Seasonal and daily variation in blood and urine concentrations of free-ranging Angolan free-tailed bats *(Mops condylurus)* in hot roosts in southern Africa

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Urine and plasma concentrations and haematocrits were measured in free-ranging Angolan free-tailed bats (*Mops condylurus*) inhabiting thermally-challenging roosts in the Komatipoort region of South Africa. Samples were collected in both autumn and summer, from bats caught emerging from roosts before feeding (pre-feeding), and those returning after foraging (post-prandial). Post-prandial bats exhibited higher body fluid concentrations, but lower haematocrits, than individuals caught prior to feeding, reflecting raised excretory mineral and nitrogenous loads and replenishment of body water pools during nocturnal foraging. Pre-feeding concentrations of both urine (2637 ± 506 mOsm/kg; n = 16) and plasma (331.5 ± 25.9mOsm/kg; n = 24) were significantly higher in summer than autumn (urine: 2157 ± 454mOsm/kg; n = 8; plasma: 294.5 ± 35.2 mOsm/kg; n = 18) reflecting the greater dehydration stresses within hotter roost microclimates, and a moderate kidney concentrating ability in this species. Haematocrits of pre-feeding animals were not, however, influenced by season and in both instances exceeded 53%, indicative of the higher oxygen carrying capacity needed for sustained flight in volant insectivores and also the defense of the rheological properties of blood. The ability of *Mops condylurus* to withstand a thermally-challenging roost milieu reflects, in part, its tolerance to dehydration, rather than the maintenance of water balance through exceptional renal concentrating ability.

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The widespread ecological success of microchiropteran bats largely reflects the employment of physiological and ethological mechanisms for conserving energy and body water (Geluso 1978; Nowak 1994). The microclimates of diurnal roosts, in which individuals may spend more than half of their lives, represent an important selective force in the ecophysiological adaptation of these animals, and can have a profound effect on energetic strategies and water turnover rates (McNab 1982; Nagy 1994; Rodrìgues-Duràn 1995).

Bats inhabiting hot roosts may have greater daily water requirements than those residing in cooler roosts because high diurnal thermal loads increase rates of pulmocutaneous evaporative cooling. Even at moderate ambient temperatures, evaporative water loss is disproportionately large in bats (Geluso 1978; Bell, Bartholomew & Nagy 1986; Morris, Curtin & Thompson 1994), and the use of hot roosts by some species may lead to considerable evaporative water losses to defend body temperature below lethal limits, thereby drawing upon water reservoirs within the body (Maloney, Bronner & Buffenstein in press). Under such potentially dehydrating conditions an animal should benefit from any decreases in other avenues of water loss, particularly those associated with urine production.

The parsimonious production of concentrated urine is, however, limited by renal morphology (such as nephron density and the lengths of the loops of Henle), which determines maximal kidney concentrating ability (Bankir & De Rouffignac 1987). The relationship between urine osmolality and the absolute length of the loop of Henle (or medullary thickness), however, is neither proportional nor direct, even though the length of the loop of Henle is a central tenet of the countercurrent multiplier theory (Beuchat 1990; 1996). Despite the fact that morphological indices for predicting urine concentrating ability lack a clear functional rationale (Beuchat 1996), and endocrine and other regulatory factors may influence urine concentrating ability (Franchini & Cowley 1996), a direct relationship between kidney structure, the ability to concentrate urine and ecological distribution exists across all taxonomic groups. Species in xeric habitats consistently show greater renal efficiencies, inner medulla/cortical area ratios, urine concentrations and urine/plasma ratios than do mesic-adapted taxa (Carpenter 1969; MacMillen, Baudinette & Lee 1972; Degen, 1977; Geluso 1980; Bassett 1982; Studier, Wisniewski, Feldman, Dapson, Boyd & Wilson 1983; Buffenstein, Cambell & Jarvis 1985; Happold & Happold, 1988; Fielden, Perrin & Hickman 1990).

Trophic niche and concomitant water and electrolyte content of the diet also affect maximal urine concentration, and thus water balance (Studier *et al.* 1983b; Bassett 1986). The high nitrogenous loads associated with a protein-rich insectivorous or carnivorous diet result in higher urine concentrations than those linked to predominantly carbohydrate, frugivorous diets (Geluso 1978). Post-feeding nitrogenous loads in microchiropteran bats may be so high that urine concentrations measured shortly (30 min) after foraging approach maximal limits allowed by renal morphology, despite the availability of water (Geluso 1978; Bassett 1986). While some bats readily drink water in captivity, other species show complete independence of free water, relying instead on the moisture content of the diet and metabolic water production (Happold & Happold 1988). Maximal urine concentrations shortly after feeding do not, therefore, necessarily reflect water stress situations, or whether a particular species naturally drinks free water. High post-prandial urine concentrations may instead result from the excretion of high levels of nitrogenous wastes using a minimum volume of water. This strategy would maximize the amount of body water available for later insensible water loss, and thereby help conserve the extracellular fluid pool. This would be particularly beneficial in very hot diurnal roosts.

