

# Optimal foraging and gut constraints: reconciling two schools of thought

Christopher J. Whelan and Joel S. Brown

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To ecologists, factors such as a forager's encounter rate with prey and its own susceptibility to predation are dominant determinants of foraging. In contrast, digestive physiologists consider foraging to be determined by factors like rates of digestion and absorption of ingested food. We reconcile these views in a model combining encounter rate, external handling, and internal handling of food in the gut. With internal food handling, two food properties become important; energy: external handling time ( $e/h$ ) and energy: bulk ( $e/b$ ). We show that internal handling is only one of a suite of rate limiting factors. The gut never reaches full capacity, indicating that spare capacity may be intrinsic to gut structure. Regardless of gut fullness, a food of sufficiently high  $e/b$  will always be harvested. Two isolegs in the state space of resource abundances determine diet selectivity. These isolegs, which we call the Mitchell and Pulliam isolegs, divide the state space into regions in which 1) the forager's optimal strategy is opportunism; 2) the forager is always selective on the food with the greater  $e/h$  and partially selective on the second food; 3) the forager is always selective on the food with the greater  $e/h$  and ignores the second food. The development and analysis of the isolegs thus reconcile the heretofore disparate perspectives of the ecological and the physiological frameworks of foraging.

*C. J. Whelan, Illinois Natural History Survey, Midewin National Tallgrass Prairie, 30239 S. State Route 53, Wilmington, IL 60481, USA (whelanc@uic.edu). – J. S. Brown, Dept of Biological Sciences, Univ. of Illinois at Chicago, 845 W. Taylor St., Chicago, IL 60607, USA.*

Energy and nutrients are essential for life and their efficient procurement has been a central interest of behavioral ecologists (Pulliam 1989). Likewise, once food resources are consumed, their efficient post-consumption processing has been a major focus of physiological ecologists (Karasov 1996). Although these two approaches to understanding animal diets are often complementary and mutually informative (Karasov and Diamond 1988, Whelan et al. 2000, Whelan and Schmidt 2006), their different emphases lead to conflicting views. Ecologists focus on how ecological factors, including food abundance and distribution, habitat structure, predation risk, and social organization affect

the ability of a consumer to search for and to capture food resources. From this perspective, the major determinants of diet are factors that occur prior to food consumption. In contrast, physiological ecologists focus on the breakdown and absorption of food after it has been consumed. From this perspective, where and how long to forage, and what items to include in the diet, are determined by factors that influence the rate and efficiency at which the gut processes the consumed food. These two views on foraging lead to controversy. Is gut processing of food sufficiently efficient so that diet is typically limited by the ecological characteristics of resources and consumers, in particular, encounter rate

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and handling time? Or does digestive processing of food determine diet and limit feeding rates?

Digestive constraints are considered more important for herbivores than for other sorts of consumers (Westoby 1974, Belovsky 1978, 1997, Farnsworth and Illius 1996, Hirakawa 1997a). The diets of herbivores, in contrast to carnivores, include low quality (i.e. low nutrient concentrations) and high fiber (bulky) items. To make up for the poor nutritional rewards, herbivore resources must be more abundant and easier to procure (Hirakawa 1997a). In this case, food consumption, which is tied importantly to nutrient absorption (Karasov and Diamond 1988), may be severely limited by digestive processing (Kenward and Sibly 1977, Sedinger and Raveling 1988, Guillemette 1994). This may be most pronounced for small herbivores because digestive capacity scales isototonically with body mass, but mass-specific nutritional requirements increase with declining body mass (Demment and Van Soest 1985).

Farnsworth and Illius (1998) extend Pulliam's (1974) foraging model to consider three ecological scenarios: consumers who are 1) purely encounter-limited, 2) purely handling-limited, and 3) mixed-process. They show that if handling of prey is expanded to include post-consumption processing, then the handling-limited case is equivalent to the digestion rate constraint mentioned above. They find that when search and handling occur simultaneously, the diet is broader than that predicted by Pulliam's (1974) model, with the optimal diet including less profitable prey. This provides an optimal foraging explanation for the mixed diets of herbivores that does not invoke relationships among resources such as nutrient and/or toxin complementarity (Rapport 1980, Tilman 1982, Schmidt et al. 1998, Whelan et al. 1998).

Here we propose a related modification of Pulliam's diet model. In our formulation, we include terms to explicitly account for both pre- and post consumption handling of food. While we are not the first to combine ecological and physiological considerations to the question of diet choice and foraging ecology (Karasov and Diamond 1988, Karasov and Hume 1997, Levey and Martínez del Rio 1999), our approach departs from previous efforts. Some (Penry and Jumars, 1986, 1987, Martínez del Rio and Karasov 1990, Martínez del Rio et al. 1994) have used optimality models founded in the physical chemistry of reactors to model digestive responses, and then applied those results to infer ecological implications. Others (Verlinden and Wiley 1989, Hirakawa 1997a, b) have incorporated constraints on gut processing into the functional response as an inequality constraint that is either turned on (operable) or off (inoperable). In contrast, we incorporate gut processing as an integral component of the standard ecological expression of the functional response. We

examine diet selection when foods vary in their bulkiness, especially the degree to which they are composed of components that are refractory to digestion and assimilation. A major goal of our model is to reconcile two schools of thought regarding what limits feeding rates and determines diet selectivity. School 1, the ecological framework, generally, but not exclusively, is associated with rich but hard to find foods. In contrast, school 2, the physiological framework, is generally associated with low quality, abundant foods. We combine these views into a single modeling and conceptual framework. In our model, both ecological food handling and physiological gut processing have a joint influence on the harvest rate and diet selection of the forager.

## The two schools

Both schools view feeding rate and diet selection to be determined by factors extrinsic and intrinsic to the forager. However, the ecological framework considers the extrinsic factors to be properties of the environment, such as abundance and distribution of resources and predators, together with properties of the resource, such as detectability and ease of capture. The physiological framework considers the extrinsic factors to be properties of the resource, such as proportion of digestible versus refractory components, nitrogen content, and energy value (reviewed by Karasov 1990). The ecological framework considers the intrinsic factors to be characteristics such as search and attack strategies, habitat preferences, and susceptibilities of the forager to predators. The physiological framework considers the intrinsic factors to be characteristics such as structure and function of the gut, including gut capacity, the suite of digestive enzymes, and transport mechanisms (active and passive) for moving nutrients from the gut lumen into the bloodstream of the forager. The approach we present below integrates key aspects of the extrinsic characters of both environment and resource, together with the intrinsic ecological and physiological characters of the forager, into a unified framework.

### School 1. Ecological framework

According to the ecological framework, feeding rates are limited by the consumer's ability to encounter and handle foods. Different food types will each have some fixed encounter rate and some fixed handling time. Handling consists of pursuing, capturing, and consuming the food item; processing of food by the gut is simply not considered. In addition, searching for and handling foods are mutually exclusive activities. Holling's disc

equation (1965, 1966) represents the classic formulation for the harvest rate, where food preference is determined by the ratio of energy to handling time ( $e/h$ ) of the respective foods and foragers should include only those foods that increase the average rate of energy gain (MacArthur and Pianka 1966). When foods are perfect substitutes (Tilman 1982, Brown and Mitchell 1989), diet selection should follow what has become known as the zero-one rule: only the abundance of the more preferred food types influence selectivity for a particular food type. Thus each food is either always accepted or always rejected for a given set of conditions.

## School 2. Physiological framework

According to the physiological framework, feeding rate can be maintained at a high level by abundant and easily procured resources until the gut reaches its maximum capacity. At this point, foraging ceases until the gut has sufficiently processed the food, after which additional foraging can resume. Gut volume is modeled as an inequality constraint that is either active (the forager cannot consume food in bulk any faster than it can be internally processed) or inactive (in which case the forager's diet choice collapses back to approach 1). Under this approach, foods offer different amounts of energy per unit bulk, but they may or may not differ in the amount of energy per (pre-consumption) handling time (Hirakawa 1997a). Feeding rate is generally limited by the abundance of foods with high energy to bulk ratios and the gut passage rate. The forager should consume all encountered items of foods with energy to bulk ratios ( $e/b$ ) above some threshold value, after which it should then fill up its remaining gut capacity (if any) with items of foods with  $e/b$  ratios below this value. For this reason, foragers are expected to show partial preferences. Although the abundance of the poor foods (those with low  $e/b$  ratios) can influence these partial preferences, their abundance will not influence the amount of the poor food consumed.

## Reconciling the two schools

The two schools of thought collide in what we shall refer to as Mitchell's paradox. The paradox is this: there are physical limits to the capacity of the gut, but is the gut ever really full? Do animals choose to feed up to this capacity limitation? Observations at banquets and ceremonial meals led our colleague, William Mitchell, to posit that there are no gut constraints. After professing to be completely "full" at the end of the main course, diners allowed that there was in fact "room" for some of the rich desert that had just entered the room. Mitchell was noting that the sensation of fullness does not necessarily equate to the stomach or gut having

reached some maximum capacity. Yet, the stomach (gut), as assumed in gut constraint models of diet, does have a maximum capacity. Thus, do animals limit their feeding based on having filled their guts to capacity (as in the case of matching some inequality constraint)? Or, as Mitchell argues, are stomachs never truly "full"? Answering these questions reconciles the two schools and resolves Mitchell's paradox. As we shall show, the gut is never really full, yet gut capacity, like many other factors associated with foraging, can be one of a suite of rate limiting factors in the foraging process.

