulation strategy B ($f_A < f_B$), and below the line the forager has a higher feeding rate using modulation strategy A ($f_A > f_B$). When resource abundances lie above the isoleg, the forager should modulate its nutrient transporters to become relatively more efficient on resource 2 (i.e. increase nutrient transporters for resource 2, and decrease nutrient transporters for resource 1). Similarly, below the isoleg, the species should modulate its nutrient transporters to become relatively more efficient on resource 1 (i.e. increase nutrient transporters for resource 1 and decrease nutrient transporters for resource 2). The net effect of modulation results in 'effective' consumption isoclines (equations 3a and 3b) that are piecewise linear, including the part of each isocline lying within that of the other. This effective consumption isocline approximates that for antagonistic resources (see Tilman, 1980, 1982), despite the fact that the model specifically treats resources as perfectly substitutable (Fig. 2).

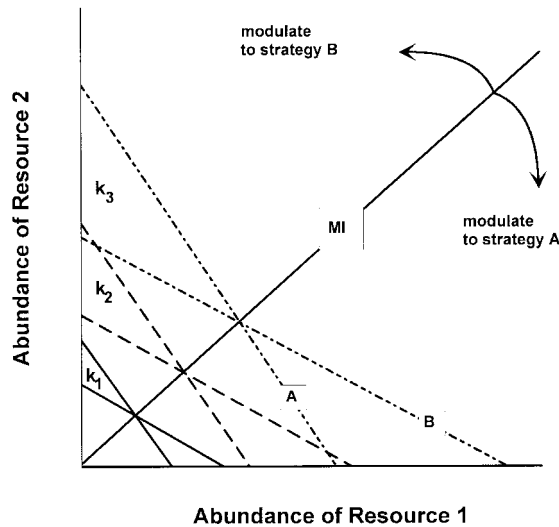


Fig. 1. Graphical representation of modulation of digestive processing on consumption isoclines. Families of paired equal consumption rate isoclines for three harvest rates or fitnesses, k , when a forager modulates between strategies A and B (labelled for harvest k_3). Each isocline represents the relative combinations of resources 1 and 2 that result in a constant harvest rate. Note that the modulation isoleg (indicated by MI) – that combination of resources 1 and 2 that results in an equal harvest rate for both modulation strategies – cuts through the intersection of each pair of consumption isoclines.

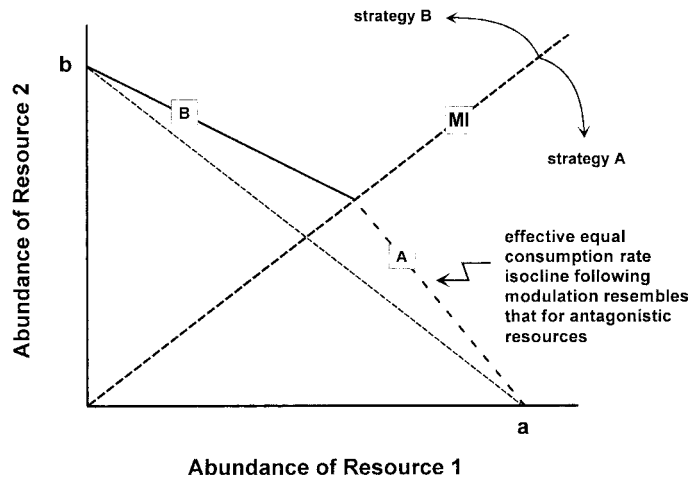


Fig. 2. Graphical representation of modulation of digestive processing on consumption isoclines. After completion of modulation to digestive strategy A and B, respectively, piecewise linear 'effective' consumption isocline approximates that for antagonistic resources. Note that this effective consumption isocline bows out from the simple line connecting the intercepts of the abscissa ('a') and ordinate ('b'), which would be the expected consumption isocline for two perfectly substitutable resources.

Modulation of gut retention time

Assume the forager can modulate the length of time food is retained in the gut for processing, denoted as mode A and mode B. This results in a model that is analogous to that for modulation of only active nutrient transporters except that the e terms are held constant and the h terms are allowed to vary. In this case, the consumption isoclines are:

$$R_2 = k/a_2(e_2 - h_{2A}k) - [a_1(e_1 - h_{1A}k)/a_2(e_2 - h_{2A}k)]R_1 \quad (5a)$$

$$R_2 = k/a_2(e_2 - h_{2B}k) - [a_1(e_1 - h_{1B}k)/a_2(e_2 - h_{2B}k)]R_1 \quad (5b)$$

Again, these two isoclines are each straight lines with negative slope. When $h_{1A} > h_{1B}$ and $h_{2B} > h_{2A}$, the lines will intersect. At the point of intersection, the two digestive modulation strategies yield equal harvest rates.

Selective retention of different food items is known in a number of taxa and can result from special structures that help retain or eliminate particles of different size or that vary in fibre content (ruminants, lagomorphs), or through anti-peristaltic contractions (some birds; reviewed by Karasov and Hume, 1997).

