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Optimization of Gut Structure and Diet for Higher Vertebrate Herbivores [and Discussion]

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Optimization of gut structure and diet for higher vertebrate herbivores

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SUMMARY

A generalized herbivore gut is modelled as (i) a well-stirred anterior chamber in which microbial fermentation occurs; (ii) a tubular reactor in which digestion but no fermentation occurs; and (iii) a posterior fermentation chamber. The rate at which the herbivore gains metabolizable energy is calculated for diets that can be eaten at different rates and contain different energy densities of easily digested cell contents, and of cell wall materials that can be fermented but not digested. The optimum gut structure for each diet is determined. Chewing probably speeds digestion and fermentation but reduces eating time. Optimal chewing times are determined for particular diets and guts.

Herbivores often have a choice between poorer food that can be eaten fast and richer food that can only be eaten more slowly. Energy costs may be incurred in travelling between patches of the richer food. Optimal diet choices are predicted for herbivores with particular gut structures.

1. INTRODUCTION

This paper tackles two main questions. What is the optimum gut structure for a herbivore eating a specified diet? And what is the optimum diet for a herbivore with specified gut structure? Such questions have often been asked before: for recent examples see Penry & Jumars (1987), Verlinden & Wiley (1989), Hume (1989), Prins & Kreulen (1990) and Murray (1991). The novel feature of this paper is its use of a simple mathematical model that predicts the energy gain of a herbivore, given the composition of the diet, the rate at which it is eaten and the volumes of the principal segments of the gut.

Penry & Jumars (1986, 1987) showed how the theory of chemical reactors can help us to understand the design of digestive systems. Plug flow reactors (PFRs) are tubes in which reagents flow with negligible mixing along the length of the tube. Continuous flow stirred tank reactors (CSTRs) are tanks in which the reagents are kept thoroughly mixed. The concentrations of reagents fall gradually along the length of a PFR, but reagents entering a CSTR are diluted immediately to the concentrations at which they will leave it. For that reason, PFRs give higher yields in reactions in which any catalysts are added at entry. However, microbial populations cannot sustain themselves in PFRs, and would soon be washed out. Penry & Jumars (1986) suggested that the fermentation chambers in herbivore guts should be modelled as CSTRs, and the rest of the gut as a PFR. Herbivorous mammals, birds (Herd & Dawson, 1984) and reptiles (Troyer, 1984) have fermentation chambers in their guts.

Penry & Jumars (1987) used the Michaelis–Menten equation to predict rates of digestion by the herbivore's own enzymes, and the Monod equation to predict fermentation rates. I will make the simpler assumption that rates of digestion and fermentation are limited only by the quantities of substrates present, and proceed according to first-order kinetics. This assumption would be unsatisfactory if the animal were taking large meals at long intervals, so that the microbial population had to build up after each meal, but seems adequate for the steady-state model that will be developed. Waldo *et al.* (1972) and Mertens & Ely (1982) also assumed first-order kinetics in their models of the rumen.

2. THE MODEL

We will consider an idealized gut consisting of an initial CSTR (a rumen), representing a fraction v_1 of total gut volume: a PFR (fractional volume v_2): and a second CSTR (a caecum or colon, v_3) (figure 1).

The animal will be assumed to feed continuously, at a constant rate. This rate will be described by the dilution rate D, the volumetric rate of food intake divided by the total volume of the gut. We will assume (as Penry & Jumars (1987) also did) that the volume of the food remains unchanged as it passes through the gut. This implies that it spends on average times v_1/D, v_2/D and v_3/D in the three segments of the gut, and that the mean residence time for the entire gut is $1/D$. The concentrations of substances and microbes in the food and in the gut will be expressed as energy densities (heat of combustion per unit volume). Subscripts will be used to distinguish energy densities in the diet (subscript 0) from those in the three segments of the gut (1, 2 and 3, see figure 1).