Hirakawa (1997a) developed a foraging model that includes the standard encounter rate and pre-consumption handling time with prey, but also incorporates a post-consumption passage rate constraint as an inequality constraint that is either on or off (the constraint operates as a step-function). This models both schools as extreme cases (ecological framework when the passage rate constraint is inactive, and physiological framework when the constraint is active). By combining aspects of both schools, it allows for novel phenomena and predictions, such as switching of prey preferences from the food with highest  $e/h$  to the food with the highest  $e/b$  as foods go from being scarce to abundant. As a consequence, it is no longer possible to make a priori rankings of food items based upon  $e/h$ . Note, however, that in this model, the passage rate constraint is either on or off.

Jeschke et al. (2002), in their review of functional response models, proposed the steady-state satiation model that incorporates both the handling and digestion of prey. Digestion influences the predator's hunger level, which in turn determines the likelihood that a predator searches for prey. While digestion is always inclusive, gut fullness influences feeding rate as a sliding motivational state that can result in the forager choosing to cease foraging – it may engage in other activities, but it does not forage when satiated. This has similarities to the "digestive pause" of Holling (1965).

Here we develop an extension of Holling's (1965, 1966) disc equation that incorporates both schools by modeling passage rate of food through the gut as an integral component of food handling time. In a manner similar to Jeschke et al. (2002), we model the extent of the "digestive pause" as a sliding scale reflecting gut fullness. Post-consumption handling time may be partially exclusive of searching for and handling, pre-consumption, additional food items. Therefore, in contrast to the models of Verlinden and Wiley (1988) and Hirakawa (1997a), in which the effect of internal gut passage on harvest rate is a step function (operable or inoperable), in our model it is continuous. We consider a forager that consumes two food types, and we use the model to determine the consequences of internal handling on harvest rate and diet selectivity.

## The model

### Scenario 1. Feeding on a single resource

We begin with a modification of the type II functional response (Holling 1965, 1966), but we explicitly consider handling of food by the gut, and additionally, a function that expresses the proportion of gut handling time that is exclusive of alternative foraging activities. For a single resource, the harvest rate is

$$H = (aR)/\{1 + aR[h + gm(B)]\} \quad (1a)$$

and

$$H = eH \quad (1b)$$

where  $H$  is rate of energy gain (joules per time);  $e$  is net assimilated energy from consuming a food item (joules of metabolizable energy content,  $MEC = 1 - [\text{excreta energy/food energy}]$ , Karasov 1990);  $R$  is resource abundance (items);  $H$  is harvest rate (items  $\times$  time $^{-1}$ );  $a$  is encounter probability (time $^{-1}$ );  $h$  is preconsumption or external handling time (time  $\times$  item $^{-1}$ );  $g$  is per item gut or internal handling time (time  $\times$  item $^{-1}$ ); and  $m(B)$  is the proportion of internal handling that is mutually exclusive of external handling. Note that  $m(B)$  affects  $h$  but not  $a$ . We consider  $m(B)$  to represent the penalty of multi-tasking. Conceptually,  $m(B)$  represents the effect of digestive load on the forager's ability to perform, simultaneously, other activities (e.g. searching, external handling). Multitasking is an inevitable penalty of shared metabolic systems at the cellular (e.g. mitochondrial activity, maintenance of cellular integrity and electrochemical gradients, etc.) and whole animal (e.g. circulatory, immune, neuronal, osmoregulatory, renal, respiratory, thermoregulatory, etc.) levels (Hulbert and Else 2000, Farrell et al. 2001, Wang 2001, Wang et al. 2001).

In Eq. 1a, per item external (preconsumption) handling,  $h$  (time  $\times$  item $^{-1}$ ), follows directly from the standard disc equation, while per item internal (post-consumption) handling is represented by the parameter  $g$  (time  $\times$  item $^{-1}$ ). The passage time per item is given by the quotient of food volume (bulk) per item  $b$  (ml A item $^{-1}$ ) and the volumetric flow rate of food through the gut  $V_o$  (ml time $^{-1}$ ):  $g = b/V_o$ . But  $V_o =$  gut capacity,  $k$  (ml) divided by retention or throughput time,  $T$  (time; Jumars and Martínez del Río 1999, McWhorter and Martínez del Río 2000). Thus passage time per item is given by  $g = (bT)/k$ . The penalty of multitasking increases with gut fullness,  $B$ . Gut fullness,  $B$ , is given by the bulk rate of intake (determined by the bulk of the resource multiplied by its ingestion or harvest rate) and the retention time of food in the gut (determined by the quotient of retention time and gut volume):  $B = (bHT)/k$ . Next,  $m(B)$ , exclusive internal handling time, can take on any functional form with a monotonically positive slope. Here we let  $m(B) = B$

(a linear function), the proportion of gut volume occupied by resource. Note that our 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. Substituting  $g$  and  $B$ , into Eq. 1a and simplifying, yields

$$H = (aR)/\{1 + aR[h + b_2H(T_2/k_2)]\} \quad (1c)$$

Similar expressions can be written for consumption of more than one resource (below). Note that in Eq. 1c, harvest rate is now one component of gut processing time.

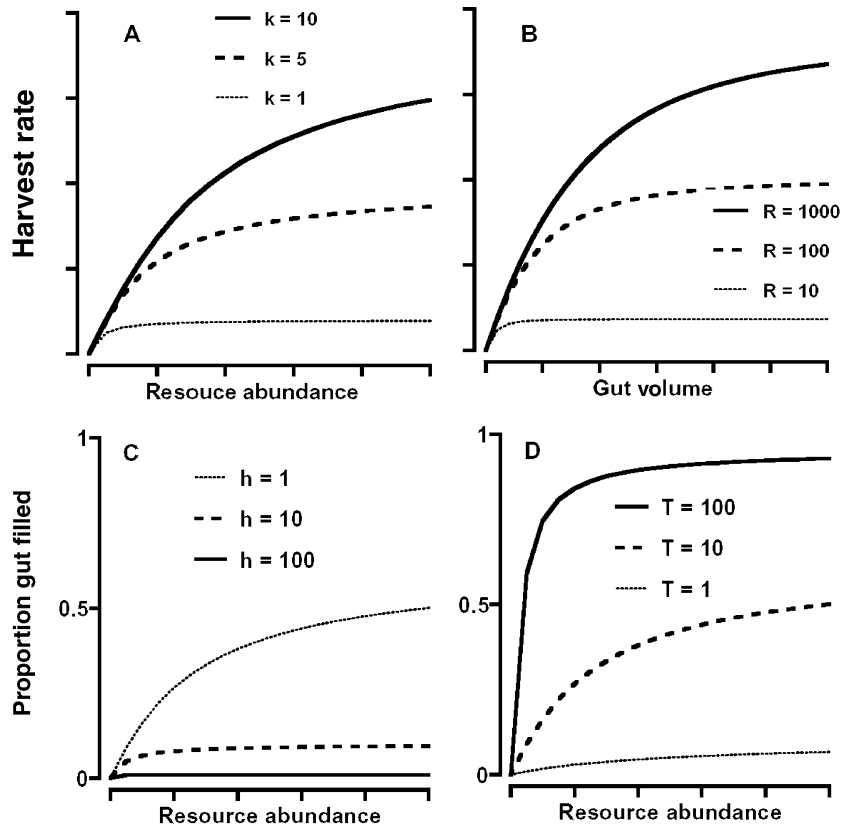
Equation 1c can be solved explicitly for  $H$  (Appendix), but this explicit expression obscures the way in which external and internal food handling influence the forager's consumption rate. Equation 1c has a number of interesting consequences. For instance, by virtue of including harvest rate as an explicit component of gut processing, gut processing in turn becomes an explicit component of harvest rate. Harvest rate and gut processing mutually feed into each other. Second, Eq. 1c makes transparent that both pre- and postconsumption food handling limit harvest rate, but they do so jointly. Third,  $h$  and  $g \times B$  are qualitatively different phenomena. External handling,  $h$ , is a fixed cost per item consumed that is paid in time – it operates qualitatively like a batch reactor (Martínez del Río et al. 1994) that is full (on) or empty (off). Internal handling,  $g \times B$ , in contrast, is a variable cost paid in time because one component, harvest rate,  $H$ , is continuous (Jumars and Martínez del Río 1999). In other words, internal handling operates as a continuous reactor, such as a plug flow reactor (PFR; Martínez del Río et al. 1994). Fourth, if we let  $h = 0$  and let  $B = 1$ , Eq. 1c collapses back to the disc equation, but now handling is exclusively internal. In contrast, if we let  $B = 0$ , (1b) collapses back to the disc equation, but handling is exclusively external. Finally, if  $B$  is a constant, and  $0 < B < 1$  and  $h > 0$ , then Eq. 1c is a disc equation with two fixed-time handling costs.

