The digestive adaptation of flying vertebrates: High intestinal paracellular absorption compensates for smaller guts

Enrique Caviedes-Vidal*, Todd J. McWhorter†‡§, Shana R. Lavin†, Juan G. Chediack*, Christopher R. Tracy†¶‖, and William H. Karasov†

*Laboratorio de Biología ''Prof. E. Caviedes Codelia,'' Facultad de Ciencias Humanas, and Departamento de Bioquímica y Ciencias Biológicas, Universidad Nacional de San Luís–Consejo Nacional de Investigaciones Científicas y Técnicas, 5700 San Luis, Argentina; †Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53717; ‡School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch 6150, Australia; ¶Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 84990, Israel; and ‖School of Science and Primary Industries, Charles Darwin University, Darwin 0909, Australia

Anecdotal evidence suggests that birds have smaller intestines than mammals. In the present analysis, we show that small birds and bats have significantly shorter small intestines and less small intestine nominal (smooth bore tube) surface area than similarly sized nonflying mammals. The corresponding >50% reduction in intestinal volume and hence mass of digesta carried is advantageous because the energetic costs of flight increase with load carried. But, a central dilemma is how birds and bats satisfy relatively high energy needs with less absorptive surface area. Here, we further show that an enhanced paracellular pathway for intestinal absorption of water-soluble nutrients such as glucose and amino acids may compensate for reduced small intestines in volant vertebrates. The evidence is that L-rhamnose and other similarly sized, metabolically inert, nonactively transported monosaccharides are absorbed significantly more in small birds and bats than in nonflying mammals. To broaden our comparison and test the veracity of our finding we surveyed the literature for other similar studies of paracellular absorption. The patterns found in our focal species held up when we included other species surveyed in our analysis. Significantly greater amplification of digestive surface area by villi in small birds, also uncovered by our analysis, may provide one mechanistic explanation for the observation of higher paracellular absorption relative to nonflying mammals. It appears that reduced intestinal size and relatively enhanced intestinal paracellular absorption can be added to the suite of adaptations that have evolved in actively flying vertebrates.

digestion | gut morphometrics | nutrient absorption | paracellular uptake

Birds have structural, physiological, and biochemical refinements that adapt them for flight (1), but basic differences in digestive processing between flying and nonflying vertebrates have never been described to our knowledge. The phrase "eating like a bird" wrongly suggests that birds have relatively small appetites, whereas in fact the typical wild bird eats about one-third more dry matter each day than does the typical nonflying mammal (2). Flight, a very energetically demanding activity, contributes to high daily energy demands, but its structural prescription for low weight also may shape an aspect of fliers' digestive apparatus in a way that runs counter to that system's role in providing fuel to meet high energy demands.

There is anecdotal evidence that birds have relatively shorter intestines than mammals (3), and shorter intestines are associated with less surface area and volume, parameters directly correlated with digestive capacity. Indeed, in both birds and mammals, digestive adjustments to higher feeding rates almost always include an increase in gut size and thus an increase in digestive enzymes and nutrient transporters (4). For birds that fly, however, the size of the digestive tract and consequently the

mass of digesta it carries may need to be minimized because the cost of flight increases with load carried, and take-off and maneuverability can be impaired at heavier masses (5–7). Individual flying vertebrates do appear to reduce the mass of digestive organs during times when capacity is not needed (e.g., during long migratory flights), suggesting that minimizing gut size might have adaptive value for increasing flight performance by reducing weight and/or the energy cost of maintaining tissue (8–13).

To test rigorously for differences in gut morphometrics, we surveyed the literature for measures of intestine length and nominal surface area (the area of an equivalent smooth bore tube) in birds, bats, and eutherian nonflying mammals. We excluded foregut fermenters, in which many substrates are fermented by microbial symbionts proximal to the small intestine and the energy-bearing products are absorbed across the foregut epithelium. In contrast, the avian and eutherian species we compared rely mainly on their small intestines for absorption of the majority of energy-bearing compounds. We excluded marsupial endotherms because we did not have measures of intestinal absorption in any species in this taxon. We focused on omnivorous species (a species was considered such if it was noted to consume both arthropods and a plant part) to control for likely effects of diet on gut morphometrics (14, 15).

A central dilemma that emerges in this consideration of birds and bats vs. nonflying mammals is how the former satisfy relatively high energy needs if they indeed possess relatively smaller intestines. Water-soluble compounds, such as glucose and amino acids, are absorbed in the small intestine mainly by two pathways, the transcellular and paracellular pathways. The transcellular absorption of sugars and amino acids is mediated primarily by membrane-bound transporter proteins that take them up from the gut lumen into the enterocyte across the apical membrane and hasten their exit from enterocyte to blood across the basolateral membrane. There do not appear to be fundamental differences between birds and mammals in the nutrient transporters of the intestinal brush border or significant differences in mediated uptake rate of D-glucose or amino acids per unit nominal area (16). Paracellular absorption involves movement of solutes through the tight junctions adjoining cells by

---

diffusion or by the process of solvent drag (17). In both mammalian and avian species, the paracellular route of absorption of water-soluble compounds has been visualized by either autoradiography (18) or confocal laser microscopy (19), its molecular size selectivity has been characterized by using a series of nonelectrolyte water-soluble probes that differ in molecular dimension (20, 21), and its charge selectivity has been characterized by using relatively inert charged peptides (22, 23). In this study, which is focused on patterns across species, we tested the hypothesis that paracellular absorption (measured as fractional absorption, or bioavailability, of metabolically inert water-soluble probes not transported by mediated mechanisms) is elevated in birds, relative to nonflying mammals, and thus may serve as compensation for smaller intestines.

Results and Discussion

Analysis of our gut morphometrics dataset [see supporting information (SI) Table 2] confirmed that birds have significantly shorter small intestine lengths than nonflying mammals, although the difference diminishes as body size increases (Fig. 1*A*). Birds also have significantly lower, by 36%, small intestine nominal surface area (Fig. 1*B*). Surface area is important because it determines the area over which nutrients can be digested and absorbed. Small intestine volume, a direct function of tube length and area, and consequently the potential mass of digesta carried, is thus relatively smaller in birds, by ≈57% (24). Our finding of lower small intestine area in birds is actually an underestimate of the difference from mammals in absorptive area for fueling metabolic demands. Commonly in mammals, but rarely in small birds, there is additional surface area in the cecum or colon where products from microbial fermentation, such as short-chain fatty acids, may be absorbed and account for up to a third of the host's energetic demand (16). Differences in total intestinal nominal surface area among birds and nonflying mammals are not likely to be counterbalanced by greater digestive surface amplification by villi in birds, at least in the case of mediated nutrient uptake. Measurements of the latter standardized per nominal surface area inherently take differences in surface amplification into account and do not differ significantly among birds and mammals (16), suggesting that total capacity for mediated uptake is indeed lower in birds.

These patterns held up in a broader analysis of >200 species of mammals and birds in which both different diets (species were classified as omnivore, carnivore, herbivore, nectarivore, or frugivore) and phylogeny (25) were taken into account (24). This analysis confirmed that small birds have significantly shorter small intestines, and avian species generally have less small intestine nominal surface area and volume than nonflying mammals. Small intestine wet mass, however, is not significantly different between taxa. Our analysis also showed that birds have significantly greater villous amplification of small intestine surface area than mammals (≈25% more amplification, $F_{1,16} = 7.12$, $P = 0.0096$), with no effect of body size. As mentioned above, greater villous surface amplification is not likely to counterbalance differences in intestine size (nominal surface area and length) in the case of mediated nutrient uptake, but it may provide one mechanistic explanation for the observation of higher paracellular absorption in birds.