As above, we can determine the modulation isoleg; that is, the combination of abundances of resources 1 and 2 for which the two gut modulation strategies are equally rewarding for all harvest rates:

$$R_2 = [a_1/a_2][(h_{1A} - h_{1B})/(h_{2B} - h_{2A})]R_1 \quad (6)$$

This is a straight line with positive slope. Above the isoleg, a forager will have a higher feeding rate using gut modulation strategy B ($f_A < f_B$); below the line, the forager has a higher feeding rate using modulation strategy A ($f_A > f_B$).

In the absence of selective retention of different food items, the phenomenon becomes considerably more complicated. For instance, assume that when in either mode A or in mode B, both resources 1 and 2 are retained for identical times, such that $h_{1A} = h_{2A} > h_{1B} = h_{2B}$. This appears to be the case for birds that increase gut retention times when feeding on insects and decrease gut retention times when feeding on fruit. For example, when a bird that is in 'fruit mode' consumes the occasional insect, the insect appears to be transported through the gut at the same rate as fruit, thus resulting in incomplete digestion (Herrera, 1984; Levey and Karasov, 1989; see below). Now, for the isoclines to cross, it is necessary that $a_1(e_1 - h_{1A}) > a_1(e_1 - h_{1B})$, while $a_2(e_2 - h_{2A}) < a_2(e_2 - h_{2B})$. Satisfying these inequalities requires additional conditions:

- When the forager is in mode A, encounter probability for resource 1, a_1 , is greater than when it is in mode B ($a_{1A} > a_{1B}$), whereas when in mode B, encounter probability for resource 2, a_2 , is greater than when in mode A ($a_{2B} > a_{2A}$). This can arise if there is co-adaptation of search modes and modulation modes. For example, the forager could adopt search images (as in Morgan and Brown, 1996), or change from incidental to directed search strategies (Schmidt, 1996), in coordination with gut modulation.
- As a consequence of modulating retention time and its effects on enzymatic processes or passive absorption, harvest rate increases for resource 1 when in mode A, and harvest rate increases for resource 2 when in mode B.

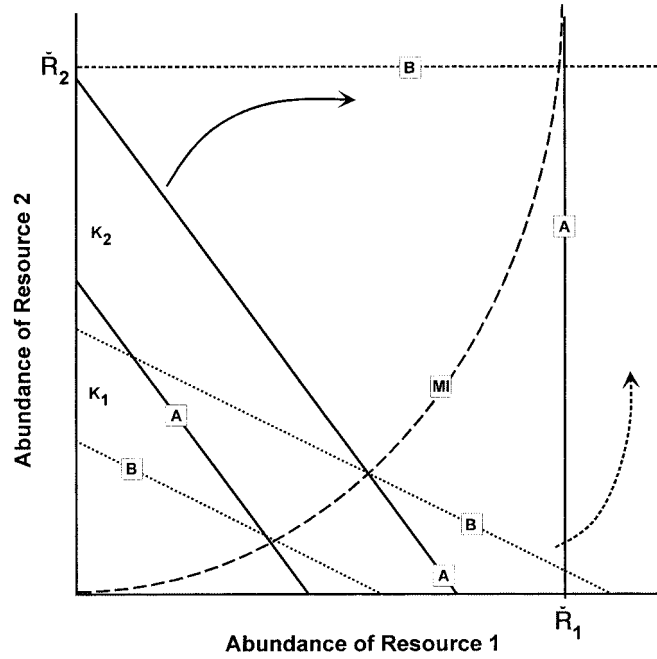


Fig. 3. Graphical representation of consumption rate isoclines when the modulation isoleg (MI) is non-linear. Two families of paired consumption isoclines corresponding to modulation mode A and B, respectively, are shown for two harvest rates, k_1 and k_2 . Note that the consumption isoclines within a modulation mode are no longer parallel.

The consumption isoclines remain the same as (5a) and (5b) except that the a terms are further distinguished by the corresponding modulation mode (a_{1A} , a_{1B} , a_{2A} , a_{2B}). The modulation isoleg is given by the positive solution of the following quadratic equation:

$$R_2^2[e_2(a_{2A}a_{2B}h_{2B} - a_{2B}a_{2A}h_{2A})] + R_2[e_2(a_{2A} - a_{2B}) + e_1R_1(a_{1A}a_{2B}h_{2B} - a_{1B}a_{2A}h_{2A}) + e_2R_1(a_{2A}a_{1B}h_{1B} - a_{2B}a_{1A}h_{1A})] + e_1R_1[(a_{1A} - a_{1B}) + R_1(a_{1A}a_{1B}h_{1B} - a_{1B}a_{1A}h_{1A})] = 0 \quad (7)$$

This modulation isoleg is a positive, accelerating curve (Fig. 3). When resource abundances lie below this line, the forager should increase its gut retention time (mode A) to increase efficiency on resource 1. When resource abundances lie above this line, the forager should decrease its gut retention time (mode B) to increase its efficiency on resource 2. Note that now, because of the parabolic shape of the modulation isoleg, the families of consumption isoclines representing higher values of k are no longer parallel (Fig. 3).

