KIDNEY STRUCTURE IN NEOTROPICAL BATS

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ABSTRACT.—Renal indices involving the relative thickness of the medulla and inner medulla were determined for Neotropical representatives of all New World bat families. Renal morphology in bats is primarily a function of diet and secondarily related to environmental dehydration pressure. Bats that are primarily frugivorous or nectarivorous possess kidneys with relatively thin and undivided medullae; those species with other feeding preferences possess kidneys with relatively thick medullae, which are subdivided into inner and outer zones. Renal indices are similar between insectivorous bats inhabiting mesic and wet habitats but are lower than ones inhabiting arid regions. The statistical relationship between renal index and body weight is enigmatic in bats, but all species have renal indices that differ according to food habits.

Renal, fecal, and evaporative routes are the primary avenues through which water is lost from mammals. Of these, evaporative water loss is determined by water vapor pressure deficit, which bats regulate primarily by behavioral mechanisms centering around appropriate roost selection, intra-roost movements, and clustering (Licht and Leitner, 1967; Studier, 1970; Wilson, 1971; Studier and O'Farrell, 1972; Bassett and Wiebers, 1979, 1980). Fecal water loss has received little attention, but renal water conserving and dissipating capacities have been studied extensively (Carpenter, 1968; Vogel, 1969; Geluso, 1975, 1978, 1980).

Eight of the nine New World families of bats contain only or mainly insectivorous species (Wilson, 1973). Species within the Family Phyllostomidae, however, exhibit widely diverse feeding habits (Gardner, 1977). Renal form and function of insectivorous species, particularly in reference to renal concentrating abilities, have been given considerable coverage (Geluso, 1980). Noninsectivorous species have been given comparatively little attention (Wimsatt and Guerriere, 1962; Carpenter, 1968, 1969; McFarland and Wimsatt, 1969; Rosenbaum, 1970).

As shown in Geluso's (1980) review, studies of renal structure and function in insectivorous bats have dealt only with species that inhabit arid or moderately mesic environments. Further, previously studied species are nearly all residents of or migrants to northern temperate zones. Perhaps bats from humid tropical environments have been ignored on the premise that lack of dehydrating roost environments combined with readily available water would minimize selective pressure for renal water conservation.

Geluso (1978) demonstrated for temperate-zone, insectivorous bats that an excellent predictive relationship exists between the ratio of inner medullary (IM) thickness to cortical (C) thickness of the kidney and the mean maximum urine concentrating capacity of the species. A somewhat less predictive relationship also was shown for total medullary (M) thickness to C ratio. By comparing renal indices (IM/C or M/C) of Neotropical bats of different feeding habits with those from temperate zone insectivorous species, we can determine whether feeding habits or environmental dehydration pressure are more directly related to renal structure and, therefore, renal water conservation capacities.

MATERIALS AND METHODS

Preserved specimens of Neotropical bats were examined from the collections of the National Museum of Natural History. Species studied and collection sites, if other than Panama, include *Cormura brevirostris* (Panama and Nicaragua), *Saccopteryx bilineata*, *Molossus aztecus* (Chiapas, Mexico; El Salvador), *Pteronotus parnellii* (Panama and Colombia), *Rhogeessa tumida*, *Myotis nigricans*, *Thyroptera tricolor* (Panama, Colombia, and Ecuador), *Furipterus horrens* (British Guiana), *Natalus stramineus* (Brazil and Dominica; Sinaloa, Mexico), *Noctilio albiventris*, *Micronycteris hirsuta* (Panama and Trinidad), *Tonatia bidens* (Brazil, Trinidad, and British Guiana), *Mimon crenulatum* (Trinidad and Colombia), *Phyllostomus discolor*, *P.*

hastatus, Trachops cirrhosus, Vampyrum spectrum (Trinidad), *Desmodus rotundus, Glossophaga soricina, Carollia perspicillata, Uroderma bilobatum, Vampyrodes caraccioli, Artibeus phaeotis, A. jamaicensis* (Nayarit, Mexico), and *A. lituratus*. Additionally, several *Artibeus jamaicensis* mist-netted on the night of 17 May 1980 on Bohio Peninsula, Panama, by two of us (EHS and DEW) were sacrificed by intra-peritoneal injection of sodium pentobarbital, perfused through the left ventricle with buffered 10% formalin solution, and saved for histologic study. All collecting sites except Nayarit and Sinaloa, Mexico, represent wet tropical habitats.