In our focal species (Table 1), absorption of water-soluble compounds by the paracellular pathway (specifically, fractional absorption or bioavailability of the metabolically inert, nontransported monosaccharide L-rhamnose) differed significantly between the avian species and the nonflying mammals, but the difference depended on body mass (Fig. 2*A*). We included body mass as a covariate in analysis of covariance (ANCOVA), because Pappenheimer (26) suggested that paracellular absorption might become increasingly important at larger body sizes, at least in mammals. However, in our focal species there was no
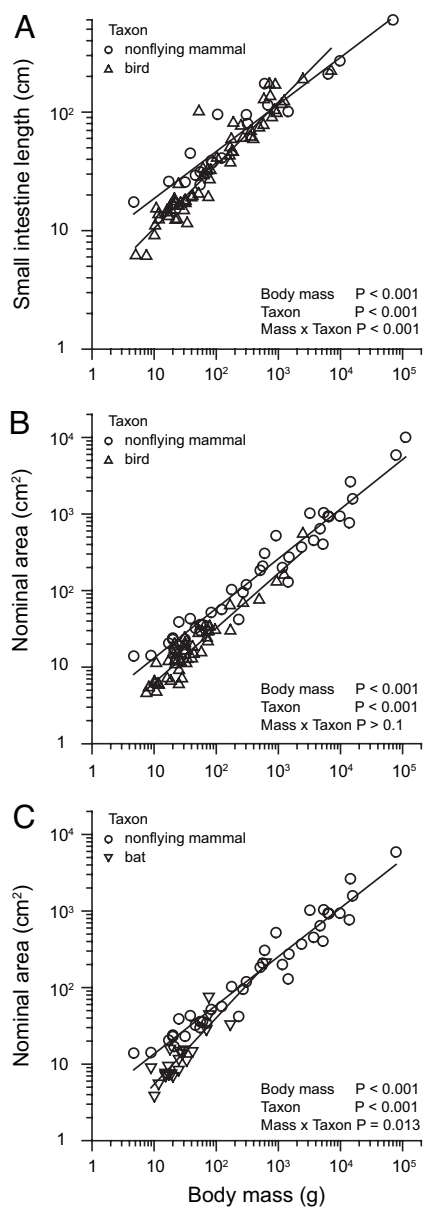

Fig. 1. Small intestine length and nominal (smooth bore tube) surface area in omnivorous birds and mammals. (*A* and *B*) A comparison of birds and nonflying mammals. (*A*) For length, the slopes of these relationships differed significantly ($F_{1,78} = 14.5$; $n = 61$ species and $n = 21$ species for birds and nonflying mammals, respectively). Birds <195 g have significantly shorter small intestines, according to the Johnson–Neyman technique (50). (*B*) For nominal surface area, there was no significant difference in slope between birds and nonflying mammals ($F_{1,83} = 2.11$; $n = 46$ species and 41 species in birds and mammals, respectively). When the lines were fit to the common slope of 0.73, the calculated proportionality coefficients (intercept at unity) were 1.14 for birds and 1.79 for mammals ($F_{1,84} = 47.31$). Hence, small intestine nominal surface area in birds is ≈36% lower than that in nonflying mammals. (*C*) Nominal surface area of bat species compared with the nonflying mammals. The slopes of these relationships differed significantly ($F_{1,60} = 7.4$; $n = 23$ species and $n = 41$ species for bats and nonflying mammals, respectively).

evidence for such a positive scaling, and in fact paracellular absorption was negatively related to body size. The analysis indicated that fractional absorption is greatest in small-sized birds. The pattern is consistent with the hypothesis that paracellular absorption is elevated in birds, relative to nonflying mammals, as compensation for smaller intestines. The differential between birds and nonflying mammals in both intestinal

Table 1. Fractional absorption (*f*), or bioavailability, of metabolically inert carbohydrate probe molecules in intact birds and mammals

Species Common name	Scientific name	Body mass, g	Probe	*f*	Source
Broad-tailed hummingbird	*Selasphorus platycercus*	3.5	L-glucose	0.59	51
Yellow-rumped warbler	*Dendroica coronata*	12	L-glucose	0.91	52
House sparrow*	*Passer domesticus*	25	L-rhamnose	0.64	21
House sparrow	*Passer domesticus*	25	L-glucose	0.603	35
House sparrow	*Passer domesticus*	25	Mannitol	0.63	53
American robin	*Turdus migratorius*	70	L-glucose	0.92	36
Rainbow lorikeet	*Trichoglossus haematodus*	125	L-glucose	0.8	54
Northern bobwhite	*Colinus virginianus*	150	L-glucose	0.7	55
Rock dove*	*Columba livia*	300	L-rhamnose	0.39	39
American coot*	*Fulica americana*	542	L-rhamnose	0.17	This study
Ring-necked pheasant*	*Phasianus colchicus*	900	L-rhamnose	0.14	This study
Mallard*	*Anas platyrhynchos*	1,200	L-rhamnose	0.22	This study
Great fruit-eating bat	*Artibeus lituratus*	70	L-rhamnose	0.90	56
Egyptian fruit bat	*Rousettus aegyptiacus*	125	L-rhamnose	0.62	37
White laboratory mouse*	*Mus musculus*	30	L-rhamnose	0.193	This study
Hamster	*Mesocricetus auratus*	156	L-rhamnose	0.0235	57
Hamster	*Mesocricetus auratus*	156	Mannitol	0.0117	57
Galea*	*Galea galea*	247	L-rhamnose	0.22	This study
Laboratory rat*	*Rattus norvegicus*	300	L-rhamnose	0.134	39, 57
Laboratory rat	*Rattus norvegicus*	300	Mannitol	0.056	This study, 57–62
Common marmoset*	*Callithrix jacchus*	370	L-rhamnose	0.302	63
Guinea pig	*Cavia aperea*	980	L-rhamnose	0.064	57
Guinea pig	*Cavia aperea*	980	Mannitol	0.054	57, 58
Cat	*Felis domesticus*	2,800	Mannitol	0.285	58
Rabbit	*Oryctolagus cuniculus*	3,000	Mannitol	0.021	58
Rhesus macaque*	*Macaca mulatta*	8,912	L-rhamnose	0.082	This study
Dog	*Canis familiaris*	12,875	L-rhamnose	0.168	64
Human	*Homo sapiens*	70,000	L-rhamnose	0.118	57, 65–76
Human	*Homo sapiens*	70,000	Mannitol	0.218	57, 58, 71, 75, 77–82

The 10 focal species of birds and nonflying mammals measured during this study are indicated by *.

length and fractional absorption declines with increasing body size (compare Figs. 1*A* and 2*A*).

If there has indeed been natural selection for smaller intestinal size in flying endotherms, and increased paracellular absorption as a compensation, then we might expect to find the same patterns in a comparison within mammals between flyers and nonfliers. Within mammals flight evolved once in the order Chiroptera, which is composed of two major suborders: the
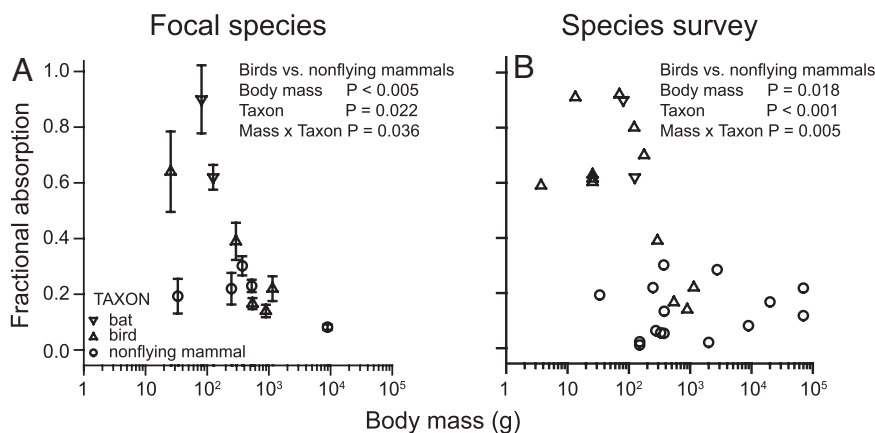

Fig. 2. Fractional absorption (bioavailability) in intact animals of inert, nonactively transported, water-soluble carbohydrates, a measure of paracellular absorption. (*A*) For all individuals in the 10 focal species (indicated by * in Table 1), absorption of L-rhamnose was measured with a standard protocol. In the comparison of birds and nonflying mammals by ANCOVA, fractional absorption declined with increasing $\log_{10}$body mass ($F_{1,6} = 19.5$) and differed significantly between the two taxa ($F_{1,6} = 9.5$), although the difference diminished with increasing size (interaction $F_{1,6} = 7.3$). Values of L-rhamnose fractional absorption in two species of bats were as high, or higher, than the values of the avian species, and above those for nonflying mammals. (*B*) The broader survey includes additional measures from the literature (Table 1) of fractional absorption of L-rhamnose or similarly sized water-soluble carbohydrate probes, L- glucose (MM = 180) and mannitol (MM = 182). Each point represents the fractional absorption of a probe by a species. In five of the 29 cases, the value shown is the mean of more than one study. In the comparison of birds, bats, and nonflying mammals by ANCOVA, fractional absorption differed significantly according to taxa ($F_{2,23} = 11.9$), although the difference diminished with increasing size (interaction $F_{2,23} = 5.46$). None of the nonflying mammals exhibited fractional absorption of these carbohydrates as high as that in small birds or bats.

