Digestive Adaptations for Fueling the Cost of Endothermy

Abstract. Little is known about the digestive adaptations that enable mammals to sustain metabolic rates an order of magnitude higher than those of reptiles. Comparison of several features of digestion in mammals and lizards of similar size eating the same diet revealed that mammals processed food ten times faster and with the same or greater extraction efficiency. Transport kinetics and rates of nutrient absorption normalized to the quantity of intestinal tissue were similar in these two classes of vertebrates. The main basis for faster absorption in mammals is their much greater intestinal surface area.

The differences in respiratory, circulatory, reproductive, and excretory physiology between mammals and reptiles have been much studied. However, little is known about the differences in digestive physiology that fuel the metabolic cost of endothermy. Mammals have metabolic rates and hence food requirements exceeding those of lizards by an order of magnitude (1), and there are at least eight types of digestive adaptations that could in theory enable mammals to meet this greater need for nutrients: faster food processing; higher extraction efficiency at the same body temperature; higher efficiency due to higher body temperature at night; greater intestinal surface area at the macroscopic, microscopic, or submicroscopic levels; and higher nutrient transport rates due to higher passive permeability or to higher capacities or binding affinities of active transport mechanisms. Although transit times (2, 3), extraction efficiencies (3, 4), and rates of transport (5–7) have been measured in some species of mammals and lizards, these quantities depend on diet and body size (5–8), and comparisons between mammals and lizards of the same size eating the same diet are lacking. The mechanisms underlying measured extraction efficiencies and transport rates in lizards remain unexplored.

Thus, quantitative assessment of the various factors that might account for the high digestive rates of mammals is

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unavailable. We therefore studied two species of herbivorous con- 
sumptive reptiles and mammals eating the same diet of alfalfa pellets to compare 
them with respect to the eight digestive features listed above (Table 1). We also 
compared seven other species of mam-
mals to these species of reptiles with 
respect to some but not all of these 
features (9).
The daily food intake required to maintain constant body weight was five 
ten times greater in mammals than in 
reptiles of similar size (Table 1). These 
higher intakes were possible because 
transit times of individual meals through 
the gut were faster in the mammals (Table 1). Faster transit 
times might be expected to yield lower 
Gastrointestinal transit time in the small intestine and for microbial digestion in the large 
intestine. However, apparent extraction 
(Dahlback ef al., 1973) was as high or higher in 
the mammals compared to the lizards (Table 1).
To study extraction of individual di-
etary components, we compared desert 
woodrats and chuckwallas as follows. 
Plant diets consist of an inorganic com-
ponent—ash (minerals)—and two pri-
marily organic components—an easily 
soluble, nonfibrous fraction composed 
mainly of cell contents and digested in 
the small intestine, and a fiber fraction 
[neutral detergent fiber (133)] composed 
mainly of cell walls and digested in non-
runnins by microbial fermentation in the 
hindgut. Woodrats and chuckwallas did not 
differ significantly in apparent 
extraction (Table 1) of ash (56 ± 3 percent 
(mean ± standard error of the mean, n = 4 per 
species); P > 0.05 [t-test]) or of the soluble 
fraction (70 ± 2 percent compared to 
68 ± 5 percent (n = 4 per species); 
P > 0.5). However, woodrats exceeded 
chuckwallas in apparent extraction of 
fiber (34 ± 2 percent compared to 
21 ± 3 percent; P < 0.05) and therefore 
also in overall extraction efficiency 
(55 ± 2 versus 46 ± 2 percent; 
P < 0.05) (Table 1). 
These results suggest that extraction 
efficiency of both the small and large 
intestine in mammals is similar to or 
greater than that of lizards, even though 
mammals must process food in shorter 
times. This difference was not due to the 
body temperatures of the ectothermic 
reptiles dropping to 24°C at night be-
cause extraction efficiency was not sign-
ificantly different [difference, 2.2 per-
cent ± 2.5 percentage units; P > 0.4 
(paired t-test)] in chuckwallas main-
tained at 37°C for 24 hours per day. 
Thus, mammals must compensate for 
their faster transit times by means of 
greater absorptive surface area or higher 
rates of nutrient transport per unit area 
(or both).
To compare rates of nutrient trans-
port, we used inverted enteral sleeves 
in vitro to measure uptake of sugar and 
ammonium across the apical (that is, 
umen-facing) cell membrane of the 
intestinal epithelium (6, 7, 14). For 
all species studied (seven mammalian 
and five reptilian), the uptake of D-glucose or 
L-proline at 30 mM—a concentration suf-
cient to saturate the active transport 
mechanisms—was maximal in the proximal 
part of the small intestine. Rates of 
uptake in this region were similar in the 
species of herbivorous mammals and 
reptiles eating alfalfa pellets (Table 2).
Mammals and reptiles (two species) 
chuckwallas, Labidolepis zonata (Benson) 
and Pseudochis alluaudi (Gray) (Table 2).
Mammals and reptiles were selected 
in four other aspects of nutrient trans-
port. First, the proportion of the total 
uptake of glucose or proline that is active 
and sodium-dependent was similar. 
For instance, passive uptake of glucose 
measured by L-glucose accounts for 3 to 25 
percent of total uptake in mammals 
(six species) and 6 to 9 percent in reptiles 
(three species). Second, the temperature 
dependencies of active glucose uptake 
between 25° and 40°C in desert iguana 
(12P, 2.51 ± 0.40; n = 6) and woodrats 
(12P, 2.28 ± 0.10; n = 4) were not 
significantly different (P > 0.5), even 
though the former is an ectothermic poi-
 kilothermal and the latter an endothermic 
homeotherm. Third, the kinetics of ac-
tive D-glucose transport is similar: both 
mammals (five species) and reptiles (two 
species) displayed Michaelis-Menten ki-
netics with an apparent binding constant 
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Table 2. Rates of uptake: minutes−1 per minute per centimeter of intestine and total transport capacities (nanomoles per minute per gram) for three species each of mammals and reptiles. Rates of uptake were measured in the proximal part of the small intestine and are given as the range of values, with the mean value in parentheses. Transport capacities are relative to the metabolic live mass (Wt)\(^{0.73}\) of the animals and are given as the mean ± standard error of the mean.

