RENAL FUNCTION IN THE NEOTROPICAL BAT,
ARTIBEUS JAMAICENSIS

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Abstract—1. When feeding on figs (*Ficus insipida*), the bat *Artibeus jamaicensis* increases dietary sodium density while decreasing potassium density by primarily extracting and ingesting pulp juices rather than other parts of the fruit.

2. Based on urine osmotic pressure, these bats are uniformly dehydrated when they leave day roosts and become rapidly rehydrated (0.5–1 hr) after initiation of feeding.

3. After 2000 hr, and throughout the night there is no difference in urine concentration of free-flying bats compared with bats held in the laboratory without food or water for the same time interval.

4. Mean maximum urine concentration in this species is 972 mOsm kg.

INTRODUCTION

Studies of renal structure and function in bats have centered strongly on insectivorous species (Geluso, 1980) with little attention given to bats in other food preference categories (Studier *et al.*, 1982; Studier & Wilson, 1982). Carpenter (1968) studied the piscivore *Myotis vivesi*; McFarland & Wimsatt (1969) reported on the sanguinivore *Desmodus rotundus*; and Carpenter (1969) dealt with the nectarivore *Leptonycteris sanborni*. These studies have primarily focused on the relationship of renal structure to maximum urine concentrating abilities.

The present study concerns some general and specific aspects of renal function in a common neo-tropical fruit bat, *Artibeus jamaicensis*. These bats show a marked feeding preference for fig fruits (*Ficus* spp.) on Barro Colorado Island in Lake Gatun of the Panama Canal (Bonaccorso, 1975). Although many aspects of the biology of *A. jamaicensis* have been studied, there is no direct evidence concerning its renal function. This paper presents data primarily on natural urine concentration and composition, maximum urine concentrating capabilities, and mechanisms of maintenance of sodium balance in *A. jamaicensis*.

MATERIALS AND METHODS

Volant *Artibeus jamaicensis* of both sexes and different ages (juveniles, sub-adults, adults) were collected at half-hour intervals throughout the night in mist nets set over trails (mostly Synder-Molino 0–2) on Barro Colorado Island (BCI) in the Isthmus of Panama. Preliminary studies were performed from 7 to 19 November 1979 and more extensive studies were done from 2 to 20 May 1980. Figs (*Ficus insipida*) carried by *A. jamaicensis* into mist nets were saved for analysis. Attempts were made, with only occasional success, to collect urine from *A. jamaicensis* immediately upon their capture in mist nets. Most of the bats were placed in cloth bags (20 × 30 cm) for temporary holding. These *A. jamaicensis* were removed after 0.5–1.5 hr and almost invariably urinated upon removal from the bag. Some netted *A. jamaicensis* were brought into the labora-

tory for use in "loading", feeding and dehydration studies. Sixteen (8 ♀, 8 ♂) *A. jamaicensis* collected between 1930 and 2000 hr local time on the night of 3 May 1980 were brought into the laboratory. An initial urine sample was taken within 0.5 hr of the time of capture for this initial starvation dehydration experiment. These 16 bats were returned to the bags and held without food or water. Attempts were made to collect sequential urine samples from these bats at 2200, 2400, 0200 and 0400 hr after which time the bats were released. A second starvation dehydration experiment was performed with 7 (4 ♀, 3 ♂) bats mist-netted between 2030 and 2100 hr the night of 7 May. A whole blood sample was collected at 2100 hr from each bat into a heparinized capillary tube by making a short longitudinal incision in the cephalic vein, which parallels the leading edge of the propatagium. Samples were centrifuged and plasma was saved for analysis. After bleeding, bats were returned to cloth bags and held overnight for further study. On 8 May, urine samples were taken at 1000, 1300, 1600, 1900 and 2200 hr and a second blood (plasma) sample collected at 1300 hr. Bats were released at 2200 hr on 8 May. This bleeding procedure apparently caused insignificant harm to these bats because one was recaptured the night of 11 May at which time the incision site was depigmented but completely healed.

In a further attempt to induce production of maximally concentrated urine and gain some insight into renal function in *A. jamaicensis*, several "loading" experiments were performed between 9 and 14 May 1980. Bats were mist-netted just after sunset, brought to the laboratory where an initial urine sample, and in some instances an initial blood (plasma) sample was taken. Individuals were then intubated and force-fed 0.5–1.0 ml of various solutions and returned to cloth bags for subsequent collections of urine and blood. Four (1 ♀, 3 ♂) individuals collected at 2000 hr were force-fed a solution of NaCl of 3350 mOsm/kg and 4 (2 ♀, 2 ♂) others collected at 2030 hr were force-fed a NaCl solution of 1550 mOsm kg. In addition to initial urine samples, urine samples were collected at 2130, 2300 and 0100 hr. Similar loading experiments were performed with additional groups: 4 individuals (3 ♀, 1 ♂) tested with a NaCl solution (3350 mOsm kg); 4 (2 ♀, 2 ♂) with a KCl solution (2220 mOsm kg); and 4 (1 ♀, 3 ♂) with distilled water. Urine and plasma samples were both taken initially (between 1915 and 2000 hr) with subsequent urine collections at 2200, 0100, and 0500 hr and subsequent plasma

samples taken at 2200 and 0500 hr. A final loading experiment was performed on 4 (1 ..3 ♂) *A. jamaicensis* the night of 14 May starting at 2200 hr with individuals fed a 10% gelatin solution. Urine samples were taken at 2200, 2400, 0230, and 0500 hr; plasma samples were collected at 2200, 2400, and 0500 hr. Bats used in all loading experiments were released after final urine and plasma samples were taken.

A single dehydration experiment was performed with 4 (1 ..3 ♂) *A. jamaicensis* netted late (after 0000 hr) the night of 13 May. Bats were held in cloth bags from the time of capture until 1900 hr on 14 May when they were placed in 0.5-in. mesh, cylindrical, hardware cloth cages (dia about 20 cm; height about 30 cm) containing about 65 g of ripe figs (*Ficus insipida*). One-fourth of the figs were fresh and 3/4 had been ehydrated about 1 week in a refrigerator. Cages were kept (over waxed paper) in approximately natural light levels in the animal room. At 30 min intervals ·between 1900 and 0500 hr on 15 May, the waxed paper was examined for urine and feces. When present, pure urine or fecal samples were taken and the waxed paper replaced. Because the air was essentially water saturated during the period of study, evaporation from urine or fecal samples was considered negligible. Bats were released after the 0500 hr samples and remaining figs were weighed and samples of pulp juice taken.

