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Use of Fibrous Diets by Small Herbivores: How Far can the Rules be 'Bent'?

William J. Foley and Steven J. Cork

Allometric considerations suggest that small mammals should be unable to eat highly fibrous diets. A combination of the selective and more rapid passage of fibrous material through the gut, together with changes in gut capacity when energy requirements increase, may allow small mammals to escape these allometric constraints. Recent evidence that birds can absorb essential amino acids from the caecum (which has hitherto been considered insignificant in mammals) suggests that birds and mammals have evolved very different ways to be a herbivore.

Nutritional ecology explores the relationships between the foods that animals eat, how those foods are obtained, and how they are processed. In recent years nutritional ecology has focused on several major themes. One of the most important has been the constraints imposed by body size on the use of fibrous diets by herbivores^{1–3}. Endothermic herbivores are believed to be constrained to particular diets by virtue of their body size: in particular, only relatively large animals should be able to subsist on a high-fibre diet. Nearly all analyses of body-size patterns in vertebrate herbivore communities depend on this assumption.

A second major theme involves the significance of different adaptations for fermentative digestion in herbivores^{2,4,5}. Herbivorous mammals can be divided into two broad groups on the basis of whether the major site of fermentative digestion is anterior to the site of true gastric digestion (forestomach fermenters) or posterior to it (hindgut

fermenters). Various advantages and disadvantages have been attributed to both groups in relation to different habitats and food resources, but one of the major postulated differences is in relation to nitrogen metabolism. Forestomach fermenters benefit from digesting, in the gastric stomach, the high-quality protein of microorganisms flowing from the forestomach, whereas this rich source of nutrient was thought to be lost to most hindgut fermenters¹.

Several recent studies have critically examined these 'two foundation stones' of nutritional ecology and they are beginning to look a little shaky.

To what extent are small herbivores constrained by limited gut capacity?

Most small endotherms feed on high-quality diets: either the tissues of other animals or else plant sources of readily available energy, such as nectar and starch- or lipid-rich seeds. Relatively few eat appreciable amounts of fibrous plant material, such as grasses or tree leaves. This pattern is believed to occur because as a mammal's body size decreases, its energy requirements per unit body mass increase, but without a comparable increase in gut capacity. In mammals, metabolic energy requirements (measured either as basal metabolic rate or field metabolic rate) scale to a power of body mass between 0.6 and 0.8 (Ref. 6), but gut capacity is directly proportional to body mass^{1–3}.

Consequently, small mammals need to acquire more energy each day, relative to their body mass, than do large mammals but they have no better relative capacity to do so because gut capacity ultimately limits both the quantity of food retained for digestion at any time and the throughput over time⁷. Small animals should therefore be restricted to diets containing very little indigestible or slowly digestible material (dietary fibre) so that they maximize energy and nutrient yields per unit of food and minimize the total amount of indigestible material they have to process daily.

There are a few species of small animals, mostly mammals, that appear to violate these 'allometric rules' by eating fibrous diets. How do they do it? Recent research has begun to provide some answers.

Some small mammals selectively retain solutes and fine particles of digesta in the hindgut while coarse material is excreted more rapidly (the mammalian hindgut usually allows solutes to pass more quickly than solids). Mechanisms that allow selective retention of this kind are consistently associated with consumption of high-fibre diets^{7–9}. The separation of the digesta in these species occurs in the proximal colon, and fine particles of food, solutes and microorganisms are retained in the caecum. Large particles include most of the indigestible fraction, so these processes allow small mammals to minimize the gut-residence time of indigestible material and to maximize the amount and

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concentration of digestible nutrients in the gut at any one time. The total daily intake of nutrients probably is maximized also. In effect, such mechanisms alleviate the allometric constraints by creating a more favourable ratio of metabolic rate to gut capacity.

Gut capacity itself may change when some mammals (for example microtine rodents) are faced with either high-fibre diets or increased energy requirements (for example during exposure to cold conditions).

Gross, Wang and Wunder¹⁰ found that the size of the caecum (measured as length or as wet or dry tissue mass) of prairie voles (*Microtus ochragaster*) increased when food quality decreased. Moreover, the size of both the caecum and small intestine increased during acclimation to cold conditions. Several recent studies have confirmed Gross *et al.*'s original observations¹¹⁻¹³. Herbivorous birds such as red grouse (*Lagopus lagopus scoticus*) appear to behave in the same way: the capacity of the caecum increases when the fibre content of the diet increases^{14,15}.

Hammond and Wunder¹³ went further to investigate whether changes in gut size affected the digestibility of the diet. Animals that were acclimated to cold conditions ate more than those maintained at 23°C but although the passage rate increased, the digestibility of the diet did not change. In Hammond and Wunder's view¹³, changes in gut size had partially offset the expected decrease in digestibility. There may also have been unidentified increases in absorptive capacity. As a result of these changes, the animals could increase their food intake without sacrificing efficiency of extraction of digestible energy. Recently, Toloza, Lam and Diamond¹⁶ and Dykstra and Karasov¹⁷ showed that two other species (omnivorous mice and insectivorous wrens (*Troglodytes aedon*) that were exposed to low temperatures behaved in a similar way. Food intake increased, the length or mass of the small intestine increased and the digestibility of the diet was unchanged.