Mops condylurus is an aerial-hunting insectivore which often uses hot diurnal roosts in tropical and subtropical Africa (Skinner & Smithers 1990; Koopman 1993; Bronner, Maloney & Buffenstein, in press). Behavioural avoidance of extreme temperatures, together with adaptive hyperthermia, are used to reduce evaporative water losses (Maloney *et al.* 1999), and help maintain water balance. Despite living in potentially dehydrating roosts, this species is apparently independent of free water, in that even pregnant individuals reportedly did not drink in captivity (Happold & Happold 1988). Predicted maximal urine concentrations (from histological examination of the relative inner medullary/cortical areas) in Malawi populations of this species are nevertheless moderate (2634 mOsm), and seemingly insufficient to maintain water balance under the extreme conditions that may be encountered in some roosts. We therefore hypothesized that Angolan free-tailed bats exposed to thermally-challenging roost microclimates would show both seasonal and daily cyclic variation in water stress, with concomitant changes in blood and urine concentrations.

Methods and materials

Study site

We captured bats at three colonies located along the Crocodile River on the southern edge of the Kruger National Park in the vicinity of Komatipoort, South Africa (25°21'S:31°50'E), during the southern hemisphere autumn (April 1996) and summer (February 1997 and January 1998) seasons. Bats from two of these colonies regularly moved between two roosts, which were located under corrugated iron roofs in buildings at Ngwenya Lodge and the nearby Tenbosch Citrus Packing Shed. The third colony occupied a structure ('Station Bat Hotel') especially erected for bats at Komatipoort Station by the South African Transport Services in 1953, as part of a malaria mosquito bio-control strategy.

Microclimatic conditions within these roosts, and the thermal biology of the Ngwenya/Tenbosch colony in particular, have been extensively studied (Bronner *et al.* 1999; Maloney *et al.* in press). Temperatures within the 'Station Bat Hotel' are cooler and temporally less variable than in the Ngwenya/Tenbosch roost, with a difference of 5.8 ± 1.0°C in mean maximum temperature during the heat of the day (11:00 – 15:00) in summer. Seasonal variability, monitored thus far only at the Ngwenya/Tenbosch roost, is marked with a mean maximum temperature differential of 9.2 ± 3.8°C during the heat of the day between summer and autumn. Maximum temperatures within both roosts exceed 50°C for approximately six hours daily in summer, and three hours daily in autumn, with an internal spatial gradient of 25–30°C (Bronner *et al.* 1999).

Sampling

Water and energy metabolism data collected under laboratory conditions, where bats are subjected to captive (particularly nutritional) stress, are of dubious applicability to animals in their natural habitats (McNab 1982; Bassett & Studier 1988). Brief periods of confinement (<12 hours), however, have no appreciable effect on the renal function of bats (Studier & Rimle 1980). This study therefore targeted only free-ranging individuals that were held captive for less than four hours.

Bat capture

Bats routinely left the roosts at dusk to forage and returned several hours later. Bats caught leaving the roost (that is before feeding) were captured using Hopper traps placed at the roost entrance (Bakken & Kunz 1988), whereas those returning to the roost were captured using mist-nets set at the roost entrances. These mist-nets were manned continuously, and bats were extracted from the net within two minutes of capture, to ensure that capture stress was minimized. The bats captured returning to the roost after two to four hours had visibly distended stomachs, and individuals weighed on average 10.5 ± 1.5% more than at emergence, implying that they had foraged intensively.

Body fluid samples

Urine samples were collected in capillary tubes upon voluntary voiding (Marienfeld, Germany), and frozen at -20°C for later analyses. Blood was collected by wing veni-puncture in heparinized capillary tubes, and immediately centrifuged at 3000 g (Heraeus Christ Haemofuge A) for 10 minutes to determine haematocrits. Plasma samples were then separated, sealed and frozen at -20°C for subsequent analysis.

Owing to the small body size of the bats, the need to minimize captive stress, and a non-removal sampling protocol dictated by a concurrent demographic study, the fluid samples obtained were generally so limited that only osmolality measurements were possible. Immediately after the samples were defrosted, the osmolalities of 10 µl sub-samples were determined using a Wescor 4400 colloidal vapour pressure osmometer. Where possible, sample measurements were made in duplicate or triplicate, and the mean for each individual was used in statistical analyses.

Statistical analysis

Statistical analyses were performed using Statistica 5.1 (StatSoft, Tulsa OK, USA). The use of parametric analytical techniques was justified by prior tests for normality (Kolmogorov-Smirnov D-statistic) and homogeneity of variances (Levene's test), which failed to reveal any significant deviation from inherent statistical assumptions. Differences between the leaving (pre-feeding) and returning to roost (post-prandial) samples, and also the extent of seasonal variation, were assessed using analysis of variance (ANOVA) and/or Student t-tests.

Results

Haematocrit

Haematocrits of pre-feeding bats did not vary significantly on a seasonal basis (Figure 1a), but haematocrits of post-prandial bats (50.75 ± 4.14; n = 47) were significantly lower than in individuals leaving the roost before feeding (53.41 ± 3.09; n = 174). This difference, although slight (6%), was highly significant ($p < 0.001$) in summer (pre-feeding 53.21± 3.36, n = 116; post-prandial 50.25 ± 4.01, n = 30). Although less pronounced in autumn, the 3% difference between the pre-feeding (53.79 ± 2.44, n = 57) and post-prandial samples (51.65 ± 4.36, n = 17) was nevertheless significant ($p < 0.02$).