Only 4 figs (*Ficus insipida*) were carried into mist nets by *A. jamaicensis*. Samples of pulp juices were taken for determination of total osmotic pressure with a Wescor vapor phase osmometer (Model 5100B). Pulp juice was also diluted for later analysis of Na^+ and K^+ concentrations by flame photometry with a Perkin-Elmer (Coleman 51) flame photometer. The concentration of reducing sugars in the pulp juice was determined by the Nelson test (Clark, 1964). These figs were then dried to constant weight and the pulp separated from the inner seed mass. Samples of dried pulp and dried seeds were homogenized with a Polytron (Brinkman Instruments) in a known volume of distilled water, filtered, and the Na^+ and K^+ concentrations of the extracts were determined by flame photometry.

All fluid samples collected (urine, plasma, feces, and pulp juices) were analyzed in similar fashion. Finally, a few of the *A. jamaicensis* urine samples collected in November 1979 were analyzed for urinary ammonia and urea nitrogen levels by using a micro-modification of a colorimetric procedure (Connerty *et al.*, 1955).

· Seven *A. jamaicensis* netted on Bohio Peninsula, Lake Gatun, Panama, were killed by intra-peritoneal injection of sodium pentobarbital, perfused through the left ventricle ·with buffered 10% formalin solution, and stored in buffered 10% formalin for later histologic study. The adrenals and portions of the salivary glands were removed, embedded in paraffin by standard histologic techniques and sectioned at 6 μm. Sections were mounted on glass slides and stained with ·hematoxylin and eosin. Salivary glands were also stained with periodic acid Shiff's reagent and Alcian blue at pH values of 2.5 and 4.0.

RESULTS

Analysis of the pulp juice from the 4 *Ficus insipida* fruits carried into mist nets by *A. jamaicensis* showed an average total osmotic pressure of 740 mOsm/kg and an average level of reducing sugars of 111 mg/ml. If the reducing sugars were composed entirely of glucose and other monosaccharides, these carbohydrates would exert an osmotic pressure of about 620 mOsm/kg. If some portion of the reducing sugars were disaccharides or larger polymers, the osmotic force exerted by these soluble carbohydrates would be reduced accordingly. The Na^+ and K^+ levels of pulp juice compared with the level of these minerals in dried pulp and dried seeds of the same 4 figs are given in Table 1.

Osmotic pressure of the urine of *A. jamaicensis* collected at various times throughout the night (mostly on 11 May) is shown in Fig. 1. Average urine osmotic pressures of samples collected at or before 1930 hr (699 ± 18 mOsm/kg, $N = 15$) are much higher ($t = 3.315$, 38 d.f., $P < 0.01$) and less variable ($F = 6.113$, 24 & 14 d.f., $P < 0.002$) than samples taken at 2000 hr (539 ± 36 mOsm/kg, $N = 25$). Values given are arithmetic mean ± SEM. Thus these bats are uniformly dehydrated when caught within the first few minutes of flight but become rapidly rehydrated within 0.5–1 hr after nighttime activity (and presumedly feeding) begins.

Figure 2 compares the urine concentrations of free-flying bats (from Fig. 1) grouped in 2 hr intervals beginning at 2000 hr with urine osmotic pressures of 16 *A. jamaicensis* collected and sampled at 2000 hr, held in cloth bags without food or water, and sequentially sampled at 2 hr intervals. There is no difference in urine concentrations of free-flying individuals compared with dehydrated, starved individuals over the same time span. This observation suggests that free-flying bats neither fed nor drank after 2000 hr on the nights they were captured. The free-flying bats were collected on several different nights, and during a variety of different moon phases. Both groups show a progressive rise in urine osmotic pressure throughout the night indicating progressive dehydration within both populations.

The Na^+ and K^+ concentrations in the urine of *A. jamaicensis* caught throughout the night are illustrated in Fig. 3. At sunset, initial urine samples show high Na^+ and moderate K^+ concentrations. During the next few hours, Na^+ concentrations remain high while K^+ concentrations decrease. These concentration changes probably relate to rehydration and

Table 1. Average sodium (Na^+) and potassium (K^+) levels in pulp juice, dried seeds, and dried pulp of 4 *Ficus insipida* fruits carried into mist nets by *A. jamaicensis*

Source	Na^+	K^+
Dried seeds	0.36 mg/g dry weight (4.02 mEq/l)	11.6 mg/g dry weight (76.0 mEq/l)
Dried pulp	0.88 mg/g dry weight (8.90 mEq/l)	17.5 mg/g dry weight (102 mEq/l)
Pulp juice	8.80 mEq/l	40.2 mEq/l

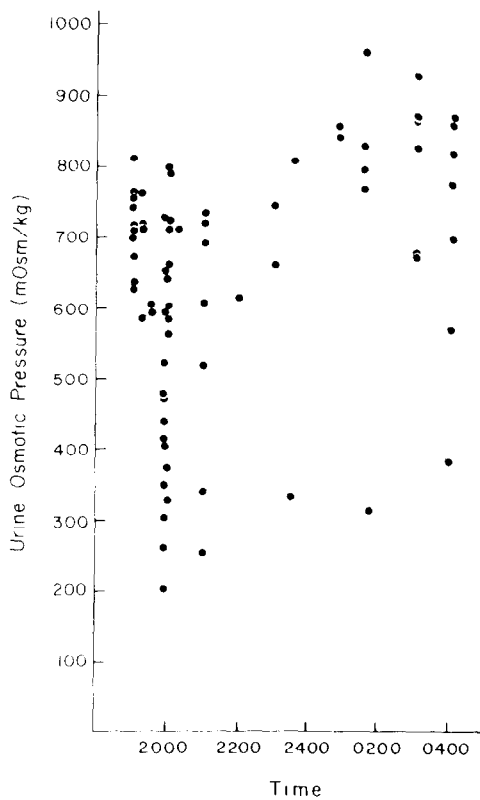Values in parentheses are average concentrations of the minerals in mEq/l of fresh fruit fluid.