These observations raise at least two important physiological questions with evolutionary implications. Firstly, how is the increase

in gut volume and/or absorptive capacity achieved; and, secondly, to what extent can changes in gut volume and/or nutrient transporters ease the allometric constraints on utilization of fibrous diets by small animals?

Buffenstein and Yahav¹⁸ have proposed several mechanisms that could increase caecal size. They include a stimulating effect of some short-chain fatty acids (one of the products of microbial digestion) on epithelial cell growth, the bulk effect of increased intake of indigestible material and changes in the populations of microfauna. Clearly, more than a simple stretching of the gut is involved since the dry mass of caecal tissue increases along with the contents¹⁰. However, it is unclear whether changes during cold adaptation reflect simply concomitant increases in food intake or whether other factors are involved. Two recent studies^{16,17} indicate that increases in the size of the small intestine are accompanied by increased numbers of nutrient transporters (particularly those of glucose and proline) thus increasing the rate of absorption of specific nutrients. Since we would not expect the mammalian caecum to play a significant role in absorption of sugars or amino acids (but see below), the mechanisms and consequences of changes in caecal size should receive further study.

If the ability to change the size of the gut in response to increased energy need is widespread amongst small herbivores, then we might expect that the ability to digest fibrous diets will not be as dependent on body size as expected previously³. There are few data to evaluate this hypothesis, partly because of the difficulty of feeding a range of animals on the same diet¹⁹. However, two recent studies^{3,20} have measured the digestibility of alfalfa fibre in a range of small, North American herbivorous mammals.

All the animals in these studies^{3,20} digest plant fibre principally in the hindgut. The extent of fibre digestion depends in part on the amount of time that it can be retained in the hindgut, which in turn depends on both input to and volume of the chamber in which retention occurs³. Consequently, increases in the size of the hindgut would tend to in-

crease fibre digestion³. Karasov and Meyer's study²⁰ showed that the extent of digestion of the cell-wall component of alfalfa pellets was similar in a range of small mammalian herbivores ranging in body mass from 30 to 1300 g. Similarly, Justice and Smith³ found that small (78 g) woodrats (*Neotoma* sp.) could digest fibre equally as well as large (250 g) woodrats. These results suggest that smaller animals were able to compensate for their relatively unfavourable ratio of metabolic rate to gut capacity. It is possible that changes in gut capacity amongst smaller species contributed to these results.

However, these trends should be viewed with caution for at least five reasons. Firstly, gut volume is a very rough relative measure of the capacity of an animal to extract digestible energy from food and an even rougher predictor of the daily rate of energy extraction. A measure of potential extraction rate rather than capacity is needed for comparison with metabolic rate. Reasonable attempts have been made to convert gut capacity to extraction rate in ruminants² but to do this meaningfully for small mammals might require closer consideration of such variables as effective gut volume and absorption rates.

Secondly, although increases in gut capacity might be sufficient to offset changes in the ratio of metabolic rate to extraction rate of the magnitude occurring in cold-stressed or reproductive mammals, it is unlikely that gut plasticity could make up for the difference in ratio between mammals of very different body size, because that ratio is predicted to increase exponentially with decreasing body mass. For example, a 15 g vole would need a 12-fold increase in gut contents to have a ratio of gut capacity to metabolic rate equivalent to that in a 50 kg ruminant (based on published relationships of Demment and Van Soest² and Nagy⁶). The maximum increases reported by Gross, Wang and Wunder¹⁰ are of the order of fivefold. Hence, mechanisms in addition to increased gut capacity should be looked for to explain results such as those of Karasov and Meyer²⁰.

Thirdly, although alfalfa contains

a high concentration of dietary fibre compared with fruits and animal matter, it is a relatively high-quality diet compared with the grasses that are the main diet of many large herbivores. If comparisons could be made amongst different-sized herbivores fed a poor-quality grass diet, it is likely that large differences in ability to utilize fibre would be apparent because the degree to which small species can compensate by expansion of the gut may decline as diet quality declines.

Fourthly, mammals of different sizes may be able to select different fractions even from well-pelleted diets³.

Finally, there is a need for caution when assessing the digestive capabilities of small animals, because of often-overlooked limitations of methods used to measure dietary fibre in faeces. Determining the digestibility of fibre requires measuring the fibre content of both diet and faeces. Nearly all nutritional ecologists measure fibre by grinding the sample and then extracting it in buffered detergents²¹. The extracted samples are then filtered through sintered glass disks and the fibre determined gravimetrically. However, some studies have shown that the finer the sample is ground, the lower the recovery of fibre²². This could result either from greater surface area exposure to the extracting solutions, or from fine particles escaping through the sintered glass filters. Both feeds and faeces are usually ground to pass sieves of similar size (normally 1 mm) but where very small mammals are concerned, the particle size of the faeces is already much finer than 1 mm. For example, in several small mammals that selectively retain digesta in the hindgut, more than half the faeces consists of particles smaller than 0.075 mm (Refs 23, 24). Differences in the preparation of faecal samples between studies on large and small species could therefore lead to artificially similar estimates of fibre digestibility. This potential problem could be avoided either by analysing particles that reflect the range of particle sizes in the faeces, or alternatively, by avoiding sintered glass disks and recovering all particles by centrifugation.