We removed kidneys and the adrenal glands whenever possible and embedded them in paraffin using standard histologic techniques. Several sagittal sections were cut at 6 or 7 μM. Periodic sections were temporarily mounted on glass slides and scanned under dark field illumination until sections showing the greatest length of renal papilla were found. Sections from that region of the ribbons were mounted permanently and stained with hematoxylin and eosin (H&E) after incubation at 60°C for 1 h in saturated picric acid. This treatment was necessary because specimens held in preservative for extended periods of time would not stain with H&E alone.

Slides were projected with a microprojector, and sections scanned until those containing the area cribrosa were found. Measurements of thicknesses of cortex, entire medulla, inner and outer medulla were taken directly from the projected images as in Geluso (1978).

Results and Discussion

Renal morphologic indices and body weights of the non-phyllostomid, insectivorous species studied are summarized in Table 1. Renal indices, body weights, and feeding preferences of phyllostomid species whose kidneys were sectioned and measured are given in Table 2. Weights were taken from skin tags of specimens in the National Museum of Natural History except for weights of *Molossus aztecus* (=*coibensis*), *Myotis nigricans*, and *Natalus stramineus*, which are from Studier (1970). There were no differences in renal indices of either *Natalus stramineus* or *Artibeus jamaicensis* taken from humid Neotropical habitats when contrasted with individuals of these species collected in much drier habitats in Mexico. Therefore, data for these localities have been pooled for inclusion in Tables 1 and 2, respectively.

Table 1.—*Arithmetic means of renal indices (IM/C and M/C) and body weights (BW) for insectivorous New World bats excluding Phyllostomidae. N(I) = sample size for index determinations; N(wt) = sample size for weights; IM/C = inner medulla/cortex; M/C = medulla/cortex.*

Family/Species	N(I)	IM/C	M/C	BW(g)	N(wt)
Emballonuridae					
Cormura brevirostris	4	4.9	7.1	9.7	5
Saccopteryx bilineata	3	4.8	6.8	11.2	5
Molossidae					
Molossus aztecus	3	4.9	6.7	14.7	11
Mormoopidae					
Pteronotus parnellii	4	4.4	6.8	23.5	5
Vespertilionidae					
Rhogeessa tumida	4	5.2	7.1	5.2	3
Myotis nigricans	8	3.5	5.3	4.0	15
Thyropteridae					
Thyroptera tricolor	3	4.0	6.8	4.4	5
Furipteridae					
Furipterus horrens	1	4.2	6.2	3.0	2
Natalidae					
Natalus stramineus	5	4.2	6.0	5.5	9
Noctilionidae					
Noctilio albiventris	6	3.8	5.7	30.8	5

TABLE 2.—*Arithmetic means of renal indices (IM/C and M/C) and body weights for phyllostomid bats. Feeding habits (FH) from Gardner (1977) include I = insects; F = fruits; P = variety of plant parts; O = omnivorous; C = carnivorous; S = sanguinivorous.*

Subfamily/Species	*FH*	N(I)	IM/C	M/C	BW(g)	N(wt)
Phyllostominae						
Micronycteris hirsuta	I, F	4	2.8	4.4	14.3	5
Tonatia bidens	I, F	3	3.0	3.6	30.0	2
Mimon crenulatum	I	2	4.2	6.3	11.7	3
Phyllostomus discolor	O	6	1.8	2.9	44.6	5
P. hastatus	O	3	2.2	4.4	133.4	5
Trachops cirrhosus	O	4	3.1	4.8	32.7	5
Vampyrum spectrum	C	5	4.5	6.3	169.4	4
Desmodontinae						
Desmodus rotundus	S	4	4.8	7.2	32.8	5
Glossophaginae						
Glossophaga soricina	P, I	6		1.8	8.8	5
Carolliinae						
Carollia perspicillata	P, I	4		2.1	21.2	5
Stenodermatinae						
Uroderma bilobatum	F, I	6		2.0	16.6	5
Vampyrodes caraccioli	F	5		2.5	37.0	5
Artibeus phaeotis	F	3		2.2	13.6	5
A. jamaicensis	F, I	8		2.4	47.1	5
A. lituratus	P, I	5		2.2	69.4	5

