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NATURAL URINE CONCENTRATIONS AND COMPOSITION IN NEOTROPICAL BATS

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Abstract—1. Among neotropical bats with subdivided renal medullae, some natural urine samples are equal in concentration to mean maximum calculated levels.

2. Natural urine osmotic pressures in frugivorous phyllostomids are less than in other phyllostomids which, in turn, are less than in insectivorous bats.

3. Urinary sodium (Na^+) concentrations show no difference between frugivorous, insectivorous, and others, but urinary potassium (K^+) levels in frugivores are higher than in other bats.

4. Natural urine concentrations are primarily related to diet and secondarily to environmental dehydration pressure.

INTRODUCTION

With few exceptions, previous studies of kidney structure (see Geluso, 1980, for review) have dealt primarily with temperate zone insectivorous species that inhabit mesic or xeric environments. We have recently expanded available data on renal morphology of bats to include a large number of neotropical species of various feeding preferences that inhabit very moist environments (Studier *et al.*, 1983).

Again, with few exceptions, studies of renal function have dealt mostly with determination of maximal urine concentrating abilities and the relationship between renal morphology, maximal concentrating abilities and environmental stress (Geluso, 1980). Together with our recent extensive study of renal function in *Artibeus jamaicensis* (Studier *et al.*, 1983a), the present study extends available data on renal function to include neotropical species. The objectives of this study are to: (1) examine the extent to which neotropical bats concentrate their urine under natural conditions, (2) determine the relationship between renal morphology and natural urine concentrations, and (3) examine the potential relationship between dietary preference, environmental dehydration pressure, and natural urine concentration and composition.

MATERIALS AND METHODS

Urine samples were taken from a variety of bats in Panama in November 1979 and May 1980. One or more individuals of the following species were collected by mist nets on Barro Colorado Island (BCI) or the nearby Bohio Peninsula, at various times throughout the night—*Mimon crenulatum*, *Micronycteris hirsuta*, *M. schmidtorum*, *M. nicefori*, *Tonatia bidens*, *T. silvicola*, *Pteronotus parnelli*, *Carollia castanea*, *C. perspicillata*, *Glossophaga soricina*, *G. commissarisi*, *Desmodus rotundus*, *Phylloderma stenops*, *Phyllostomus hastatus*, *P. discolor*, *Trachops cirrhosus*, *Vampyrum spectrum*, *Artibeus phaeotis*, *A. jamaicensis*, *A. lituratus*, *A. watsoni*, *Vampyrodes carracioli*, *Uroderma bilobatum*, *Vampyrops helleri*, *Chiroderma villosum* and *Vampyressa pusila*. Data on *Artibeus jamaicensis* was reported elsewhere (Studier *et al.*, 1983). Six *Molossus aztecus* were collected at dawn (0600 hr local time) in a mist net placed over the entrance to a day roost. One *M. bondae* and many *Noctilio albiventris* were collected at sunset (1800 hr local time) with a hand net as they left a day roost under the roofing tiles of a pump house in Gamboa. One *Rhogeesa tumida* was caught in a Tuttle trap at night on BCI. One *Thyroptera tricolor* and 13 *Myotis nigricans* (seven in November, six in May) were collected by hand at various times throughout the day from day roosts on BCI. Five *Cormura brevirostris* were collected with hand nets at dawn from a day roost on BCI. Several *Saccopteryx bilineata* and *Micronycteris hirsuta* were collected by hand nets in mid-afternoon from day roosts on Orchid Island.

Urine samples were collected from *T. tricolor* and *M. nigricans* immediately upon capture because bats almost invariably urinate immediately upon being handled when captured in day roosts. A few urine samples were collected from mist-netted bats immediately upon capture. All other bats were placed in cloth bags (20 × 30 cm) for temporary holding. These bats were removed after 1/2–1 1/2 hr and usually urinated upon removal from the bag. Urine samples were analyzed for total osmotic pressure (= total concentration) with a Wescor vapor phase osmometer (Model 5100 B) as soon as possible after collection. Times between collection and analysis ranged from a few seconds to a few hours with most samples analyzed within a few minutes of collection. When urine samples were held for more than a few minutes before analysis, they were kept in small (0.5 ml), sealed microtubes (Coy Laboratory Products, Inc., Ann Arbor, MI). This precaution, together with the normal high humidity in Panama, permitted only negligible evaporation of urine samples prior to testing. When urine samples were sufficiently large, aliquots were diluted for analysis of Na^+ and K^+ concentrations with a Perkin–Elmer (Coleman 51) flame photometer. Some of the urine taken in the November sampling was diluted for determination of urinary ammonia and urea nitrogen levels (Connerty *et al.*, 1955).