Two groups of substrates will be distinguished. Sugars, starch, oils, protein and other easily digestible

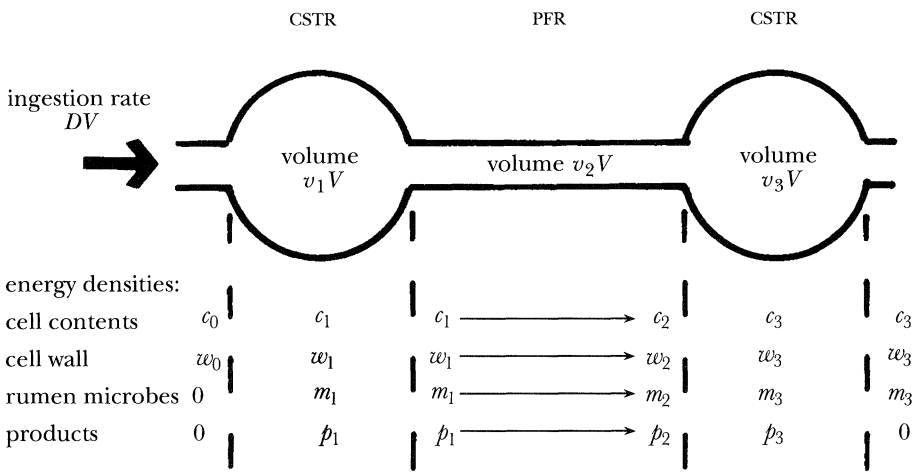

Figure 1. A diagram of the gut model.

materials will be referred to as 'cell contents' because that is their main origin. Their energy density is c_0 in the food, c_1 in the first CSTR, and so on. They can be fermented by microbes with fractional rate constant $r_{\mathrm{ferm,c}}$ or digested by the herbivore's own enzymes with rate constant r_{dig}. Cellulose and other materials that can be fermented but not digested are referred to as 'fermentable cell wall'. Their energy density in the food is w_0 and the rate constant for their fermentation is $r_{\mathrm{ferm,w}}$. This fraction excludes any of the cell wall polysaccharides that are protected from fermentation by their association with lignin.

The energy densities of rumen microbes (i.e. of microbes produced in the first CSTR) will be represented by the symbol m, with appropriate subscripts. That of absorbable products of digestion will be represented by p. We will assume that all these products are eventually absorbed but will not distinguish at any stage in the calculation between products that are still in the gut and those that have been absorbed into the bloodstream.

We will assume that fermentation of any substrate yields absorbable products and microbes whose heats of combustion are fractions Y_{ferm}, Y_{micr}, respectively of that of the substrate. Digestion of any substrate gives a fractional energy yield Y_{dig}.

We will now consider the segments of the gut in turn, starting with the first CSTR. Food travels through it (as through the rest of the gut) at a rate DV (dilution rate multiplied by gut volume). The energy density of cell contents is c_0 in the material entering the CSTR and c_1 in the material leaving, so the rate at which cell contents are broken down is $DV(c_0-c_1)$. The volume of the CSTR is v_1V and cell contents are fermented at a fractional rate $r_{\mathrm{ferm,c}}$, so the rate of breakdown of cell contents is also $v_1Vc_1r_{\mathrm{ferm,c}}$.

$$DV(c_0-c_1) = v_1Vc_1\,r_{\mathrm{ferm,c}},$$
$$c_1 = Dc_0/(D+r_{\mathrm{ferm,c}}\,v_1). \qquad (1)$$

Similarly, for fermentable cell wall materials

$$w_1 = Dw_0/(D+r_{\mathrm{ferm,w}}\,v_1). \qquad (2)$$

The energy density of fatty acids and other absorbable products formed by these fermentations is

$$p_1 = Y_{\mathrm{ferm}}(c_0-c_1+w_0-w_1), \qquad (3)$$

and the energy density of microbes produced is

$$m_1 = Y_{\mathrm{micr}}(c_0-c_1+w_0-w_1). \qquad (4)$$

Now consider the PFR. The energy density of the remaining cell contents falls along its length from c_1 to c_2 as digestion proceeds at a rate r_{dig}. Each particle travels the length of the PFR in time v_2/D so

$$c_2 = c_1\exp(-r_{\mathrm{dig}}\,v_2/D). \qquad (5)$$

Cell wall materials (by our definition) cannot be digested, so

$$w_2 = w_1. \qquad (6)$$

However, microbes that are carried out of the first CSTR with the food are digested here,