Caviedes-Vidal *et al.*

Microchiroptera and Megachiroptera (27). Several biologists noted that bats tend to have less intestinal tissue than comparably sized nonflying mammals (28, 29), a pattern confirmed with our dataset. Bats had significantly shorter intestines (data not shown) and less small intestinal nominal surface area than nonflying mammals, although the difference diminished as body size increased (Fig. 1C). We measured fractional absorption of L-rhamnose in Egyptian fruit bats (*Rousettus aegyptiacus*; Megachiroptera) and in the great fruit-eating bat (*Artibeus lituratus*, Microchiroptera) with our standard pharmacokinetic protocol. The mean fractional absorption values for both bat species were as high, or higher, than the values of the avian species, and above those for nonflying mammals (Fig. 2A), indicating relatively higher paracellular absorption.

To broaden our comparison and test the veracity of our finding we surveyed the literature for other studies of fractional absorption of water-soluble carbohydrates (Table 1). Our broader survey includes studies that used similar methodology to ours (either serial blood or urine sampling postinjection and/or postoral administration) to measure fractional absorption of L-rhamnose or the similarly sized water-soluble carbohydrate probes L-glucose [molecular mass (MM) = 180] and mannitol (MM = 182), which are also metabolically inert and lack affinity for mediated transport mechanisms. Fractional absorptions were similar within a species when measured with two or more different compounds. Although paracellular absorption should decline with increasing MM, because of sieving at the tight junction (21, 30), there was no significant difference in the adjusted least-square mean fractional absorption (arcsine square root transformed) according to MM over this small range for either nonflying mammals ($F_{1,12} = 1.07, P > 0.3$) or birds ($F_{1,7} = 1.18, P > 0.3$). Fractional absorptions were similar within a species when measured with two or more different compounds (Table 1). For three species (guinea pigs, laboratory rats, and humans) of a total of 23 species, we calculated a single species mean value for fractional absorption of L-rhamnose and/or mannitol because there were data available from several studies. In the comparison of taxa we did not distinguish between measurements of fractional absorption that were made in the presence of luminal nutrients vs. their absence (i.e., in fasted animals). Although permeability of the paracellular pathway is increased when Na$^+$-coupled glucose and amino acid transport occurs (17, 31, 32), the increase in fractional absorption in rats and house sparrows ($+0.06 \pm 0.03$, $n = 4$ studies with L-rhamnose, L-glucose, and mannitol; refs. 21, 33, and 34) was small relative to the large difference in fractional absorption between birds and nonflying mammals. The patterns in fractional absorption in our focal species held up when we included other species surveyed (Fig. 2B). None of the nonflying mammals exhibit fractional absorption of these carbohydrates as high as occurs in small birds or bats. High paracellular absorption in small birds from seven different avian families with varied diets (omnivores, nectarivores, and granivores) suggests that it is an important pathway of absorption of water-soluble compounds in small avian species generally, rather than being associated with a specific diet type. Thus, the data from uniform methods on our focal species and the data from less uniform methods in the broader species survey are consistent with the hypothesis that paracellular absorption is elevated in flying birds and mammals, relative to nonflying mammals, as compensation for smaller intestines.

It appears that reduced intestinal size and elevated intestinal paracellular absorption can be added to the suite of adaptations (1) that have evolved in actively flying vertebrates. Our demonstration of a difference in digestive physiology between flyers and nonfliers begs many questions in physiology and ecology.

The differences in paracellular absorption between fliers and nonfliers do not extend to absorption generally. For example,

whereas the nonflying mammals had relatively low fractional absorption of L-rhamnose, their absorption (measured by our standard protocol) of 3-O-methyl-D-glucose, a nonmetabolizable analogue of D-glucose that is actively as well as passively absorbed, was universally high (0.76 ± 0.06, $n = 5$ species) and not significantly different from that of flying species (0.90 ± 0.04, $n = 4$, 2 bird and 2 bat species, $t_7 = 2.02$, $P > 0.08$). Paracellular absorption can account for the majority of glucose absorption in at least two avian species (35, 36) and at least two bat species (37, 38) according to our comparison of simultaneous apparent rates of absorption of paracellular probes (such as L-rhamnose or L-glucose) and 3-O-methyl-D-glucose or D-glucose. In accordance with August Krogh's dictum (83), the study of the cellular and subcellular details of paracellular absorption might be advanced by study of such species with relatively high paracellular absorption.

The difference in paracellular absorption between fliers and nonfliers is not simply explained by mediated absorption in birds of the carbohydrate probes that are presumed to be absorbed passively or by longer retention of digesta in fliers than in nonfliers. In studies using radiolabeled L-glucose and L-rhamnose, we have failed to find evidence that their uptake by intestine *in vitro* is inhibited by high concentrations (50–100 mM) of unlabeled L-glucose, L-rhamnose, or D-glucose (24, 33, 39). Nor is the difference in paracellular absorption between fliers and nonfliers explained by longer retention of digesta in the gut of the former relative to the latter. Avian species typically have shorter mean retention time of digesta than do similarly sized nonflying mammalian species (24), and a shorter retention time probably occurs in bats relative to nonflying mammals (28). Because small vertebrate flyers typically achieve higher paracellular absorption with less intestinal length and surface area than do similarly sized nonflying mammals, there apparently are differences in intestinal permeability per unit intestinal tissue. We have confirmed this elsewhere in a comparison of pigeons and laboratory rats (39). Under similar recirculating duodenal perfusion conditions, we found that anesthetized rats and pigeons absorbed D-glucose at a comparable rate, but that pigeons had significantly greater ($>2\times$ higher) absorption of inert carbohydrate probes (24, 34).

The mechanisms responsible for relatively higher paracellular absorption in some species are unknown, but could include the following: (*i*) Greater villous area per unit intestinal nominal surface area might be associated with more cell junctions across which paracellular transport occurs, if villous area is increased mainly by increase in number of similar-sized enterocytes. Barry (40) and Mayhew and coworkers (41, 42) have made measurements on a bat species and a similar-sized nonflying mammal species by using uniform methodology, and in all cases the ratio of villous area relative to nominal surface area in the bat species exceeded that in the nonflying mammal by ≥59%. We have found this same pattern in our comparisons of small birds with relatively high paracellular absorption and nonflying mammals with relatively lower paracellular absorption (24). (*ii*) Larger effective pore radius in the junction, caused by differences in claudins and other proteins that create the sieving effect, will increase paracellular permeation over certain size ranges of molecules (21, 30). (*iii*) Greater water flux across the tight junction will increase solute permeation by increased solvent drag (17).

From an evolutionary perspective, one can argue that there are both benefits and costs to high intestinal permeability to hydrosoluble biochemicals, which would explain why it is present in some, but not all, vertebrates. We have suggested that a selective advantage in the case of active fliers is that it can compensate for smaller intestines, and Pappenheimer (43) suggested that passive absorption may confer a selective advantage because it requires little energy and provides a mechanism

whereby rate of absorption is matched to rate of substrate hydrolysis in the intestine. The significant negative correlation of paracellular absorption with body mass revealed by our analysis, opposite to Pappenheimer's prediction (43), supports the notion of adaptive value for nutrient absorption in active fliers with reduced guts. Although carbohydrate probes have primarily been used to measure paracellular absorption, other hydrosoluble molecules, including peptides (23) and dyes (19), also show high fractional absorption in small omnivorous birds. Taken in the context of the present analysis, it is reasonable to predict that paracellular absorption of peptides and amino acids might be similarly important in small volant vertebrates consuming diets primarily composed of protein and fat. A possible cost is that a high intestinal permeability that permits passive absorption is less selective than a carrier-mediated system for nutrient absorption and might permit water soluble toxins made by humans (e.g., carbamate insecticides, glyphosate herbicide) and naturally occurring in foods (e.g., caffeine, nicotine, some flavonoids) to be absorbed to a greater extent in the intestine (44). Opposing costs and benefits can lead to variation among species in intestinal permeability to hydrosoluble biochemicals. For vertebrates with high intestinal permeability, vulnerability to hydrophilic toxins could be an important ecological driving force, constraining food exploratory behavior, limiting the breadth of the dietary niche, and selecting for compensatory behaviors such as searching for and ingesting specific substances that inhibit hydrophilic toxin absorption (45).