Plasma concentration

Two-way ANOVA revealed a significant difference ($p < 0.05$) in the plasma concentrations of pre-feeding and post-prandial bats (Figure 1b), but no direct seasonal effect was evident. There was, however, a significant interactive effect between season and nutritional status on plasma concentration levels (Figure 1b).

Plasma concentrations in post-prandial animals did not differ significantly on a seasonal basis (t = 1.73; df = 30; $p >$ 0.05), and in autumn were significantly higher (337.46 ± 37.36 mMol/Kg; n =13) than in pre-feeding bats (294.47 ± 35.24 mMol/Kg; n = 16; fig. 1b). During summer, however, plasma concentrations of pre-feeding bats (333.51 ± 25.90 mMol/Kg; n = 24) were significantly higher (t = 4.04; df = 38; $p < 0.01$) than in autumn, and approached levels observed in post-prandial individuals (320.9 ± 15.59 mMol/Kg; n = 19). Opposing trends in the plasma concentrations of pre-feeding and post-prandial bats during summer and autumn thus resulted in synergistic interaction.

Urine concentration

Variation in urine concentration followed a similar trend to that shown by plasma osmolality (Figure 1c). Two-way ANOVA revealed no direct effect of season, but urine concentrations differed significantly in relation to nutritional status during autumn, and a significant interaction between these two variables was evident (Figure 1c). This may be attributed to a significant seasonal difference (t = 2.26; df = 22; $p <$ 0.05) in pre-feeding urine osmolalities, which were 22% higher in summer (2637.00 ± 505.70mMol/kg; n =16) compared to autumn (2156.75 ± 453.88 mMol/Kg; n = 8). Post-prandial urine concentrations, however, did not differ significantly on a seasonal basis (t = 1.03; df = 18; p >0.05).

Pre-feeding summer osmolalities, and post-prandial concentrations in both autumn (2997.65 ± 647.00 mMol/Kg; n = 12) and summer (2705.21 ± 577.33 mMol/Kg; n = 8), exceeded the maximum (2634 mMol/Kg) predicted from renal morphology (Happold & Happold 1988). The maximum urine concentrations recorded in post-prandial bats were 39% higher than predicted in summer, and 45% above the predicted value in autumn. The proportion of individuals with urine osmolalities 20% or more above the predicted value was 14.9% in the summer pre-feeding sample (Z = 1.04), and 17.9% in both the summer and autumn post-prandial samples (Z = 0.93).

Urine/plasma ratios

Urine/plasma (U/P) ratios, calculated from the mean values for the four groups similarly reflected seasonal and nutritional trends. In autumn, U/P ratios increased. from 7.4 to 9.0 with feeding, while in summer U/P ratios showed a smaller increment (7.9 to 8.4) owing to greater urine and plasma concentrations in bats caught emerging from their roosts before feeding.

Mean U/P ratios, based on plasma and urine samples taken from the ***same*** individuals in autumn, were markedly higher in post-prandial bats (8.7 ± 2.1, n=9), and about 22% greater than in animals that had not fed (7.1 ± 2.4, n=6).

Discussion

Although seasonal differences in roost temperatures during 1996/97 were comparatively small (Bronner *et al.* in press), the duration of exposure to high temperatures was longer during summer than autumn. The substantial elevation in pre-feeding urine and plasma concentrations during summer, in the absence of any significant seasonal change in haema-concentration, suggest that longer periods of exposure to hot roost conditions led to greater dehydration stress, and elicited physiological mechanisms to both conserve water and defend haematocrit. Seasonal effects in post-prandial samples, however, were ameliorated, and elevated body fluid concentrations probably reflected nitrogenous loads associated with rapid digestion of a protein rich insectivorous diet, rather than dehydration associated with flight activity.

The mean urine concentration of free-ranging *M. condylurus* recorded during this study is appreciably lower than in xeric-adapted bats (Table 1; Figure 2), such as the neotropical molossid *Tadarida brasiliensis* (Carpenter 1969; Geluso 1978), but nevertheless fall within the range of values reported for other insectivorous and carnivorous microchiropterans from mesic habitats (Bassett 1986; Busch 1988; Figure 2). Maximum urine concentrations recorded in insectivorous bats are significantly higher than those recorded in omnivorous or frugivorous microchiropterans (1-WAY ANOVA: $F_{3,36}$ = 60.84; $p > 0.001$. Urine concentrating ability amongst the broadly-distributed Microchiroptera is thus dependent upon trophic niche, rather than habitat aridity or phylogeny (Geluso 1975; Studier & Wilson 1983).