A few bats were used in dehydration/starvation experiments as described by Studier *et al.* (1983a) for *Artibeus jamaicensis*.

Table 1. Natural urine osmotic pressures (mOsm/kg) of some Panamanian, frugivorous, phyllostomid bats

Species	Month	N	(♂/♀)	$\bar{X}$	SE	(Range)
Carollia castanea	May	4	(4/0)	806	146	(422–1131)
C. perspicillata	Nov.	1	(1/0)	238		
	May	19	(10/9)	742	67	(271–1189)
Glossophaga soricina	May	1	(1/0)	832		
G. commissarisi	May	2	(2/0)	744		(478–1010)
Artibeus phaeotis	May	9	(3/6)	655	51	(379–922)
A. lituratus	May	10	(5/5)	454	53	(132–699)
	Nov.	8	(3/5)	497	74	(56–766)
A. watsoni	May	2	(0/2)	519		(369–668)
Vampyrodes caraccioli	May	9	(5/4)	645	56	(342–840)
	Nov.	3	(2/1)	484		(312–714)
Uroderma bilobatum	May	5	(1/4)	456	118	(195–844)
	Nov.	8	(2/6)	530	60	(254–749)
Vampyrops helleri	May	2	(0/2)	488		(365–610)
Chiroderma villosum	May	3	(2/1)	553		(481–491)
Vampyressa pusilla	May	2	(0/2)	359		(168–550)

RESULTS

Data on natural urine of neotropical bats have been subdivided to correspond to significant differences in renal morphology (Studier *et al.*, 1983b). Accordingly, data on urine osmotic pressure in frugivorous phyllostomids are presented in Table 1, non-frugivorous phyllostomids in Table 2, and non-phyllostomid, insectivorous bats in Table 3. There are no significant differences in urine osmotic pressures between May and November samples for those species in which sample sizes are large enough for comparison (*Artibeus lituratus*, *Vampyrodes carracioli* and *Uroderma bilobatum* from Table 1, and *Myotis nigricans* from Table 3).

Urinary sodium and potassium concentrations in neotropical bats are summarized in Table 4. Because there were no significant differences in the levels of these ions between the May and November samples, data are pooled. Urinary ammonia and urea nitrogen levels are given in Table 5.

Preliminary dehydration/starvation experiments with small numbers of two species of frugivorous phyllostomid bats showed that six (2♀/4♂) *Carollia perspecillata* produced urine of highest concentration after 21–29 hr without food or water with average urine osmotic pressure reaching 1090 mOsm/kg (SEM = 16; N = 6; range = 1045–1137) and two male *Artibeus lituratus* produced maximally concentrated urine after 23–24 hr without food or water when urine osmotic pressure reached 784 and 809 mOsm/kg.

DISCUSSION

The collection of urine from live-trapped animals that have been held briefly in captivity was shown to yield samples that do not reflect either total or component concentrations present in urine in free-living

Table 2. Natural urine osmotic pressures (mOsm/kg) of some Panamanian, non-frugivorous, phyllostomid bats