Most of the physiological and ecological issues suggested by our findings remain to be studied in vertebrate, and possibly invertebrate, fliers. Also, we could not consider diet as a factor in our analysis of paracellular absorption, so we do not know whether the difference between fliers and nonfliers occurs for all types of feeders (as it does for intestinal surface area) or mainly those that eat carbohydrate-rich foods. An enlarged comparative dataset (e.g., including insectivorous/carnivorous birds varying in body size and insectivorous bats) will permit the most robust, phylogenetically informed test of the hypothesis that increased intestinal paracellular absorption has evolved as a compensation for smaller intestinal size in flying vertebrates.

Materials and Methods

As a measure of passive, paracellular absorption, we used standard methods from pharmacokinetics to measure the whole-organism fractional absorption of water-soluble compounds that are similar in molecular size to water-soluble nutrients such as amino acids and glucose (which range in MM from 75 to 204) but are metabolically inert and lack affinity for intestinal-mediated uptake mechanisms. We applied the standard methods to five each of avian and nonflying mammalian species chosen to cover a wide range in body size (focal species) and two bat species (Table 1). For all individuals in our focal species, L-rhamnose (MM = 164) was injected, and also administered orally (typically 30–40 mM, volume ≈1% of body mass) to intact animals in separate experiments, and blood and/or urine samples were serially collected and analyzed for probe molecules. Probes were analyzed by HPLC (37). Fractional absorption (f) was calculated as [AUC postgavage]/[AUC postinjection] (AUC = dose-corrected area under the curve of plasma or urine probe concentration vs. time). This simple pharmacokinetic method does not require assumptions about pool sizes (e.g., one or two pools) or kinetics (e.g., first order) (46). In mammals, the probes can be recovered in urine, and estimates of oral absorption take account of possible differential recovery of probes when injected. In our studies with laboratory mice, rats, and marmosets, recoveries of carbohydrate probes were uniformly high, which is in agreement with measures by others in rats and humans (47). Fractional absorption of L-rhamnose in laboratory rats measured by serially sampling blood (0.24 ± 0.03) did not differ significantly from that measured by urine recovery (0.22 ± 0.03, $n = 4$, by repeated measures $F_{1,3} = 1.14$; $P > 0.3$). Here, and elsewhere, statistical analyses of fractional absorption were made on arcsin-square-root transformed values (48). In some cases test solutions included 50 mM 3-O-methyl D-glucose. L-rhamnose is commonly used in humans in tests of passive (noncarrier-mediated) intestinal permeability (49), and 3-O-methyl D-glucose is an actively transported, nonmetabolizable D-glucose analogue.

1. Maina JN (2000) *J Exp Biol* 203:3045–3064.
2. Nagy KA (2001) *Nutr Abstr Rev B* 71:21R–31R.
3. McLelland J (1979) in *Form and Function in Birds*, eds King AS, McLelland J (Academic, London), pp 69–181.
4. Karasov WH, McWilliams SR (2005) in *Physiological and Ecological Adaptations to Feeding in Vertebrates*, eds Starck JM, Wang T (Science Publishers, Enfield, NH), pp 87–112.
5. Nudds RL, Bryant DM (2002) *Am J Physiol* 283:R249–R256.
6. Norberg UM (1995) *Funct Ecol* 9:48–54.
7. Guillemette M (1994) *Auk* 111:900–909.
8. Piersma T (1998) *J Avian Biol* 29:511–520.
9. Piersma T, Gill REJ (1998) *Auk* 115:196–203.
10. Karasov WH, Pinshow B (1998) *Physiol Zool* 71:435–448.
11. Piersma T, Gudmundsson GA, Lilliendahl K (1999) *Physiol Biochem Zool* 72:405–415.
12. Landys-Ciannelli MM, Piersma T, Jukema J (2003) *Funct Ecol* 17:151–179.
13. Battley PF, Piersma T (2005) in *Physiological and Ecological Adaptations to Feeding in Vertebrates*, eds Starck JM, Wang T (Science Publishers, Enfield, NH), pp 201–228.
14. Chivers DJ, Hladik CM (1980) *J Morphol* 166:337–386.
15. Ricklefs RE (1996) *Condor* 98:279–292.
16. Karasov WH, Hume ID (1997) in *Handbook of Comparative Physiology*, ed Dantzler W (Am Physiol Soc, Bethesda), pp 409–480.
17. Pappenheimer JR, Reiss KZ (1987) *J Membr Biol* 100:123–136.
18. Ma TY, Hollander D, Riga R, Bhalla D (1993) *J Lab Clin Med* 122:590–600.
19. Chang MH, Karasov WH (2004) *Zoology* 107:121–133.
20. Hamilton I, Rothwell J, Archer D, Axon TR (1987) *Clin Sci* 73:189–196.
21. Chediack JG, Caviedes-Vidal E, Fasulo V, Yamin LJ, Karasov WH (2003) *J Comp Physiol B* 173:187–197.
22. He YL, Murby S, Warhurst G, Gifford L, Walker D, Ayrton J, Eastmond R, Rowland M (1998) *J Pharmacol Sci* 87:626–633.
23. Chediack JG, Caviedes-Vidal E, Karasov WH (2006) *J Comp Physiol B* 176:303–309.
24. Lavin SR (2007) PhD thesis (University of Wisconsin, Madison).
25. Felsenstein J (1985) *Am Nat* 125:1–15.
26. Pappenheimer JR (1998) *Comp Biochem Physiol* 121:45–58.
27. Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) *Science* 307:580–584.
28. Klite PD (1965) *J Bacteriol* 90:375–379.
29. Keegan DJ, Mödinger R (1979) *S Afr J Zool* 14:220–223.
30. Chang RLS, Robertson CR, Deen WM, Brenner BM (1975) *Biophys J* 15:861–886.
31. Turner JR, Madara JL (1995) *Gastroenterology* 109:1391–1396.