Fig. 1. Osmotic pressures in mOsm/kg of urine samples collected from free-flying *Artibeus jamaicensis* throughout the night. Each point represents a sample from a different individual.

ing sunset. Urinary Na^+ is low at sunset (about 10 mEq/l), rises rapidly at emergence and remains elevated (20–60 mEq/l) for about 3 hr and then returns to low levels throughout the rest of the day. Urinary K^+ concentrations, although variable, are about 100 mEq/l at sunset, fall rapidly to about 50 mEq/l for 2–3 hr, rise greatly during the next 5–6 hr with most concentrations ranging from 120 to 200 mEq/l, and finally decline from sunrise to sunset to a level of about 100 mEq/l. Plasma osmotic press-
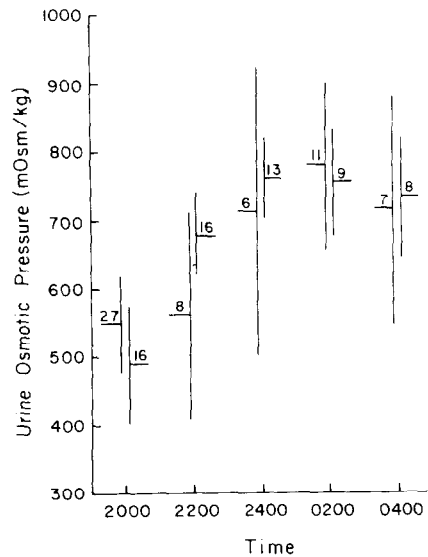

Fig. 2. Urine osmotic pressures of *A. jamaicensis* in 2 hr intervals throughout the night. Horizontal line is the mean; vertical line is 95% confidence interval. The left side member of each pair represents urine of free-flying bats (from Fig. 1) and the right side represents sequential urine samples from 16 captive individuals (see text).

influx of dietary Na^+. After 2200 hr, urinary Na^+ levels fall to very low levels while K^+ concentrations increase markedly.

Results of a second starvation–dehydration experiment are shown in Table 2. Seven bats were collected the night of 7 May at 2000 hr. Plasma samples were taken immediately, bats were kept in bags; and urine and plasma samples were taken at various times on 8 May. Urine osmotic pressure after 14 hr of dehydration starvation (733 mOsm/kg; see Table 2) are no different from urine osmotic pressures either after 8 hr without food or water (736 mOsm/kg; see Fig. 2 at 0400 hr) or in free-flying bats at 0400 hr (718 mOsm/kg; see Fig. 2). Four of the 1900 hr urine samples shown in Table 2 were diluted for determination of Na^+ and K^+ levels; with average concentrations of 8.6 and 103 mEq/l, respectively. A diurnal cycle in urinary osmotic pressure as well as Na^+ and K^+ levels can be outlined to summarize the preceding results as follows: urine osmotic pressure is uniform and relatively high at the time of emergence (1900 hr) from day roosts (699 mOsm/kg). Within 0.5–1.5 hr after leaving day roosts, urine osmotic pressure falls greatly, indicating rehydration probably associated with ingestion of pulp juices of fruit. After this re-hydration period, bats become progressively and rapidly dehydrated; peak natural urine osmotic pressures were reached by 0200 hr. Urine osmotic pressure may show a slight decrease around dawn but probably remains constant from 0200 hr until the follow-
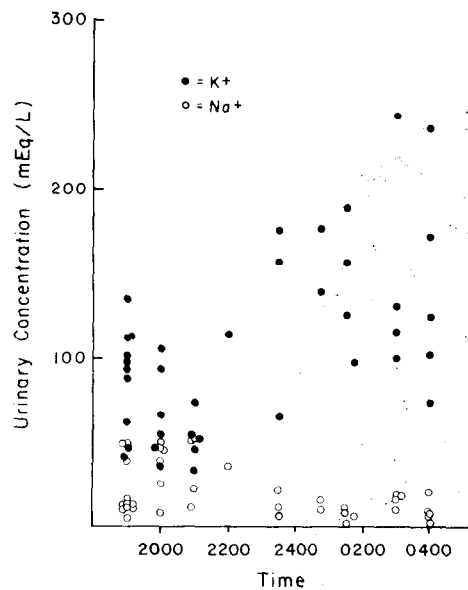

Fig. 3. Sodium and potassium concentrations of urine samples collected from free-flying *A. jamaicensis* throughout the night. Each point represents a sample from a different individual (see Fig. 1).

Table 2. Plasma and urine osmotic pressures (mOsm/kg) of *A. jamaicensis* caught at 20:00 hr on 7 May

Date: Time: Sample:	7 May 20:00 Plasma	 10:00 Urine	 13:00 Urine	8 May 13:00 Plasma	 16:00 Urine	 19:00 Urine
Osmotic pressure	304.4(7) ±2.2	733(7) ±20	782(7) ±17	334.6(7) ±2.7	785(6) ±26	799(5) ±32

Values are mean ± SEM. Sample size in parentheses.

ure rises significantly during the 17 hr dehydration period given in Table 2 ($t = 8.14$, d.f. $= 12$, $P < 0.001$).

From the preceding results, it is apparent that total urinary osmotic pressure is most uniform at sunset. Therefore, seasonal comparison of urinary concentration and composition values in urine samples collected at or just after sunset should be the most valid. Urinary samples from *A. jamaicensis* collected at sunset in November show significantly greater variability and lower osmotic pressure than May samples ($F = 4.751$, 21 & 14 d.f., $P < 0.005$; $t = 6.644$, d.f. $= 21$ & 14, $P < 0.001$). There is no difference in the November–May urinary Na^+ levels; however, urinary K^+ levels are higher in November than in May ($t = 2.181$, 9 & 19 d.f., $P < 0.05$). Nineteen urine samples taken just after sunset in November were analyzed for ammonia and urea nitrogen levels. Average concentration was $495 ± 115$ mg%. If urinary nitrogen were all urea, the 495 mg% would exert an osmotic pressure of about 180 mOsm/kg or 44% of total urinary osmotic pressure.

Results of all the "loading" experiments are summarized in Table 4 with one example, forced ingestion of a NaCl solution with an osmotic pressure of 3350 mOsm/kg, illustrated in Fig. 4.