$$m_2 = m_1\exp(-r_{\mathrm{dig}}\,v_2/D). \qquad (7)$$

Thus, if no absorption had occurred through the gut wall, the energy density of absorbable products would increase to

$$p_2 = p_1 + Y_{\mathrm{dig}}(c_1-c_2+m_1-m_2). \qquad (8)$$

Finally, the food enters the second CSTR, where fermentation proceeds as in the first. Any microbes that arrive undigested will be dead and liable to fermentation at the same fractional rate as cell contents. Note that m_2, m_3 are energy densities of microbes originating in the first CSTR: microbes produced in the second will be lost in the faeces so there is no need for us to calculate their density. By the same arguments as for equations (1) to (3)

$$c_3 = Dc_2/(D+r_{\mathrm{ferm,c}}\,v_3), \qquad (9)$$
$$w_3 = Dw_2/(D+r_{\mathrm{ferm,w}}\,v_3), \qquad (10)$$
$$m_3 = Dm_2/(D+r_{\mathrm{ferm,c}}\,v_3), \qquad (11)$$
$$p_3 = p_2 + Y_{\mathrm{ferm}}(c_2-c_3+w_2-w_3+m_2-m_3). \qquad (12)$$

The rate of flow through the gut is DV so the rate of formation of absorbable products in the entire gut is p_3DV. We will assume that these are completely absorbed (but see Dade *et al.* (1990)).

Equations (1) to (12) have been incorporated in a computer program that calculates $p_3\,D$ for any specified diet (described by D, c_0 and w_0) and gut structure (v_1, v_2, v_3).

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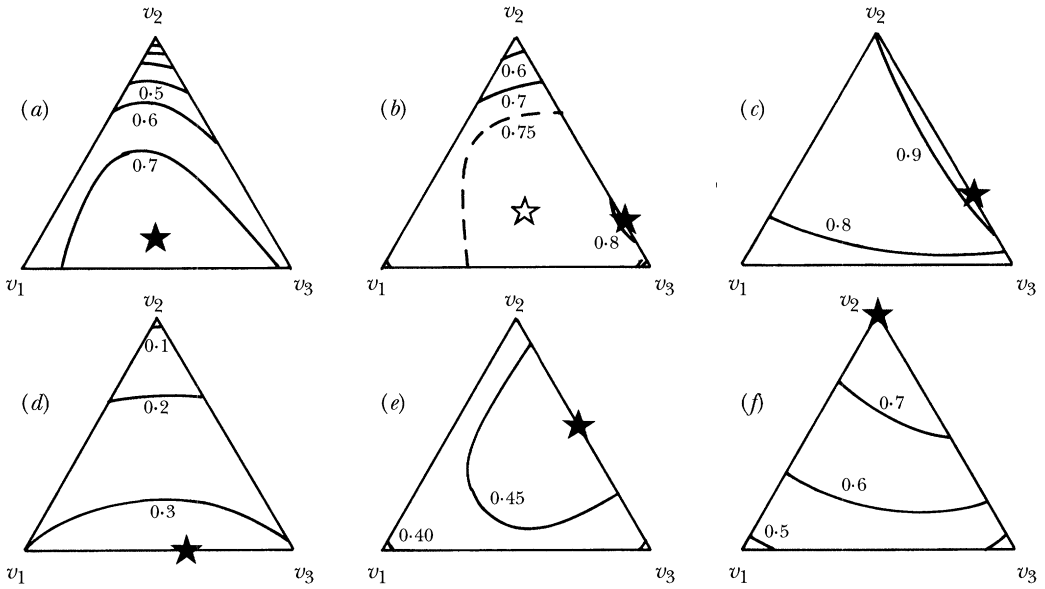

Figure 2. Rates of energy gain from specified diets in different guts. Each triangular graph represents the set of all possible gut structures (v_1, v_2, v_3), with contours representing rates of energy gain (expressed as $p_3/(c_0+w_0)$). Filled stars represent global maxima and the hollow star a local maximum. Relative feeding rates D/r_{dig} are 0.05 in (*a*) to (*c*); and 0.5 in (*d*) to (*f*). The proportion of cell contents in the food, $c_0/(c_0+w_0)$ is 0.1 in (*a*) and (*d*); 0.5 in (*b*) and (*e*); and 0.9 in (*c*) and (*f*).