Species	Month	N	(♂/♀)	$\bar{X}$	SE	(Range)
Desmodus rotundus	Nov.	1	(1/0)	3550		
	May	1	(0/1)	1146		
Phylloderma stenops	Nov.	1	(1/0)	230		
	May	1	(0/1)	1978		
Phyllostomus hastatus	Nov.	1	(0/1)	44		
	May	7	(5/2)	1143	63	(858–1359)
P. discolor	Nov.	1	(0/1)	370		
	May	5	(2/3)	728	80	(428–911)
Trachops cirrhosus	May	4	(2/2)	1926	225	(1481–2552)
Vampyrum spectrum	Nov.	1	(1/0)	2198		
Micronycteris hirsuta	Nov.	1	(1/0)	1879		
	May	7	(5/2)	1948	131	(1332–2418)
M. schmidtorum	May	2	(2/0)	2004		(1202–2806)
M. nicefori	May	3	(1/2)	1638		(1036–2059)
Mimon crenulatum	May	1	(1/0)	2852		
Tonatia bidens	Nov.	1	(0/1)	1944		
	May	2	(1/1)	1622		(1852–2392)
T. silvicola	May	1	(0/1)	2370		

Table 3. Natural urine osmotic pressures (mOsm/kg) of some Panamanian, non-phyllostomid, insectivorous bats

Species	Month	N	(♂/♀)	$\bar{X}$	SE	(Range)
Cormura brevirostris	May	2	(0/2)	2735		(2010–3460)
Saccopteryx bilineata	May	6	(1/5)	2122	146	(1656–2540)
Molossus aztecus	May	6	(1/5)	3171	81	(2906–3394)
M. bondae	May	1	(1/0)	1703		
Pteronotus parnelli	May	6	(1/5)	1666	265	(1050–2808)
Rhogeesa tumida	May	1	(1/0)	2328		
Myotis nigricans	Nov.	7	(4/3)	1598	241	(1140–2048)
	May	6	(5/1)	1754	286	(918–2916)
Thyroptera tricolor	May	1	(1/0)	1551		
Noctilio albiventris	May	7	(5/2)	2694	119	(2180–3178)

Table 4. Levels of urinary sodium (Na^+) and potassium (K^+) in mEq/l in some neotropical bats

Species	N	Na^+	K^+
Carollia perspicillata	12	14.5 ± 4.1 (2.0–48.0)	58.7 ± 10.7 (14.0–131.0)
C. castanea	3	17.2 ± 9.4 (7.0–36.0)	73.0 ± 26.1 (38.0–124.0)
Vampyrops helleri	1	53.0	47.0
Chiroderma villosum	2	36.0 (35.5–36.5)	81.0 (65.0–97.0)
Artibeus phaeotis	5	19.9 ± 10.7 (6.0–62.5)	63.6 ± 10.0 (33.0–89)
A. lituratus	16	12.4 ± 2.5 (3.0–38.0)	81.8 ± 15.2 (5.0–212.0)
Vampyrodes carracioli	7	7.2 ± 1.8 (2.0–16.0)	111.7 ± 16.6 (81.0–210.0)
Uroderma bilobatum	10	15.8 ± 4.1 (2.0–38.0)	90.0 ± 18.4 (27.0–210.0)
Vampyressa pusilla	1	5.0	33.0
Phylloderma stenops	2	25 (3.0–4.7)	26.5 (11.0–42.0)
Phyllostomus hastatus	8	9.2 ± 2.6 (2.5–26.0)	20.9 ± 3.6 (7.0–36.0)
P. discolor	3	4.8 ± 1.0 (3.0–6.5)	34.7 ± 15.9 (3.0–53.0)
Trachops cirrhosus	2	24.2 (11.0–37.5)	42.0 (35.0–49.0)
Micronycteris hirsuta	4	12.5 ± 4.1 (5.0–20.0)	56.0 ± 13.2 (31.0–90.0)
Tonatia bidens	3	6.3 ± 2.6 (1.5–10.5)	80.7 ± 42.2 (27.0–164.0)
T. silvicola	1	3.0	32.0
Mimon crenulatum	1	15.5	101.0
Myotis nigricans	5	44.6 ± 9.9 (16.0–74.0)	81.2 ± 20.6 (41.0–144.0)
Molossus aztecus	3	22.8 ± 2.9 (17.0–26.0)	61.0 ± 8.1 (45.0–71.0)
Noctilio albiventris	2	10.5 (6.0–15.0)	22.5 (16.0–29.0)
Pteronus parnelli	6	5.8 ± 1.1 (3.0–9.5)	27.0 ± 3.2 (19.0–37.0)

May and November urine samples are lumped. Values given are mean ± SEM. Range is in parentheses

red squirrels (Bakko, 1977). Methods that are generally useful in collection of natural urine from small mammals were recently reviewed by Studier & Rimle (1980). They showed that temporary holding of big brown bats (*Eptesicus fuscus*) had no discernible effect on total urine or component concentrations. There were no differences in total or component concentrations of urine collected immediately from bats and those held briefly in cloth bags prior to urine collection for any of the species reported here (see also Studier *et al.*, 1983a).