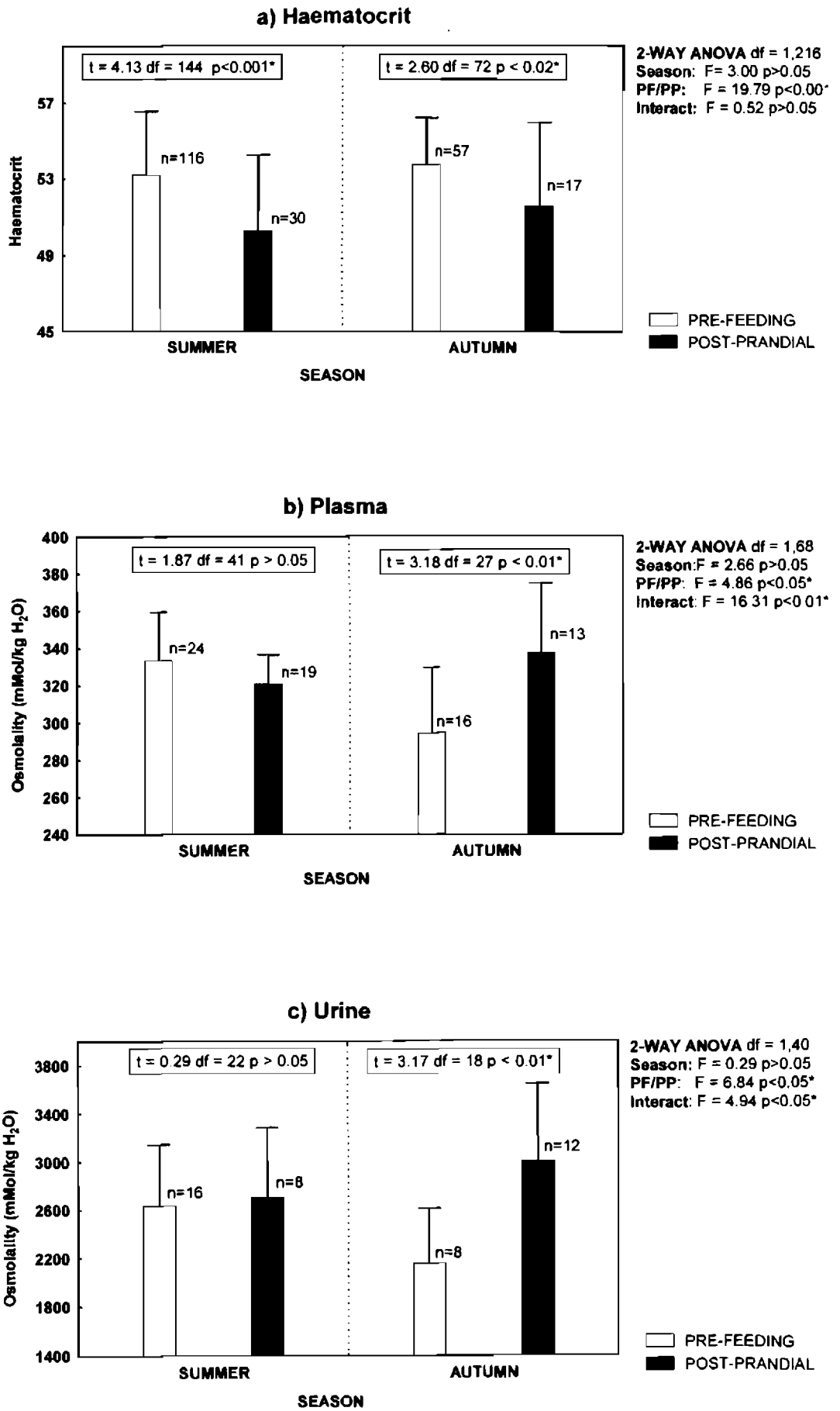

Figure 1 Haematocrits (a), plasma concentrations (b) and urine concentrations (c) in free-ranging *Mops condylurus* caught emerging from roost entrance(s) prior to feeding (PF), and in post-prandial (PP) individuals returning to the roost(s) after foraging, during summer and

Under laboratory conditions, urine concentrations of insectivorous bats approach maximal levels (as predicted by renal inner medulla/cortical ratios) within 30 minutes of eating a protein-rich meal (Geluso 1975). Digestion and absorption in bats thus appears to be very rapid, with transient nitrogenous and mineral loads excreted within two hours of foraging. In contrast, urine concentrations of frugivorous bats decline after a high-carbohydrate meal in response to the high water and low nitrogen content of the diet (Geluso 1978). Although we could not separate the effects of flight activity from feeding, we speculate that the nocturnal increase in urine and plasma concentrations observed in *M. condylurus* was linked predominantly to high nitrogen and electrolyte loads following rapid digestion and absorption of a protein-rich diet, rather than increased activity. This is supported by the similarity, both in magnitude and over time, between body fluid concentrations in post-prandial *M. condylurus* (Figure 1) and experimental results reported for other volant insectivores following feeding (Geluso 1978; Basset 1986). While exercise could also elevate body fluid concentrations, in the absence of feeding it would also lead to greater dehydration and an elevated haematocrit, instead of haemodilution as observed.

The urine of insectivorous and carnivorous microchiropterans is, therefore, concentrated maximally after feeding to facilitate the excretion of excess dietary metabolites with minimal water loss. Rather than being lost in urine, dietary water can thus be saved to replenish body water compartments (most notably the plasma water pool), as indicated by the significant, albeit slight, reduction of haematocrit values in post-prandial samples relative to those in pre-feeding individuals during both seasons. The replenished body water pools may then be drawn upon, if necessary, to thermoregulate during the day, a tactic that would confer a considerable adaptive and survival value in species that inhabit hot diurnal roosts.