We can explore the behavior of the model graphically. For instance, several relationships result in monotonically increasing curves with decelerating slope (Fig. 1), as exhibited by the standard disc equation. The type II curve results when plotting:

- harvest rate,  $H$ , as a function of resource abundance,  $R$  (Fig. 1a);
- harvest rate,  $H$ , as a function of gut volume,  $k$  (Fig. 1b);
- gut fullness,  $(bHT)/k$ , as a function of  $R$  with different values of  $h$  (Fig. 1c) or of  $T$  (Fig. 1d).

Remarkably, gut fullness asymptotes below the full capacity of the gut. Inspection of Eq. 1c indicates that there are three conditions, each unlikely, that can result in achieving full gut capacity:

Fig. 1. Graphical results of harvest rate model incorporating both external (pre-consumption) and internal (post-consumption) handling of food when the forager feeds on a single resource. (A) Harvest rate as a function of resource abundance when gut volume ( $k$ ) available for internal handling increases from 1 to 10. Harvest rate rises monotonically with decreasing slope, and increased gut volume allows greater maximal harvest rate. (B) Harvest rate as a function of increasing gut volume as resource abundance ( $R$ ) increases from 10 to 1000. Harvest rate rises monotonically with decreasing slope, and increased resource abundance allows greater maximal harvest rate. (C) Proportion of gut filled as a function of increasing resource abundance as external handling time ( $h$ ) increases from 1 to 100. The proportion of the gut filled rises monotonically with decreasing slope, but the decrease is more pronounced for shorter external handling times. (D) Proportion of gut filled as a function of increasing resource abundance as internal handling time ( $T$ ) increases from 1 to 100. The proportion of the gut filled rises monotonically with decreasing slope, but the decrease is more pronounced for longer internal handling times.



- gut volume,  $k$ , reaches 0;
- retention time,  $T$ , reaches infinity;
- external handling,  $h$ , approaches 0 while encounter probability,  $a$ , approaches infinity.

We can also examine the effect of particular parameters. For instance, harvest rate,  $H$ , decreases with increasing:

- external handling time,  $h$  (Fig. 2a);
- internal handling time (retention time),  $T$  (Fig. 2b);
- food bulk,  $b$  (Fig. 2c).

In addition, we can examine the relative effects of total food handling ( $h + gB$ ), external food handling ( $h$ ) alone, and internal food handling ( $gB$ ) alone (Fig. 2d).

## Scenario 2. Feeding on two resources

We now consider two resources, 1 and 2. The messages emerging from consuming only one food type still apply. Both pre- and post consumptive handling influence harvest rates on the two resources. And, despite the significant impact of gut capacity on harvest rates, actual

gut fullness generally remains well below maximum gut capacity. In this section we are interested in how pre- and post consumptive handling jointly or separately influence diet choice.

The two resources can differ in their abundances,  $R_1$  and  $R_2$ , metabolizable energy content,  $e_1$  and  $e_2$ , external handling times,  $h_1$  and  $h_2$ , and bulkiness,  $b_1$  and  $b_2$ . Food preferences should be influenced by external handling efficiency ( $e/h$ : the ratio of energy to external handling) and food richness ( $e/b$ : the ratio of energy to bulk). In the absence of gut capacity considerations, food qualities are ranked in descending order of external handling efficiency. External handling efficiency matters because the forager handling a particular food item is precluded from searching for and handling a food item of higher quality. With gut capacity limitations, richness matters. Depending upon the degree of gut fullness, consuming an item with a particular bulk costs the forager time in terms of searching for better foods. The internal time cost of consuming a food item increases with gut fullness.

We begin by considering an opportunistic forager that harvests and consumes all encountered food items. Let  $H_1$  and  $H_2$  be harvest rates (items per unit time) of food

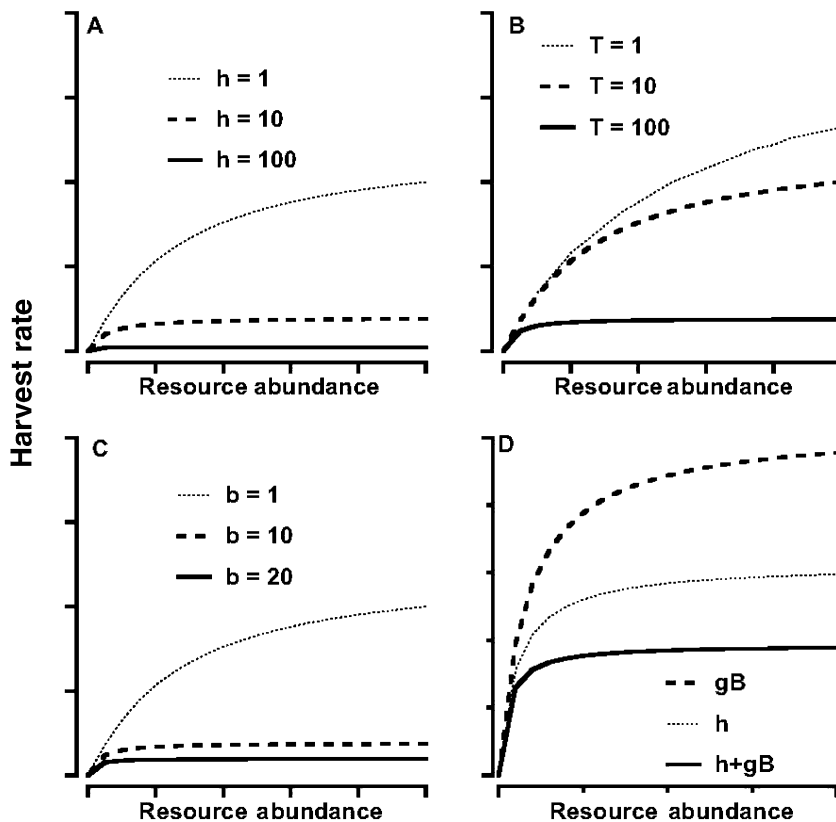


Fig. 2. Relationship between harvest rate and resource abundance when either external handling time, internal handling time, of food bulk varies, but all other parameters are fixed. Harvest rate increases monotonically with decreasing slope as a function of resource abundance with: (A) external food handling time ( $h$ ); (B) internal food handling time ( $T$ ); (C) bulk volume ( $b$ ) of food. Note that maximal harvest rate decreases with increasing external handling time, internal handling time and bulk volume of food. (D) Harvest rate curve when handled only internally ( $gB$ ), only externally ( $h$ ), or both internally and externally ( $h + gB$ ).

one and food two, respectively. Gut fullness is now determined by the volume and passage rate of both foods. So,  $B = (b_1H_1 + b_2H_2) \times (T/k)$ , and the per item internal handling time is:  $g_i = (b_i \times T)/k$  where  $i=1,2$ . Substituting these expressions for  $B$  and  $g_i$  into Eq. 1a for each of the two food types and simplifying yields

$$H_1 = (a_1R_1) / [1 + a_1R_1(h_1 + b_1(T^2/k^2)(b_1H_1 + b_2H_2) + a_2R_2(h_2 + b_2(T^2/k^2)(b_2H_2 + b_1H_1))] \quad (2a)$$

$$H_2 = (a_2R_2) / [1 + a_1R_1(h_1 + b_1(T^2/k^2)(b_1H_1 + b_2H_2) + a_2R_2(h_2 + b_2(T^2/k^2)(b_2H_2 + b_1H_1))] \quad (2b)$$

where the rate of energy gain of an opportunistic forager is:

$$H = e_1H_1 + e_2H_2$$

or

$$H = (a_1e_1R_1 + a_2e_2R_2) / [1 + a_1R_1(h_1 + b_1(T^2/k^2) \times (b_1H_1 + b_2H_2) + a_2R_2(h_2 + b_2(T^2/k^2) \times (b_1H_1 + b_2H_2))] \quad (2c)$$

Equation 2a and 2b can be solved explicitly for  $H_1$  and  $H_2$  (Appendix), but as with the solution to Eq. 1c, these explicit expressions obscure the ways in which the presence of one food type influences the forager's consumption rate on the other. We can explore the

behavior of Eq. 2a and 2b by three-dimensionally plotting  $H_1$  and  $H_2$  as functions of  $R_1$  (Fig. 3a) and  $R_2$  (Fig. 3b). In all cases increasing  $R_i$  increases  $H_i$  and decreases  $H_j$ ,  $i \neq j$ . The presence of food 1 (or food 2) reduces the forager's consumption of food 2 (or food 1) through both external and internal handling times. By handling an item of food 1, the forager spends less time looking for food. The external handling time is independent of the forager's overall harvest rates on foods one and two. However, the internal handling time increases with harvest rates and gut fullness.