Among the phyllostomids (Table 2), members of the primarily frugivorous and nectarivorous subfamilies Glossophaginae, Carolliinae, and Stenodermatinae possess renal medullae that cannot be readily subdivided into inner and outer zones. Thus, IM/C ratios cannot be determined for these species. Members of the phyllostomid subfamilies Phyllostominae and Desmodontinae, as well as all members thus far studied in all other New World bat families, do have renal medullae that are readily subdivided into zones, thus permitting the calculation of IM/C ratios for these species (Tables 1 and 2). Fig. 1, although not intended to show histologic detail, illustrates this point: The insectivorous vespertilionid, *Myotis nigricans*, has a divided renal medulla, but the frugivorous phyllostomid, *Artibeus jamaicensis*, has an undivided renal medulla.

Both renal indices show considerable variability within species. Some of this variability could be introduced by differences in orientation of kidneys in paraffin blocks prior to sectioning, although care was taken to avoid this problem. Much of the variability may relate to previously observed effects on renal morphology such as aging or long term dietary changes (for example, see Arataki, 1926; Lewis and Alving, 1938; Epstein, 1979; Johnson and Barrows, 1980; Bengele et al., 1981).

Results of Student-Newman-Keuls tests of the data in Tables 1 and 2 show that among Neotropical bats, the M/C ratio for frugivores (mean = 2.2; species = 7; range = 1.8–2.5) is lower than in other phyllostomids (mean = 4.7; species = 8; range = 2.9–7.2), which in turn is lower than the M/C ratio of non-phyllostomid insectivores (mean = 6.5; species = 10; range = 5.3–7.1). In each test $P < 0.001$.

In addition to differences in number of medullary zones among these Neotropical bats, species that are primarily frugivorous have the thinnest of medullae (Table 2). Those species that are solely insectivorous possess the thickest of medullae (Table 1). Also note that *Desmodus rotundus* (a blood feeder), *Vampyrum spectrum* (a carnivore), and *Mimon crenulatum* (an insectivore) have medullary thicknesses similar to insectivorous species (Table 2). The remaining phyllostomids with mixed diets have intermediate values. Animalivorous bats seem to require a kidney capable of excellent water conservation compared with that required by frugivorous bats.