Urine voided prior to feeding in summer was 22% more concentrated than that in autumn. This suggests that longer periods of exposure to high temperatures within the roost during summer were more stressful than in autumn, and elicited maximal urine concentrating mechanisms. Similar reports of dehydration stress within daytime roosts have been reported for the fig-eating neotropical bat, *Artibeus jamaicensis* (Studier, Boyd, Feldman, Dapson & Wilson 1983), which rapidly rehydrates within 0.5 – 1h of feeding.

Urine produced by free-ranging Angolan free-tailed bats during both seasons of this study was eight times more concentrated than plasma (U/P > 8), reflecting a concentrating ability superior to man, and of the same magnitude as the camel (Maloiy 1972). Urinary concentrating ability is, however, inversely correlated with body size (Greenwald & Stetson 1988; Beuchat 1990), with small mammals better able to concentrate urine than larger ones. In comparison to similar-sized mammals, the urine concentrating ability of *M. condylurus* is moderate, with U/P values less than half those in some desert rodents (Table 1). Maximum urine concentrations and the kidney concentrating ability of this species is instead comparable to that of other insectivores, both terrestrial and volant, and mesic-adapted rodents.

In both pre-feeding and post-prandial *M. condylurus*, urine concentrations often exceeded the maximum predicted by renal morphology. Given that the predicted values were obtained from a Malawi population, this discrepancy could be the result of geographic variability in renal properties, as reported for several neotropical species (Bassett 1982). Alternatively, it may reflect the inefficiency of morphological predictors of urine concentrating ability, thereby supporting Beuchat's (1996) conclusion that such indices should not be used as a substitute for empirical measurements. Regardless, the similarity of maximum urine concentrations in post-prandial and pre-feeding individuals during summer implies that little or no renal reserve in concentrating ability is available should these bats encounter more severe dehydrating stresses. The ability of this species to survive in hot, potentially dehydrating roosts is not, therefore, based on any exceptional renal concentrating ability.

Table 1 Maximum urine concentrations of *Mops condylurus* recorded (during summer) in this study, and U/P ratios determined from the same individuals in autumn, compared with values reported for other taxa in xeric and mesic habitats. A = arid; M = mesic; F = frugivore; G = granivore; I = insectivore; S = sanguinivore; O = omnivore; nd = no data

Group	Zone/diet	Urine Σ (n) [mMol/Kg]	U/P (n)	Source
Rodentia	A/G	4840–9370 (10)	12–22 (10)	MacMillen & Lee (1972); MacMillen *et al.* (1967)
	A/O	3468–5000(5)	9–12 (5)	Brownfield & Wunder (1976); Louw & Seely (1982); Buffenstein *et al* (1985)
Insectivora	A/I	3634–4010 (3)	9–12 (2)	Yaakobi & Shkolnik (1974); Fielden *et al* (1990)
Microchiroptera	A/I	3566–5010 (4)	(nd)	Geluso (1978); Studier & Wilson (1983)
	M/S	2630–3550 (2)	(nd)	Studier & Wilson (1983); Busch (1988)
	M/I	1551–4340 (9)	(nd)	Geluso (1978); Studier & Wilson (1983)
	M/I	2637 (16)	7.1	**Pre-feeding** *M. condylurus*
		2705 (8)	8.7	**Post-prandial** *M. condylurus*
	M/O	728–2198 (5)	(nd)	Studier & Wilson (1983); Studier *et al* (1983a)
	M/F	359–806 (12)	(nd)	Studier & Wilson (1983)
Insectivora	M/I	1820–3062 (2)	12 (1)	Yaakobi & Shkolnik (1974)
Rodentia	M/O	3250–3804 (5)	7–9 (5)	Brownfield & Wunder (1976); Buffenstein *et al* (1985)
Homo sapiens	A-M/O	1350	4	Brownfield & Wunder (1976)