3. VALUES FOR PARAMETERS

We will assume for lack of information that cell contents can be fermented or digested at equal rates: $r_{ferm,c} = r_{dig}$. However, we must assume that cell wall materials are fermented more slowly (Van Soest *et al.* 1988). We will generally assume $r_{ferm,w}/r_{dig} = 0.3$ but will also try other values.

Waldo *et al.* (1972) found that the mean fractional rate of fermentation of cellulose by rumen microbes from cattle was 0.07 h^{-1}. Mean retention times $(1/D)$ in the guts of herbivorous birds and mammals range from about 3 h to 130 h (Warner 1981). These data suggest that we should consider a wide range of values of D/r_{dig}: results will be presented for values ranging from 0.01 to 1.00. Values greater than 1.00 seem unlikely, as they would imply loss in the faeces of at least $1/e$ (37 %) of cell contents.

The fractional yield of fermentation products Y_{ferm} will be taken to be 0.75 and the yield of microbes Y_{mier} will be taken to be 0.10. (Blaxter 1962). It will be assumed that no energy is lost in digestion: $Y_{dig} = 1.00$.

Figure 2 shows calculated energy gains for animals with different gut structures, on particular diets. Figure 2*a*, *d* shows results for food containing a very low proportion of cell contents, lower than would be expected even in mature grass (Blaxter (1962) gives compositions by mass of grass and other foods from which compositions by energy content can be estimated). At a low rate of feeding (figure 2*a*) the optimum gut has two large CSTRs ($v_1 \doteq v_2 \doteq 0.45$) and a very small intervening PFR ($v_2 \doteq 0.1$); and at a high rate of feeding (figure 2*d*) it consists entirely of two CSTRs. (Two CSTRs are not equivalent to one large one because their contents do not intermix.)

Figure 2*b*, *e* shows results for food with a moderate proportion of cell contents, at the same two feeding rates. The optimum gut now has no first CSTR: at the lower feeding rate it has a small PFR and a large second CSTR (figure 2*b*) but at the high rate it has a larger PFR (figure 2*e*). Notice the local maximum in figure 2*b*, close to the position of the global maximum in figure 2*a*. The loss of the first CSTR from the optimum gut as food quality increases occurs abruptly at a bifurcation, when $c_0/(c_0+w_0) = 0.45$ (at $D = 0.05$) or 0.47 (at $D = 0.5$).

Finally, figure 2*c*, *f* shows results for a diet with a very high proportion of cell contents, higher even than mangolds or grain (Blaxter 1962). At a low feeding rate, the optimum gut still consists of a small PFR and a large second CSTR (figure 2*c*); but at a high rate it consists of a PFR and nothing else (figure 2*f*).

There must be a maximum dilution rate for any CSTR, above which it cannot function as a fermentation chamber because microbial reproduction cannot keep pace with the dilution, and the microbial population is lost. The optimal gut for operation above this rate will consist of a PFR alone, for any food.

The results shown in figure 2 were all calculated for $r_{ferm,w}/r_{dig} = 0.3$. In other calculations, this ratio was given values of 0.2 and 0.5. The positions of the maxima were altered very little, with one exception: when figure 2*b* was recalculated for $r_{ferm,w}/r_{dig} = 0.5$, only one maximum was found, at the position of the local maximum in the figure. Increasing the ratio increases the relative feeding rate (D/r_{dig}) at which the bifurcation occurs.

In yet other calculations, the fractional yield of fermentation products Y_{ferm} was changed from the value used for figure 2 (0.75) to 0.50, with or without a further change of the microbial yield Y_{mier} from 0.10 to 0.25. These changes moved the optima only slightly, from the positions shown in figure 2.