Joint modulation of gut retention time and active nutrient uptake

Assume the forager can now switch between modulation strategies A and B through joint modulation of gut retention time, h , and active nutrient transport, e , as described above. The result again will be two consumption isoclines:

$$R_2 = k/a_2(e_{2A} - h_{2A}k) - [a_1(e_{1A} - h_{1A}k)/a_2(e_{2A} - h_{2A}k)]R_1 \quad (8a)$$

$$R_2 = k/a_2(e_{2B} - h_{2B}k) - [a_1(e_{1B} - h_{1B}k)/a_2(e_{2B} - h_{2B}k)]R_1 \quad (8b)$$

Once again these isoclines are straight lines with negative slopes. When $e_{1A}/h_{1A} > e_{1B}/h_{1B}$ and $e_{2A}/h_{2A} < e_{2B}/h_{2B}$, the isoclines will intersect at the point in the state space at which the two strategies of gut modulation are equally efficient for both resources. Also as before, the effective consumption isoclines for the two digestive modulation strategies are piecewise linear and resemble that for antagonistic resources (Fig. 2).

The modulation isoleg, under joint modulation, is given by the positive solution of the following quadratic equation:

$$R_2^2[a_2^2(e_{2A}h_{2B} - e_{2B}h_{2A})] + R_2[a_2(e_{2A} - e_{2B}) + a_1a_2R_1(e_{1A}h_{2B} - e_{1B}h_{2A} + e_{2A}h_{1B} - e_{2B}h_{1A})] + a_1R_1[(e_{1A} - e_{1B}) + a_1R_1(e_{1A}h_{1B} - e_{1B}h_{1A})] = 0 \quad (9)$$

This modulation isoleg is a positive, accelerating curve (Fig. 3). When resource abundances lie below this line, the forager should modulate its gut to mode A, thereby increasing its efficiency on resource 1. When resource abundances lie above this line, the forager should modulate its gut to mode B, thereby increasing its efficiency on resource 2.

Ecological scenarios

Consumers that do not deplete their resources

For species that are resource ‘takers’ (those that live off the ‘fat of the land’ without depleting resources), the above models predict that foragers should exhibit a gut modulation strategy that reflects the availability of resources. If this availability changes seasonally, and seasonal availabilities cross the forager’s modulation isoleg, then foragers should exhibit synchronous and seasonal changes in gut modulation strategies each time standing crops of food cross the modulation isoleg (Witmer and Van Soest, 1998). Migratory birds that consume either fruit or insects may provide examples of this phenomenon where spring and summer bring more insects and less fruit.

It may not always be optimal for the forager to harvest resources opportunistically. For example, assume that resource 1 is preferred when in digestive mode A, and that resource 2 is preferred when in digestive mode B. Then, as k increases, the modulation-A isocline becomes vertical (at \check{R}_1) and the modulation-B isocline becomes horizontal (at \check{R}_2), respectively. We can thus delimit four distinct regions of the state space (see Fig. 3). At resource abundances less than points \check{R}_1 , \check{R}_2 , and in accord with the theory of optimal diets, the forager should be opportunistic and modulate to strategy A or B, respectively, depending upon the modulation isoleg. When $R_1 > \check{R}_1$ and $R_2 < \check{R}_2$, the forager should be selective for resource 1 and modulate to strategy A. Similarly, if $R_2 > \check{R}_2$ and $R_1 < \check{R}_1$, the forager should be selective for resource 2 and modulate to strategy B. Finally, when $R_1 > \check{R}_1$ and $R_2 > \check{R}_2$, when consuming resource 1 the forager should modulate to strategy A, and when consuming resource 2 the forager should modulate to strategy B.

Consumers that deplete their resources

In the case of consumers that deplete their resources from the resource carrying capacity to some reduced level of abundance (resource ‘depleters’ as opposed to resource ‘takers’),

the situation differs slightly from the previous presentation. For these consumers, resource depletion occurs at a much faster time scale than gut modulation. Therefore, the optimal modulation strategy results from an equilibrium between consumption and renewal, rather than a predetermined standing crop of resources at the beginning of a foraging bout.