<table>
<thead>
<tr>
<th>Class</th>
<th>Rate of uptake (mean)</th>
<th>Transport capacity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D-Glucose(^{+})</td>
<td>L-Proline(^{+})</td>
</tr>
<tr>
<td>Reptiles</td>
<td>294 to 831 (485)</td>
<td>249 to 377 (329)</td>
</tr>
<tr>
<td>Mammals</td>
<td>401 to 615 (487)</td>
<td>329 to 676 (511)</td>
</tr>
</tbody>
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\(^{+}\)Carrier-mediated uptake. \(^{\circ}\)Total uptake.

Dietary intake from mouth to anus is 4.1 ± 0.5 for the eight species of small mammals studied but only 1.6 ± 0.3 for the five species of reptile. The key adaptive feature of surface area of the intestine is 4 to 13 times greater than that of the corresponding smoothbore cylinder (compare columns 7 and 8 of Table 1) because of elaborations of the intestinal mucosa at the microscopic level (fingerlike villi in mammals and long ridges in lizards) and is increased another order of magnitude by microvilli. The factor for increase in surface area at the microscopic level may be higher for mammals (7.4 ± 1.6 for five species studied) than for lizards [4.0 for one species; see (16)]. When rates of uptake were integrated over the whole length of the small intestine to yield the total transport capacity [see (6, 7) and Table 1], these capacities, whether related to weight or to metabolic live mass, were an average of 6.8 times greater for mammals than for reptiles, for both glucose and proline (Table 2).

Thus, in the evolution of mammals from reptiles, the key adaptive feature of the digestive system to the need for higher nutrient uptake is analogous to the key adaptation of the respiratory system to the need for higher oxygen uptake (17), that is, a great increase in absorptive surface area. Through lengthening of the gut (and possibly by microscopic elaborations), the intestine is enabled to process food in a shorter time without any sacrifice in extraction efficiency. This pattern of intestinal adaptation during the evolution of endothermy resembles the adaptations, within an individual animal's lifetime, to many other conditions associated with increased requirements for nutrient uptake, such as pregnancy, lactation, diabetes, intestinal resection, and perhaps reduced environmental temperatures (5). Under these conditions, the intestine adapts by a proliferation of mucosal surface per unit length of intestine. Such mucosal proliferation has the same result as lengthening of the gut: namely, increased rates of uptake for all nutrients. These anatomical responses contrast with the other main adaptive pattern of the gut, that is, induction or repression of specific transport mechanisms that enable animals to adapt phenotypically or evolutionarily to changes in diet (5-7).

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References and Notes


9. The four species listed in Table 1, plus box turtles (*Terrapene carolina*) and hamsters, were given diets of alfalfa pellets and free access to water. Lizards were fed hydrated pellets by

10. For mean retention times (t) in Table 1 were calculated from the mass of digests in the gut (m) at the rate at which food enters the gut (r), and the rate at which feces leave the gut (K). (m)/[r(t) + K(t)] > 6. (Mor.), J. H. Scholander, in *Physiological Ecology*, C. R. Townsend and P. Calow, Eds. (Sinauer, Sunderland, Mass., 1981), p. 109. These estimates t, values were confirmed for lizards by direct measurements with food dried in a Sudan III [digestal iguanas, 93 ± 2.4 hours (n = 5); chuckwalla, 74 ± 2.4 hours (n = 4); mean ± standard error of the mean].


12. Apparent extraction efficiency was calculated as [(m/m) - (m/x)] × 100, where m/x is the flux of total digested weight or of a specific diet component per day. This calculation underestimates actual efficiencies if lizards contain significant amounts of organic matter from intestinal secretion or microbes.


15. Similar conclusions were obtained whether the rates of transport were normalized to the length, dry or wet weight, metabolic weight, or metabolic surface area unless otherwise noted (Table 1).

16. Microscopic surface area was measured as described (7). The ratio of microscopic to nominal area (Table 2) was 2.2 for mouse, and 12.8 for woodrat; corresponding figures for these other small mammals are 7.4 (Langaroo rat), 7.1 (Carollia perspicillata), and 4.3 (Arvicanthis jamaicensis). Mean surface area measurements and allometric analysis of gut dimensions in these species are needed to test whether mammals really do exceed reptiles in the ratio of microscopic to nominal area and to compare the contributions of an increase in this ratio and of the increased gut length to the increased gut area of mammals.


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