Four *A. jamaicensis* (1., 3 ♂) collected after 2400 hr the night of 13 May were caged with excess *Ficus insipida* at 1900 hr the night of 14 May after collecton of an initial urine sample. Figs were either freshly collected ripe figs (one-fourth) or dehydrated ripe figs (three-fourths). The osmotic pressure of the pulp juices of the dehydrated figs averaged $1636 ± 89$ mOsm/kg ($N = 9$). Pure urine and fecal samples were collected, when present, at half-hourly intervals for the next 10 hr. Bats were then released. Average consumption of figs was 38.7 g. Two of the bats began eating almost immediately (1900 and 1930 hr) and consumed over 50 g of figs while the other 2 bats began eating at 2200 hr and each consumed less than

30 g. Fecal samples were collected from all four bats within 30 min of their initial food consumption. Thus, passage time in *A. jamaicensis* is less than 30 min. Although highly variable, there is an apparent progressive erratic increase in total urine osmotic pressure throughout the night after eating dehydrated figs in *A. jamaicensis* (Fig. 5). Because of the small sample size of bats tested, regression analyses were not performed. The most uniform maximum total urine osmotic pressure in the 4 bats was reached at 0430 hr with an average urine osmotic pressure of 972 mOsm/kg. There may also be an erratic and slow rise in urinary K^+ level throughout the night after ingestion of dehydrated figs (Fig. 5). Two very high urinary K^+ levels (227 and 245 mEq/l) found in the 2100 hr urine samples were matched by similarly high fecal K^+ levels for those individuals at that time (118 and 147 mEq/l, respectively). No apparent trends were found for urinary or fecal Na^+ concentrations nor fecal K^+ concentration or osmotic pressure throughout the night in this experiment. Two abnormally high urinary Na^+ levels found in 2230 hr samples (69.0 and 67.5 mEq/l) were matched by similarly high

Table 3. Osmotic pressure (mOsm/kg). and Na^+ and K^+ (mEq/l) concentrations in *A. jamaicensis* urine collected just after sunset in May and November

	May	November
Osmotic pressure	699 ± 19 (15)	411 ± 33 (22)
Na^+	22.25 (10) ± 5.26	15.95 (20) ± 2.25
K^+	89.0 (10) ± 9.58	127.7 (20) ± 11.5

Values are mean ± SE_x: sample size in parentheses.

Table 4. Mean urine and plasma osmotic pressures (mOsm/kg) of *Artibeus jamaicensis* in "loading" experiments

Soln	Soln o.p.	Sex	$\bar{X}$ Urine o.p.			
			2000	2130	2300	0100
NaCl	3350	1.:3 ♂	708*	705	768*	805
NaCl	1550	2.:2 ♂	734*	658	772*	810
			1930	2200	2430	0330
NaCl	3350	3.:1 ♂	707	691	773	866*
KCl	2220	2.:2 ♂	744	728	802	798*
D.W.	0	1.:3 ♂	763	502*	750	856*
			2200	2400	0230	0500
Gel.	0	1.:3 ♂	508	645	713	854
			$\bar{X}$ Plasma o.p.			
			1930	2200	0330	
NaCl	3350	3.:1 ♂	306	352	364	
KCl	2220	2.:2 ♂	310	347	370	
D.W.	0	1.:3 ♂	312	312	346	
			2200	2400	0500	
Gel.	0	1.:3 ♂	303	305	314	

Sample size is 4 except values marked with an asterisk(*) where sample size is 3.
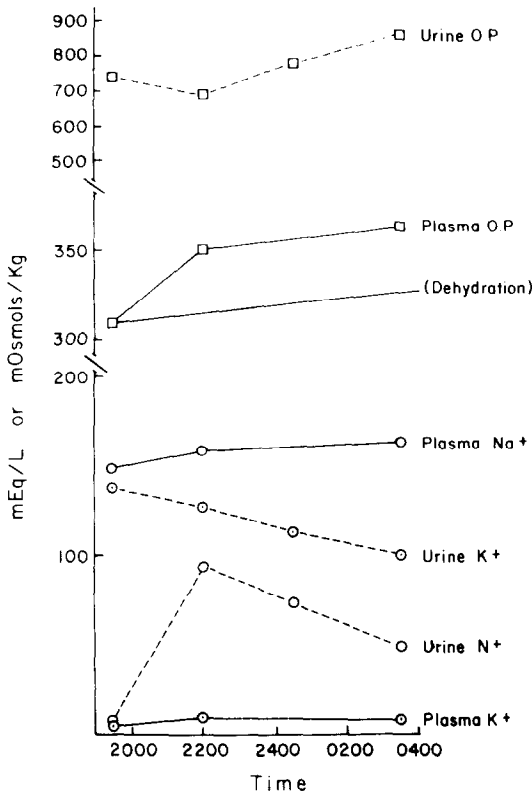
Fig. 4. Sequential average osmotic pressure and sodium and potassium concentrations of urine and plasma samples of four *A. jamaicensis* forced to ingest 0.5 1.0 ml of a sodium chloride solution (osmotic pressure = 3350 mOsm kg) at 1930 hr. The line labelled dehydration represents the average rate of increase of plasma osmotic pressure in these bats when they are deprived of food and water.
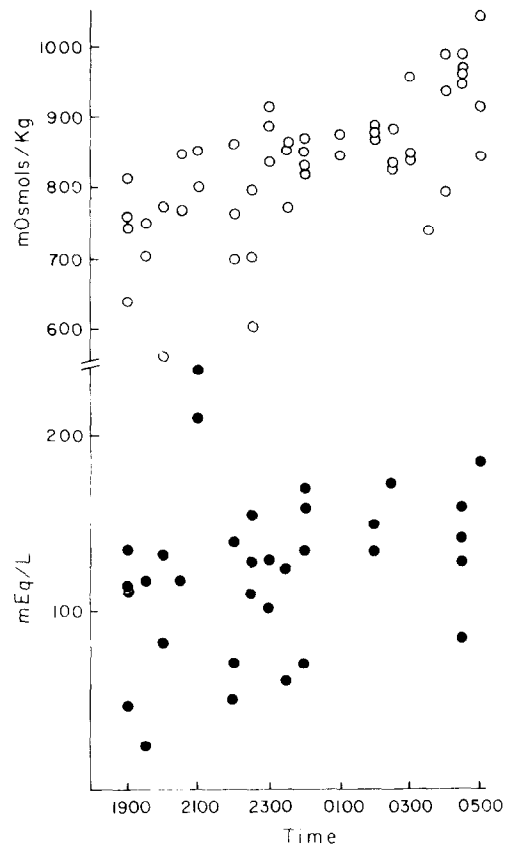

Fig. 5. Osmotic pressures (circles) and potassium concentrations (dots) of the urine of caged *A. jamaicensis* throughout the night with bats allowed free access to dehydrated figs.

fecal Na$^+$ levels for those individuals at that time (31.5 and 11.5 mEq/l, respectively). Urine and fecal osmotic pressures, as well as Na$^+$ and K$^+$ concentrations, of all samples collected in this experiment are summarized in Table 5. At 17 times throughout the night, urine and fecal samples were obtained from single individuals for the same 30 min collection interval. Paired sample t-tests show urinary osmotic pressure and K$^+$ concentrations to be higher than fecal levels (t = 11.86, d.f. = 16, P < 0.001; and t = 14.20, d.f. = 16, P < 0.001, respectively). Urinary Na$^+$ levels were nearly significantly higher than simultaneously collected fecal Na$^+$ concentration (t = 1.97, d.f. = 16, 0.05 < P < 0.10).