Let resource renewal follow Monod's (1950) equation in the absence of consumption and let resource consumption result from N foragers harvesting foods 1 and 2 opportunistically (Tilman, 1980, 1982). Resource dynamics are given by:

$$dR_1/dt = r_1(K_1 - R_1) - a_1R_1N/(1 + a_1h_1R_1 + a_2h_2R_2) \quad (10a)$$

$$dR_2/dt = r_2(K_2 - R_2) - a_2R_2N/(1 + a_1h_1R_1 + a_2h_2R_2) \quad (10b)$$

The depletion trajectory gives all of the combinations of R_1^* and R_2^* that result from increasing the population size of foragers (Vincent *et al.*, 1996). This can be found by setting equations (5a,b) equal to zero, solving each for N , setting each equal to each other (dropping the N), and then solving for R_2^* (where * denotes dynamic equilibrium):

$$R_2^* = (a_1r_2K_2R_1^*)/[a_2r_1K_1 + R_1^*(a_1r_2 - a_2r_1)] \quad (11)$$

As N goes from 0 to infinity, the values for R_1^* and R_2^* form a line going from the resource supply point (K_1, K_2) to the origin (0, 0). The shape of the line depends upon the products of encounter probabilities and resource growth rates: a_1r_2 and a_2r_1 . When $a_1r_2 = a_2r_1$, the depletion trajectory is a straight line; when $a_1r_2 > a_2r_1$ (or $<$), then the depletion trajectory is decelerating (or accelerating). When the depletion trajectory is linear, it corresponds exactly to the linear modulation isoleg obtained under the models of modulation of only active nutrient transporters or only gut retention time when foods are transported differentially through the gut.

Any point on the depletion trajectory represents an abundance of resources that will result from a unique value of N . Increasing the size of the forager's population shifts the equilibrium resource abundances down the depletion trajectory. The position of the depletion trajectory with respect to the isoleg determines the optimal gut modulation strategy (Fig. 4). If population size, N , is such that resource abundances come to rest on a portion of the depletion trajectory that lies above (or below) the isoleg, then the forager should choose modulation strategy B (or A). If the depletion trajectory lies wholly above or below the gut modulation isoleg, then a single gut modulation strategy of B or A, respectively, is optimal regardless of forager population size.

Any parameter that shifts the depletion trajectory upwards with respect to the modulation isoleg tends to increase the region over which modulation strategy B is optimal. This leads to the following predictions. Increasing the resource supply point or growth rate of resource 2 increases the likelihood of B as the optimal modulation strategy. Increasing the forager's encounter probability on resource 2 simultaneously depresses both the depletion trajectory and the modulation isoleg. This also favours B as the optimal modulation strategy.

Two types of changes may cause seasonal changes in the forager's gut modulation strategy. First, the resource supply point for the two resources may change seasonally, causing changes in the positions of the depletion trajectories with respect to the modulation isoleg. Second, seasonal changes in the population sizes of consumers will shift the position of resource availabilities along the depletion trajectory. For changes in resource supply

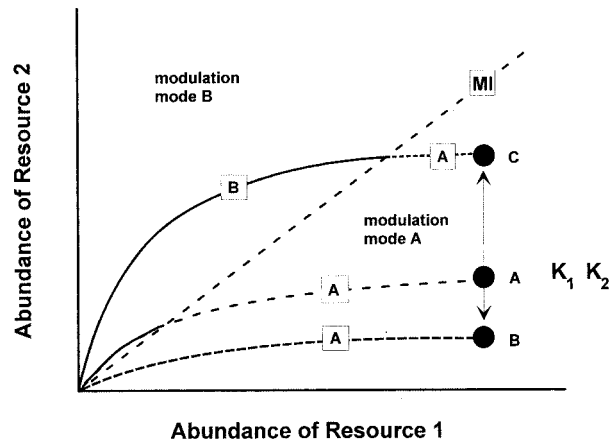


Fig. 4. Graphical representation of a consumer resource model when the consumer depletes its resources to some standing crop equilibrium and modulates between digestive physiology strategies A and B, respectively. K_1 and K_2 represent the carrying capacity of resources 1 and 2, respectively, for three different resource supply points, A, B and C. A fixed population size of consumers results in resource depletion, and the standing crop of resources results from a dynamic equilibrium between resource renewal and resource consumption. Under this scenario, the optimal gut-modulation strategy is determined by this dynamic equilibrium between renewal and consumption in relation to the modulation isog. Note that when in the state space below the depletion vector cutting through the 'elbow' of the zero net growth isocline (Vincent *et al.*, 1996), the consumer should always be in modulation mode A (resource supply point B). When above this depletion vector, the consumer may use either modulation mode A or B, depending on where the equilibrium standing crop lies with respect to the modulation isog (resource supply points A and C).

points to change modulation strategies, seasonal changes in depletion trajectories must at different times place the equilibrium abundance of resources above and below the modulation isog. For changes in N to change the modulation strategy, the depletion trajectory must cross the modulation isog and changes in N must be severe enough to explore regions of the depletion trajectory that lie above and below the isog.

Voles, which experience large seasonal and large year-to-year changes in resource productivities and vole densities, may provide a possible illustration. Either seasonal changes in resource productivities (more foliage in the spring and summer, more seeds in the fall and winter; Batzli and Cole, 1979) or year-to-year variation in vole numbers may be enough to drive both seasonal and irregular patterns of gut modulation towards or away from the efficient assimilation of foliage (low quality) or seeds (high quality).

