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SPRINGER VERLAG
NUTRIENT REQUIREMENTS AND THE DESIGN
AND FUNCTION OF GUTS IN FISH,
REPTILES, AND MAMMALS

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Abstract. What changes in gut design and nutrient absorption are associated with differences in daily nutrient intake between fish, reptiles, and mammals? To answer this question I compared glucose and proline uptake rates in 23 species from the three classes using uniform methodology. The uptake rate for the entire gut for these nutrients in mammals was 13 times higher than in fish and four times higher than in reptiles. The main basis for faster absorption in the mammals and reptiles was that the intestine operates at a higher temperature (both mammals and reptiles) and that the area of the intestine is greater (mammals only).

Introduction. This paper is concerned with the design and function of the intestine in its absorptive role in relation to the nutrient requirements of vertebrates. A major difference between fish and terrestrial vertebrates is that the latter tend to have higher daily energy requirements, due possibly to low transport costs in fish, higher body temperatures in ectothermic reptiles and to endothermy in the case of mammals and birds. Predictive relationships for daily energy requirements in kJ/d as a function of body mass in grams, for example, are 0.14 g/m^0.81 in fish at a temperature of 15 °C (Ric 1981), 0.22 g/m^0.80 in free-living iguanid lizards and 7.4 g/m^0.67 in rodents (New 1982). Higher metabolic rates must be fueled by more food. The higher food intake rates of mammals, as compared with reptiles, are possible because transit times of individual meals are about ten times faster in the mammals (Karasov et al. 1986a). Are the higher food intake rates and faster transit times met by a higher absorptive capability of the intestine? We will see that the answer to this question in most cases is yes, and we will attempt to assess quantitatively the basis for this within and between taxa.

A priori we can list several ways in which the intestine could achieve a higher absorptive capability and thereby make possible increased feeding rates: (1)
higher passive permeability to nutrients; (2) higher affinity carriers; (3) more active transport sites; (4) greater intestinal surface area at the macroscopic and microscopic level; (5) the advantage of operating the intestine at high temperatures all day (as in most mammals and birds) or part of the day (as in reptiles, amphibiens, and some fish) rather than at low temperatures (as in most fish). Passive permeability to nutrients appears to be similar in ectothermic reptiles and endothermic mammals (Karasov et al. 1983a), but there are too few data for fish for comparison and so we will omit detailed consideration of the first possibility. Because it is also difficult for technical reasons to establish unambiguously differences between species in carrier affinity (Karasov et al. 1983b), we will focus on the latter three factors affecting absorptive capability. A sixth factor which affects the extent of absorption is the retention time of digesta in the gut and we shall consider this near the end of the paper.

For simplicity, let us view the apportioning of intestinal nutrient uptake capacity between physiological, environmental, and anatomic causes as follows (Karasov et al. 1983a):

$$J_{a,T} = (J_0/T)(X)$$

where \( J_{a,T} \) is the summed uptake rate over the entire length of the small intestine at a given temperature \( T \), \( J_0/T \) is the uptake rate per unit intestine (e.g. cm length or cm\(^2\) nominal area) at the temperature, and \( X \) is an anatomic measure of the small intestine. \( J_{a,T} \) can be conveniently measured using the everted sleeve method (Karasov and Diamond 1983) by measuring solute uptake per cm at saturating concentrations at several positions along the small intestine and then interpolating uptake rates linearly between successive positions and summing over the length of the small intestine (Karasov et al. 1983). Because we are attempting to account for most of the transport activity in the gut, and because fish and terrestrial vertebrates differ in their gastrointestinal tract morphology, it is necessary to consider first where transport occurs in the gut.

**Three transport occurs.** Intestines of fish are generally a single unreeioned tube and have transport activity all along the length (Huddington and Diamond 1987a,b). In many terrestrial vertebrates there is a distinct hind gut which is separated from the small intestine by a valve and which functions in the conservation of electrolytes and water. The existence of carrier-mediated uptake of sugars and amino acids in this region is disputed. Should the large
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Intestine be included in the quantitation of $J_{a,T}$ in terrestrial vertebrates? Uptake rates in the large intestine have been found to be less than 10% of those in the small intestine (Hundal and Haftin 1981, Karasov et al. 1985a). In desert iguanas, chuckwallas, and desert woodrats the large intestine constitutes a third to a half of the total surface area of the gut but its contribution to $J_{a,T}$ is less than 7% for both glucose and proline (Karasov et al. 1985a). Thus, the large intestine can be excluded from quantitation of $J_{a,T}$ because its contribution appears to be negligible.