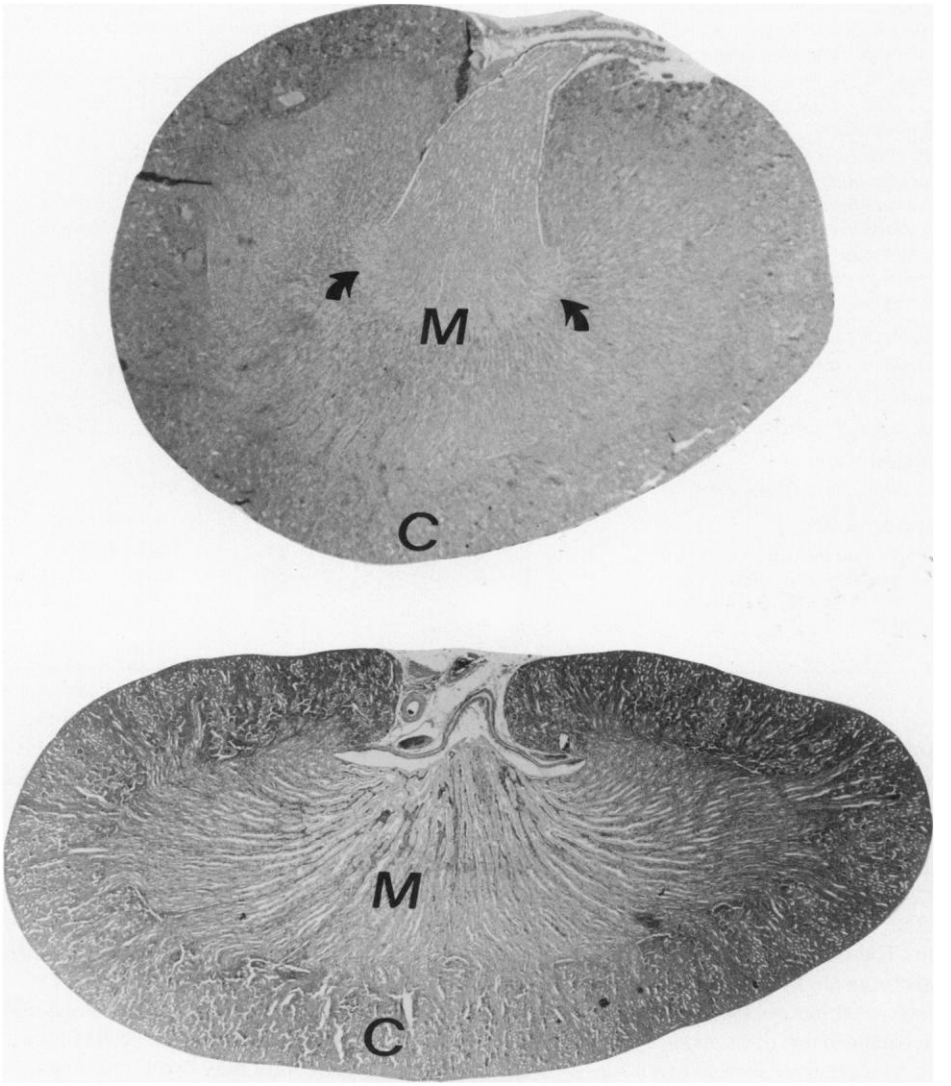

FIG. 1.—Midsagittal sections of the kidneys of an insectivorous vespertilionid, *Myotis nigricans* (above), with a medulla subdivided into inner and outer zones (arrows), and a frugivorous phyllostomid, *Artibeus jamaicensis*, with an undivided medulla (below). Both micrographs are 27×. Abbreviations are: C, cortex; M, medulla.

Sperber (1944) examined the kidneys of several bats and found that the frugivorous megachiropteran *Pteropus* possess medulla not subdivided into zones, whereas two insectivorous microchiropteran species have renal medullae that are readily separable into inner medullary (IM) and outer medullary (OM) regions. This observation led Sperber to postulate that megachiropterans possess a "two part" (medulla and cortex) kidney, whereas, microchiropterans possess a "three part" (cortex plus inner medulla and outer medulla) kidney. Table 2 shows that Sperber's postulate is not valid.

Among microchiropterans of the family Phyllostomidae, members of the subfamilies Carolliinae, Glossophaginae, and Stenodermatinae (the frugivores) possess two part kidneys whereas

TABLE 3.—*Renal indices (IM/C = inner medulla/cortex; and, M/C = total medulla/cortex) of insectivorous bats of various habitats. Values are arithmetic mean, range (in parentheses) and number of species represented in brackets. Data for xeric and mesic bats are taken from Geluso (1980).*

Habitat	IM/C	M/C
Xeric (desert)	6.6 (5.3–7.8) [5]	8.8 (7.5–9.9) [6]
Mesic (moist-temperate)	4.1 (3.2–4.7) [8]	5.8 (4.6–6.8) [9]
Wet (humid-tropical)	4.4 (2.8–5.2) [11]	6.4 (3.6–7.1) [11]

members of the subfamilies Phyllostominae and Desmodontinae possess three part kidneys (Table 2; see also Carpenter, 1969; McFarland and Wimsatt, 1969; Rosenbaum, 1970; Lu and Bleier, 1981). This dichotomy reflects the feeding habits of the two groups. Leaf-nosed bats with undivided renal medullae are vegetarian (frugivorous) species that feed on nectar, flowers, and fruit; and phyllostomids with subdivided renal medullae, although highly diverse in dietary habits, contain no species that are primarily vegetarians (Gardner, 1977). All non-phyllostomid New World bats thus far examined are insectivorous or piscivorous and have three part kidneys (see Tables 1 and 2 and Geluso, 1980). In short, frugivorous bats have undivided renal medullae whereas bats of other feeding preferences (omnivores, carnivores, insectivores, sanguinivores, and piscivores) possess medullae subdivided into inner and outer zones.