Consumer and resource dynamics

Lastly, we include consumer population dynamics and consider situations where the abundance of consumers equilibrates with respect to resource availabilities and productivities. Let c be the forager's subsistence rate of resource consumption. When feeding rate is above c ($f > c$), the population size of consumers increases ($dN/dt > 0$); below c ($f < c$), the population size of consumers declines ($dN/dt < 0$). For such a system, N^* , R_1^* and R_2^* occur at the intersection of the depletion trajectory with the forager's zero net growth

may prefer to settle in the habitat that favours its current modulation strategy. Conversely, when an animal does disperse from one habitat to the next, it can be expected to shift its modulation strategy appropriately. So residents may exhibit a more constant modulation strategy, while floaters may exhibit frequent changes in modulation strategy.

Illustration with seasonally frugivorous/insectivorous birds

Many bird species are seasonally frugivorous or insectivorous (Martin *et al.*, 1951; Herrera, 1984, 1987; Wheelwright, 1986, 1988; Bairlein, 1990; Levey and Stiles, 1991; Witmer, 1996; Parrish, 1997, 1999). In many species, the switch can be from virtually 100% of the diet derived from insects to 100% of the diet derived from fruit (Bairlein, 1990). Although many of these species migrate between temperate and tropical latitudes (Bairlein, 1990; Levey and Stiles, 1991), many others remain within the temperate latitudes throughout the year (e.g. Ehrlich *et al.*, 1988; Root, 1988). For these species, the relative abundances of fruits and insects will vary tremendously from season to season: insects reach peak abundance during the summer months (e.g. Rabenold, 1978, 1979) and most fruit species reach peak abundance in the fall months (Thompson and Willson, 1979; Parrish, 1997). Insects (and other arthropods) at temperate latitudes are relatively scarce during the winter months (represented mainly as eggs, over-wintering larvae and pupae, and some propylene-glycol enhanced spiders), whereas some fruits persist for months through the winter. Thus, for year-round resident bird species, late winter and early spring probably represent the period of least food availability, with standing crops of fruit and insects having been consumed throughout the previous months, and before new populations of the upcoming growing season's arthropods are becoming available. Figure 6 represents such a scenario. In Fig. 6a, seasonally fluctuating resource abundances result in seasonally shifting resource standing crops. These, in turn, lead to large advantages in gut modulation (Fig. 6b).

Fruit and insects differ in chemical composition, digestibility and subsequent nutritional rewards (Snow, 1971; Moermond and Denslow, 1985; Debussche *et al.*, 1987; Herrera, 1987; Bairlein, 1990; Levey and Karasov, 1992). Fruits tend to be bulky with a substantial amount of indigestible seed mass, and although they may often be relatively high in concentrations of nutrients such as sugars or fatty acids, they are usually low in concentrations of amino acids. Insects, in contrast, can be more completely digested and contain high concentrations of proteins or amino acids (Karasov, 1990; Levey and Karasov, 1992). For many bird species, these differences in composition between fruits and insects lead to adaptive gut modulation when the diet is switched from the one food type to the other. For instance, Levey and Karasov (1992) switched American robins (*Turdus migratorius*) from a mixed diet consisting of three native fruit species to that of house crickets (*Acheta domestica*); transport of food through the gut decreased significantly (i.e. retention of food in the gut increased significantly). According to our model of gut retention time, such gut modulation would be reflected by an altered consumption isocline (Fig. 6b), which, in turn, will lead to increased efficiency of food utilization.

As a result of gut modulation, therefore, a consumer species can profitably harvest available resources at lower resource standing crops than is otherwise possible. Consequently, an individual can maintain itself on lower abundances of resources due to the gut modulation. This is illustrated in Fig. 7, which shows two families of consumption isoclines corresponding to a lower (the joint isoclines lying closest to the origin) and a higher (the joint isoclines lying farthest from the origin) fitness, respectively. Note that when in the state