Table 5. Urine and fecal osmotic pressures (mOsm/kg) and Na$^+$ and K$^+$ concentrations (mEq/l) of all samples taken in the dehydrated fig feeding experiment

Sample	Osmotic pressure	Na$^+$	K$^+$
Urine	837 ± 14 (51)	13.9 ± 2.8 (34)	125.5 ± 8.5 (33)
Feces	441 ± 11 (31)	8.2 ± 1.3 (24)	50.5 ± 6.1 (24)

Values are mean ± SE: sample size in parentheses.

Sections of salivary glands of *A. jamaicensis* showed no hyperdevelopment of ducts. Secretory substance stained heavily with PAS but not Alcian blue, at pHs of 2.5 and 4.0, indicating the presence of neutral polysaccharides.

DISCUSSION

Ingestion of adequate amounts of dietary Na$^+$ among a wide variety of herbivorous mammals has generated considerable interest (Cowan & Brink, 1949; Stockstad *et al.*, 1953; Dalke *et al.*, 1965; Blair-West *et al.*, 1968; Herbert & Cowan, 1970; Jordan *et al.*, 1973; 1978a, Weeks & Kirkpatrick, 1976, 1978). Critically low sodium availability has been suggested as a major controlling factor in regulating population density in some mammals (Aumann, 1965; Aumann & Emlen, 1965; Botkin *et al.*, 1973; Belovsky, 1978). Sodium levels in a wide variety of plants and plant parts are routinely very low (Sauchelli, 1969; Likens & Bormann, 1970; Weeks, 1978b) and related to soil Na$^+$ levels which are in turn highly affected by the Na$^+$ levels in rainfall (Blair-West *et al.*, 1968) and the frequency of rainfall. Tropical rain forests may be particularly susceptible to leaching loss of nutrients due to rapid decomposition of litter and heavy, frequent rains (Jordan & Herrera, 1981). Although many characteristics and composition data on the soils of

Barro Colorado Island (BCI) are known (Knight, 1975), we have found no information on soil sodium levels on BCI. Mineral compositon of a variety of figs has been reported that shows fig fruits to uniformly contain very little sodium (Documenta Geigy, 1962; Heinz International Research Center, 1964; Oates, 1978). Sodium levels in a variety of plants and plant parts on BCI, including ripe figs, *Ficus insipida* and *F. yoponensis*, have been measured at very low levels of 0.49 and 0.48 mg/g dry weight, respectively (Nagy & Milton, 1979).

Minimal sodium requirements have been estimated for few small mammals. Growth requirements for laboratory rats and mice are estimated at 10 and 18 mg/animal per day, respectively (National Research Council, 1978). Assuming similar minimal requirements for 40–60 g *A. jamaicensis*, these bats would appear to require minimal nightly consumption of 91–164 g of ripe *F. insipida* at 0.11 mg of Na^+/g fresh weight (Nagy & Milton, 1979) to maintain sodium balance. Although minimal daily energy requirements of *A. jamaicensis* are calculated at 5 feeding passes to a *F. insipida*, actual feeding passes were measured as 7 by Morrison (1978a). The *F. insipida* fruits selected for ingestion have an average weight of 9.5 g (Bonaccorso, 1975) which is 1.7 times the average wet weights of ripe *F. insipida* figs (Morrison, 1978a). This yields a nightly consumption of 66.5 g of *F. insipida* figs, a value markedly lower than apparent required intake for maintenance of Na^+ balance. Howler monkeys which also feed heavily on the products of *Ficus* trees on BCI are estimated to also receive marginal amount of dietary Na^+ from this diet (Nagy & Milton, 1979).

We made careful observations of *Artibeus* feeding on *Ficus insipida* fruit. These bats primarily consume the pulp of the figs. This fleshy outer portion is taken into the mouth in small pieces where it is rolled back and forth by the tongue against the heavily corrugated hard palate. Pulp juice is then extracted by chewing and squeezing the shredded pulp against the hard palate with the tongue. Juices are swallowed and the shredded pulp is spat out. This "chop" of shredded, extracted fig pulp is characteristically found under active night roosts of *A. jamaicensis*. These bats feed preferentially on the pulp juices of *Ficus insipida* fruits. Similar observations have been reported by Morrison (1980b). Table 1 shows sodium and potassium levels in figs carried and, therefore, about to be consumed by *A. jamaicensis*. The Na^+ levels are similar to those found by Nagy & Milton (1979) but potassium concentrations are somewhat lower than theirs. Dried pulp sodium density is about 2.4 times the sodium level of dried seeds and is identical to the sodium level of pulp juices, thus the specific consumption of pulp juice rather than ingestion of the entire fig greatly increases dietary Na^+ density in *A. jamaicensis*. The elevated Na^+ density and specific ingestion of pulp juices combined with the fact that the pulp portion contributes the greatest fraction of fresh weight of the figs would significantly reduce the necessary weight of figs estimated to be required for maintenance of Na^+ balance. It should also be noted that the K^+ level of pulp juices is less than half the concentration of that ion in dried pulp. This observation implies that K^+ is perhaps concentrated in specific organelles within the fig pulp and not extracted by *A. jamaicensis*, but is released in the process of homogenization of the dried pulp. The lowered dietary K^+ level obtained from pulp juices as opposed to whole pulp probably also lowers the Na^+ requirements of *Artibeus jamaicensis* as it does in other mammals (Meyer et al., 1950; Weeks & Kirkpatrick, 1978; Staaland et al., 1980).