Ruminant guts consist of a very large first CSTR (the reticulorumen), a small PFR (the abomasum and small intestine) and a second, smaller CSTR (the caecum and

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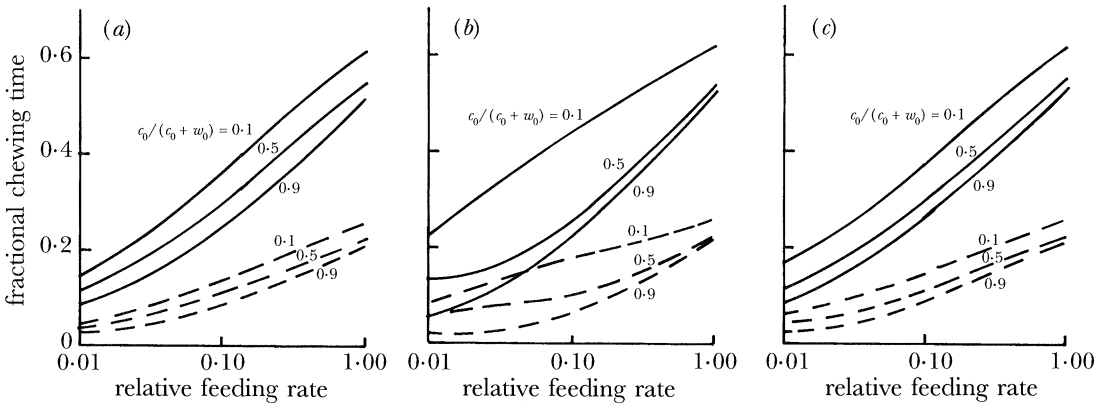

Figure 3. Graphs of optimal fractional chewing time against relative feeding rate D_{max}/r_{dig} for (*a*) a ruminant with $v_1 = 0.80$, $v_2 = 0.05$ and $v_3 = 0.15$; (*b*) a non-ruminant with $v_1 = 0$, $v_2 = 0.70$ and $v_3 = 0.30$; and (*c*) a non-ruminant with $v_1 = 0$, $v_2 = 0.30$ and $v_3 = 0.70$. The constant q is 1 (continuous lines) or 10 (broken lines).

colon): typical proportions, estimated from masses of gut contents, are $v_1 = 0.8$, $v_2 = 0.06$, $v_3 = 0.14$ (Maloiy *et al.* 1982). The model indicates that these proportions would give near-optimal energy gains from poor food (figure 2*a*, *b*). It suggests that a gut with a smaller rumen and a larger caecum and colon would be even better, but this suggestion may be misleading because the model takes no account of the reduction of volume that presumably occurs as the food travels along the gut, or the movement of food back and forth between rumen and mouth during rumination. Some ruminants eat poor food such as mature grasses but others select richer food (Jarman 1974).

Figure 2*b*, *e* show that a gut with no rumen but with a large posterior fermentation chamber (as in horses) may be optimal for diets containing moderate proportions of cell contents. This accords with Penry & Jumars' (1986) statement that horses outcompete ruminants when food is abundant and good. However, the model gives no support for Janis' (1976) contention that hindgut fermentation is better than a rumen for very poor as well as for rich diets.

Milton (1981) compared the monkeys *Alouatta*, which eats leaves, passing them through its gut relatively slowly; and *Ateles* which eats fruit, passing it through fast. The leaves presumably contain a moderate proportion of cell contents and the fruit a high one. Appropriately, as it seems from figure 2, the colon (the posterior fermentation chamber) is much smaller in *Ateles* than in *Alouatta*.

The model presented above takes no account of the habit of lagomorphs and some rodents, of eating faeces and so passing material through the gut for a second time.

5. OPTIMUM CHEWING TIME

In this section we ask, how long should a herbivore chew its food? Chewing breaks food up into small particles, damages cells and presumably speeds fermentation and digestion. There is some evidence from *in vitro* experiments that finely-ground food is fermented faster than larger pieces of the same food (Mertens & Ely 1982). However, the more an animal chews the less food, presumably, it has time to eat.