32. Sadowski DC, Meddings JB (1993) *Can J Physiol Pharmacol* 71:835–839.
33. Chang MH, Chediack JG, Caviedes-Vidal E, Karasov WH (2004) *J Comp Physiol B* 174:181–188.
34. Lavin SR, McWhorter TJ, Karasov WH (2004) *Integr Comp Biol* 44:717.
35. Chang MH, Karasov WH (2004) *J Exp Biol* 207:3109–3121.
36. McWhorter TJ, Karasov WH, Green AK (2004) *Integr Comp Biol* 44:602.
37. Tracy CR, McWhorter TJ, Korine C, Wojciechowski MS, Pinshow B, Karasov WH (2007) *J Exp Biol* 210:1726–1734.
38. Caviedes-Vidal E, Chediack JG, Cruz-Neto AP, Karasov WH (2004) *Integr Comp Biol* 44:534.
39. Lavin SR, McWhorter TJ, Karasov WH (2007) *J Exp Biol* 210:2754–2764.
40. Barry RE, Jr (1976) *J Mammal* 57:273–289.
41. Mayhew TM, Middleton C (1985) *J Anat* 141:1–17.
42. Makanya AN, Maina JN, Mayhew TM, Tschanz SA, Burri PH (1997) *J Exp Biol* 200:2415–2423.
43. Pappenheimer JR (1993) *Am J Physiol* 265:G409–G417.
44. Diamond J (1991) *News Physiol Sci* 6:92–96.
45. Diamond J, Bishop KD, Gilardi JD (1999) *Ibis* 141:181–193.
46. Welling PG (1986) *Pharmacokinetics: Processes and Mathematics* (Am Chem Soc, Washington, DC).
47. Riviere JE (1999) *Comparative Pharmacokinetics: Principles, Techniques and Applications* (Iowa State Univ Press, Ames).
48. Wilkinson L (1992) *Systat for Windows: Statistics* (Systat, Evanston, IL), version 5.
49. Travis S, Menzies I (1992) *Clin Sci* 82:471–488.
50. White CR (2003) *Physiol Biochem Zool* 76:135–140.
51. McWhorter TJ, Hartman Bakken B, Karasov WH, Martínez del Rio C (2006) *Biol Lett* 2:131–134.
52. Afik D, McWilliams SR, Karasov WH (1997) *Physiol Zool* 70:370–377.
53. Chediack JG, Caviedes-Vidal E, Karasov WH, Pestchanker M (2001) *J Exp Biol* 204:723–731.
54. Karasov WH, Cork SJ (1994) *Am J Physiol* 267:G16–G26.
55. Levey DJ, Cipollini ML (1996) *Comp Biochem Physiol* 113:225–231.
56. Caviedes-Vidal E, Karasov WH, Chediack JG, Fasulo V, Cruz-Neto AP, Otani L (2007) *PLoS*, in press.
57. Delahunty T, Hollander D (1987) *Comp Biochem Physiol* 86:565–567.
58. Bijlsma PB, Peeters RA, Groot JA, Dekker PR, Taminiau JAJM, Meer RvD (1995) *Gastroenterology* 108:687–696.
59. Schwartz RM, Furne JK, Levitt MD (1995) *Gastroenterology* 109:1206–1213.
60. Sigalet DL, Kneteman NN, Fedorak RN, Kizilisik T, Madsen KE, Thomson ABR (1996) *J Surg Res* 61:379–384.
61. Sigalet DL, Martin GR, Poole A (2000) *J Ped Surg* 35:661–664.
62. Martin GR, Meddings JB, Sigalet DL (2003) *J Parenter Enter Nutr* 27:65–70.
63. McWhorter TJ, Karasov WH (2007) *Am J Primatol*, 69:1399–1411.
64. Sørensen SH, Proud FJ, Adam A, Rutgers HC, Batt RM (1993) *Clin Chim Acta* 221:115–125.
65. Menzies IS, Pounder R, Heyer S, Laker MF, Bull J, Wheeler PG, Creamer B (1979) *Lancet* 1107–1109.
66. Menzies IS, Noone C, Bull J, Mount JN (1983) *Gut* 24:A488.
67. Menzies IS (1984) in *Intestinal Absorption and Secretion*, eds Skadhauge E, Heintze K (MTP Press, Lancaster, UK), pp 527–543.
68. Saweirs WM, Andrews DJ, Low-Beer TS (1985) *Age Ageing* 14:312–315.
69. Maxton DG, Bjarnason I, Reynolds AP, Catt SD, Peters TJ, Menzies IS (1986) *Clin Sci* 71:71–80.
70. Noone C, Menzies IS, Banatvala JE, Scopes JW (1986) *Eur J Clin Invest* 16:217–225.
71. Erikson RA, Epsten RM (1988) *Am J Gastroenterol* 83:541–544.
72. Menzies IS, Jenkins AP, Heduan E, Catt SD, Segal MB, Creamer B (1990) *Scand J Gastroenterol* 25:1257–1264.
73. Bjarnason I, Maxton D, Reynolds AP, Catt S, Peters TJ, Menzies IS (1994) *Scand J Gastroenterol* 29:630–639.
74. Dinmore AJ, Edwards JSA, Menzies IS, Travis SPL (1994) *J Appl Physiol* 76:1903–1907.
75. Munkholm P, Langholz E, Hollander D, Thornberg K, Orholm M, Katz KD, Binder V (1994) *Gut* 35:68–72.
76. Menzies IS, Zuckerman MJ, Nukajam WS, Somasundaram SG, Murphy B, Jenkins AP, Crane RS, Gregory GG (1999) *Gut* 44:483–489.
77. Elia M, Behrnes R, Northrop C, Wraight P, Neale G (1987) *Clin Sci* 73:197–204.
78. Cobden I, Hamilton I, Rothwell J, Axon ATR (1985) *Clin Chim Acta* 148:53–62.
79. Brunetto AL, Pearson ADJ, Gibson R, Bateman DN, Rashid MU (1990) *Eur J Clin Invest* 20:279–284.
80. Fleming SC, Kapembwa MS, Laker MF, Levin GE, Griffin GE (1990) *Clin Chem* 36:797–799.
81. Fleming SC, Kynaston JA, Laker MF, Pearson ADJ, Kapembwa MS, Griffin GE (1993) *J Chromatogr* 640:293–297.
82. Farhadi A, Keshavarzian A, Holmes EW, Fields J, Zhang L, Banan A (2003) *J Chromatogr B* 784:145–154.
83. Krogh A (1929) *Am J Physiol* 90:243–251.

Table 2. Small intestine (SI) length and nominal surface area (NSA) of omnivorous birds and eutherian mammals [common names were extracted from the Integrated Taxonomic Information System (ITIS; www.itis.gov) and ref. 1]

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
			BIRDS				
Mottled duck	*Anas fulvigula*	Anseriformes	Anatidae	742	135.85		2, 3
Mallard	*Anas platyrhynchos*	Anseriformes	Anatidae	1,237.2	122.9	160	3-6
Lesser scaup	*Aythya affinis*	Anseriformes	Anatidae	718	172.1		6, 7
Greater scaup	*Aythya marila*	Anseriformes	Anatidae	892	169.6		6, 7
Muscovy duck	*Cairina moschata*	Anseriformes	Anatidae	585	127.8		3
Herring gull	*Larus argentatus*	Charadriiformes	Laridae	787.9	90		3
Ring-billed gull	*Larus delawarensis*	Charadriiformes	Laridae	359.7	69		3
Glaucous gull	*Larus hyperboreus*	Charadriiformes	Laridae	1,132	116.5		3
Pigeon	*Columba livia*	Columbiformes	Columbidae	270.4	60.3	68.6	3, 4, 8, 9
Northern bobwhite	*Colinus virginianus*	Galliformes	Odontophoridae	166.7	50.3	63.84	3, 10, 11
Montezuma quail	*Cyrtonyx montezumae*	Galliformes	Odontophoridae	186	46		11
Rock partridge	*Alectoris graeca*	Galliformes	Phasianidae	576	77.5		11
Scaled quail	*Callipepla squamata*	Galliformes	Phasianidae	175	59		11
Japanese quail	*Coturnix coturnix japonica*	Galliformes	Phasianidae	169.1	37.4	29.85	12, 13
Chicken	*Gallus g. domesticus*	Galliformes	Phasianidae	2,481	188.4	550	3, 9
Gambel's quail	*Lophortyx gambelii*	Galliformes	Phasianidae	188	81		11
Wild turkey	*Meleagris gallopavo*	Galliformes	Phasianidae	7,050	222		3, 11
Mountain quail	*Oreortyx picta*	Galliformes	Phasianidae	250	76.5		11
Hungarian partridge	*Perdix perdix*	Galliformes	Phasianidae	395	59		11
Ring-necked pheasant	*Phasianus colchicus*	Galliformes	Phasianidae	938.3	97.8	130	3-5, 11
American coot	*Fulica americana*	Gruiformes	Rallidae	491	73.8	75.5	3, 4
Purple gallinule	*Porphyrula martinica*	Gruiformes	Rallidae	163.9	42.9		3
Waxwing	*Bombycilla garrulus*	Passeriformes	Bombycillidae	62.1	29.19		14
Raven	*Corvus corax*	Passeriformes	Corvidae	874	103.5		3
Rook	*Corvus frugilegus*	Passeriformes	Corvidae	359.5	61.75		15
Blue jay	*Cyanocitta cristata*	Passeriformes	Corvidae	61	33.3		3

Caviedes-Vidal et al.   Table 2

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm^2	Source
Song sparrow	*Melospiza melodia*	Passeriformes	Fringillidae	21.2	18.4	16.87	16
Pine grosbeak	*Pinicola enucleator*	Passeriformes	Fringillidae	52.6	100.99		14
Rufous-sided towhee	*Pipilo erythrophthalmus*	Passeriformes	Fringillidae	41.5	19.49	18.29	5, 16, 17
Scarlet tanager	*Piranga olivacea*	Passeriformes	Fringillidae	31.4	17.9	20.52	16
Scarlet-rumped tanager	*Ramphocelus passerinii*	Passeriformes	Fringillidae	30.3	14.8	16.4	16
Variable seedeater	*Sporophila aurita*	Passeriformes	Fringillidae	10.4	11	6.11	16
Silver-throated tanager	*Tangara icterocephala*	Passeriformes	Fringillidae	22	12.3	12.47	16
Blue-gray tanager	*Thraupis virens*	Passeriformes	Fringillidae	34	11.5	12.71	16
Red-winged blackbird	*Agelaius phoeniceus*	Passeriformes	Icteridae	57.5		15.5	18
Streak-backed oriole	*Icterus pustulatus*	Passeriformes	Icteridae	28.2		7.08	C. Martínez del Rio, personal communication
Orchard oriole	*Icterus spurius*	Passeriformes	Icteridae	18.5		6.57	C. Martínez del Rio, personal communication
Brown-headed cowbird	*Molothrus ater*	Passeriformes	Icteridae	40.8		12.9	C. Martínez del Rio, personal communication
Boat-tailed grackle	*Quiscalus major*	Passeriformes	Icteridae	178.2	46.2		3
Great-tailed grackle	*Quiscalus mexicanus*	Passeriformes	Icteridae	95.9		30.4	C. Martínez del Rio, personal communication
Common grackle	*Quiscalus quiscula*	Passeriformes	Icteridae	81.1	32.3		3
Gray catbird	*Dumetella carolinensis*	Passeriformes	Mimidae	32	17	18.7	19
Northern mockingbird	*Mimus polyglottos*	Passeriformes	Mimidae	51.9	20.4	27.74	16
British robin	*Erithacus rubecula*	Passeriformes	Muscicapidae	16.3	14.82		20, 21
North American thrush	*Hylocichla guttata*	Passeriformes	Muscicapidae	31	17.6	23.87	16