A relationship between various indices of renal morphology and maximal urine concentrating ability is well established for mammals (Sperber, 1944; Brownfield & Wunder, 1976). For insectivorous bats, Geluso (1978) demonstrated that renal indices involved with medullary thickness are highly correlated with maximum concentrating ability; the best predictors being the ratio of the inner medullar zone to cortex (IM/C) and ratio of medulla to cortex (M/C). Our previous observation that renal indices of frugivorous species are less than those of other phyllostomids, which are lower than those of insectivorous bats (Studier *et al.*, 1983b), argues for parallel differences in maximal urine concentrating abilities in

Table 5. Urinary ammonia and urea nitrogen (N level in mg %) level for some neotropical bats collected in November

Species	N	N level
Artibeus jamaicensis	19	495 ± 115 (12–1794)
A. lituratus	5	519 ± 260 (19–1453)
Uroderma bilobatum	2	205 (147–263)
Carollia perspicillata	1	234
Phyllostomus discolor	1	1629
P. hastatus	1	3
Phylloderma stenops	1	534
Desmodus rotundus	1	8337
Myotis nigricans	4	1887 ± 106 (1674–2084)

Values are mean ± SEM with range in parentheses. Values for *Artibeus jamaicensis* are from Studier *et al.* (1983a)

these three groups. A Student–Newman–Keuls (SNK) analysis of the data on natural urine concentrations given in Tables 1, 2 and 3 yields significant differences ($P < 0.001$ in each case) between each group.

Mean urine osmotic pressure of naturally collected urine in insectivores (2172 mOsm/kg for 43 samples from 9 species) is higher than that of non-frugivorous phyllostomids (1580 mOsm/kg for 41 samples from 12 species) which is, in turn, higher than the mean urine osmotic pressure in frugivorous species (557 mOsm/kg for 148 samples from 13 species).

As suggested earlier by Studier *et al.* (1983b), based on renal morphology, these three groupings are best explained by differences in normal dietary protein density and perhaps to differences in preformed water in the food. The frugivorous phyllostomids (subfamilies Carolliinae, Glossophaginae and Stenodermatinae) feed primarily on nectar, flowers or fruit, and the non-frugivorous phyllostomids (subfamilies Phyllostominae and Desmodontinae), although highly diverse in dietary habits, all routinely consume food of animal origin and contain no species that are primarily frugivorous (Gardner, 1977). The non-phyllostomid insectivorous bats feed, of course, on insects (Wilson, 1973). Rasweiler (1977) tabulated nutritional data on many foods consumed by bats and found protein levels in animal tissues to be much higher than in plant tissues. He also pointed out that animal proteins have amino acid compositions that correspond more closely to mammalian requirements and may be more readily digestible than proteins of plant origin. It is unlikely that dietary mineral densities would exert a selective pressure relative to maximal urine concentrating abilities. Whereas specific ion concentrations (especially sodium and potassium) differ markedly, total mineral levels of plant and animal tissue fluid are comparable (Altman & Dittmer, 1972; Rasweiler, 1977).

Geluso (1980) presented a highly predictive equation relating mean maximum urine concentrating abilities of insectivorous bats to renal indices (IM/C or M/C) in which mean maximum urine osmolality (mOsm/kg) = 658 + 558 (IM/C) or = 702 + 387 (M/C). He further suggested that these relationships apply only to insectivorous bats. Renal index (M/C) and maximum urine concentration values in the nectarivore, *Leptonycteris sanborni*, from Carpenter (1969) and in the frugivore, *Artibeus jamaicensis*, from Studier *et al.* (1983a, 1983b) fall well below those derived by Geluso's equations. His equations, then, do not apply to those phyllostomids with undivided renal medullae (Studier *et al.*, 1983b).