A modification of the digestive tract which is unique to fish is the presence of blind diverticula located in the proximal gut adjacent to the pyloric sphincter. These pyloric caeca are present among certain families of fish, sometimes within only certain species within a family (Buddington and Diamond 1987a). Although the caeca of some fish species constitute a significant portion of the post-gastric surface area, their function in digestion and absorption has been uncertain. Buddington and Diamond (1987a) quantitated the caecal contribution relative to that of the rest of the intestine in four fish species in which the caeca contributed 16-70% of the total post-gastric area of the gut. They found that for glucose and proline the caeca contribute about the same percentage to uptake as to total gut area. Hence, the caeca are an adaptation for increasing gut area and in some fish species may be the most important region of nutrient absorption.

Having identified the regions of the digestive tract where most transport activity occurs in fish, reptiles, and mammals, we shall now analyze the patterns of variation in intestinal nutrient uptake as they relate to metabolic requirements.

Relationships between intestinal summed uptake, body size, and taxa. If higher metabolic rates and hence feeding rates are met by a higher absorptive capability of the intestine, then we should find that endothermic mammals have higher summed uptake rates than ectothermic reptiles and fish, and that within each group summed uptake rate increases with increasing body mass. Summed uptake rates for the entire gut (including pyloric caeca when present) in 11 fish species are plotted in Fig. 1 along with summed uptake rates for the small intestine in nine mammal species and three reptile species. The measurements on fish were performed at 20 °C, all others at 37 °C, though I will take into consideration below the effect of temperature. The clearest illustration of how summed uptake varies among these groups can be made by adding together for each species the summed uptake rates for glucose and
Figure 1. Relationships between the sum of glucose and proline summed uptake rates and body mass in fish, reptiles, and mammals. For each species summed uptake for both solutes is at either 25 or 50 mM. The relationships do not differ significantly in slope. When fitted to a common slope (0.57) the calculated proportionality coefficients are: fish, 0.17; reptiles, 0.58; mammals, 2.15. Species designations and sources are as follows: mammals (Karasov et al. 1985a,b unless otherwise indicated) - 1, mouse; 2, kangaroo rat; 3, Antilocapra fruit bat; 4, hamster; 5, desert woodrat; 6, Belding’s ground squirrel; 7, green monkey; 8, lab rat (Karasov and DeBoo 1986); 9, vole (Karasov and Mayer, unpublished data); fish (Buddington and Diamond 1987a,b unless otherwise indicated) - 10, opaleye (Karasov et al. 1985b); 11, common carp; 12, channel catfish; 13, white sturgeon; 14, striped bass; 15, cod; 16, rainbow trout; 17, largemouth bass; 18, striped bass; 19, grass carp; 20, tilapia; reptiles (Karasov et al. 1985a) - 21, desert iguana; 22, chuckwalla; 23, box turtle

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proline. We might consider this an index of the total absorptive capability of the intestine for sugars and amino acids. The physiological rationale for this is that glucose transport, and possibly amino acid transport too, varies with dietary composition (see the chapter by JM Diamond in this volume) and so analysis of the transport of only one of these nutrients might introduce a bias when comparing vertebrates with different dietary habits.

Within each taxon summed uptake rate is an increasing function of body mass. The relations are usefully described by allometric equations of the general form \( Y = aX^b \) and are linear when plotted on logarithmic coordinates. The small differences in slope are not statistically significant (analysis of covariance; Dunn and Clark 1974) and so data for each taxon are fitted to the common slope of 0.57. When the resultant proportionality coefficients (intercept at unity) are compared, mammals significantly exceed both reptiles and fish, by four times and thirteen times respectively (p<0.001). Reptiles significantly exceed fish by about three times (p<0.05). What is the basis for differences in summed uptake within and between taxa within the context of equation 17?

**Physiological, anatomical, and environmental components of intestinal nutrient uptake.** To determine whether differences in tissue specific uptake rates (U/X) exist, we can compare uptake rates per cm² nominal surface area (Table 1). Comparing uptake per cm length intestine would be complicated by the fact that luminal diameter, and hence amount of intestine per cm, increases with increasing body size. A complication in making any comparison at the tissue level is that in most species sugar and amino acid transport varies with position (cf. Karasov et al. 1985a, Buddington and Diamond 1987b). To make our comparisons here, we will use the uptake rates at the position where uptake is highest, usually the proximal or mid intestine.

Plots of uptake per cm² as a function of body size (not shown) indicated that there was no dependence of tissue specific transport activity on body size for either glucose or proline transport for any of the taxa over the following body mass ranges: mammals (30-5000 g), reptiles (71-386 g), fish (43-1871 g). Thus, within each taxon the dependence of summed uptake rate on body size (Fig. 1) is probably not due to changes in uptake rate at the tissue level.