The anatomical basis for the subdivision of the medulla into inner and outer zones has never been demonstrated adequately. Our data show a definite relationship between this subdivision and concentrating ability (Studier and Wilson, in press). This argues strongly for a structural difference in the nephrons causing the clear demarcation between inner and outer zones. The line may represent the area where the tubules of juxtamedullary nephrons uniformly change from thick to thin. Thickness of the inner medulla would then be a relative measure of the length of the thin segments of the loops of Henle. It is these thin segments and the vasa recta associated with them that ultimately control urine concentration through the amount of sodium in the medulla (Rosenbaum, 1970). Perhaps those species with no clear line of demarcation have fewer juxtamedullary nephrons or juxtamedullary nephrons with variable length thin segments, which do not therefore form a distinct line. The detailed histological study necessary to test these hypotheses has yet to be done.

Renal indices of the insectivorous bats reviewed by Geluso (1980) and the insectivorous species included in Tables 1 and 2 are summarized in Table 3. Examination of Table 3 shows that tropical (humid-zone) insectivorous species have M/C and IM/C ratios similar to those of temperate (mesic) species and both have ratios substantially lower than species inhabiting temperate deserts.

Based on renal morphology, Neotropical insectivorous bats should be tolerant of generally drier habitats. However, renal and fecal water losses, which are primarily under physiological control, account for only a minor fraction of total water loss in insectivorous bats (Bassett, 1980). Pulmocutaneous water loss accounts for the great bulk of daily water loss. Evaporative water loss is determined primarily by the water vapor pressure deficit, which is poorly regulated by physiological mechanisms but extensively modified by behavioral activity through habitat selection and diurnal microhabitat selection movements (Licht and Leitner, 1967; Wilson, 1971). The invasion of generally drier habitats by Neotropical insectivorous bats, therefore, would not be limited by renal function but by the availability of roosting sites characterized by consistently high humidity. This is supported by observations that the northernmost roosting sites of *Natalus stramineus* and *Pteronotus parnellii* in Sonora, Mexico are characterized by standing water within the roosts or high water vapor pressures (Studier, 1970).

There was no difference in M/C ratios of Panamanian *A. jamaicensis* when compared to

M/C ratios of conspecifics inhabiting a much drier climate in Nayarit, Mexico. Similarly, the average renal indices (IM/C = 4.2; M/C = 5.9) of two *Natalus stramineus* collected from a generally much drier habitat in Sinaloa, Mexico are not different from the renal indices of Panamanian *Natalus*. Differences in renal ratios and urine concentrating capability have been shown between two populations of insectivorous bats (*Myotis lucifugus*) with those from drier habitats having higher renal ratios (Bassett, 1979) and better able to conserve urinary water (Bassett and Wiebers, 1979). Comparable differences have been demonstrated in other small mammals (Heisinger and Breitenbach, 1969; Blake, 1977). Based on the limited samples studied here, such renal anatomical adaptations do not occur in *A. jamaicensis* or *N. stramineus*.

Aside from free water in food, the primary dietary components that would most likely relate to renal structural modifications are dietary protein or mineral densities. Although specific ion concentrations differ greatly between plant and animal tissue fluids, total mineral levels are comparable (Altman and Dittmer, 1972; Rasweiler, 1977). Crude protein levels of animal tissues, however, are markedly higher than in plants (Altman and Dittmer, 1972; Rasweiler, 1977). Additionally, as pointed out by Rasweiler (1977), animal proteins generally have amino acid compositions that correspond more closely to mammalian requirements and may be more readily digestible than proteins of plant origin. Thus, among bats, the existence of a subdivided renal medulla probably relates to higher dietary protein density, with such a kidney expected in any bat that eats significant amounts of animal food.

An inverse relationship between M/C and weight has been shown for mammals having several dietary habits and encompassing a wide span of body weights (Greegor, 1975; Blake, 1977). Insectivorous bats from both xeric and mesic habitats exhibit M/C ratios that are markedly higher than predicted from the M/C ratio to weight relationship found in other insectivorous mammals (Geluso, 1980). Available data are insufficient to establish the existence of a relationship between M/C and body weight for insectivorous mammals other than bats from tropical humid habitats. M/C ratios of Neotropical insectivorous bats (Tables 1 and 2), however, all lie well above the relation derived by Geluso (1980) for moist temperate-zone insectivores other than bats. The abnormally high M/C ratios of insectivorous bats compared with those of other insectivorous mammals of the same weight suggest more efficient renal water conservation by bats. Geluso (1980) has suggested that this may offset high pulmonary water losses during flight and additional losses through wing membranes while flying or resting.