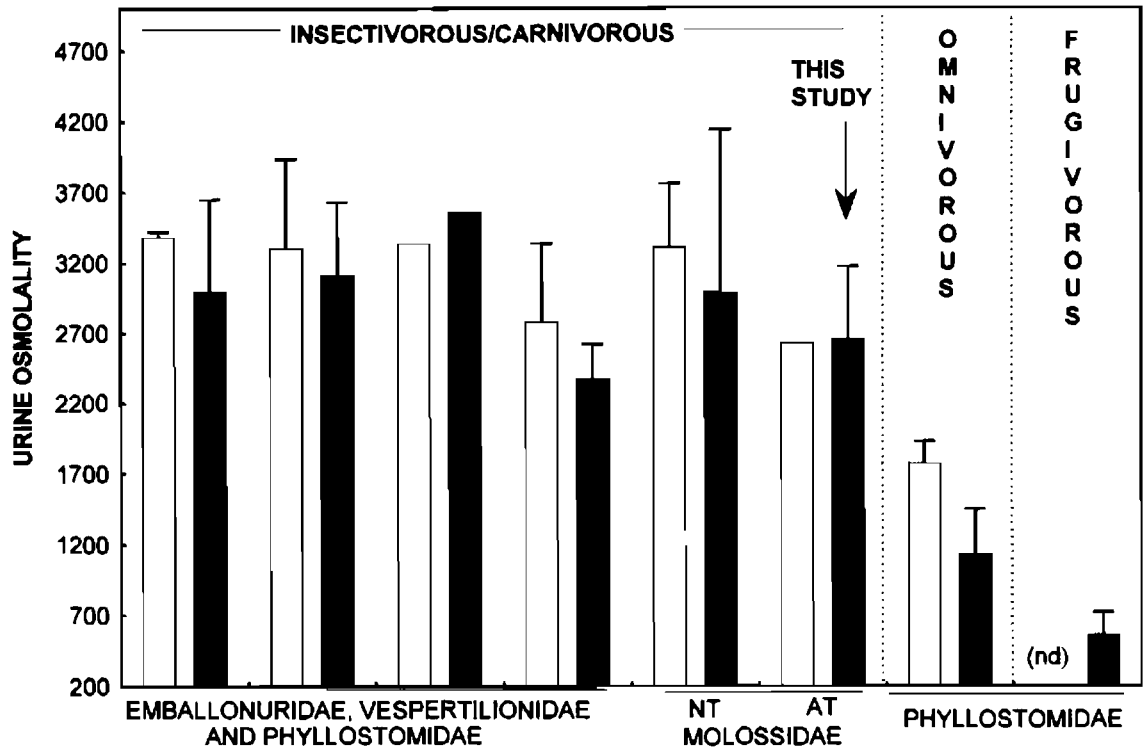

Figure 2 Predicted (open blocks) and recorded (solid blocks) maximum urine concentrations in free-ranging *Mops condylurus* relative to reported values for other microchiropteran trophic groups, including neotropical (NT) and afrotropical (AT) molossids

Despite raised urinary concentrations in individuals emerging from the roost during summer, plasma concentrations of these bats were still markedly higher (±10%) than in autumn. This suggests that the bats were indeed dehydrated, and that water from the plasma pool was probably drawn upon to defend body temperature by evaporative cooling (Maloney *et al.* in press). Despite this substantial reduction in the plasma pool of *M. condylurus*, we observed no obvious deleterious effects, as commonly shown by other animals enduring similar dehydration stresses (Horowitz & Adler 1983). Since a 15% reduction in total body water is generally fatal (Louw & Seely 1982), the 10% reduction in the vascular pool constituted a considerable loss in body water, indicating that this species is extremely tolerant of dehydration on a daily basis.

Regardless of season or nutritional status, haematocrit values were higher than expected for mammals at this altitude, but similar to values (47–63%) reported for other volant insectivores (Studier & Ewing 1971; Riedesel 1977; Jurgens, Bartels & Bartels 1981; Arevalo, Perez-Suarez & Lopez-Luna 1987; Wolk & Bogdanowicz 1987) and some frugivorous bats (Valdivieso & Tamsitt 1971; Van der Westhuysen 1988). Such high haematocrits with concommitant increased haemoglobin concentration most likely reflect the high oxygen-carrying capacity needed for the increased oxygen demands of prolonged powered flight in bats (Jurgens, Bartels & Bartels 1981; Agar & Godwin 1992; Arevalo Perez-Suarez & Lopez-Luna 1992).

Haematocrit exceeded 60% in four individuals caught before feeding, and was greater than 58% in a substantial proportion (8%) of bats caught before feeding in summer and autumn. In most mammals, such high haematocrit values increase blood viscosity and resistance, thereby impeding blood flow to the brain and peripheral tissues, and increasing the workload of the heart, often with fatal effect (Horowitz & Samueloff 1979). Although volant mammals may require high haematocrits to ensure adequate oxygen delivery during sustained flight, superimposed dehydration stresses could severely compromise the rheological properties of blood. Indeed, long-term survival of dehydration stresses demands the protection of haematocrit for normal cardiovascular function (Horowitz & Adler 1983). In most terrestrial vertebrates routinely faced with dehydration, haematocrit and plasma volume are maintained at the expense of other body water compartments, with initial reliance on interstitial and intracellular water pools (Degen 1977; Horowitz & Adler 1983; Carmi, Pinshow, Horowitz & Bernstein 1993). These water compartments, although not measured in the present study, may also have been drawn upon to meet evaporative water requirements and conserve blood volume

The similarity of haematocrit measurements in the two seasons, despite markedly higher plasma concentrations in summer, could reflect active haematocrit defence, as observed in the Egyptian fruit bats (*Rosettus aegyptiacus)* deprived of water (Arad & Korine 1993). Haematocrit maintenance could be achieved by water efflux from the erythrocytes into the more concentrated plasma fraction, with a concomitant reduction in red blood cell volume that would maintain haematocrit despite elevated plasma osmolalities. Similar changes in red blood cell volume have been previously reported in arid-adapted camels and goats subjected to dehydration (Meyerstein, Etzion, Mazor & Yagil 1987). Another possible, although untested, explanation is that withdrawal of some red blood cells from the vascular pool into the spleen may be used to actively maintain haematocrit and blood viscosity,

and thus facilitate blood flow, when the rheological properties of blood are threatened.