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Clay-colored robin	*Turdus grayi*	Passeriformes	Muscicapidae/ Turdidae	74.7	19.1	29.51	16
Tufted titmouse	*Parus bicolor*	Passeriformes	Paridae	21.3	17.6	19.9	16
Carolina chickadee	*Parus carolinensis*	Passeriformes	Paridae	10.1	9.1	6.43	16
Great tit	*Parus major*	Passeriformes	Paridae	16.2	14.2	7.11	21, 22
Yellow-rumped warbler	*Dendroica coronata*	Passeriformes	Parulidae	11.9	12.37	5.83	23, 24
Pine warbler	*Dendroica pinus*	Passeriformes	Parulidae	11.7	13.7	6	25
Orange-crowned warbler	*Vermivora celata*	Passeriformes	Parulidae	8.2		5.4	26
House sparrow	*Passer domesticus*	Passeriformes	Passeridae	26.6	17	11.8	4, 27
Thrush-like manakin	*Schiffornis turdinus*	Passeriformes	Pipridae/ Cotingidae	32	17.8	16.26	16
Tree sparrow	*Passer montanus*	Passeriformes	Ploceidae	25	16.12	5.96	28
Goldcrest	*Regulus regulus*	Passeriformes	Regulidae	5.1	6.17		20
White-breasted nuthatch	*Sitta carolinensis*	Passeriformes	Sittidae	20.9	16.2	14.65	16
European starling	*Sturnus vulgaris*	Passeriformes	Sturnidae	73	32.24	29.05	5, 14, 18, 19
Garden warbler	*Sylvia borin*	Passeriformes	Sylviidae	18.5	15		21, 29
Orange-billed nightingale-thrush	*Catharus aurantiirostris*	Passeriformes	Turdidae	25.2		9.12	C. Martínez del Rio, personal communication
Hermit thrush	*Catharus guttatus*	Passeriformes	Turdidae	33		11.2	30
Gray-cheeked thrush	*Catharus minimus*	Passeriformes	Turdidae	43.5		14.8	30
American robin	*Turdus migratorius*	Passeriformes	Turdidae	78.4	26.97	33.79	3, 5, 16, 19
Fieldfare	*Turdus pilaris*	Passeriformes	Turdidae	102.7	41.08		14
Rufous-backed robin	*Turdus rufopalliatus*	Passeriformes	Turdidae	70.4		24.23	C. Martínez del Rio, personal communication
Yellow-bellied elaenia	*Elaenia flavogaster*	Passeriformes	Tyrannidae	23.5	12.5	14.99	16

| Species | | | | Body | SI length, | SI NSA, | Source |
Common name	Scientific name	Order	Family	mass, g	cm	cm²	
Western flycatcher	*Empidonax difficilis*	Passeriformes	Tyrannidae	10.9		4.74	C. Martínez del Rio, personal communication
Ochre-bellied flycatcher	*Mionectes oleagineus/ Pipromorpha oleaginea*	Passeriformes	Tyrannidae	10.8	15.3	11.24	16
Great kiskadee	*Pitangus sulphuratus*	Passeriformes	Tyrannidae	73.3		21.58	C. Martínez del Rio, personal communication
	Terrenotricus erythrurus	Passeriformes	Tyrannidae	7.5	6.1	4.56	16
Tropical kingbird	*Tyrannus melancholicus*	Passeriformes	Tyrannidae	39.8	19		16
Yellow-breasted chat	*Icteria virens*	Passeriformes	Vireonidae	21.9		10.82	C. Martínez del Rio, personal communication
Blue-headed vireo	*Vireo solitarius*	Passeriformes	Vireonidae	17	13.2	11.9	16
Lesser honeyguide	*Indicator minor*	Piciformes	Indicatoridae	24.7	24.6		31
TERRESTRIAL EUTHERIAN MAMMALS							
Pig	*Sus scrofa*	Artiodactyla	Suidae	111,850		10,047	32, 33
Dog	*Canis familiaris*	Carnivora	Canidae	9,782.5	271	907	32-37
Red fox	*Vulpes vulpes*	Carnivora	Canidae	6,320	210	939.2	32, 34
Leopard	*Panthera pardus*	Carnivora	Felidae	15,700		1,580	32
African golden cat	*Profelis aurata*	Carnivora	Felidae	5,230		404	32
African palm civet	*Nandinia binotata*	Carnivora	Nandiniidae	2,363.3		370	32
Servaline genet	*Genetta servalina*	Carnivora	Viverridae	1,480		274	32
African linsang	*Poiana richardsoni*	Carnivora	Viverridae	510		184	32
South American squirrel monkey	*Saimiri sciureus*	Primates	Cebidae	675.4	114.88		38
Grey-cheeked mangabey	*Cercocebus albigena*	Primates	Cercopithecidae	3,700		453	32

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Vervet monkey	*Cercopithecus aethiops*	Primates	Cercopithecidae	4,700		643.5	39
Western black-and-white colobus	*Colobus polykomos*	Primates	Cercopithecidae	6,500		925	32
Long-tailed macaque	*Macaca fascicularis*	Primates	Cercopithecidae	3,216.7		1,024.3	32
Rhesus macaque	*Macaca mulatta*	Primates	Cercopithecidae	13,885		768.67	32, 40
Talapoin monkey	*Miopithecus talapoin*	Primates	Cercopithecidae	915		522.5	32
Mandrill	*Papio sphinx*	Primates	Cercopithecidae	14,450		2,644.5	32
Greater dwarf lemur	*Cheirogaleus major*	Primates	Cheirogaleidae	230		42	32
Fork-crowned lemur	*Phaner furcifer*	Primates	Cheirogaleidae	270		95	32
Demidoff 's dwarf bushbaby	*Galago demidovii*	Primates	Galagonidae	60		36	32
Human	*Homo sapiens*	Primates	Hominidae	70,000-78,300	600	5897.5	33, 34, 41, 42
Calabar potto	*Arctocebus calabarensis*	Primates	Loridae	176.7		103	32
Potto	*Perodicticus potto*	Primates	Loridae	1,160		200	32
Northern jumping mouse	*Zapus hudsonius*	Rodentia	Dipodidae	20		23	43
Spiny mouse	*Acomys spinosissimus*	Rodentia	Muridae	17.2	25.99	20.53	44
Cape short-eared gerbil	*Desmodillus auricularis*	Rodentia	Muridae	86.2	37.51		44
Griselda's striped grass mouse	*Lemniscomys griselda*	Rodentia	Muridae	54.9	24.38	29.99	44
Gerbil	*Meriones unguiculatus*	Rodentia	Muridae	70.1	30.5	34.3	33, 36
Syrian hamster	*Mesocricetus auratus*	Rodentia	Muridae	122.6	41	56.7	33, 35, 36, 46, 47
Harvest mouse	*Micromys minutus*	Rodentia	Muridae	8.9		14.2	33
Pygmy mouse	*Mus minutoides*	Rodentia	Muridae	4.7	17.45	13.96	44