Although the relationship between M/C and body weight for mammals in general seems unequivocal, the picture within smaller subsets is less so. Geluso (1981) presented data for temperate zone insectivorous species that showed no significant correlation between M/C and body weight. Adding tropical insectivores increases the sample size and demonstrates that there are no differences between these two groups, but the slight positive relationship is not significant (Fig. 2). Note that *Mimon crenulatum*, the only completely insectivorous phyllostomine of those we examined (Table 2), falls clearly towards the center of the cluster of insectivorous species.

Adding the remainder of the animalivorous-omnivorous phyllostomids changes the regression to the expected inverse one seen in mammals as a whole, but it remains non-significant. *Desmodus rotundus*, a blood feeder, and the carnivorous *Vampyrum spectrum* have high M/C ratios in spite of heavy body weights. *Phyllostomus discolor* is the phyllostomine that is probably most frugivorous (Gardner, 1977). These bats are frequently captured with pollen covering their heads, suggesting some nectar and flower feeding as well. The kidney structure data lend support to this hypothesis, as they fall very close to the frugivorous group (Fig. 2).

When the fruit and flower feeders are added to the data set, the regression line for all species decreases in slope, and the regression coefficient ($r = 0.35$; $n = 52$) gains significance ($P < 0.01$). However, as can be seen in Figure 2, this significance is likely an artifact of comparing species across food habits. When the frugivorous species are analyzed separately, the relationship is again positive and non-significant. Note that *Glossophaga soricina*, the only nectar feeder in our sample, has the lowest M/C ratio of all of the species we have studied.

In summary, animalivorous bats in all New World bat families possess kidneys in which the

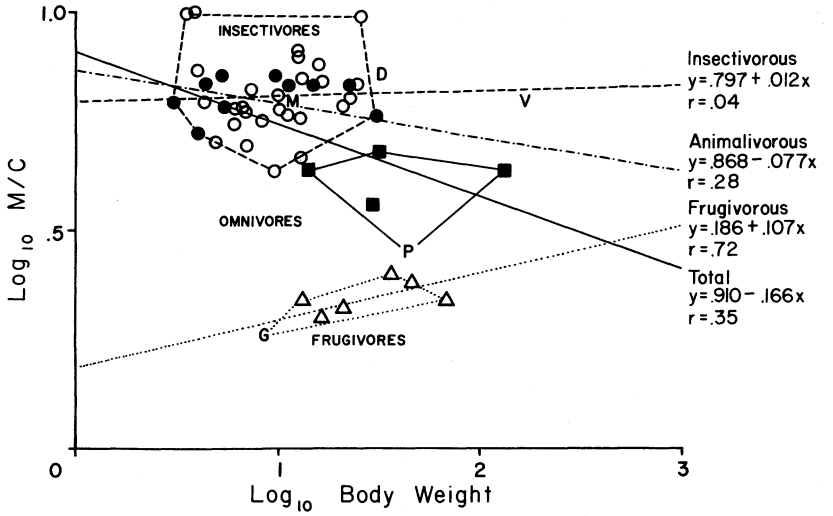

FIG. 2.—Regression analyses of the relationship between medulla/cortex ratio and body weight in bats. Open circles are temperate zone insectivores, closed circles are tropical insectivores, squares are omnivores, and triangles are frugivores, D = *Desmodus rotundus*, a blood feeder; G = *Glossophaga soricina*, a nectar feeder; M = *Mimon crenulatum*, an insectivore; P = *Phyllostomus discolor*, an omnivore; V = *Vampyrum spectrum*, a carnivore.

medullae have well-marked outer and inner zones. The renal index (M/C) of frugivorous bats is markedly lower than that of insectivorous species, independent of habitat. Among insectivorous bats, the renal index, IM/C is the same for Neotropical residents and species that inhabit mesic regions although the IM/C of bats inhabiting arid regions is significantly higher. In Neotropical bats, the M/C ratio may be related directly to dietary protein density. M/C ratios for frugivorous phyllostomids are less than those for non-frugivorous phyllostomids, whose ratios are less than those in non-phyllostomids (insectivores). The statistical relationship between renal index and body weight is enigmatic in bats but all species have renal indices that differ according to food habits. Renal morphology is primarily a function of diet and is less dependent on environmental dehydration pressure. The tolerance of more arid environments by Neotropical insectivorous bats does not seem limited by renal structure and function.

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