Clearly, digestive responses of small herbivores to plant cell-walls are more plastic than nutritional ecologists have previously thought. Understanding how and to what extent plasticity of gut function compensates for allometric constraints on utilization of fibrous plant matter is one important key to understanding the comparative nutritional ecology of small mammals. It is equally clear that care must be taken in the design and interpretation of experiments to investigate these processes.

How can small hindgut fermenters utilize microbial protein?

A second area where recent work has overturned established ideas concerns the site of absorption of amino acids from the gut. Herbivores have two major sources of protein available to them. The first is dietary proteins. These can be digested directly by species in which gastric digestion is not preceded by microbial digestion and can serve as the source of essential amino acids. The second protein source, rich in essential amino acids, is that in microbial cells that have grown as a result of the fermentation processes within the gut.

It has long been believed that microbial protein is only available to forestomach fermenters or those hindgut fermenters that practice caecotrophy (the ingestion of special nutrient-rich faecal pellets formed from caecal contents after concentration of microorganisms in the caecum by selective retention of solutes and fine particles). Species without either of these adaptations would need to absorb essential amino acids of microbial origin intact across the wall of the hindgut. This process is traditionally considered to be either nonexistent or insignificant in comparison with absorption of nitrogen as ammonia after breakdown of amino acids in the gut lumen. However, two recent reports^{25,26} suggest that amino acids made available through lysis of microbial protein are actively transported across the wall of the caecum of a range of birds.

Obst and Diamond²⁵ measured the transport of sugars and amino acids from the gut of five species of birds, including both granivorous

and more strictly herbivorous forms. Small sections of the caecum were incubated with labelled sugars and amino acids (proline, leucine, lysine and aspartic acid). Proline was taken up in all species and, importantly, Obst and Diamond²⁵ showed that in three species studied more intensively – the chicken, goose (*Branta canadensis*) and rock dove (*Columba livia*) – 20–30% of the uptake of proline was sodium dependent and thus almost certainly carrier mediated.

These were surprising results for several reasons. Previous studies had only demonstrated this transport ability in new-born chickens; studies in which the caecum of adult birds (e.g. willow ptarmigan, *Lagopus lagopus lagopus*) was perfused with amino acids showed no evidence of the uptake of amino acids, even by diffusion²⁷. Secondly, the tissue-specific uptake rates of amino acids were greater in the caecum of all species studied than in the small intestine, but the contribution of the caecum to the integrated uptake capacity of the gut depended on the size of the caecum. For example, the caeca contributed between 2% (rock dove) and 25% (sage grouse, *Centrocercus urophasianus*) of the total gut uptake of proline.

In another study, Moreto and Planas²⁶ showed that, in adult chickens, only the proximal parts of the caecum absorbed amino acids. However they suggested that the overall importance of the process might be limited because the absorptive region is not continuously in contact with digesta.

The range of species studied by Obst and Diamond²⁵ suggests that the active transport of amino acids from the caecum of birds is widespread. It would be interesting to see whether the use of similar techniques in a range of mammalian species gives similar results. If so, then it would be profitable to try to document the importance of caecal amino acid transport in species eating poor-quality diets. In particular, it would be important to look at mammals, such as koalas (*Phascolarctos cinereus*) and greater gliders (*Petauroides volans*), that selectively retain bacteria in the hindgut for long periods but that do not practise

caecotrophy^{23,24}. If such species do obtain significant amounts of essential amino acids from the hindgut, it would explain why they have evolved the important physiological mechanisms needed for production of caecotrophs but not the final steps of excretion and ingestion of caecotrophs. If they do not, then the full significance of digesta separation and retention in non-caecotrophic mammals remains an important and intriguing area for future research.

If no active amino acid transport could be demonstrated in the caecum of a range of mammals of differing diet and caecal morphology, this would have major implications for our understanding of the evolution of herbivorous vertebrates. Our current understanding is that the major differences between herbivorous birds and mammals are probably in initial mechanical processing of the food. Additional major differences at the transport level would suggest that the two groups differ much more than previously expected in the strategies that they have evolved to utilize poor-quality diets.

Obst and Diamond²⁵ recommended future studies of caecal transport functions in a variety of ecological and phylogenetic groups. They also recommended investigation of how the caeca of different species of birds could express all

potential functions such as water and electrolyte transport, degradation of fibre and amino acid transport. We strongly support these recommendations and urge that attention also be given to other vertebrates such as herbivorous lizards.

Conclusion

In this article we have provided examples, in two areas of nutritional ecology, of how small animals bend what we thought were reasonably rigid 'rules'. The major challenge for nutritional ecologists in the future is to investigate just how far these rules can be bent because this will help us to understand how physiological constraints might have directed the evolution of digestive and metabolic adaptations in herbivores.

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