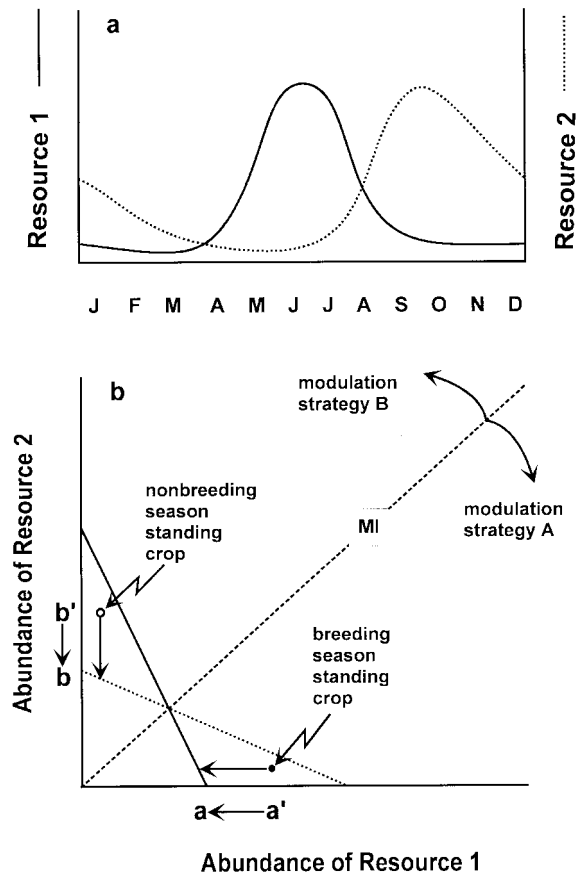


Fig. 6. Graphical representation of hypothetical relation between fluctuating resource abundances and gut modulation. (a) Hypothetical depiction of varying relative abundances of two resources, 1 and 2, throughout the year. Resource 1 might represent changing abundances of insects, while resource 2 might represent changing abundances of fruits at temperate latitudes. (b) As the resource standing crop shifts through the state space of relative resource abundances, modulation to the appropriate digestive strategy allows increased efficiency of resource utilization. The axes represent the relative abundances of two resources, 1 and 2. Consumption isoclines and modulation isogonals indicated as in previous figures. The open circle represents resource standing crop in September and the solid circle represents the resource standing crop in June. As depicted, in June the resource standing crop indicates abundant supply of resource 1 and short supply of resource 2, and the forager should modulate to modulation strategy A. In September, resource 1 is in short supply and resource 2 is abundant, and the forager should modulate to modulation strategy B. Note that, following modulation, resource consumption can decline with no loss of fitness (e.g. a' to a ; b' to b , respectively).

space corresponding to the breeding season levels of resource standing crops, the consumer can maintain itself at the higher fitness when using the breeding season digestive strategy, but only at the lower fitness when using the non-breeding season digestive strategy. The converse is true in the state space of non-breeding season levels of resource standing crops.

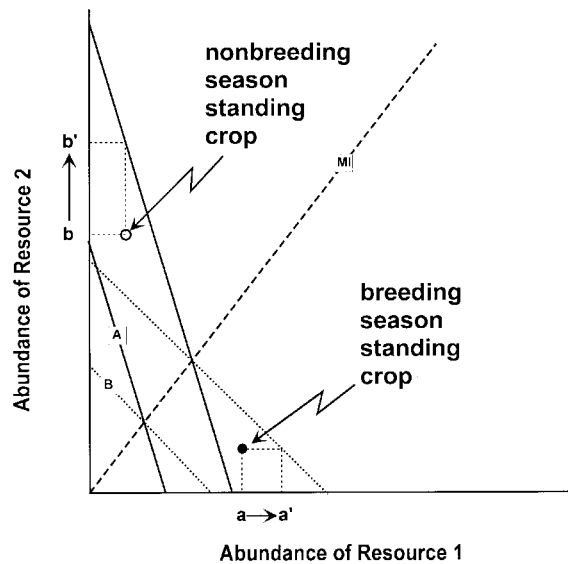


Fig. 7. Graphical depiction of relation between modulation strategy, standing crop abundance and attainable harvest rate when resource standing crops differ. Two families of paired consumption isoclines corresponding to modulation strategies A and B. As in Fig. 1, the pair farthest from the origin represents a higher harvest rate or fitness. The solid circle represents resource standing crop in June and the open circle represents the resource standing crop in September. Note that, in the breeding season, the resource standing crops permit maintenance at the higher fitness when the gut is modulated to digestive mode A, but the converse is true in the non-breeding season.

Other sorts of seasonal changes in food availability can also result in diet shifts. For instance, some grouse species (e.g. spruce grouse, *Dendragapus canadensis*, and blue grouse, *D. obscurus*) subsist during winter on a diet almost exclusively composed of conifer needles, but both species incorporate significant amounts of fruit during the summer and fall, according to availability (Johnsgard, 1983). Note that conifer needles do not become seasonally unavailable (although it is possible that the preferred age-class of needles might; see Remington and Hoffman, 1996), indicating that diet shifts are not necessarily caused by lack of resources. Regardless, we would expect some digestive modulation in response to such diet shifts.

DISCUSSION

Modulation of digestive physiology alters the minimum resource requirements for a given level of self-maintenance. An alternative, although equivalent, way of stating this is that modulation allows the forager to attain higher foraging rates at a given abundance of resources. This agrees with the suggestion of Levey and Karasov (1992) that direction of the modulation of gut retention times in the American robin when switched from an insect to a fruit diet 'is a key factor' allowing them 'to subsist on a diet of mostly fruit'. Furthermore, the models also agree with their (Levey and Karasov, 1992; also Karasov, 1996) suggestion that the inability to rapidly (instantaneously) modulate will impose an initial

cost to switching diets. We see this readily by noting the increased amounts of resources necessary to maintain the organism when the gut is inappropriately modulated (as would be the case when first commencing the diet switch; points a' or b' in Fig. 7) compared to the amounts necessary when the gut is appropriately modulated (points a or b in Fig. 7). Our models clearly imply that gut modulation leads to increased efficiency of resource use in the face of fluctuating resources and thus constitutes an adaptive digestive strategy.