Equation 2c has many of the same properties as Eq. 1b. When we plot  $H$  as a function of  $R_1$  and  $R_2$ , we see a monotonically increasing surface with decelerating slope over the regions in which opportunistic foraging is optimal (Fig. 4). Consider the case where food 1 is both richer ( $e_1/b_1 > e_2/b_2$ ) and has a higher external handling efficiency ( $e_1/h_1 > e_2/h_2$ ) than food 2. For sufficiently high values of  $R_1$  and  $R_2$ , the forager's net rate of energy gain actually declines for increasing values of  $R_2$ . This is because opportunistic foraging ceases to be optimal. The time spent externally and internally handling an item of food 2 no longer exceeds what could be gained from looking for and consuming an item of food 1. Below we explore how external and internal handling times shift a forager's diet from opportunism to either partial or complete selectivity for a single food type. To

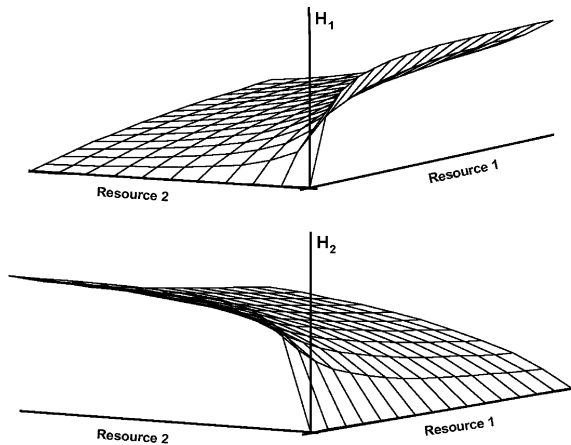


Fig. 3. Harvest rate surface for a single resource when forager feeds on two resources, resource 1 and resource 2. Harvest rate surface of (A) resource 1 or (B) resource 2 as a function of abundance of both resources 1 and 2. In both figures, resource 2 has half the energetic value and 10 times the bulk volume of resource 1. Note that harvest rate on the “focal” resource is greatest when only that resource is consumed (value of other resource is 0). Joint consumption of both resources depresses the rate of harvest on focal resource (1 or 2) through competition for internal handling by the gut. The extent of depression of harvest rate of resource 1 by consumption of resource 2 is greater than depression of harvest rate of resource 2 by consumption of resource 1.

do so, we develop the Pulliam isoleg and the Mitchell isoleg.

#### Pulliam isoleg

An isoleg is a line in some state-space of consumer or resource densities along which the fitness of two behaviors is equal. Important isolegs thus separates regions of quantitatively or qualitatively different optimal behaviors (Rosenzweig 1981). For our purposes, the relevant state space has  $R_1$  as the x-axis and  $R_2$  as the y-axis. And, the relevant behaviors concern the selectivity of the forager for one food type or the other. We define the Pulliam isoleg as the combinations of  $R_1$  and  $R_2$  such that a forager feeding selectively on just one

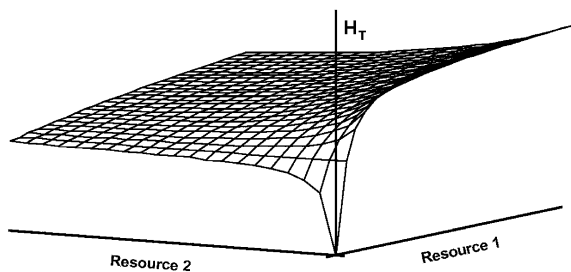


Fig. 4. Harvest rate surface for both resources 1 and 2 as a function of their abundance. As in Fig. 3, resource 2 has half the energetic value and 10 times the bulk volume of resource 1. Note that because the forager has greater external handling efficiency on resource 1, and because resource 1 is more rich than resource 2, total harvest is maximal when the forager consumes only resource 1.

food type has an average harvest rate that equals the energy gain from simply handling an item of the other food type (Brown and Mitchell 1989). This isoleg is a direct extension of Pulliam’s (1974) result from his model of diet selection.

In Pulliam, there was a term analogous to external handling time, but no consideration of gut fullness. Our model collapses to Pulliam’s when  $m(B) = 0$ . The Pulliam isoleg pertains only to the resource which has the higher external handling efficiency, because it is never optimal to reject the food item with the highest energy to handling time ratio. For the remainder of this paper we assume that food 1 has a greater external handling efficiency than food 2:  $e_1/h_1 > e_2/h_2$ . The Pulliam isoleg satisfies the condition where searching for and handling items of food 1 yields the same net energy return as simply handling an item of food 2 (Pulliam 1974, Brown and Mitchell 1989):

$$a_1 e_1 R_1 / (1 + a_1 h_1 R_1) = e_2 / h_2$$

which rearranges to:

$$\hat{R}_1 = e_2 / a_1 (e_1 h_2 - e_2 h_1) \quad (3)$$

The Pulliam isoleg in the absence of gut fullness thus yields a vertical isoleg when plotted in the state space of  $R_1$  and  $R_2$ . To the left of the isoleg (for values of  $R_1 < \hat{R}_1$ ) the forager should be opportunistic and consume all encountered food items regardless of type. To the right of the isoleg ( $R_1 > \hat{R}_1$ ) the forager should be completely selective on food 1 and reject all encountered items of food 2. In the above case, diet choice is bang-bang in that the forager switches from complete opportunism to complete selectivity, and the optimal behavior is influenced only by the abundance of the food with the higher external handling efficiency.

Consider the Pulliam isoleg when gut fullness influences internal handling time. The Pulliam isoleg for food 1 exists when:

$$(a_1 e_1 R_1) / \{1 + a_1 R_1 [h_1 + b_1^2 H_1' (T^2/k^2)]\} = e_2 / [h_2 + b_1 b_2 H_1' (T^2/k^2)]$$

where  $H_1'$  denotes the forager’s harvest rate (items per unit time) when only items of food 1 are harvested. The left term gives the harvest rate from foraging selectively on 1, and the right hand side gives the energy gain achieved from externally and internally handling an item of food 2 when gut fullness has been determined by feeding selectively on food 1. Solving for  $R_1$  yields:

$$\hat{R}_1 = e_2 / a_1 \{ (e_1 h_2 - e_2 h_1) + [(T^2/k^2)(b_1 H_1') \times (e_1 b_2 - e_2 b_1)] \} \quad (4)$$

where  $R_1$  also exists in the term  $H_1'$ , although  $H_1'$  in the case of selective foraging is independent of  $R_2$ . Hence,

the Pulliam isoleg on food 1 remains a vertical line independent of  $R_2$ .

The position of the isoleg is determined by the differences among foods in external handling efficiency and in richness. If the foods have equal richness ( $e_1b_2 = e_2b_1$ ), then the Pulliam isoleg collapses to the "classical" model without internal handling time. If food 1 is also richer than food 2 ( $e_1b_2 > e_2b_1$ ) then the Pulliam isoleg with gut fullness will have a lower  $\hat{R}_1$  than the model without, and vice-versa when food 2 is richer than food 1. In fact, when food 2 is sufficiently richer than food 1, the Pulliam isoleg for food 1 ceases to exist. Hence, when food 1 has a higher handling efficiency than food 2, there is likely, but not necessarily, a Pulliam isoleg for food 1 when  $e_1/b_1 > e_2/b_2$ ; but when  $e_2/b_2 > e_1/b_1$  there is unlikely, but possibly, a Pulliam isoleg for food 2.

For there to be a Pulliam isoleg for food 2 under these circumstances, food 2 must be considerably richer than food 1. This yields the following isoleg for food 2:

$$\hat{R}_2 = e_1/a_2 \{ (e_2h_1 - e_1h_2) + [(T^2/k^2)(b_2H_2) \times (e_2b_1 - e_1b_2)] \} \quad (5)$$

This isoleg is horizontal and independent of the abundance of  $R_1$ . For there to be an isoleg for food 2, expression 5 must yield a positive value for  $\hat{R}_2$ . Because food 1 has a higher external handling efficiency, the first term in the denominator will be negative. Hence, the second term must be positive (food 2 richer than food 1, and food 2 must have some bulk), and it must be sufficiently positive to outweigh the first term (this can be insured by making food 1's bulkiness sufficiently large). Note that if the two foods have the same handling efficiency, then the Pulliam isoleg exists for the food that has the higher richness.

For resource densities that lie outside of a Pulliam isoleg, the forager should be completely selective on the appropriate resource. For instance, if  $R_1 > \hat{R}_1 > 0$  then the forager should ignore food 2 and have a diet composed only of 1. But, what happens when  $R_1 < \hat{R}_1$ ? Unlike the classical case (Eq. 3), the forager's optimal diet may not necessarily be opportunistic. With gut fullness, the Pulliam isoleg simply separates a region where it is never optimal to consume a food item from one where it is optimal to consume some of the less preferred food items. When the Pulliam isoleg exists for food 1, we need to consider an additional isoleg that separates the region of food abundances at which the forager should be opportunistic from that in which it should be merely partially selective. In reference to Mitchell's paradox, we shall call this isoleg the Mitchell isoleg.