The bulk of the total osmotic pressure of pulp juices is due to reducing sugars (Widdowson & McCance, 1935; Eckart & Mason, 1967). If all reducing sugars are glucose or other hexoses these substances are responsible for 620 mOsm/kg or 84% of the total 740 mOsm/kg osmotic pressure of fig pulp juice. The sugar content of fig fruits is exceptionally high in comparison to other fruits (Whiting, 1970). The glucose solution would then represent, at 686 kcal/mol, 425 kcal/l or 0.425 kcal/ml of pulp juice. The value of 0.425 kcal/ml of pulp juices is distinctly higher than the level of 0.315 found by Morrison (1980b). This discrepancy may be attributed to the fact that we analyzed figs carried into nets by *A. jamaicensis* whereas Morrison studied ripe fruit picked from trees. These bats selected abnormally large ripe fruit (Morrison, 1978a) which August (1981) suggests is significantly softer than other ripe fruit and, based on our data, contains more reducing sugars, and potentially more energy than other ripe fruit. Hladik et al. (1971) found 5.8 g carbohydrate/100 g wet weight for *F. insipida* fruit. Assuming the carbohydrate to be glucose yields an energy equivalent of 0.221 Kcal/g for the entire fig. Morrison (1980b) has calculated the minimum daily energy requirement for *A. jamaicensis* on BCI to be 50.2 kJ (12.0 kcal). Thus, this bat requires a minimum of 28.2 ml of fig pulp juices at 100% assimilation efficiency to maintain energy balance. Such a volume should be easily extracted from the 66.5 g of figs estimated to be consumed nightly by *A. jamaicensis* (Morrison, 1978a). Additionally, the presence of apparently high concentrations of free glucose in pulp juices would decrease somewhat the need for amylytic enzymes and time required for digestion. This would, of course, relate to the rapid passage times of less than 0.5 h found for this species (also see Morrison, 1980b). Assimilation of the glucose from pulp juices reduces its total osmotic concentration to 120 mOsm/kg, a fluid concentration that is extremely hypotonic to plasma (ca. 300 mOsm/kg). Pulp juices are then an excellent source of water for *A. jamaicensis* and presumably represent, together with metabolic water, all of the water intake for this species. There is no indication that *A. jamaicensis* require free drinking water in either the wild or captive state.

Mammals suffering Na^+ deficiency characteristically exhibit hypertrophy and hyperplasia of the zona glomerulosa of adrenal glands and greater development of both striated and excretory ducts within salivary glands (Blair-West et al., 1968). These features, through the renin-angiotensin-aldosterone system, result in renal and salivary Na^+ retention. The adrenal zona glomerulosa of *A. jamaicensis* shows no obvious hypertrophy or hyperplasia in comparison to insectivorous neotropical species although possible subtle differences remain to be studied. Like many frugivores, *A. jamaicensis* has exceptionally large salivary

glands (Phillips *et al.*, 1977). The functions of salivary glands include the production and release of salivary amylase and mucous plus participation in the maintenance of water and mineral balance. Results of our histologic examination of salivary glands of *A. jamaicensis* are in agreement with those of Wimsatt (1956).

There is no relative increase in numbers of ducts within the glands nor is there evidence of relative excess production of serous secretion. Excessive relative occurrence of mucus producing cells, however, is obvious. The functional significance of these structural observations include possible increases in salivary amylase production and increased involvement of these glands in mineral and water balance regulation together with overall increase in production of saliva simply because the glands are oversized. Mucus content of saliva, however, should be abnormally high.

In general, mucus functions to protect the gastrointestinal tract from physical or chemical abrasive contact or damage. The only physically abrasive material present regularly in the gut of *A. jamaicensis* would seem to be fig seeds. Low power microscopic examination of *Ficus insipida* seeds show them to have smooth surfaces with no angular or sharp projections which could readily excoriate the gastrointestinal mucosa.

It is possible that salivary mucus may act chemically to neutralize alkaloids which may be present in fig fruits. Dalquest (1952) suggested that the mucus functions to hold together the pellets that are formed and subsequently ejected during feeding. We offer another hypothesis which seems a more probable explanation. We suggest that the abundant saliva rich in mucus may strongly buffer gastric secretions thus preventing gastric contents from becoming acidic while simultaneously coating the gastric epithelium with an extensive buffering barrier. If gastric fluid remains above pH 4, salivary amylase should continue to function, which may be of considerable importance in view of the rapid passage time exhibited by this species. Histologic examination of the stomach and duodenum of a wide variety of frugivorous bats (Rouk & Glass, 1970; Forman, 1972; Bhide, 1980) shows the gastric glands to contain typical parietal and zymogen cells. Frugivorous bats, including *Artibeus*, characteristically have reduced or absent Brunner's glands. Although the importance of Brunner's glands among mammals is still debated, these glands have long been associated with protection of the duodenum from damage by highly acidic chyme leaving the stomach. If saliva of *A. jamaicensis* has sufficient buffering capacity to prevent chyme from becoming highly acidic, the reduction or absence of Brunner's glands in these frugivores would be compensated. Additionally, it has been demonstrated that salivary bicarbonate concentration is directly proportional to the rate of saliva formation (Burgen & Emmelin, 1961). Since the bicarbonate buffer system accounts for the bulk of the buffering power of the saliva (Izutsu, 1981), increased or high relative rates of saliva production may indicate elevated salivary buffering capacity in *A. jamaicensis*.

Urine samples taken from *A. jamaicensis* at sunset in May are significantly more concentrated and less variable than samples collected in November. This observation may relate to the fact that the May samples were collected at the very end of the dry season associated with greater and more uniform dehydration while the November sampling occurred toward the end of the wet season (Smythe, 1974). Additional factors which may relate to the observed seasonal differences include reduced reproductive effort in November with reduced water, mineral, and energy requirements compared with May (Fleming *et al.*, 1972) and ripe fig availability, which, based on our observations in 1979 and 1980, was much greater in November than May. This observed pattern of ripe fig availability is not consistent with the normal pattern on BCI (Smythe, 1970; Morrison, 1978a). Elevated K^+ levels in the November sample seem inconsistent but could relate to increased K^+ load associated with increased fig availability.

The osmotic concentrations of urine of free-flying vs capative *A. jamaicensis* throughout the night (see Figs 1 and 2) are essentially identical. The markedly rapid decrease in total urine concentration 0.5–1.5 hr after flight initiation parallels the very rapid food passage time in this species, the ingestion of adequate hypotonic fluid for rehydration, and rapid assimilation and equilibration with ingested fig pulp juice. The existence of a single main bout of rehydration coupled to the similarities in urine concentration patterns of free-flying and captive bats strongly indicates a single feeding period which occurs shortly after flight initiation. Because *A. jamaicensis* characteristically carry figs to night roosts before eating (Morrison 1978b, 1980a), and in view of a single intense feeding period observed in this study, it is perplexing that so few bats carried figs into mist nets at the time of capture. Capture success peaked at about 3 hr after sunset (Fig. 6).