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Mouse	*Mus musculus*	Rodentia	Muridae	38.2	45	43	33, 34, 48; R. Ferraris and J.M. Diamond, personal communication
Long-tailed deer mouse	*Peromyscus leucopus*	Rodentia	Muridae	25		39	43
Woodland deer mouse	*Peromyscus maniculatus*	Rodentia	Muridae	20		24	43
Laboratory rat	*Rattus norvegicus*	Rodentia	Muridae	305	95.1	119.2	4, 33-35, 49-53
House rat	*Rattus rattus*	Rodentia	Muridae	105.2	95.64		44
Four-striped grass mouse	*Rhabdomys pumilio*	Rodentia	Muridae	46.2	29.35	32.29	44
Acacia rat	*Thallomys paedulcus*	Rodentia	Muridae	55.2	31.3	36	44
Nutria	*Myocastor coypus*	Rodentia	Myocastoridae	5,358.4		1,040.1	33, 36, 54
Woodland dormouse	*Graphiurus murinus*	Rodentia	Myoxidae	20.9	17.01	17.01	44
Pouched mouse	*Saccostomus campestris*	Rodentia	Nesomyidae	82.9	38.93	51.78	44
Fat mouse	*Steatomys pratensis*	Rodentia	Nesomyidae	31.5	25.69	23.12	44
Ebien squirrel	*Epixerus ebii*	Rodentia	Sciuridae	560		208.5	32
Red squirrel	*Sciurus vulgaris*	Rodentia	Sciuridae	600	174	306.5	32, 34
Belding's ground squirrel	*Spermophilus beldingi*	Rodentia	Sciuridae	318	80		W.H.K., unpublished data
FLYING EUTHERIAN MAMMALS (BATS)							
Mariana sheath-tailed bat	*Emballonura semicaudata*	Chiroptera	Emballonuridae	7	9		55
Proboscis bat	*Rhynchonycteris naso*	Chiroptera	Emballonuridae	4	12		55
Black-bearded tomb bat	*Taphozous melanopogon*	Chiroptera	Emballonuridae	22.7	53.6		55
Yellow-winged bat	*Lavia frons*	Chiroptera	Megadermatidae	23.4	16.1		55

Species		Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Common name	**Scientific name**						
Greater false vampire bat	*Megaderma lyra*	Chiroptera	Megadermatidae	35.3	15.7		55
Lesser false vampire bat	*Megaderma spasma*	Chiroptera	Megadermatidae	23.8	11.5		55
Hairless bat	*Cheiromeles torquatus*	Chiroptera	Molossidae	168.5	34		55
Pallas's mastiff bat	*Molossus major*	Chiroptera	Molossidae	10.7	12.3		56
Egyptian free-tailed bat	*Tadarida aegyptiaca*	Chiroptera	Molossidae	17.7	16.6		55
Brazilian free-tailed bat	*Tadarida brasiliensis*	Chiroptera	Molossidae	11.2	15.95		57
Ghost-faced bat	*Mormoops megalophylla*	Chiroptera	Mormoopidae	15.3		7.15	58
Parnell's moustached bat	*Pteronotus parnellii*	Chiroptera	Mormoopidae	20.1	14.7	7.04	57, 58
Greater bulldog bat	*Noctilio leporinus*	Chiroptera	Noctilionidae	59.2	34.2		57
Large slit-faced bat	*Nycteris grandis*	Chiroptera	Nycteridae	29.4	24.3		55
Egyptian slit-faced bat	*Nycteris thebaica*	Chiroptera	Nycteridae	8.95	11.7		55
Geoffrey's hairy-legged bat	*Anoura geoffroyi*	Chiroptera	Phyllostomidae	15.5		7.37	58
Fringed fruit-eating bat	*Artibeus fimbriatus*	Chiroptera	Phyllostomidae	63.9	34.68		57
Jamaican fruit-eating bat	*Artibeus jamaicensis*	Chiroptera	Phyllostomidae	39.3	31.3		55
Great fruit-eating bat	*Artibeus lituratus*	Chiroptera	Phyllostomidae	69.6	42.18	28.7	57, This study
Antillean fruit-eating bat	*Brachyphylla cavernarum*	Chiroptera	Phyllostomidae	46.8	30.3		55
Silky short-tailed bat	*Carollia breviccauda*	Chiroptera	Phyllostomidae	17.2		7.5	58
Short-tailed bat	*Carollia perspicillata*	Chiroptera	Phyllostomidae	16.1	20.85		56, 57
Wrinkle-faced bat	*Centurio senex*	Chiroptera	Phyllostomidae	26		15.01	58

Table 2

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Salvin's big-eyed bat	*Chiroderma salvini*	Chiroptera	Phyllostomidae	25		11.77	58
Hairy big-eyed bat	*Chiroderma villosum*	Chiroptera	Phyllostomidae	24.8	37		55
Godman's long-tailed bat	*Choeroniscus godmani*	Chiroptera	Phyllostomidae	10.1		3.89	58
Big-eared woolly bat	*Chrotopterus auritus*	Chiroptera	Phyllostomidae	96.1	32		57
Toltec fruit-eating bat	*Dermanura tolteca*	Chiroptera	Phyllostomidae	15.2		7.76	58
Vampire bat	*Desmodus rotundus*	Chiroptera	Phyllostomidae	29	26.95	14.02	57, 58
Hairy-legged vampire bat	*Diphylla ecaudata*	Chiroptera	Phyllostomidae	27.8	20.5		57
Pallas's long-tongued bat	*Glossophaga soricina*	Chiroptera	Phyllostomidae	10.2	11.75		57
Lesser long-nosed bat	*Leptonycteris curasoae*	Chiroptera	Phyllostomidae	24.8	18	8.48	57, 58
Waterhouse's leaf-nosed bat	*Macrotus waterhousii*	Chiroptera	Phyllostomidae	18.9		7.59	58
Pale spear-nosed bat	*Phyllostomus discolor*	Chiroptera	Phyllostomidae	41.5		14.9	58
Greater spear-nosed bat	*Phyllostomus hastatus*	Chiroptera	Phyllostomidae	87.1	38		57
White-lined broad-nosed bat	*Platyrrhinus lineatus*	Chiroptera	Phyllostomidae	21.9	30.33		57
Greater broad-nosed bat	*Platyrrhinus vittatus*	Chiroptera	Phyllostomidae	36.6	36.2		55
Little yellow shouldered bat	*Sturnira lilium*	Chiroptera	Phyllostomidae	16.8 - 21.9	21.8	9.58	57, 58
Pygmy round-eared bat	*Toniata brasiliensis*	Chiroptera	Phyllostomidae	11.8		5.62	58
Fringe-lipped bat	*Trachops cirrhosus*	Chiroptera	Phyllostomidae	33.5		11.29	58
Little yellow-eared bat	*Vampyressa pusilla*	Chiroptera	Phyllostomidae	8.8	17.9		57
Great stripe-faced bat	*Vampyrodes caraccioli*	Chiroptera	Phyllostomidae	31		15.64	58

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm^2	Source
Straw-colored fruit bat	*Eidolon helvum*	Chiroptera	Pteropodidae	266.8	170		55
Lesser dawn bat	*Eonycteris spelaea*	Chiroptera	Pteropodidae	51.6	35		57
Wahlberg's epauletted fruit bat	*Epomophorus wahlbergi*	Chiroptera	Pteropodidae	76	73.3	76.49	59
Franquet's epauletted bat	*Epomops franqueti*	Chiroptera	Pteropodidae	118.3	80		55
Hammer-headed fruit bat	*Hypsignathus monstrosus*	Chiroptera	Pteropodidae	324.6	115		55
Angola fruit bat	*Lisonycteris angolensis*	Chiroptera	Pteropodidae	76.9	72.2	45.05	59
Black flying fox	*Pteropus alecto*	Chiroptera	Pteropodidae	540	163		60
Gray-headed flying fox	*Pteropus poliocephalus*	Chiroptera	Pteropodidae	630 – 645	169	215	57, 60, 61
Egyptian fruit bat	*Rousettus aegyptiacus*	Chiroptera	Pteropodidae	126 - 168.3	103.45	33.3	57, This study
Southern blossom bat	*Syconycteris australis*	Chiroptera	Pteropodidae	18.8	36.1		62
Trident leaf-nosed bat	*Asellia tridens*	Chiroptera	Rhinolophidae	12.8	11.7		55
Diadem roundleaf bat	*Hipposideros diadema*	Chiroptera	Rhinolophidae	43.6	24		55
Geoffroy's horseshoe bat	*Rhinolophus clivosus*	Chiroptera	Rhinolophidae	20.1	10.2		55
Greater horseshoe bat	*Rhinolophus ferrumequinum*	Chiroptera	Rhinolophidae	23.5	17.9		57
Lesser horseshoe bat	*Rhinolophus hipposideros*	Chiroptera	Rhinolophidae	4.6	8.05		55
Lesser mouse-tailed bat	*Rhinopoma hardwickei*	Chiroptera	Rhinopomatidae	12.9	5.27		55
Greater mouse-tailed bat	*Rhinopoma microphyllum*	Chiroptera	Rhinopomatidae	27.1	7.73		55
Big brown bat	*Eptesicus fuscus*	Chiroptera	Vespertilionidae	18		16	43
Serotine	*Eptesicus serotinus*	Chiroptera	Vespertilionidae	27	16.1		57
Eastern red bat	*Lasiurus borealis*	Chiroptera	Vespertilionidae	12.2	8		57