#### *Mitchell isoleg*

This isoleg exists only when foods differ in richness and when gut fullness influences internal handling times. The

Mitchell isoleg for food 1 (or food 2) gives all combinations of  $R_1$  and  $R_2$  such that the net energy gain from feeding opportunistically just equals the energy gain from simply handling an item of food 2 (or food 1). The Mitchell isoleg for food 1 satisfies:

$$(a_1e_1R_1 + a_2e_2R_2) / [1 + a_1R_1(h_1 + b_1(T^2/k^2)(b_1H_1 + b_2H_2) + a_2R_2(h_1 + b_2(T^2/k^2)(b_2H_2 + b_1H_1))] = e_2/h_2 + (b_2(T^2/k^2)(b_2H_2 + b_1H_1)]$$

where  $H_1$  and  $H_2$  are the rate of harvest of food items of 1 and 2, respectively, when the forager is opportunistic. Rearranging this equation gives:

$$R_1 = e_2/a_1 \{ (e_1h_2 - e_2h_1) + [(T^2/k^2)(b_1H_1 + b_2H_2) \times (e_1b_2 - e_2b_1)] \} \quad (6)$$

where both  $R_1$  and  $R_2$  are present in the terms for  $H_1$  and  $H_2$ . An explicit expression for the Mitchell isoleg can be found in the appendix. In the following, we characterize the Mitchell isoleg, particularly in relation to the Pulliam isoleg.

If food types 1 and 2 do not differ in richness, then the Mitchell isoleg collapses to the Pulliam isoleg. The Mitchell isoleg and the Pulliam isoleg share the same  $R_1$  intercept. As  $R_2$  goes to zero,  $H_2$  goes to zero,  $H_1$  goes to  $H_1'$ , and the Mitchell isoleg converges on the Pulliam isoleg.

When food 1 is also richer than food 2, the Mitchell isoleg is a curve that has negative slope. At  $R_2 = 0$ , it emerges from the Pulliam isoleg, bends to the left and then asymptotes on

$$R_1 = (2e_2b_2) / \{ 2a_1b_2(e_1h_2 - e_2h_1) + a_1(e_1b_2 - e_2b_1) \times [-h_2 + [h_2^2 + 4e_2b_2(T^2/k^2)]^2] \} \quad (7)$$

as  $R_2$  goes to infinity (Fig. 5). The greater the richness of food 1 relative to food 2, the greater the spread between the Mitchell and Pulliam isolegs.

The combination of the Mitchell and Pulliam isolegs divides the state space into three regions. To the left of the Mitchell isoleg, the forager's optimal strategy is opportunism. Between the isolegs, the forager should be partially selective and consume all encountered items of food 1 and only a portion of encountered items of food 2. To the right of the Pulliam isoleg the forager should be selective and consume only food 1 (Fig. 5).

What happens when food 1 is less rich than food 2? Once  $(e_1b_2 - e_2b_1) < 0$ , (i.e.  $e_1/b_1 < e_2/b_2$ ) the Mitchell isoleg emerges to the right of the Pulliam isoleg. As  $R_2$  goes to infinity, the Mitchell isoleg now asymptotes at values of  $R_1$  greater than the value of the Pulliam isoleg. This paradoxical arrangement of the two isolegs returns the arrangement of optimal behaviors to that of the classical model without gut processing limitations. To the left of the Pulliam isoleg the forager will be opportunistic and to the right the forager will be

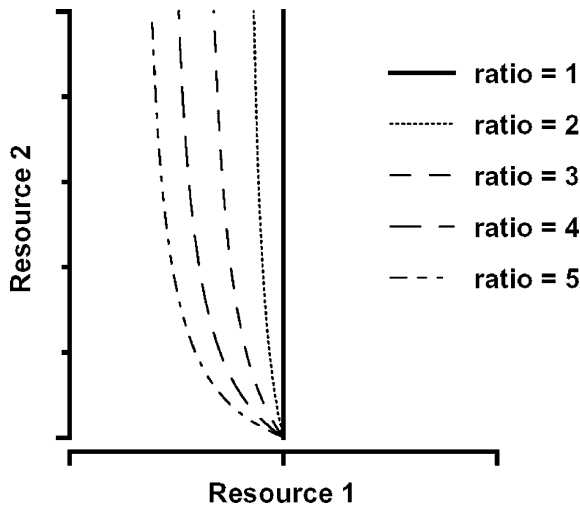


Fig. 5. Pulliam isoleg and Mitchell isolegs in state space of abundance of resources 1 and 2. Pulliam isoleg is the solid vertical line, and in the region of the state space to the right of it, the forager will be selective on resource 1. Mitchell isoleg emerges from the Pulliam isoleg, curving to the left and asymptoting parallel to the resource 2 ( $y$ ) axis. The degree of spread between the two isolegs is determined by the ratio of their relative richnesses ( $e_i/b_i$ ,  $i=1, 2$ ). As this ratio increases, the spread between the isolegs increases. In between the two isolegs, the forager will always select resource 1, but take only some of encountered resource 2. To the left of the Mitchell isoleg, the forager will take both resources opportunistically.

selective on food 1. The Mitchell isoleg still separates the region where opportunism is better than partial selectivity, but it becomes meaningless in terms of the optimal diet because this behavioral switch occurs in a region where pure selectivity on food 1 trumps either opportunism or partial selectivity.

Food 1 can be made less rich than 2 by selecting  $b_1$  sufficiently large. As  $b_1$  continues to increase, the Pulliam isoleg is 'pushed' by the increasing bulk of resource 1 to ever increasing values of  $R_1$ . As the bulk of resource 1 continues to increase, eventually a threshold value of  $b_1$  is exceeded, at which point the Pulliam isoleg goes to infinity. As the Pulliam isoleg is pushed to ever increasing values of  $R_1$ , the range of resource abundances over which the forager will be opportunistic on food types also increases. Interestingly, at the moment the Pulliam isoleg reaches infinity for resource 1, the Mitchell isoleg for resource 1 disappears, and it reappears as the Mitchell isoleg for food 2. At this point, the Mitchell isoleg for food 2 is a monotonically decreasing curve that eventually becomes parallel to the  $R_1$ -axis (Fig. 6). The forager is opportunistic on both food types at values of  $R_2$  below this line, and partially selective on resource 2 above it. At still greater levels of bulk for resource 1, the Pulliam isoleg reappears for resource 2 (it is a horizontal line that intersects the  $R_2$ -axis), and the forager is selective on resource 2 above this line and partially selective on resource 2 between it and the Mitchell line

below it. The forager remains opportunistic at values of  $R_2$  below the Mitchell line.

### Food preference reconsidered

When there are no gut capacity limitations, food preference is determined by a descending ranking of  $e_i/h_i$ , external handling efficiency. Whether a food item is included in the diet is determined by the position of the Pulliam isoleg. Once gut capacity limitations enter, however, the world of food preference gets more complicated and interesting. Now preference is determined by relative ranking of  $[e_i/(h_i + b_i[T/k]B)]$ , where  $B = (\sum b_i H_i)/(T/k)$ , the extent to which the gut is "bulked up" from previous consumption. Now let

$$\rho = e_i/(h_i + b_i[T/k]B) \quad (8)$$

where  $\rho$ , which has units of (energy  $\cong$  time $^{-1}$ ), represents an equal acceptability threshold for a food item to be included in the diet. Noting the similarity of Eq. 8 to the Michaelis-Menton equation for enzyme kinetics, we make use of reciprocals of both sides to allow a solution for a straight line:

$$(b_i/e_i) = k/\rho(TB) - (k/TB)(h_i/e_i) \quad (9)$$

Equation 9, a straight line with negative slope within the state space of ( $h_i/e_i$ ) and ( $b_i/e_i$ ), represents an equal preference isocline such that all food items lying on it are

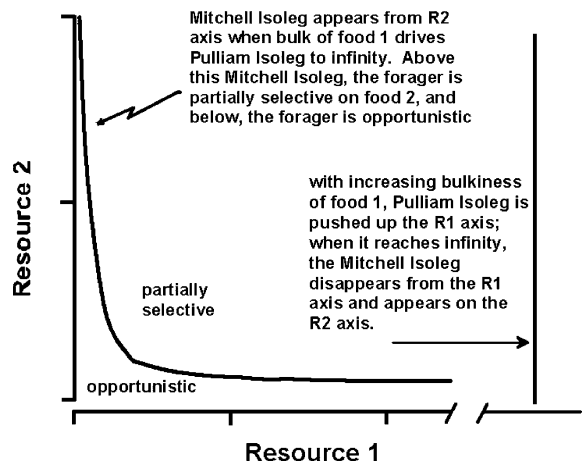


Fig. 6. Mitchell isoleg for resource two as Pulliam isoleg for food one goes to infinity. When resource 2 is considerably more rich than resource 1 ( $e_2/b_2 \gg e_1/b_1$ ), the Pulliam isoleg for resource 1 is "pushed" to infinity by increasing bulk of resource 1. When the Pulliam isoleg reaches infinity, the Mitchell isoleg for resource 1 vanishes and a Mitchell isoleg for resource 2 appears. This isoleg emerges from the resource 2 ( $y$ ) axis with a negative slope, and asymptotes parallel to the resource 1 ( $x$ ) axis. Above this isoleg, the forager will always select resource 2, but will select only some of encountered resource 1. Below this isoleg the forager is opportunistic. Values for the Mitchell isoleg in this figure are:  $a_1 = a_2 = 1$ ,  $e_1 = 2$ ,  $h_1 = 1$ ,  $e_2 = 1$ ,  $h_2 = 0.6$ ,  $b_1 = 9$ ,  $b_2 = 2$ ,  $T = 1$ ,  $k = 10$ ,  $R_1 = 0-20$ ,  $R_2 = 10$ .

of equal acceptability. The region outside the line, because of the reciprocals, represents higher ratios of bulk: energy and handling: energy. Any food item lying in this outer region is therefore less preferred. The region lying below it, because of the reciprocals, represents lower ratios of bulk: energy and handling: energy. All items lying in this inner region are therefore more preferred. When the line is a threshold of acceptability, then it is an isoleg separating acceptable (below) from unacceptable (above) food items.