Table 6 compares our measured maximum osmotic pressure for natural urine samples with the expected mean maximum level estimated by Geluso's (1980) equation. Only those neotropical species with a subdivided renal medulla are included (Studier *et al.*, 1983b). Several of the species are not insectivorous (Wilson, 1973). Figure 1 compares natural urine maximum concentrations to expected levels based on the renal index, IM/C, using Geluso's (1980) equation. It is apparent in Fig. 1 that for nearly all species where sufficient samples were taken, natural and expected urine maxima are equal. Points 8 (*Rhogeesa tumida*), 10 (*Thyroptera tricolor*) and 16 (*Vampyrum spectrum*) are species represented by a single urine sample.

Table 6. Mean maximum urine concentrations predicted from ratio of inner medulla:cortex and actual maximum concentration values in natural urine of neotropical bats with subdivided renal medullae

Species	Exp. max.	Act. max.	*N*
Cormura brevirostris	3409	3460	2
Saccopteryx bilineata	3353	2540	6
Mimon crenulatum	3002	2852	1
Micronycteris hirsuta	2209	2418	8
Tonatia bidens	2315	2392	3
Molossus aztecus	3364	3394	6
Pteronotus parnelli	3085	2808	6
Rhogeessa tumida	3560	2328	1
Myotis nigricans	2600	2916	13
Thyroptera tricolor	2879	1552	1
Noctilio albiventris	2795	3178	7
Desmodus rotundus	3336	3550	2
Phyllostomus hastatus	1886	1359	8
P. discolor	1662	911	6
Trachops cirrhosus	2388	2552	4
Vampyrum spectrum	3169	2198	1

Concentrations are expressed in mOsm/kg. Sample size (*N*) is the total number of natural urine samples collected.

Points 13 and 14 represent species (*Phyllostomus hastatus* and *P. discolor*) that are truly omnivorous (Gardner, 1977). Data shown in Fig. 1, therefore, provide some support for expanding Geluso's (1980) equation relating mean maximal renal concentrating abilities to IM/C in insectivorous bats to include all bats with a subdivided renal medulla, regardless of feeding habits. Furthermore, it seems that most species with a subdivided renal medulla produced

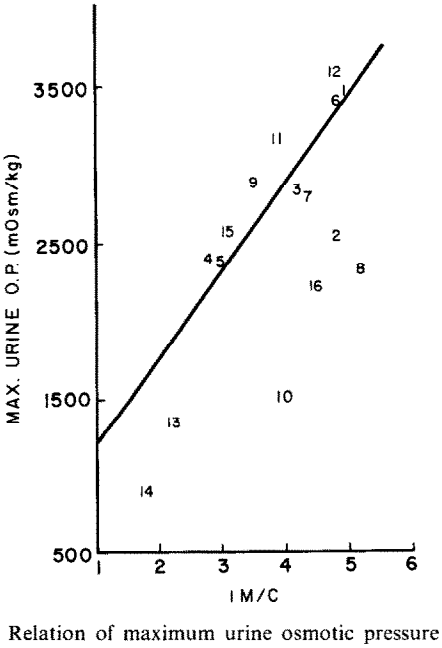

Fig. 1. Relation of maximum urine osmotic pressure and IM/C in insectivorous bats (solid line) from Geluso (1978). Numbers show maximum natural urine concentrations for species listed in Table 6. Renal indices are from Studier *et al.* (1983a).

urine, at some time in the day, that is equal in concentration to their maximum capabilities. As previously discussed, the production of such highly concentrated urine probably relates to dietary protein density. Thus, insectivorous species (numbers 1–11 in Fig. 1), a sanguinivorous species (*Desmodus rotundus*, number 12 in Fig. 1) and a carnivorous species (*Trachops cirrhosus*, number 15 in Fig. 1), all of which consistently consume high-protein diets, produce maximally concentrated urine to eliminate the large dietary nitrogen load. We assume that the consumption of both plant and animal food by the two species of *Phyllostomus* represents an intermediate dietary protein load and does not require the production of maximally concentrated urine.