The preference of *Mops condylurus* for hot roosts in which microclimates are spatially quite variable confers several ecophysiological advantages relating to sustained reproduction, the minimization of thermoregulatory energy costs and the exploitation of habitats where more clement roosts are limited (Bronner *et al.* 1999). But this tactic also has inherent hazards in terms of body water regulation. Faced with a thermally-challenging roost milieu, these bats apparently compensate for an only moderate kidney concentrating ability through behavioural means, as well as physiological mechanisms such as adaptive hyperthermia, tolerance of plasma concentration and haematocrit defense. Although apparently tolerant of cyclic dehydration and rehydration during feeding, these bats may lack the physiological resilience to sustain water balance should more debilitating conditions prevail, or if prevented from feeding. It therefore seems likely that they may need to forage regularly not only for energetic reasons, but also to meet the daily water needs associated with the hot roost microclimates experienced in summer and autumn.

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References

AGAR, N.S. & GODWIN, I.R. 1992. Erythrocyte metabolism in two species of bats: common bent-wing bat (*Miniopterus schreibersii)* and the red fruit bat (*Pteropus scapulatus) Comp Biochem. Physiol.* 101B: 9–12.

ARAD, Z. & KORINE, C. 1993. Effect of water restriction on energy and water balance and osmoregulation of the fruit bat *Rosettus aegyptiacus. J. Comp Physiol* 163B: 401–405.

AREVALO, F., PEREZ-SUAREZ, G. & LOPEZ-LUNA, P. 1987. Hematological data and hemoglobin components in bats (*Vespertilionidae). Comp. Biochem. Physiol* 88A: 447–450.

AREVALO, F., PEREZ-SUAREZ, G. & LOPEZ-LUNA, P. 1992. Seasonal changes in blood parameters in the bat species *Rhinolopus ferrumequinum* and *Miniopterus schreibersi. Arch. Int. Physiol. Biochim. Biophys.* 100: 385–387.

BAKKEN, G.S. & KUNZ, T.H. 1988. Microclimate methods. In: Ecological and behavioral methods for the study of bats. (ed.) T.H. Kunz. Smithsonian Institution Press, Washington D.C., pp. 303–332.

BANKIR, L. & DE ROUFFIGNAC, C. 1987. Urine concentrating ability: insights from comparative anatomy. *Am J. Physiol.* 249. 643–666.

BASSETT, J.E. 1982. Habitat, aridity and intraspecific differences in the urine concentrating ability of insectivorous bats. *Comp Biochem. Physiol.* 72A: 703–708.

BASSETT, J.E. 1986. Habitat aridity and urine concentrating ability of nearctic insectivorous bats. *Comp. Biochem. Physiol.* 83A: 125–131.

BASSETT, J.E. & STUDIER, E.H. 1988. Methods for determining water balance in bats. In: Ecological and behavioral methods for the study of bats, (ed.) T.H. Kunz. Smithsonian Institution Press, Washington D.C., pp. 373–386.

BELL, G.P., BARTHOLOMEW, G.A. & NAGY, K.A. 1986. The roles of energetics, water economy, foraging behaviour and geothermal refugia in the distribution of the bat, *Macrotus californicus. J. Comp. Physiol. B.*, 156: 441–450.

BEUCHAT, C.A. 1990. Body size, medullary thickness and urine concentrating ability in mammals. *Am. J. Physiol.* 258: R298–R308.

BEUCHAT, C.A. 1996. Structure and concentrating ability of the mammalian kidney: correlations with habitat. *Am. J Physiol.* 271. R157–R179.

BRONNER, G.N., MALONEY, S. & BUFFENSTEIN, R. Xxxx. Survival tactics within thermally-challenging roosts: heat tolerance and cold sensitivity in the Angolan free-tailed bat, *Mops condylurus. S. Afr. J. Zool.* 34(1):1–10.

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

BUFFENSTEIN, R., CAMBELL, W. & JARVIS, J.U.M. 1985. Identification of crystalline allantoin in the urine of African cricetidae (Rodentia) and its role in their water economy. *J. Comp. Physiol.* B 155: 493–499.

BUSCH, C. 1988. Consumption of blood, renal function and utilization of free water by the vampire bat, *Desmodus rotundus. Comp. Biochem Physiol.* 90A: 141–146.

CARMI, N., PINSHOW, B., HOROWITZ, M. & BERNSTEIN, M.H. 1993. Birds conserve plasma volume during thermal and flight incurred dehydration. *Physiol Zool.* 66: 829–846.

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

DEGEN, A.A. 1977. Responses to dehydration in fat tailed awassi and imported German Mutton Merino Sheep. *Physiol. Zool.* 50: 284–293.

FIELDEN, L.H., PERRIN, M.R. & HICKMAN, G.C. 1990. Water metabolism in the Namib desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Comp. Biochem. Physiol.* 96A: 227–234.