Species Common name	Scientific name	Order	Family	Body mass, g	SI length, cm	SI NSA, cm²	Source
Greater long-fingered bat	*Miniopterus inflatus*	Chiroptera	Vespertilionidae	8.9	19.6	9.13	59
Schreibers's long-fingered bat	*Miniopterus schreibersi*	Chiroptera	Vespertilionidae	10.9	15.97		57
Daubenton's bat	*Myotis daubentoni*	Chiroptera	Vespertilionidae	7.8	17.6		55
Mouse-eared bat	*Myotis myotis*	Chiroptera	Vespertilionidae	25	17.55		57
Whiskered bat	*Myotis mystacinus*	Chiroptera	Vespertilionidae	4.85	13		55
Natterer's bat	*Myotis nattereri*	Chiroptera	Vespertilionidae	7.15	14.8		55
Noctule bat	*Nyctalus noctula*	Chiroptera	Vespertilionidae	26	17.05		55
Kuhl's pipistrelle	*Pipistrellus kuhlii*	Chiroptera	Vespertilionidae	6.3	9.3		55
Common pipistrelle	*Pipistrellus pipistrellus*	Chiroptera	Vespertilionidae	6.6	9.6		57
Brown big-eared bat	*Plecotus auritus*	Chiroptera	Vespertilionidae	11.4	12		57
Lesser Asiatic yellow bat	*Scotophilus kuhlii*	Chiroptera	Vespertilionidae	19.6	20		55
Parti-colored bat	*Vespertilio murinus*	Chiroptera	Vespertilionidae	33.3	25.5		55

1. Wilson DE, Reeder DM (1993) *Mammal Species of the World: A Taxonomic and Geographic Reference* (Smithsonian Institution, Washington, DC), 2nd Ed.
2. Moorman TE, Baldassare GA, Richard DM (1992) *Condor* 94: 401-417.
3. DeGolier TF, Mahoney SA, Duke GE (1999) *Condor* 101: 622-634.
4. Lavin SR (2007) PhD thesis (University of Wisconsin, Madison).
5. Karasov WH (1990) *Stud Avian Biol* 13: 391-415.
6. Barnes GG, Thomas VG (1987) *Can J Zool* 65: 1812-1817.
7. Kehoe FP, Ankney CD (1985) *Can J Zool* 63: 2339-2342.
8. Verzar F, McDougall EJ (1936) *Absorption From the Intestine* (Longmans and Green, London).
9. Obst BS, Diamond JM (1989) *J Exp Zool Suppl* 3: 117-126.
10. Karasov WH, Afik D, Darken BW (1996) *Comp Biochem Physiol* 113A: 233-238.
11. Leopold AS (1953) *J Wildl Manag* 2: 197-203.
12. Christaki E, Babidis V, Florou-Paneri P, Kufidis D, Spais AB (1997) *Anim Feed Sci Tech* 65: 287-292.
13. Starck JM, Rahmaan GHA (2003) *J Exp Biol* 206: 1887-1897.

Caviedes-Vidal et al.

Table 2

14. Pulliainen E, Helle E, Tunkkari P (1981) *Orn Fenn* 58: 21-28.
15. Przystalski A (1985) *Zool Polon* 32: 14-21.
16. Ricklefs RE (1996) *Condor* 98: 279-292.
17. Davis J (1961) *Condor* 63: 313-321.
18. Martínez del Rio C, Brugger KE, Rios JL, Vergara ME, Witmer M (1995) *Physiol Zool* 68: 490-511.
19. Karasov WH. Levey DJ (1990) *Physiol Zool* 63: 1248-1270.
20. Przystalski A (1984) *Act Biol Cracov* 26: 89-99.
21. Herrera CM (1984) *Ecology* 65: 609-617.
22. Przystalski A (1986) *Zool Polon* 35: 5-20.
23. Afik D, Karasov WH (1995) *Ecology* 76: 2247-2257.
24. Afik D, Darken BW, Karasov WH (1997) *Physiol Zool* 70: 213-221.
25. Levey DJ, Place AR, Rey PJ, Martínez del Rio C (1999) *Physiol Biochem Zool* 72: 576-587.
26. Schondube JE, Martínez del Rio C (2004) *J Comp Physiol B* 174: 263-273.
27. Caviedes-Vidal E, Afik D, Martínez del Rio C, Karasov WH (2000) *Comp Biochem Physiol A-Mol Integr Physiol* 125: 11-24.
28. Przystalski A (1987) *Act Biol Cracov* 29: 93-104.
29. Hume ID, Biebach H (1996) *J Comp Physiol B* 166: 388-395.
30. Witmer MC, Martínez del Rio C (2001) *Physiol Biochem Zool* 74: 584-593.
31. Downs CT, van Dyk RJ, Iji P (2002) *Comp Biochem Physiol A* 133: 125-134.
32. Chivers DJ, Hladik CM (1980) *J Morph* 166: 337-386.
33. Snipes RL (1997) *Adv Anat Embry Cell Biol* 138: 1-88.
34. Pappenheimer JR (1998) *Comp Biochem Physiol* 121A: 45-58.
35. Anderson JH, Taylor AB (1973) *J Morph* 141: 281-291.
36. Snipes RL, Kriete A (1991) *Zeitschrift für Säugetierkunde* 56: 225-244.
37. Fahey GC, Merchen NR Jr, Corbin AK, Hamilton AK, Serbe KA, Hirakawa DA (1990) *J Anim Sci* 68: 4229-4235.
38. Fooden J (1964) *Am J Phys Anthropol* 22: 227-231.
39. Bruorton MR, Perrin MR (1991) *Zeitschrift für Säugetierkunde* 56: 65-71.
40. Young Owl M (1982) *Allometry in Primate Digestive Systems* (University of California, Los Angeles).
41. Marsh MN, Swift JA (1968) *Gut* 9: 727-728.
42. Wilson TH (1962) *Intestinal Absorption* (Saunders, Philadelphia).
43. Barry RE Jr (1976) *J Mammal* 57: 273-289.
44. Perrin MR, Curtis BA (1980) *S Afr J Zool* 15: 22-33.
45. Knight MH, Knight-Eloff AK (1987) *J Zool* 213: 7-22.
46. Karasov WH, Solberg DH, Diamond JM (1985) *Am J Physiol* 249: G271-G283.
47. Sakaguchi E, Itoh H, Uchida S, Horigome T (1987) *Br J Nutr* 58: 149-158.
48. Diamond JM, Karasov WH (1984) *J Physiol* 349: 419-440.
49. Wood HO (1944) *J Anat* 78: 103-105.

50.   Palay SL, Karlin LJ (1959) *J Biophys Biochem Cytol* 5: 373-383.
51.   Keegan DJ, Mödinger R (1979) *S Afr J Zool* 14: 220-223.
52.   Mayhew TM, Middleton C (1985) *J Anat* 141: 1-17.
53.   Clemens ET, Stevens CE (1980) *J Agric Sci* 94: 735-737.
54.   Sakaguchi E, Nabata A (1982) *Comp Biochem Physiol A* 103: 601-604.
55.   Jones KE, MacLarnon AM (2004) *Am Nat* 164: E20-E31.
56.   Klite PD (1965) *J Bacteriol* 90: 375-379.
57.   Cruz-Neto AP, Jones KE (2006) in *Functional and Evolutionary Ecology of Bats*, eds Zubaid A, McCracken G, Kunz TH (Oxford University Press, Oxford), pp 59-78.
58.   Schondube JE, Herrera-M. LG, Martínez del Rio C (2001) *Zool-Anal Compl Syst* 104: 59-73.
59.   Makanya AN, Maina JN, Mayhew TM, Tschanz SA, Burri PH (1997) *J Exp Biol* 200: 2415-2423.
60.   Tedman RA, Hall LS (1985) *Aust J Zool* 33: 625-640.
61.   Tedman RA, Hall LS (1985) *Aust Mammal* 8: 271-278.
62.   Law BS (1992) *Funct Ecol* 6: 257-264.