Equation 9 illustrates a number of important relationships. First, if the external handling of food is fast relative to internal handling, preference will be determined by the intercept of the richness (y) axis of Eq. 9,  $k/\rho(TB)$ . In this case, the preference isocline is a horizontal line, and all foods on or below it are acceptable (Fig. 7A). Second, if internal handling is fast relative to external handling, preference will be determined by the intercept of the external handling efficiency axis (x) of Eq. 9,  $1/\rho$ . In this case, the preference isocline is a vertical line, and any food on or to the left of it is acceptable (Fig. 7B). Third, when both internal and external handling operate, preference is represented by a straight line with slope of  $(-k/TB)$ , Fig. 7C). The negative slope of this line indicates a tradeoff between external handling efficiency ( $e/h$ ) and food richness ( $e/b$ ) in affecting preference. Fourth, preference is influenced by previous consumption, so that as the gut takes on bulk,  $B$ , fewer items will be included in the diet. As  $B$  increases due to past consumption, both the y-intercept and the slope of Eq. 9 may decline.

In Pulliam's (1974) model, preference is influenced by the environment but in a simpler more transparent manner, namely the abundance of preferred food(s) with respect to  $e/h$ . In our case, two environments may offer equal net energy returns to a forager, but if they differ in the relative abundances of foods that differ in bulk, then a forager can have different food preference rankings in them. Pulliam's (1974) preference criterion,  $e/h$ , can now be seen to be a special case of this environment-dependence of food preferences. With differences in bulk, foods can become complementary resources, which creates the possibility for partial preferences.

## Discussion

Both ecological and physiological characteristics of foragers influence diet. However, foraging ecology and digestive physiology are usually investigated in isolation from each other (Whelan and Schmidt 2006). It is not unreasonable to enquire why either should care about the other. Our model shows why they should. By explicitly incorporating internal food handling in the gut into an ecological framework, our model shows how

both ecological (encounter rate, external handling efficiency) and physiological (gut volume, internal handling of food in the gut) parameters limit harvest rate, and how both may interact to influence diet preference. By integrating internal handling into an ecological frame-

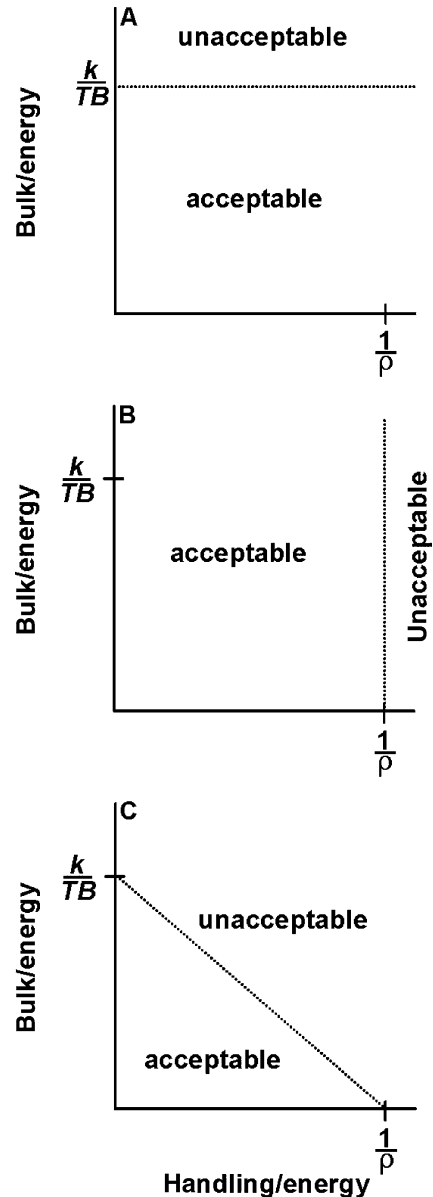


Fig. 7. Preference isoleg in state space of bulk:energy (y-axis) and external handling:energy (x-axis). (A) When external handling is fast relative to internal handling, the isoleg is a horizontal line at the value of  $k/TB$ , and any food on or below it is preferred. (B) When internal handling is fast relative to external handling, the isoleg is a vertical line at the value of  $1/\rho$ , and any food on or to the left of it is preferred. (C) As the forager takes on bulk through resource consumption, the isoleg takes on a negative slope  $(-k/TB)$ , "pushing" the isoleg toward the y-axis. Consumption thus decreases the universe of preferred food items.

work, our model adds physiological characteristics to the intrinsic characteristics of foragers that influence feeding rate and diet selection. This in turn adds properties of the food items not previously considered in ecological models, specifically their bulk properties, to the extrinsic factors influencing diet and harvest rate. Our model thus integrates the ecological and physiological frameworks of foraging. In contrast to the models of Verlinden and Wiley (1988) and Hirakawa (1997a), our model incorporates the effect of gut processing as a continuous function, rather than as an on/off inequality constraint. In contrast to the model of Jeschke et al. (2002), we consider a forager consuming two foods, and in addition, in our model, a “satiated” forager will always accept a food item provided it is of sufficient richness. In the following, we first show how our integration of gut physiology into an ecological model lends insight into the question of constraints versus limitations on harvest rate and diet selection. We next consider the physiological feasibility and the physiological implications of the model. We finally illustrate how the resolution of Mitchell’s paradox provides an application of foraging theory to the design of the successful multi-course meal.

### Constraints vs limits

To a foraging ecologist operating within the paradigm of optimal control theory, ‘constraint’ pertains to limits or restrictions on the value of a control variable. In a typical foraging model, such control variables would include the probability of accepting or rejecting a food item, or the amount of time spent foraging in a patch. This is a more restrictive use of the word than the standard use, in which a constraint is simply anything that places a limit on some process or value. In this standard sense, our model clearly shows that digestive processing can limit feeding rate and diet selection in the short run of instantaneous feeding behavior. In the current formulation of our model, internal handling time, like external handling time, is simply a rate-limiting parameter. Digestive system structure or function can be considered a control variable only over longer time scales when modulation or evolution may come into play. So in the restrictive sense, over these longer time scales digestive system properties like retention time and gut capacity could be modeled as control variables that can impose constraints on foraging.

Our model also allows a comparison of how the ecological versus the physiological parameters influence harvest rate, gut fullness, etc. For instance, in Fig. 1c, 1d and Fig. 2a, 2b we depict gut fullness and harvest rates, respectively, when varying either *h*, external handling time, or *T*, internal handling time, while all other variables were held constant. While it is obvious that both *h* and *T* influence (limit) both gut fullness and

harvest rate, they appear to do it differently. To investigate their effects further, we show the asymptote achieved for harvest rate, *H*, and gut fullness for different values of *h* and *T* (Fig. 8).

When inspecting Fig. 8, note that in moving across a row, external handling time, *h*, increases 10 fold from cell to cell at constant values of internal handling time, *T*. Similarly, when moving down a column, *T* increases 10-fold from cell to cell at constant values of *h*. Note also that cells along upper left to lower right diagonals have the same *h/T* ratio. From Fig. 8, it is clear that increasing either *h* or *T* while holding the other constant decreases both *H* and gut fullness. And, external handling, *h*, limits *H* to a greater degree than does internal handling, *T*. For instance, in moving from *h*=*T*=1 to *h*=100 and *T*=1, *H* decreases by a factor of 470. In contrast, in moving from *h*=*T*=1 to *h*=1 and *T*=100, *H* decreases by a factor of 19. Interestingly, *h* also has a relatively greater limit on the extent of gut filling. The relatively greater limiting effect of *h* compared to *T* is due to the batch-reactor-like processing of *h* and the continuous-flow-like processing of *T*. Finally, equal ratios of *h/T* result in identical amounts of gut filling irrespective of the particular values of *h* and *T*.