We do not know the functional relation between chewing time and rates of fermentation or digestion, but will assume that the rates r_{ferm} and r_{dig} are very low for unchewed food and are increased by chewing, approaching asymptotic values after long chewing times. Let τ be the fraction of the time available for eating or chewing, that is spent chewing, and let R (with appropriate subscripts) be the asymptotic value of a rate of fermentation or digestion. We assume

$$r(\tau) = R(1-\exp(-q\tau/(1-\tau))), \qquad (13)$$

where q is a constant: a high value of q would indicate that the asymptotic rate was approached rapidly. The effect of chewing time on energy gain was investigated by using $r(\tau)$ (with appropriate subscripts) instead of r in equations (1), (2), (5), (9) and (10). However r_{dig} in equation (7) and $r_{ferm,c}$ in equation (11) were left independent of chewing time, because they refer to the breakdown of microbes. We will assume $R_{ferm,c} = R_{dig} = r_{dig}$ and $R_{ferm,w} = 0.3\ r_{dig}$.

Account was taken of the reduced time available for eating by replacing D in equations (1) to (12) by

$$D(\tau) = (1-\tau)D_{max} \qquad (14)$$

A computer program found the fractional chewing time that maximized the rate of energy gain $p_3VD(\tau)$ for given gut structures and diets. Figure 3 shows that optimal chewing times are generally longer for foods that break down slowly when chewed ($q = 1$) than for foods that break down faster ($q = 10$). They are longer for foods that can be eaten rapidly (large values of D_{max}) than for those that can only be eaten slowly. They are also longer for foods that contain large proportions of fermentable cell wall materials. We should not be surprised that cattle chew for about 8 hours per day (Welch & Hooper 1988). The model implies that chewing occurs before swallowing, so tells us nothing about the special advantage of rumination.

Long chewing times imply rapid tooth wear, especially if the food contains abrasive particles, such as the silica particles in grass, or is contaminated by soil particles. Grazing mammals including cattle, horses and lagomorphs have hypsodont (high crowned) teeth.

Herbivorous birds grind food between stones in a muscular gizzard (see Herd & Dawson 1984) but the

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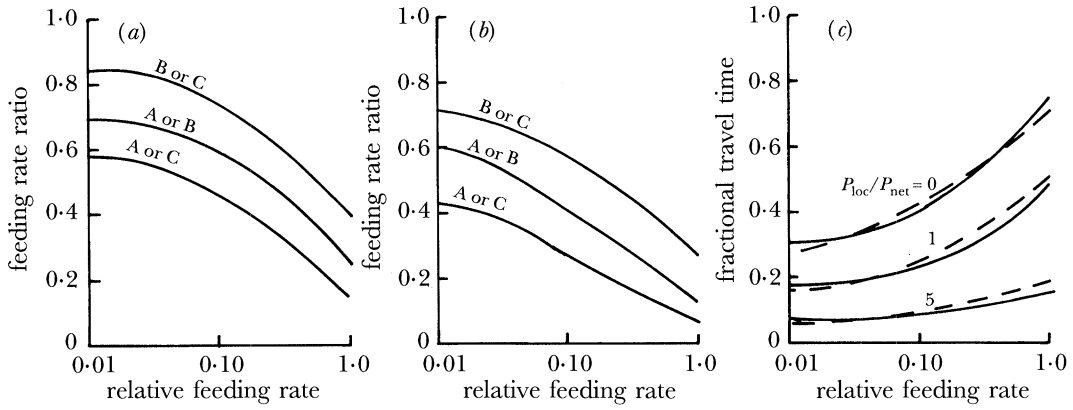

Figure 4. Graphs showing when a rich food that can be eaten only slowly gives the same rate of energy gain as a poor food that can be eaten fast, for the same two herbivores as in figure 3*a*, *b*. (*a*) Breakeven feeding-rate ratios D_{rich}/D_{poor} for the ruminant, for three pairs of foods, when energy costs of travel are negligible; (*b*) shows the same for the non-ruminant and (*c*) shows breakeven fractional travel time τ' for the ruminant choosing between foods A and B (continuous lines) and the non-ruminant choosing between B and C (broken lines). The energy densities of cell contents and fermentable cell wall materials in the foods are A, $c_0/E = 0.05$, $w_0/E = 0.50$; B, $c_0/E = 0.30$, $w_0/E = 0.50$; C, $c_0/E = 0.75$, $w_0/E = 0.20$.

arguments of this section do not apply to them because the storage capacity of the crop enables them to eat while grinding.