However, most of the individuals were captured in an area some distance from their feeding and night-roosting trees, so we may have been sampling them only on their way between day roost and feeding area. Thus, based on capture success, the greatest period of flight activity occurred shortly after the intense feeding period. The few bats collected later in the night may have been involved primarily in searching rather than feeding flights.

Phase of the moon profoundly affects flight activity patterns in *A. jamaicensis* (Morrison 1978c, 1980a). Lunar phobia exhibited by *A. jamaicensis* may also be involved in the flight activity we observed in May, 1980 (Fig. 7). Peak capture times seem to be earlier immediately after a full moon. Perhaps they feed early and quickly on these nights, and then spread the feeding period out later in the moon cycle, when captures seem to peak later (Fig. 7). We know from other netting experiences on BCI that feeding activity is not always concentrated in early evening. These results may be a reflection of the age structure of the population at the times of our study, when juveniles and subadults are a major part of the sample.

The Na^+ and K^+ urinary concentration patterns (Fig. 3) are consistent with rapid, early assimilation and equilibration with ingested fig pulp juice resulting in an elevation of urinary Na^+ coupled to a depression of urinary K^+. This early pattern is followed by a marked depression of urinary Na^+ combined with an elevation of urinary K^+ consistent with the
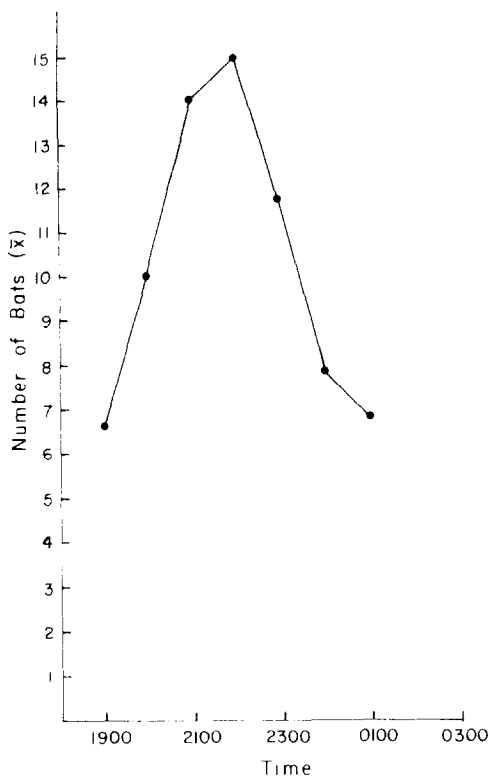
Fig. 6. Average numbers of *A. jamaicensis* mist-netted at hourly intervals. Each point represents 8 to 15 nights between 2 and 18 May 1980.

release of aldosterone causing renal tubular Na^+ reabsorption coupled to K^+ exchange. Thus Na^+ is retained.

In view of the rapid assimilation and equilibration of ingested fluids by *A. jamaicensis*, the loading experiments (Fig. 4; Table 4) are of little value. Renal adjustments to the ingested fluids should have been most pronounced during the first hour after fluid ingestion when no samples were taken, e.g. urinary Na^+ concentration probably peaked before the 2200-hr sample was taken in the loading experiment shown in Fig. 4. General patterns of plasma and urinary osmotic concentrations and mineral concentrations are consistent with renal adjustments expected to accompany the ingestion of the various experimental fluids. It is of interest, however, that marked rises in plasma osmotic pressure are not accompanied by the production of maximally concentrated urine. There appears to be a slow or minimal release of anti-diuretic hormone (ADH) or a slow or reduced renal tubular response to ADH associated with dehydration resulting from ingestion of the experimental solutions.

Table 2 shows a rise in plasma osmotic pressure of 30.2 mOsm/kg associated with a period of starvation/ dehydration lasting 17 hr (1.78 mOsm/kg hr), which also is not accompanied by the production of maximally concentrated urine. This rate of increase in plasma osmotic pressure associated with starvation/ dehydration is also shown in Fig. 4 as a reference. The initial (2–2.5 hr) rise in plasma osmotic pressure associated with mineral loading experiments is the result of the nearly complete assimilation of and equilibration with the ingested salts within body fluids. As an example, when the 3350 mOsm/kg NaCl solution is ingested, the plasma osmotic pressure after 2.5 hr has risen from 306 to 352 mOsm/kg. If average body fluid osmotic pressure starts at 306 mOsm/kg and the average *A. jamaicensis* tested weighs 45 g with 70% of body wt equal to body water (= 31.5 ml), then total body mOsm before ingestion is 9640 mOsm. Ingestion of an average of 0.5 ml of the NaCl solution will then add 1675 mOsm yielding a final average body fluid osmotic pressure of 354 mOsm/kg (= 9640 + 1675/31.5 + 0.5). Similar calculations can be made for ingestion of other solutions.

The ingestion of dehydrated figs by *A. jamaicensis* illustrated in Fig. 5 and summarized in Table 5 is the functional equivalent of Geluso's (1975, 1978) "water-denied" experiments with insectivorous bats. In those experiments, bats were allowed to feed but had no access to drinking water. That experimental protocol resulted in the insectivorous bats forming maximally concentrated urine. Because *A. jamaicensis* on a natural diet apparently requires no drinking water, the best replication of Geluso's "water-denied" experiments was the feeding of dehydrated natural food while allowing no access to water. In insectivorous bats, "water-denied" experiments resulted in urine concentration cycles following feeding that were described as exhibiting an inverted "V" pattern or a plateau pattern with a horizontal period of the plateau cycle lasting 7–12 hr after feeding (Geluso, 1978).

For *A. jamaicensis* in the present study, both the natural urine concentration cycle (Fig. 1) and the urine concentration cycle associated with the ingestion of dehydrated figs (Fig. 5) show similar patterns with urine concentrations reaching peak levels about 6 hr after feeding in the free-flying bats and 6.5–9.5 hr after feeding on dehydrated figs. Peak urinary osmotic concentration in 4 free-flying bats at 0130 hr was only 848 mOsm/kg whereas 4 bats feeding on dehydrated figs produced a mean maximum urine concentration of 972 mOsm/kg at 0430 hr. We believe that this latter value is a reasonably accurate estimate of maximum urine concentrating ability in *A. jamaicensis*. Much of the variability in urine concentrations shown in Fig. 5 probably results from bats having access to some ripe (not dehydrated) figs during testing and the observation that bats tested did not all begin feeding at the same time.