Migration and gut modulation have an interesting relationship. Many species of arctic-tropical migrant bird species are opportunistically as well as seasonally frugivorous (Bairlein, 1990; Parrish, 1997, and references therein). Because lipogenesis and mass gain are particularly critical for migrants (Jenni and Jenni-Eiermann, 1998), gut modulation that leads to greater energy assimilation should be strongly favoured (Piersma, 1998). However, there is a lag between switching from, say, an insect to a fruit diet, and modulating to peak digestive efficiency on the new diet (Levey and Karasov, 1992; see Fig. 7). More recently, Witmer and Van Soest (1998) showed a similar lag in modulation to a switch from sugar-rich/lipid-poor fruits to lipid-rich/sugar-poor fruits. This lag suggests that gut modulation could potentially affect various characteristics of migration, such as stopover location, stopover length, flight distances and resource selection. Thus, speed of modulation could influence whether migration tends to be rapid and smooth or slow and jerky.

Moore *et al.* (1995) discussed the myriad problems associated with inadequate mass gain or overly slow refuelling during stopover, including being poorly buffered against adverse weather at later stopover sites, delayed arrival on breeding or wintering grounds, and other effects (Piersma, 1990; Moore *et al.*, 1995). Parrish (1997) investigated the relationship between diet and energetic condition in passerine migrants on Block Island, Rhode Island, USA, a major stopover site for southbound land migrant passerines in northeastern North America. Although most of the 47 species studied are insectivorous during the breeding season, their diets expand during migration. More than 90% of the species show substantial frugivory. Omnivorous migrants (those consuming > 33% fruit by gut volume) typically gained mass between successive captures in mist nets. In contrast, insectivores (those consuming < 33% fruit by gut volume) tended to exhibit declines in energetic condition between successive captures. Parrish (1997) suggested that the insectivores may quickly depart Block Island after assessing that the available resources (abundant fruit but, presumably, scarce insects) are not adequate for refuelling and mass gain. These results may be explained from the perspective of gut modulation. For instance, the omnivores may be those species that had, before reaching Block Island, commenced a switch to fruit resources, and thus had modulated to a digestive strategy appropriate for a largely fruit diet. In contrast, the insectivores may have been in the wrong modulation mode or may be able to modulate their digestive physiology for efficiency on fruit. This suggestion awaits testing.

Our model clearly applies to species that migrate only short distances or remain resident in temperate latitudes; they surely experience a seasonally fluctuating resource base. For many other species, however, long-distance migration from the tropics in the non-breeding season to the temperate zone in the breeding season is also accompanied by a switch in diet. For instance, Levey and Stiles (1991; but see Chesser and Levey, 1998) argued that bird species that migrate from tropical to temperate latitudes tend to rely on seasonally fluctuating resources, such as fruit and nectar, in their tropical habitats, and switch to insect resources in their temperate habitats. Note that, for both temperate residents and long-distance migrants, the diet switch from fruit to insects, and then from insects to fruits, will

be gradual and will scale favourably to the time-course of gut modulation (which often takes only several days).

Other species, however, migrate between the tropics and temperate zone without shifts in diet. For example, American redstarts, *Setophaga ruticilla*, remain almost totally insectivorous throughout the year (R.T. Holmes, personal communication; Parrish, 1997). In such cases, migration may be viewed as an effort to move through real space to remain in areas with equivalent resource supply points or standing crops in resource abundance state space, thus avoiding the need for gut modulation. From the perspective advanced here, migration could thus be viewed as an alternative digestive strategy to modulation. This, in turn, suggests that, when an organism's diet changes little throughout its annual cycle, selection for a single digestive strategy is likely, but when the diet changes substantially, selection for digestive modulation is likely. Ecologically, this again suggests that foraging in a fine-grained manner (either spatially or temporally) selects for no (or minimal) gut modulation, whereas foraging in a course-grained manner selects for gut modulation (see also Sabat *et al.*, 1998).

Sabat *et al.* (1998) recently pointed out the critical relationship between the time-course for induction of digestive enzymes and transporters in the modulation process and the rapidity of the diet shift. If the diet changes rapidly relative to the time-course of modulation of gut physiology, they suggest that natural selection will favour constant (constitutive) levels of enzymes and transporters that are not 'optimal for the composition for each individual dietary item, but that reflect the average intake of the nutrients hydrolyzed and transported by the intestinal diet proteins' (p. 234). They further suggest that such animals should be more likely to forage in a 'fine-grained' manner that will not require gut plasticity. Their suggestion may correspond to our second environmental scenario of a fixed population of consumers depleting resources to some equilibrium level of abundances (see Fig. 4, depletion vectors for resource supply points A and C). In this case, foragers consume resources so that the depletion vector crosses the modulation isocline: one modulation strategy (strategy B in Fig. 4) will always be favoured when resource depletion reaches these levels.