The quality of food (represented by $c_0/(c_0+w_0)$) has much more effect on optimal chewing time for a herbivore with a small fermentation chamber (figure 3*b*) than for those with larger ones (figure 3*a*, *c*).

6. OPTIMIZATION OF DIET

Animals will generally gain energy faster by eating a richer diet (one containing a higher proportion of cell contents) if the alternative foods can be eaten at the same rate. This section examines choices between poor foods that can be eaten fast and richer food that can only be eaten more slowly, for example between eating grass indiscriminately in large mouthfuls or selecting the small but richer young shoots. Initially we will ignore the energy costs of any locomotion that may be involved in seeking out the richer food.

We will consider pairs of foods. In each case, rates of energy gain have been calculated for the poorer food, by using equations (1) to (12), for specified feeding rates D_{poor}. The feeding rate D_{rich} for the richer food, that gave the same rate of energy gain, was then found. Figure 4 shows breakeven feeding rate ratios D_{rich}/D_{poor} for pairs chosen from three foods. Food (A) is intended to represent mature leaves (either grass or dicotyledons); (B) young leaves; and (C) very rich food such as fleshy fruit or grain (Blaxter 1962).

Figure 4*a*, *b* shows that when feeding rates are low, the better quality of a rich food will compensate for only a small reduction in feeding rate. At higher feeding rates, cell wall materials are less completely fermented and breakeven feeding rate ratios are lower. This helps to explain two observations. First, grazing antelopes are less selective when feeding on low biomass pastures (Murray 1991). Secondly, very large bovids (which have relatively low mass-specific metabolic rates, and correspondingly low values of D) tend to be less selective than smaller ones (Jarman 1974). An additional reason for large herbivores being less selective is that they can take larger bites, so their feeding rates may be reduced more, when they eat food that is available only in small mouthfuls.

At any particular value of D_{poor}, breakeven feeding-rate ratios are lower for the non-ruminant of figure 4*b* than for the ruminant of figure 4*a*; this particular non-ruminant ferments cell wall materials less completely than the ruminant, so gains more advantage from better food. The differences would be reduced if the non-ruminant were given a larger posterior CSTR. They show however that in some circumstances one herbivore should prefer the poorer but more plentiful of two foods, whereas another, even of the same size, should prefer the richer.

Thorns reduce the rate at which herbivores can eat a plant's leaves (Cooper & Owen-Smith 1986), so reduce the probability of their being preferred over other food.

The relative merits of diets may depend on the energy costs of feeding on them; for example, herbivores may have to travel further between bites of a richer but less common food. We will assume (unlike Murray 1991) that the rate of intake of food is reduced in proportion to the fraction τ' of the available time that is spent travelling

$$D = (1-\tau')D_{max}. \qquad (15)$$

This implies that the foods being compared could be eaten at the same rate D_{max}, if there were no need to travel. This is realistic for some pairs of foods but not (as discussed above) for others.

We will assume that metabolic power P_{loc} is required for locomotion, so that the net rate of energy gain by feeding (with its associated locomotion) is given by

$$\begin{aligned} P_{net} &= p_3 DV - P_{loc}\tau' \\ &= (1-\tau')p_3 D_{max} V - P_{loc}\tau'. \end{aligned} \qquad (16)$$

We will again consider a pair of foods: a poorer, continuously distributed food that can be eaten with

negligible travel costs and a richer dispersed food. A computer program has been used to find the fractional travel time for the richer food that makes P_{net} the same as for the poorer one.

Figure 4*c* shows results for the ruminant of figure 4*a*, choosing between foods A and B and for the non-ruminant of figure 4*b* choosing between foods B and C. The results for these two cases are almost identical. P_{loc} is expressed as a multiple of P_{net}; that is, approximately, as a multiple of metabolic rate. The graphs show that when $P_{loc}/P_{net} = 1$ or 5, the proportion of time, that the animal can spend travelling and still benefit from the richer food, is greatly reduced. $P_{loc}/P_{net} = 1$ represents approximately the energy cost of walking at speeds around 1 ms^{-1} (Taylor *et al.* 1982). P_{loc}/P_{net} might perhaps reach 5 if the animal ran between patches of food or if it had to climb trees to reach them.