Geluso (1980) has conclusively demonstrated a direct relationship for insectivorous bats between maximal urine concentrating ability and renal morphology. The most useful parameter is the ratio of medullary thickness (M) to cortex thickness (C) (Geluso, 1978). Using the equation developed by Geluso (1980) for insectivorous bats where maximum urine concentrating ability, in mOsm/kg, equals 702 plus 387 (M/C). *A. jamaicensis*, with an M/C of 2.37 (Studier et al., 1982), would produce maximally concentrated urine of 1619 mOsm/kg. This value is well above the mean maximum observed level of 972 mOsm/kg. The only available comparable data for phyllostomid bats are for *Leptonycteris sanborni* which has an M/C of 1.4 and produces maximally concentrated urine at 342 mOsm/kg (Carpenter, 1969). This
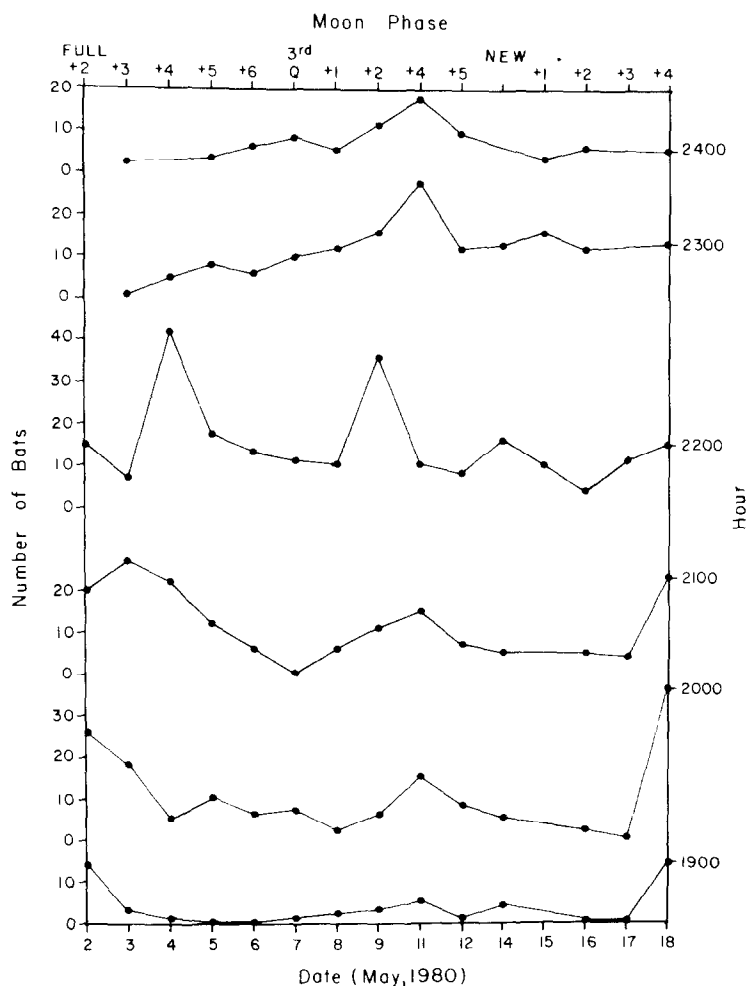
Fig. 7. Total number of *A. jamaicensis* collected (left ordinate) at hourly intervals (identified on right ordinate) on various nights in May, 1980. Moon phase is shown on the top.

value falls 898 mOsm/kg below the level predicted by Geluso's (1980) equation. We concur with Geluso (1980), therefore, that his equation for insectivorous bats does not apply to frugivorous species such as *A. jamaicensis*.

In summary, figs (*Ficus insipida* and *F. yoponensis*) are a staple in the diet of *A. jamaicensis* on BCI. Based on published data, these figs would provide, at best, a marginally adequate dietary Na^+ source. When feeding on *F. insipida* fruits, *A. jamaicensis* primarily ingest pulp juice which markedly increases dietary Na^+ level and decreases dietary K^- level in comparison to ingestion of whole pulp or whole fruit. Other adaptations that might be associated with severely restricted Na^+ intake in mammals include hypertrophy or hyperplasia in the zona glomerulosa of the adrenals and excessive development of striated and excretory ducts in salivary glands. There is no obvious hyperdevelopment of the zona glomerulosa in this species, but subtle differences remain to be studied.

Although there is no relative increase in the occurrence of ducts within the salivary glands, the relatively large size of these glands indicates an above normal ratio of salivary ducts to body mass. Histologic exam-

ination of salivary glands in *A. jamaicensis* indicates disproportionately large development of mucus-producing cells. Hyperproduction of mucus-laden saliva is hypothesized to prevent extreme acidity of gastric contents allowing prolonged action of salivary amylase and reducing the need for Brunner's glands. Gut passage time in *A. jamaicensis* is rapid (less than 30 min) as is assimilation of sugars, water, and minerals. Over 80% of the osmotically active material of pulp juice is reducing sugar. After assimilation of sugars from pulp juices, the remaining fluid (osmotic pressure 120 mOsm/kg) is very hypotonic to plasma (osmotic pressure 300 mOsm/kg) and apparently provides the only external source of water for this species.

Based on urine osmotic pressure, bats are uniformly dehydrated at the initiation of flight and become rapidly rehydrated from ingestion of figs within 0.5–1 hr after flight initiation. Urine then becomes more concentrated throughout the remainder of the night. Osmotic concentrations of urine of captive rehydrated individuals are identical throughout the night with urine concentrations of free-flying bats. Thus, these bats exhibit a nightly single feeding/rehydration period that occurs shortly after leaving day roosts. Urinary concentration patterns for Na^+

and K^+ in free-flying *A. jamaicensis* show elevation of Na^+ levels shortly after emergence from day roosts followed by a marked depression of this cation throughout the remainder of the night. Urinary K^+ concentration decreases rapidly during the first few hours of flight followed by considerable elevation of this ion later in the night. Plasma osmotic pressure of rehydrated bats averages 304 mOsm/kg and rises at a rate of about 1.8 mOsm/kg/hr in bats denied access to food or water. Plasma Na^+ and K^+ concentrations in rehydrated bats are 148.8 and 6.4 mEq/l, respectively. Loading of bats through forced ingestion of highly concentrated salt (NaCl, KCl) and protein solutions did not cause the production of maximally concentrated urine. Ingestion of dehydrated figs by caged bats resulted in the formation of mean uniform maximal urine concentration of 972 mOsm/kg.

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