Table 1 compares across the three classes of vertebrates glucose and proline uptake rates normalized to cm² nominal area. Uptake rates of reptiles do not differ significantly from those of mammals for either glucose or proline.
Uptake rates for proline by fish intestine, however, are significantly lower than for mammal or reptile intestine (p<.005 and p<.01, respectively, by the t-test). Within fish, glucose uptake rates were significantly higher in the herbivorous/omnivorous species than in the carnivores (p<.05), but still below those in herbivorous/omnivorous mammals and reptiles (p<.001 in both cases). Notice that the factorial difference between mammals and fish in uptake per cm² (ca. 3-5X) does not account for the thirteen-fold difference in summed uptake between mammals and fish. Uptake in fish was measured at 20 °C, and so Table 1 also compares glucose uptake in the three classes at more similar temperatures. This comparison suggests only a modest difference, if any, between these groups.

Table 1. Comparison of total L-proline uptake and carrier-mediated D-glucose uptake at the tissue level in vertebrates

<table>
<thead>
<tr>
<th>TAXA</th>
<th>FISH</th>
<th>REPTILES</th>
<th>MAMMAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Carnivore</td>
<td>Herbivore/Omnivore</td>
<td>Herbivore/Omnivore</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>PROLINE (µmoles/min/cm²)</td>
<td>21±4</td>
<td>50-186</td>
<td>15±266</td>
</tr>
<tr>
<td>Range</td>
<td>117±41</td>
<td>86±24</td>
<td>271±57</td>
</tr>
<tr>
<td>Mean±S.E.M.</td>
<td>6.50</td>
<td>20-99</td>
<td>129-689</td>
</tr>
<tr>
<td>GLUCOSE (µmoles/min/cm²)</td>
<td>16±4</td>
<td>62±16</td>
<td>357±45</td>
</tr>
<tr>
<td>Range</td>
<td>6.0±5</td>
<td>62±16</td>
<td>357±45</td>
</tr>
<tr>
<td>Mean±S.E.M.</td>
<td>16±4</td>
<td>62±16</td>
<td>357±45</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Q10 (between 20-37°C)</td>
<td>3.4,2.0</td>
<td>3.4</td>
<td>3.4</td>
</tr>
</tbody>
</table>

Uptake rates are at saturating concentrations (i.e. 25-50 mM). Incubation temperatures were 20°C for fish and 37°C for all others, unless otherwise indicated. Tissues were taken from the region where transport activity was greatest (i.e. the proximal or mid intestine). Sources for data were: Buddington and Diamond 1986a,b; Karamov et al. 1986a,b; Karamov and Dobson 1986).

If there are only modest differences in uptake per cm² (i.e. 3-5X) between these groups, and no differences in uptake per cm² among different-sized species with attributed explore quantitatively the normal sur.

Thus, at least the uptake rate temperature of more need exceed that of reptiles (e.g. don't bask). Fish (15-20 °C) show differences in day time and account for equally imp.
species within each group, presumably the differences in summed uptake can be attributed to differences in surface area (i.e. X in Eq. 1). In order to explore quantitatively this possibility, I summarized in Fig. 2 estimates of nominal surface area (i.e. that of the corresponding smooth tube) in species of varying sizes from the three vertebrate classes. For the mammals and reptiles I drew on several sources (listed in the figure legend) in which measurements were usually made on intestine opened and flattened out. For the fish I took the values reported by Buddington and Diamond (1987a,b), though in their studies they estimated gut diameter differently; as the diameter of a rod giving a good fit to a sleeve of intestine or caecum. (I have found that this latter method yields consistently higher values of nominal surface area than the former method [1.75 ± 0.11 times higher in two mammal and two reptile species; unpublished data]).

As was the case for summed uptake rate (Fig. 1), intestinal surface area increases with body mass within each class, differences between classes in the mass exponent (i.e. slope) are negligible, and so data for mammals and fish are fitted to the common slope (0.63 ± 0.04). When the resultant proportionality coefficients are compared, mammals significantly exceed fish by 2.3 times (p < 0.001). Considering the differences in measurement methodology mentioned above, the actual difference is probably closer to four times. The two reptile species have small intestinal surface areas similar to gut areas of similar-sized fish.