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Discussion

L. De Bruyn (*Laboratory of General Zoology, University of Antwerp, Belgium*). Some groups of insects (e.g. the Diptera family Chloropidae) infest their host plant with phytopathogenic symbionts. The larvae damage the host-plant's tissues and inoculate them with the bacteria. This leads to the development of local bacteriosis in the injured tissues, with maceration and lysis effects, and a number of reactive changes in the plant's structures. The insects' larvae develop in a pool of disintegrating plant tissues saturated with nutritive bacteria. In the process of feeding, the larvae ingest the bacteria along with the plant-tissue juice and use them for food. In this way the larvae have developed a sort of external CSTR.

When extrapolating the model for plant food processing by higher vertebrates to invertebrates, this phenomenon has to be taken into consideration to resolve observed deviations from the expected digestive system.

R. McN. Alexander. I have nothing to add to this interesting point.

R. N. Hughes (*School of Biological Sciences, University College of North Wales, Bangor, U.K.*). By scaling for size, does Professor Alexander's model ignore constraints imposed by size itself? For example, a unit of cell wall material may take a certain time to be broken down by fermentation. The smaller the body, the shorter will be the residence time within an CSTR. Insects may be too small for an CSTR to be worthwhile. On the other hand, *Diplodocus*, with its huge CSTR could probably prolong fermentation long enough to make a nutritious broth even out of cycads!

R. McN. Alexander. The model finds the optimum gut structure for a particular diet, but even the optimum gut may not break food down fast enough to support the high mass-specific metabolic rate of a very small herbivore. The model shows that guts consisting largely of CSTRs are optimal for poor diets containing a lot of cell wall and very little cell contents. Such a diet may be incapable of supporting a small herbivore with a gut consisting mainly of CSTRs, but with any other gut structure the herbivore would do even worse. Small herbivores may need fairly rich diets.

P. W. Skelton (*Department of Earth Sciences, The Open University, Milton Keynes, U.K.*). Why does Professor Alexander have two CSTRs in his initial herbivorous gut model? Is this a theoretically predicted ideal arrangement?

R. McN. Alexander. My model, consisting of two CSTRs and an intervening PFR (any of which may be omitted), is the simplest capable of imitating reasonably well the whole

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observed range of herbivore guts. Ruminants, for example, have a rumen (CSTR), a small intestine (PFR) and a hind gut (CSTR). A CSTR can always be improved by replacing it with two CSTRS in series (with the same total volume), so that substrate concentrations do not fall immediately to their final values. Some herbivore fermentation chambers (for example, the stomachs of kangaroos) are relatively long, so there may be little mixing between the contents of their proximal and distal ends, and they may perhaps function as several CSTRS in series, but this has not been shown.

I did not consider the possibility of two PFRS with an intervening CSTR, because I do not know of any animal with such a gut.

C. G. JONES (*Institute of Ecosystem Studies, Millbrook, New York, U.S.A.*). Under what circumstances and with what consequences would coprophagy (e.g. rabbits) or internal recycling (e.g. koalas) be advantageous, based on Professor Alexander's model?

R. MCN. ALEXANDER. The model is concerned only with energy, so cannot take account of the possible value of re-ingested faeces or caecotrophs as sources of nitrogen and vitamins. Faeces will presumably have lower metabolizable energy contents than the food from which they are derived, so animals are unlikely to be able to gain energy by eating faeces in preference to other food. However, if part of the day is spent resting or hiding where fresh food is not available, any energy obtained by re-ingesting faeces then is pure gain. Caecotrophs could have higher metabolizable energy content than the food from which they are derived, if they are formed selectively from the more digestible constituents of the food.

C. G. JONES. Given that detoxification of plant secondary metabolites can be done by the herbivore and its symbiotic microorganisms, would it be possible to develop similar models for detoxification? Could such models be coupled with Professor Alexander's model?

R. MCN. ALEXANDER. My model can take account of plant secondary metabolites, only in so far as they affect rates of digestion or fermentation of the food.

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