Studies of gut modulation have used captive (or domestic) animals in controlled laboratory conditions. Our models suggest that gut modulation can also be studied with free-ranging animals in the field. Giving-up densities (GUDs) of foods in experimental foraging patches (Brown, 1988) allow determination of the consumption isocline (e.g. Brown and Mitchell, 1989; Morgan and Brown, 1996). GUDs can therefore be used to determine experimentally the shape of the consumption isocline after completion of modulation and in response to different combinations of food abundances in experimental food patches. In the absence of modulation, the consumption isocline should be linear with negative slope when two resources are perfectly substitutable (Brown and Mitchell, 1989; Vincent *et al.*, 1996). This line should lie between the two intercepts for resources 1 and 2, when the gut is modulated to be most efficient on each of the two resources, respectively (indicated by a and b in Fig. 2). As can be seen from an inspection of Fig. 2, an animal that modulates should have an effective consumption isocline that lies outside of this line. This prediction constitutes a definitive test of the models. An experimental test could follow the methods described by Morgan and Brown (1996) in their test of search images.

Furthermore, by using GUDs to determine the shapes of equal consumption isoclines on different diet combinations and in different seasons (which correspond to different digestive

modulation modes), it should be possible to measure directly the benefit (or cost) of gut modulation. GUDs indicate the quitting harvest rate for a consumer and thus provide a measure of the consumer's efficiency (Brown, 1988). Therefore, differences in GUDs collected at different times in a consumer's yearly budget that also correspond to different modulation modes will reflect resource utilization. This proposition would best be tested with joint ecological and physiological studies, where the physiological work validates the ecological findings and conclusions. This field technique has the additional benefit of estimating physiological costs and benefits without the use of invasive methods that sometimes include sacrificing the subject organism.

Gut modulation is not limited to avian foragers. Nor is it restricted to diets that shift from being predominantly fruit to predominantly insect. For instance, omnivorous bears (*Ursus* spp.) modulate mean retention time (which is related to passage rate) when shifting from a diet of white clover (*Melilotus alba*) to meat (Pritchard and Robbins, 1990). Similarly, Brody and Pelton (1988) suggested that black bears (*U. americanus*), prior to denning, increase their ability to assimilate fat and carbohydrate at the expense of protein assimilation. This change facilitates weight gain. Spencer *et al.* (1998) found that Australian short-necked turtles (*Emydura macquarii*) increased mean gut retention time when fed plants (possibly to increase time for fermentation) and decreased mean gut retention time when fed animals. McCauley and Björndal (1998) found that both small and large size classes of turtles increased food intake when given a diluted diet, presumably due to increased transit of food through the gut (decreased retention time). Karasov (1992) reviewed evidence for the hypothesis that adaptive modulation of intestinal nutrient transport is under dietary control in a variety of carnivores, omnivores and herbivores. Animals that exhibited adaptive digestive modulation included desert iguana (*Dipsosaurus dorsalis*), mink (*Mustela vison*), bullfrog tadpole (*Rana catesbeiana*), carp (*Cyprinus carpio*), rabbit (*Sylvilagus* sp.) and sheep (*Ovis aries*). Together, these studies suggest that adaptive gut modulation is widespread.

Changes in energy needs related to seasonally varying temperatures can also lead to changes in diet composition or quantity. This, in turn, has been shown to result in gut modulation. For instance, Gross *et al.* (1985) found that, in prairie voles (*Microtus ochrogaster*), the mass of the small intestine, large intestine and caecum increased in response to decreased temperatures (increased energy demands). Dykstra and Karasov (1992) found that when house wrens (*Troglodytes aedon*) increased food consumption due to lowered temperatures and forced exercise, the length of the small intestine and retention time of non-aqueous digesta increased, but stomach size, retention time of aqueous digesta and intestinal absorption of L-proline \cdot cm⁻¹ did not. The digestive modulation resulted in increased digestive efficiency compared to that expected in the absence of modulation (Karasov, 1996).

Our models illustrate the utility of considering how fluctuations in resource abundances in space and time, coupled with adaptive modulation of gut-processing capabilities, influence resource selection and harvest rate. A major objective of this paper was to demonstrate one means of incorporating digestive flexibility into an ecological framework of consumer–resource dynamics and optimal foraging. For instance, in the simple models presented, we implicitly consider *h*, the term for food handling time, to include both pre- and post-consumption handling times. Whelan and Brown (in prep.) are developing a modified approach, in which pre- and post-consumption handling of food is modelled explicitly. Combining advances in our understanding of gut physiology with optimal foraging

approaches should lead to greater realism in optimal foraging models and greater understanding of how digestive physiology influences diet selection and its ecological consequences.

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