It seems that non-omnivorous, neotropical bats with a subdivided renal medulla have little or no reserve renal concentrating capacity and probably could not tolerate increased dietary protein density or environmental change that would markedly increase habitat dehydration stress. A similar situation exists for at least one temperate zone bat, *Myotis lucifugus* (Geluso & Studier, 1979), which in New Mexico produces natural urine equal in concentration to its mean maximum. For another, *Eptescus fuscus* (Studier & Rimle, 1980), natural urine concentrations fall well below their expected mean maximum. The latter statement assumes that the renal index of *Eptesicus fuscus* is identical for bats from Michigan and New Mexico. We believe that both structural and functional renal adaptations for water conservation throughout the geographic ranges of species of bats should reflect the most extreme conditions of water availability and dehydration stress that will exist over time periods measured in units of at least decades. Thus bats occupying temperate, mesic environments would be expected to possess greater renal water conserving reserves than bats in Panama where water availability and dehydration stress is less variable.

It is, then, not surprising that neotropical frugivorous bats, which possess an undivided renal medulla, produce relatively dilute urine and are poorly adapted to produce urine of high osmotic pressure (Carpenter, 1969; Studier *et al.*, 1983a). Their foods are readily available and of low protein density and high water content, and environmental dehydration stress is not so variable. As indicated by Gardner (1977), neotropical frugivorous bats, especially glossophagine and carolliine species, do erratically consume some insects precipitating a discussion of whether the ingestion of insects is purposeful or accidental. In view of these dietary observations, it is useful to note that several urine samples collected from *Carollia* spp. (6 of 23) and *Glossophaga* spp. (1 of 3) in May exceeded 1000 mOsm/kg. These levels far exceed the average natural urine concentration (557 mOsm/kg) found for frugivorous bats. During May, these species consume significant numbers of insects (see Fig. 3, Fleming *et al.*, 1972), adult females are in late pregnancy or lactation, and volant young are rapidly growing (Fig. 4, Fleming *et al.*, 1972). We suggest that insects are purposefully ingested by these species during those portions of the reproductive cycle when protein synthesis involved in embryonic or neonatal growth, and milk synthesis is high. The ingestion of foods of high dietary protein density is then reflected by the production of highly concentrated urine.

Sodium and potassium balance of the frugivorous phyllostomid, *Artibeus jamaicensis*, was discussed by Studier *et al.* (1983a). Total mineral densities ingested by frugivores and insectivores are probably comparable; however, the ingested loads of specific ions, particularly sodium and potassium, are extremely different. For frugivores, dietary sodium density is very low while potassium density is very high. For insectivores, dietary sodium density is much higher and potassium density somewhat lower. These dietary differences might well be expected to reappear in similar concentrations in the urine of bats of different dietary preferences. Urinary sodium and potassium concentrations for the species studied are summarized in Table 4. An SNK analysis of urinary sodium levels shows no differences between frugivores (15.4 mEq/l for 54 samples from 8 species), non-frugivorous phyllostomids (14.7 mEq/l for 26 samples from 9 species), and non-phyllostomid insectivores (21.7 mEq/l for 16 samples from 4 species). An SNK analysis of urinary potassium levels, however, shows urinary potassium concentration of frugivores (80.3 mEq/l for 54 samples from 8 species) to be significantly higher ($P < 0.005$) than that of non-frugivorous phyllostomids (41.4 mEq/l for 26 samples from 9 species) and also higher ($P < 0.05$) than that of non-phyllostomid insectivores (49.8 mEq/l for 16 samples from 4 species). There is no significant difference in urinary potassium concentrations in the latter two groups. Urinary mineral (Na^+ and K^+) densities of frugivores, therefore, are reflective of dietary mineral densities but urinary mineral densities of insectivores are not. This observation suggests that strategies for maintenance of sodium and potassium balance in frugivores may differ from those of insectivores. Frugivores seem to use rapid and efficient assimilation of these minerals at the intestinal epithelium (supported also by mineral loading experiments with *Artibeus jamaicensis* by Studier *et al.*, 1983a) with renal regulation of significance in retention of sodium and loss of potassium. Unless sodium and potassium are sequestered in the body, in insectivorous species these ions would appear to be assimilated much more slowly and selectively at the level of intestinal epithelium leading to a lesser rate of sodium and potassium influx followed by renal sodium reclamation and potassium excretion.