Thus, at least three differences in intestinal transport between endothermic mammals and ectothermic fish and reptiles contribute to higher summed uptake rates in mammals. The least important difference appears to be differences in uptake rate at the tissue level, when uptakes are measured at the same temperature. It appears that mammals may exceed fish, if at all, by a factor of no more than two times in uptake per cm² at 20 °C, and that they don't exceed reptiles at all. The next most important difference may be that fish intestine operates at a lower temperature than mammal intestine all day, and reptile intestine usually for part of the day (during inactivity when they don't bask). Considering the almost 20 °C difference in temperature between fish (15-20 °C) and mammals (ca. 37 °C) and a Q₁₀ for carrier-mediated uptake of 2-3 (Table 1), the temperature difference could account for a four-fold difference in summed uptake. For a reptile thermoregulating at 37 °C during daytime and cooling to 24 °C at night, the temperature difference could account for a ca. 1.5X difference in summed uptake (Karasov et al. 1986a). An equally important difference between endotherms and ectotherms appears to be
Figure 2. Relationships between nonintestinal surface area of the small intestine and body mass in fish, reptiles, and mammals. Surface areas for fish include pyloric ceca when present. Data for each taxa are fitted to a common slope of 0.63 and the calculated proportionality coefficients are: fish, 1.68; mammals, 3.94. Species designations and sources are as follows: mammals - #1-16 domestic and temperate and tropical wild mammal species weighing 43-2100 g from Tables 7 and 8 of Chivers and Nilsen (1980); 17, lab rat (Wood 1944); 18, cat (Wood, 1944); 19-20, mouse and woodrat (Karasov et al. 1986a); #21-27, small mammal species from (Barry, 1976); fish - #28-36 species from (Buddington and Diamond, 1987a,b); reptiles - 37,38 desert iguana and chuckwalla (Karasov et al. 1986a).
in amount of intestine. Mammals appear to have about four times more intestinal nominal surface area than fish and reptiles, though this conclusion is based on relatively few data.

The increased metabolic rates associated with increasing body size or associated phylogenetically with the evolution of endothermy involve increased requirements for all nutrients. This increase is met by the evolution of more intestinal tissue, the simplest solution to the problem of absorbing more of everything. The design features of the lung provide an attractive analogy. Increased lung capacity with increasing body size in mammals, or in mammals compared with reptiles, is achieved largely by increasing the surface area of the lung rather than by increasing the gas exchange through each centimeter squared of lung surface (Temney and Remmers 1965, Temney and Temney 1970).

Allometric relations in gastrointestine tract structure and function. The analysis so far suggests that morphometric analysis is an important area of research in the comparative study of intestinal transport. I have applied allometric scaling procedures in order to understand how morphological parameters such as intestinal surface area are related to nutrient requirements, body size, and so on. (Scaling deals with the structural and functional consequences of changes in size or scale among otherwise similar organisms [Schmidt-Nielsen 1984]). The analysis suggests several areas for future research:

1. Does the scaling of gut area fully account for the scaling of intestinal nutrient uptake? In this analysis the mass exponents for summed uptake \(n^{0.57}\) and gut nominal surface area \(n^{0.63}\) are close, but the analysis is based on relatively small sample sizes.

2. Will summed uptake and nominal surface area in amphibians and birds scale in a similar fashion, and will the birds exceed the ectotherms as do the mammals? A recent study of three bird species applying similar techniques to those used here (Karasov et al. 1986b) recorded intestinal glucose and proline uptake rates per cm² nominal area which were comparable to those in Table 1. Thus, some simple measurements of nominal surface area in bird species of differing sizes would shed some light on this question.

3. Why does summed uptake rate not scale with mass raised to the 0.75 power, as does metabolism? One answer might be that nutrient absorption rate does not need to keep pace with metabolism (in contrast to \(O_2\) movement across the
lungs which must equal the body tissues' O₂ consumption in order to maintain aerobic steady state. Instead, many nutrients in a meal are absorbed during a restricted period of the day (after a meal) and are stored in body tissues for use throughout the day. The length of that restricted period for absorption can vary, and so instantaneous maximal nutrient absorption rates can vary independently of the time-averaged rates over a whole day.

Probably, an important factor to consider is the retention time of food in the gut. Extraction efficiency can be viewed as follows:

\[
\text{retention time (min)} \times \text{(summed uptake rate (mole/min))} = \frac{\% \text{ absorbed}}{\text{(quantity of nutrient in gut (moles))}}
\]

(eq. 2)

In order for nutrient extraction efficiency to be independent of body size (which is by no means certain), the following relation should hold:

\[
\% \text{ absorbed} \propto 1.0 \propto \left( \frac{N^V_{\text{upt}}}{N^V_{\text{cap}}} \right) / N^V_{\text{cap}}
\]

(eq. 3)

where \( N^V_{\text{cap}} \) is the manner in which retention time in the digestive tract scales with body size, \( N^V_{\text{upt}} \) is the manner in which summed uptake scales, and \( N^V_{\text{cap}} \) is the manner in which gut capacity scales. The integration in this manner of nutrient transport with other aspects of the digestive process (e.g., Karasov et al. 1984b) would be a challenging but possibly rewarding exercise.

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REFERENCES


Buddington RK, Diamond JM (1987b) Genotypic regulation of intestinal nutrient
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