### Physiological feasibility and implications

The disc equation forms the basis for our model. For the extension of this model to be useful to physiologists, the

		External handling time, <i>h</i>		
		1	10	100
Internal handling time, <i>T</i>	1	<i>h</i> / <i>T</i> : 1 <i>H</i> : 0.941 Gut fullness: 0.19	<i>h</i> / <i>T</i> : 10 <i>H</i> : 0.099 Gut fullness: 0.02	<i>h</i> / <i>T</i> : 100 <i>H</i> : 0.002 Gut fullness: .01
	10	<i>h</i> / <i>T</i> : 0.1 <i>H</i> : 0.386 Gut fullness: 0.78	<i>h</i> / <i>T</i> : 1 <i>H</i> : 0.096 Gut fullness: 0.19	<i>h</i> / <i>T</i> : 10 <i>H</i> : 0.009 Gut fullness: 0.02
	100	<i>h</i> / <i>T</i> : 0.01 <i>H</i> : 0.049 Gut fullness: 0.975	<i>h</i> / <i>T</i> : 0.1 <i>H</i> : 0.039 Gut fullness: 0.78	<i>h</i> / <i>T</i> : 1 <i>H</i> : 0.009 Gut fullness: 0.19

Fig. 8. Effect of external (*h*) and internal (*T*) handling times on harvest rate and gut fullness (proportion of gut volume occupied by ingested food) when forager takes only one resource. The values in each cell represent the approximate asymptote for each relationship. Harvest rate is given by Eq. 1c, with encounter rate, *a*=1, food bulk, *b*=2, and gut volume, *k*=10, with *R* varying from 1 to 20. Gut fullness is determined by  $[(bHT)/k]$  as a function of resource abundance, *R*, using the same values for each parameter as for harvest rate.

physiological parameters must be feasible, measurable, and accessible to manipulation (C. Martínez del Río, pers. comm.). Our model meets those requisites. We model movement of food through the gut as retention time ( $T$ ), which is the appropriate parameter when considering both digestion and absorption of food (Warner 1981). In our model, we assume all food types will have the same value for  $T$ , which may often, but not always, be the case (there can be some reflux of certain lumen contents, for example; Clench and Mathias 1992, Levey and Duke 1992). However, as a first approximation, this is a robust assumption. For instance, several studies have shown that modulation of retention time following a diet switch imposed under laboratory conditions requires a number of days (Levey and Karasov 1989, 1992).

Like many physiological models (Penry and Jumars 1986, 1987, Martínez del Río et al. 1994), we model gut volume as a constant. While this assumption is not strictly true for all species (Levey and Duke 1992), again, for a first approximation it is adequate. As we show below, this assumption can be relaxed, and gut volume can be allowed, over relatively short time scales, to be modulated in response to the forager's switching among different diets (Whelan et al. 2000) or, over long time scales, to evolve. Finally, foods obviously differ in both energy content and their bulkiness (Karasov 1990).

An important result of our model is that, for any particular level of gut fullness, there can exist a food type that is rich enough (sufficiently high energy to bulk ratio,  $e/b$ ), that the forager will always consume it. This runs counter both to the view that gut capacity sets an upper limit to consumption and to the view that some foragers feed until capacity is reached and then cease foraging until the gut has sufficiently processed its contents (Diamond et al. 1986, Krebs and Harvey 1986). The differences between these perspectives raises the question of how the gut may signal to a forager's central nervous system pertinent information regarding gut capacity and gut contents.

The gut possesses both mechanical and chemical receptors that allow matching food intake with digestive and absorptive capacity (Raybould 1998, Höfer et al. 1999, Savory 1999, Feinle et al. 2001, Jensen 2001, Batterham et al. 2002, Schwartz and Morton 2002). The mechanoreceptors detect distension and deformation or stretch of stomach mucosa resulting from food intake or contraction of smooth muscle. The chemoreceptors detect nutrients, such as glucose, amino acids, and lipid, as well as osmolarity, pH and temperature. These receptors allow unconscious communication between the gut and the central nervous system (Ranson 1921, Raybould 1998) and influence gastric motility, food intake, and gastrointestinal sensations such as dyspepsia and nausea (Feinle et al. 2001). In addition to such direct communication between the viscera and the central

nervous system, indirect communication pathways involving regulatory peptides or neuroactive modulators (e.g. cholecystokinin) also influence food intake (Jensen 2001).

Of particular interest from the new perspective of our model is that some gastric sensations appear to require triggering by both chemoreceptors in the small intestine in addition to mechanoreceptors in the stomach (Feinle et al. 2001). For instance, in humans a high-lipid liquid test meal increased susceptibility to motion sickness and nausea compared to a lipid-free meal as long as the motion sickness stimulus was applied after the meal emptied from the stomach into the small intestine (Feinle et al. 2001). Perfusion of the intestine with the local anesthetic benzocaine reduces gastric distension-induced sensations induced by small intestine receptors (Feinle et al. 2001). This in turn implies that feelings of satiety (gut fullness) likewise are modulated by chemoreceptors in the intestine in combination with mechanoreceptors in the stomach. For instance, the apolipoprotein AIV (apoAIV), which is involved with lipid uptake, may signal intestinal lipid content to other organ systems. Intraperitoneal injection of exogenous apoAIV inhibits food intake in rats (Merrill 1996), suggesting that its presence in the small intestine induces sensation of satiety. Taken together, these findings suggest that the gut can detect the quality as well as the quantity of its contents, and use this information to contribute to appropriate regulation of food intake (Behmer et al. 2001, Schwartz and Morton 2002).

Why the gut should detect both quality and quantity of its contents is answered by our definition of food preference (Eq. 8). Food choice should depend upon the food's external handling efficiency ( $e:h$  ratio), its richness ( $e:b$  ratio) and on the animal's current state with respect to how full and how "richly full" (both indicated by parameter  $B$  in Eq. 8) it is. In other words, to gauge its state, the forager needs more than just a "gas gauge", which detects how full the tank is; it also wants to know whether the gas is regular or premium. In the gut, mechanoreceptors gauge fullness while chemoreceptors gauge richness. Further, gustatory senses (taste and smell) serve to assess the value and richness of the currently encountered food item (Drewnowski 1997). All of these sensations integrated together provide sufficient information to motivate an optimal perception of a food item's current value to the forager.

How can our model be used by physiologists? To illustrate, consider Eq. 8, our expression for food preference. In Eq. 8 we define  $\rho$  as an equal acceptability threshold. There are several related biological interpretations of  $\rho$ . For instance,  $\rho$  can be interpreted as the energetic state of the animal. In this case, Eq. 8 indicates what foods enable the animal to maintain its energetic state at  $\rho$ . Now consider the case in which a forager is changing diets, perhaps in response to seasonal changes

in resources. Such diet changes often induce modulation of digestive physiology (Karasov and Hume 1997, Whelan et al. 2000), which may include adjustments of digestive enzymes and/or absorptive proteins, retention time, and even changes in gut mass. An example is provided by passerine bird species switching from insects in the breeding season to fruit in the nonbreeding season (Whelan et al. 2000). Insects tend to be relatively completely digestible and of low bulk, while fruits, despite readily available nonstructural carbohydrate or lipid in the pulp, also contain seeds, which for most frugivores represent bulky ballast (Karasov 1990). Hence insects have relatively larger  $e:b$  ratios than do fruits. As is apparent from Eq. 8, if the animal is to maintain its energetic state at a constant value of  $\rho$  while the value of  $b$ , food bulk, is increasing, the animal may either decrease retention time,  $T$ , increase gut volume,  $k$ , or do both. As has been demonstrated with a variety of bird species, retention time is a commonly modulated physiological characteristic accompanying switches in diet (Levey and Karasov 1989, 1992, Karasov and Hume 1997).

Animals can maintain their energetic state by burning fuel reserves in addition to active consumption and processing of food. For instance, many bird species, during migration, fuel their migratory flights with fat and fat-free tissue reserves, which are replenished during stop-overs of various length (Biebach 1996, 1998, Jehl 1997, Piersma 1998). In this case, energetic state,  $\rho$ , is maintained either by active consumption and processing of food or through the expenditure of fuel reserves (Fig. 9). It is now well established that fuel tissue

deposition involves hypertrophy of both fat and fat-free tissue (e.g. adipose deposits and pectoral muscle), often in concert with atrophy of various organs, notably the digestive tract and liver (Piersma and Gill 1998). Atrophy of organs such as the digestive tract likely is a tactic to offset the increase in overall body mass resulting from fuel deposition (Piersma 1998). As shown in Fig. 9, when fuel reserves maintain energetic state, gut volume,  $k$ , which is proportional to gut mass, can be reduced with no effects on  $\rho$ . When the animal switches back to active consumption,  $k$  will have to be increased in order to maintain  $\rho$  at a constant value. Karasov and Pinshow (2000) provide evidence that the long-distance migratory blackcap, *Sylvia atricapilla*, experience reduced assimilation rates following two days of fasting, but quickly (within three days) increased assimilation rate. Their findings are consistent with our expectations based on Eq. 8 and Fig. 9.

### Foraging theory and the successful multi-course meal

Let us return to Mitchell's paradox. Yes, gut volume and passage rate influence feeding rate, diet choice, and partial preferences. Nonetheless, Mitchell is right. In the sense of an absolute inequality constraint acting on diets, there are no gut constraints. The gut is never quite full, and in fact it may be quite empty. Moreover, there will always be room for a food with sufficiently high richness, even when the gut may be signaling the sensation of satiety or fullness. The sensation of fullness may be a means of indicating both the current bulk and value of the gut's contents. This sensation may thus serve to set the threshold of acceptability on foods varying in richness (Behmer et al. 2001). Given an array of foods with different richness, a forager should feel full and little interested in continuing to consume foods of low richness. This feeds into a variety of human dining issues. The proverbial, "Do not eat those cookies or sweets before dinner, it will spoil your appetite", may recognize the heightened sense of fullness caused by placing rich food in the gut. Suddenly a whole variety of lower richness (but healthy!) foods served at dinner may be of little interest.