The limited urinary ammonia and urea nitrogen data summarized in Table 5 further support the relationship between dietary protein density, urine osmotic pressure, and urinary ammonia and urea nitrogen levels. Although too few data are available for analysis, the frugivorous species ingest low protein density foods and produce the most dilute urine, which contains little ammonia and urea nitrogen. The insectivorous species (*Myotis nigricans*) ingests a high protein diet and produces concentrated urine high in ammonia and urea nitrogen. The non-frugivorous phyllostomids have diets of variable protein density in which protein level is directly related to urinary concentration and ammonia and urea nitrogen level. A few anecdotal observations provide additional support. The only reference to the feeding habits of *Phylloderma stenops* is the ingestion of the larvae and pupae of a social wasp (Jeanne, 1970), although

Gardner (1977) suggests that they also consume plant material. This was certainly true of the single individual taken in November (Table 5). While being held in a cloth bag prior to urine collection, this individual defecated a very large number of seeds (*Passiflora ambigua*), indicating the very recent ingestion of fruit. Its urine osmotic pressure was very low (230 mOsm/kg), and contained little ammonia or urea nitrogen (534 mg%). The single *Phyllostomus hastatus* taken in November was coated with pollen, indicating the recent ingestion of nectar; this bat produced an unmeasured but very large volume of urine. Its urine osmotic pressure was the lowest measured for any individual (44 mOsm/kg) and contained the least ammonia and urea nitrogen (3.0 mg%). At the other end of the spectrum, the single vampire sampled in November produced urine of highest total concentration (3550 mOsm/kg) and highest ammonia and urea nitrogen level (8337 mg%) of any individual examined.

Dehydration/starvation experiments with *A. jamaicensis* (Studier *et al.*, 1983a) did not cause individuals of that species to form maximally concentrated urine. In limited studies with *Carollia perspicillata*, urine became maximally concentrated, after approximately one day without food or water, at 1090 mOsm/kg, approximating the maximum osmotic pressure for natural urine (Table 1). *Carollia*, then, with an M/C ratio of 2.1 (Studier *et al.*, 1983b) can produce urine considerably more concentrated than that of *Artibeus jamaicensis*, which has an M/C of 2.4 and produces maximally concentrated urine of 972 mOsm/kg (Studier *et al.*, 1983a, 1983b) when feeding on dehydrated figs. *Glossophaga*, with an M/C ratio of 1.8, also is capable of producing urine that is more concentrated than the maximum level attained by *A. jamaicensis*. Unlike results for *A. jamaicensis*, urine produced by *A. lituratus* after approximately one day without food or water was more concentrated than any natural urine samples. We suspect that dehydration/starvation stress, as with *Artibeus jamaicensis* (Studier *et al.*, 1983a), did not force these frugivores to produce maximally concentrated urine. The existence of a relationship between M/C and maximum urine concentrating ability of bats that possess an undivided medulla remains to be established. Major hindrances in establishing such a relationship, if it indeed exists, is the very small range of M/C values and the difficulty in determining maximal urine concentrating abilities in these species.

In summary, natural urine of frugivorous phyllostomids is less concentrated than that of non-frugivorous phyllostomids, which is less concentrated than urine of non-phyllostomid, insectivorous bats. Osmotic pressure of natural urine relates directly to dietary protein density. Geluso's (1980) equation relating mean maximum urine concentrating abilities in xeric- and mesic-zone insectivorous bats to renal indices seems to hold for any bats that possess subdivided renal medullae and regularly ingest food of animal origin. Included are all New World non-phyllostomids and those phyllostomids in the subfamilies Phyllostominae and Desmodontinae. Some natural urine samples within each species of such bats are equal in concentration to their mean maximum urine concentrations. These bats, therefore, possess no reserve renal concentrating or water retention capacity. Urine concentrating abilities are primarily a function of diet and are less dependent on environmental dehydration pressure. The invasion of more arid environments by neotropical bats with subdivided renal medullae does not seem limited by renal function.

Geluso's (1980) equation does not hold for bats with undivided renal medullae (phyllostomids in the subfamilies Carolliinae, Glossophaginae and Stenoderminae). The possible existence of a relation between the renal index M/C and mean maximum urine concentrating ability in bats with undivided renal medullae has yet to be established.

Average urinary sodium concentrations show no differences between frugivorous phyllostomids, non-frugivorous phyllostomids and non-phyllostomids. Average urinary potassium levels of frugivorous phyllostomids are, however, significantly higher than in both non-frugivorous phyllostomids and non-phyllostomids, which are not different from each other. Relative to mineral balance, frugivorous bats seem to use rapid and extremely efficient assimilation of dietary minerals with renal regulation of lesser importance whereas insectivorous species seem to assimilate dietary minerals less readily and utilize a greater range of renal regulation. Urinary ammonia and urea nitrogen levels are directly related to normal dietary protein density.

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REFERENCES

ALTMAN P. L. & DITTMER D. S. (1972) *Biology Data Book*, 2nd edn, Vol. 1. Fed. Amer. Soc. Exptl. Biol., Bethesda.

BAKKO E. B. (1977) Influence of collecting techniques on estimate of natural renal function in red squirrels. *Am. Midl. Nat.* **97**, 502–504.

BROWNFIELD M. S. & WUNDER B. A. (1976) Relative medullary area: a new structural index for estimating urinary concentrating capacity of mammals. *Comp. Biochem. Physiol.* **55**, 69–75.

CARPENTER R. E. (1969) Structure and function of the kidney and the water balance of desert bats. *Physiol. Zool.* **42**, 288–302.

CONNERTY H. V., BRIGGS A. R. & EATON E. H., JR (1955) Determination of blood urea nitrogen using a simple stabilizing agent. *Am. J. clin. Path.* **25**, 1321–1325.

FLEMING T. H., HOOPER E. T. & WILSON D. E. (1972) Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology* **53**, 555–569.

GARDNER A. L. (1977) Feeding habits. In *Biology of Bats of the New World Family Phyllostomatidae*. Part III (Edited by BAKER R. J., JONES J. K., JR & CARTER D. C.), pp. 293–350. Special Publ. No. 13, The Museum, Texas Tech. University, Lubbock.

GELUSO K. N. (1978) Urine concentrating ability and renal structure of insectivorous bats. *J. Mammal.* **59**, 312–323.

GELUSO K. N. (1980) Renal form and function in bats: an ecophysiological appraisal. In *Proceedings Fifth International Bat Research Conference* (Edited by WILSON D. E. & GARDNER A. L.), pp. 403–414. Texas Tech. Press, Lubbock.

GELUSO K. N. & STUDIER E. H. (1979) Diurnal fluctuation in urine concentration in the little brown bat, *Myotis lucifugus*, in a natural roost. *Comp. Biochem. Physiol.* **62A**, 471–473.

JEANNE R. L. (1970) Note on a bat (*Phylloderma stenops*) preying upon the brood of a social wasp. *J. Mammal.* **51**, 624–625.

RASWEILER J. J. IV (1977) The care and management of bats as laboratory animals. In *The Biology of Bats*, Vol. III (Edited by WIMSATT W. A.), pp. 519–617. Academic Press, New York.

SPERBER I. (1944) Studies on the mammalian kidney. *Zool. Bidr. Upps.* **22**, 249–431.

STUDIER E. H. & RIMLE D. A. (1980) Concentration and composition of natural urine of some Michigan small mammals. *Comp. Biochem. Physiol.* **67A**, 163–165.

STUDIER E. H., BOYD B. C., FELDMAN A. T., DAPSON R. W. & WILSON D. E. (1983a) Renal function in the Neotropical bat *Artibeus jamaicensis*. *Comp. Biochem. Physiol.* **74A**, 199–209.

STUDIER E. H., WISNIEWSKI S. J., FELDMAN A. T., DAPSON R. W., BOYD B. C. & WILSON D. E. (1983b) Kidney structure in Neotropical bats. *J. Mammal.*, in press.

WILSON D. E. (1973) Bat Faunas: A trophic comparison. *Syst. Zool.* **22**, 14–29.