Finally, our resolution of Mitchell's paradox may have been anticipated by conventions designed to present the successful multi-course meal. Here success means keeping the diners at the table for a lengthy and continuous period without inducing a sense of fullness or satiation until meal's end (Stewart 1982, Waters 1982). An example of such a meal in the United States would be that characteristically served on Thanksgiving. Typically, such meals progress from items of greater bulk and lower richness (e.g. salad), to items of lower bulk and greater richness (dessert). In terms of our model, as the meal

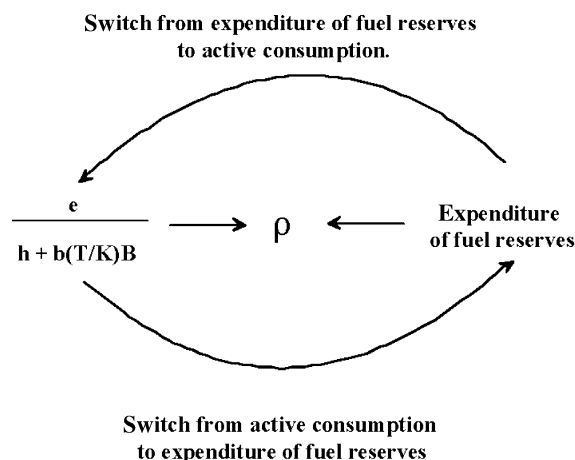


Fig. 9. Schematic depiction of a forager's switching between maintenance of its energetic state ( $\rho$ ) through active consumption and through expenditure of fuel reserves. When maintaining  $\rho$  by active consumption, only foods satisfying Eq. 8,  $\rho = e_i / (h_i + b_i[T/k]B)$ , will be accepted. When the forager maintains its energetic state by expenditure of fuel reserves, it is free to modulate terms in Eq. 8, such as gut volume,  $k$ . See text for details.

progresses and diners consume the dishes, their guts become increasingly bulked up. As predicted by our definition of preference (Eq. 9 and 10), as the gut becomes bulked up, the universe of acceptable food items declines. It takes foods of increasing richness to induce continued dining. Close to the meal's end, diners should feel satisfied and satiated ("I can't possibly eat another thing!"). And that is when dessert is introduced, for typically, desserts possess little bulk but great richness. By adding analysis of the effect of food bulk and internal handling to classical optimal foraging theory, we show that Mitchell's paradoxically "full" dinner guest, who nonetheless squeezes in that luscious dessert, is not only understandable, but to be expected. Animals, in nature, likely do no less.

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## Appendix

To solve for explicit solutions to Eq. 1c, 2a and 2b, we must use the formula for the solution to quadratic equations,  $x = [-b \pm \sqrt{b^2 - 4ac}] / 2a$ . We illustrate with Eq. 1c:

$$H = (aR) / \{1 + aR[h + b^2H(T^2/k^2)]\}$$

We multiply by the denominator on the rhs:

$$H\{1 + aR[h + b^2H(T^2/k^2)]\} = aR$$

and then simplify and set equal to zero:

$$H^2[ab^2(T^2/k^2)R] + H(1 + ahR) - aR = 0$$

Now, letting  $a = [ab^2(T^2/k^2)R]$ ,  $b = (1 + ahR)$ , and  $c = -aR$ , and keeping in mind that we are seeking only the positive solution,

$$H = \{-(1 + ahR) + [(1 + ahR)^2 + 4ab^2(T^2/k^2)R^2]^{1/2}\} / (2ab^2(T^2/k^2)R) \quad (A1)$$

Similar algebraic manipulations produce the following solutions for Eq. 2a and 2b, respectively:

$$H_1 = \{-(1 + a_1h_1R_1 + a_2h_2R_2) + [(1 + a_1h_1R_1 + a_2h_2R_2)^2 + 4(T^2/k^2) \times [a_1b_1^2R_1^2 + b_1b_2R_1a_2R_2 + a_2b_1b_2R_2 + (a_2b_2R_2)^2/(a_1R_1)]a_1R_1]^{1/2}\} / (2(T^2/k^2) \times [a_1b_1^2R_1^2 + b_1b_2a_1R_1a_2R_2 + a_2b_1b_2R_2 + (a_2b_2R_2)^2/(a_1R_1)]) \quad (A2)$$

$$H_2 = \{-(1 + a_1h_1R_1 + a_2h_2R_2) + [(1 + a_1h_1R_1 + a_2h_2R_2)^2 + 4(T^2/k^2) \times [a_2b_2^2R_2^2 + b_1b_2R_2a_1R_1 + a_1b_1b_2R_2 + (a_1b_1R_1)^2/(a_2R_2)]a_2R_2]^{1/2}\} / (2(T^2/k^2) \times [a_2b_2^2R_2^2 + b_1b_2R_2a_1R_1 + a_1b_1b_2R_2 + (a_1b_1R_1)^2/(a_2R_2)]) \quad (A3)$$

Finally, the exact expression for the Mitchell isoleg is given by the following:

$$\begin{aligned}
 & (a_1^3 e_1^3 (b_1^2 b_2^2 - a_1^3 e_1^2 h_2^2 b_1^2 - a_1^3 e_1 h_2 h_1 b_1 b_2 e_2 - 4a_1^3 e_1^2 (b_1^3 b_2 e_2 + a_1^3 e_1 (b_1^4 e_2^2 + a_1^3 h_1^2 e_2^2 b_1 b_2 - a_1^3 h_1^2 e_2^2 b_1^2 + a_1^3 e_1^2 h_2 h_1 b_1 b_2 \\
 & + 4a_1^3 e_1 h_1 e_2 h_2 b_1^2 - a_1^3 h_1^2 e_2 b_1 e_1 b_2) R_1^4 + (4a_1^2 h_1 e_2^2 b_1 b_2 - 4a_1^2 e_1 h_2^2 a_2 R_2 b_1 b_2 e_2 + 4a_1^2 e_1^2 (b_1 b_2^3 a_2 e_2 R_2 + 4a_1^2 e_1 e_2 h_2 b_1^2 \\
 & - 8a_1^2 e_1 (b_1^2 b_2^3 a_2 e_2^2 R_2 + a_1^2 e_1^2 h_2 b_1 b_2 - 4a_1^2 (b_1^3 e_2^3 a_2 b_2 R_2 - a_1^3 e_1^2 h_2^2 b_1 b_2 R_2 + 4a_1^2 h_1 e_2^3 h_2 b_1 a_2 b_2 R_2 - 4a_1^2 h_1 e_2 b_1 e_1 b_2 \\
 & + a_1^2 e_1 h_2 h_1 a_2 b_2^2 e_2 R_2 + a_1^2 e_1^2 h_2^2 a_2 R_2 b_1 b_2 - a_1^2 e_1 h_2 b_1 b_2 e_2 - a_1^2 h_1 e_2 a_2 h_2 R_2 b_1 e_1 b_2 - a_1^2 h_1^2 e_2^2 a_2 b_2^2 R_2 \\
 & + 4a_1^3 e_1 h_1 e_2 h_2 b_1 b_2 R_2 - a_1^3 h_1^2 e_2^2 b_1 b_2 R_2 - 4a_1^2 h_1 e_2^2 b_1^2) R_1^3 + (a_1 h_1 e_2^3 a_2^2 h_2 R_2^2 [b_1/e_1] b_2 + a_1 e_1 h_2 a_2 b_2^2 e_2 R_2 \\
 & + a_1 e_1 (a_2^2 b_2^4 e_2^2 R_2^2 + b_1 b_2 e_2^2 + 4e_2^2 a_1 h_2 b_1 a_2 b_2 R_2 + [a_1/e_1] (b_1^2 a_2^2 b_2^2 e_2^4 R_2^2 + a_1 h_1 e_2^2 h_2 a_2^2 b_2^2 R_2^2 - e_2 a_2 h_2 R_2 a_1 b_1 e_1 b_2 \\
 & - e_2^2 a_1 b_1^2 - a_1 h_1^2 [e_2^3/e_1] a_2^2 b_2^2 R_2^2 - 4a_1^2 h_1 e_2^2 b_1 b_2 R_2 - 4a_1 h_1 e_2^2 a_2 b_2^2 R_2 - e_2 a_1 b_1 e_1 b_2 - 4a_1 (a_2^2 b_2^3 e_2^3 R_2^2 b_1 \\
 & - a_1 h_2^2 a_2^2 R_2^2 b_1 b_2 e_2^2) R_1^2 + (e_2^2 a_2^2 h_2 R_2^2 b_2^2 + e_2^3 a_2^2 h_2 R_2^2 [b_1/e_1] b_2 - a_1 b_1 b_2 e_2^2 R_2 - 4h_1 [e_2^3/e_1] a_2^2 b_2^2 R_2^2 - a_2 b_2^2 e_2^2 R_2) R_1 \\
 & - [e_2^3/a_1 e_1] a_2^2 b_2^2 R_2^2 = 0
 \end{aligned}$$