FRANCHINI, K.G. & COWLEY, A.W.Jr. 1996. Renal cortical and medullary flow responses during water restriction: the role of vasopressin. *Am. J. Physiol.* 270: R1257–R1264.

GELUSO, K.N. 1975. Urine concentration cycles of insectivorous bats in the laboratory. *J. Comp. Physiol.* 99: 309–319.

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 of the Fifth International Bat Research Conference, (eds.) Wilson, D.F. & Gardner, A.L. Texas Tech Press, Lubbock, Texas, pp. 403–414.

GREENWALD, L. & STETSON, D. 1988. Urine concentration and the length of the renal papilla. *News in Physiological Sciences* 3: 46–49.

HAPPOLD, D.C.D. & HAPPOLD, M. 1988. Renal form and function in relation to the ecology of bats (Chiroptera) from Malawi, Central Africa. *J. Zool., Lond.* 215: 629–655.

HOROWITZ, M. & ADLER, J.H. 1983. Plasma volume regulation during heat stress: albumin synthesis vs. capillary permeability. A comparison between desert and non-desert species. *Comp. Biochem. Physiol.* 75A: 105–110.

HOROWITZ, M. & SAMUELOFF, S. 1979. Plasma water shifts during thermal dehydration. *J Appl Physiol.* 47: 738–744.

JURGENS, K.D., BARTELS, H & BARTELS, R. 1981. Blood oxygen transport and organ weights of small bats and small non-flying mammals. *Respir. Physiol.* 45: 243–260.

KOOPMAN, K.F. 1993. Order Chiroptera. In: Mammal species of the world: a taxonomic and geographic reference, (eds.) D.E. Wilson & D.M. Reeder, 2nd. edn. Smithsonian Institution Press, Washington D.C., pp. 137–242.

LOUW, G.N. & SEELY, M.K. 1982. Ecology of desert organisms. Longmans, London, 184 pp.

MACMILLEN, R.E., BAUDINETTE, R.V. & LEE, A.K. 1972. Water economy and energy metabolism of the sandy inland mouse *Leggadina hermansburgensis*. *J Mammal.* 53: 529–539.

MACMILLEN, R.E. & LEE, A.K. 1967. Australian desert mice: independence of exogenous water. *Science* 158: 383–385.

MALOIY, G.M.O. 1972. Renal salt and water excretion in the camel *(Camelus dromedarius)*. *Symp. Zool. Soc., Lond.*, 31: 243–259.

MALONEY, S.K., BRONNER, G.N. & BUFFENSTEIN R. *in press.* Thermoregulation in the Angolan free-tailed bat (*Mops condylurus*): a small mammal that uses hot roosts. *Physiol Zool*

McNAB, B.K. 1982. Evolutionary alternatives in the physiological ecology of bats. In: Ecology of Bats, (ed.) T. Kunz, 9th edn. Plenum, New York, 425 pp.

MEYERSTEIN, N., ETZION, Z., MAZOR, D. & YAGIL, R. 1987. Adaptation to the environment: the role of red blood cells. In: Adaptive Physiology to Stressful Environments.(Samueloff S. & Yousef M.K.) CRC Press, Boca Raton, Florida. pp. 131–137.

MORRIS, S., CURTIN, A.L. & THOMPSON, M.B. 1994. Heterothermy, torpor, respiratory gas exchange, water balance and the effect of feeding in Gould's long-eared bat *Nyctophilus gouldi*. *J. Exp Biol.* 197: 309–335.

NAGY, K.A. 1994. Seasonal water, energy and food use in free-living arid habitat mammals. *Aust. J. Zool.* 42: 55–63.

NOWAK, R.M. 1994. Walkers bats of the world. Johns Hopkins University Press, Baltimore, 287 pp.

RIEDESEL, M.L. 1977. Blood physiology. In: Biology of bats (ed. Wimsatt W.A.) Vol III, Academic Press, New York, pp. 485–517.

RODRIGUES-DURÁN, A. 1995. Metabolic rates and thermal conductance in four species of neotropical bats roosting in hot caves. *Comp. Biochem. Physiol.* 110A: 347–355.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. The mammals of the southern African subregion. University of Pretoria Press, Pretoria, 771 pp.

STUDIER, E.H. & EWING, W.G. 1971. Diurnal fluctuation in weight and blood composition in *Myotis nigricans* and *Myotis lucifugus*. *Comp. Biochem. Physiol.* 38A: 129–139.

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. & WILSON, D.E. 1983. Natural urine concentrations and composition in neotropical bats. *Comp Biochem. Physiol.* 75A: 509–515.

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

STUDIER, E.E., WISNIEWSKI, S.J., FELDMAN, A.T., DAPSON, R.W., BOYD, B.C. & WILSON, D.E. 1983(b). Kidney structure in neotropical bats. *J. Mammal.* 64: 445–452.

VALDIVIESO, D. & TAMSITT, J.R. 1971. Hematological data from tropical American bats. *Can. J. Zool.* 49: 31–36.

VAN DER WESTHUYSEN, J. 1988. Haematology and iron status of the Egyptian fruit bat, *Rousettus aegyptiacus*. *Comp. Biochem. Physiol.* 90: 117–120.

WOLK, E. & BOGDANOWICZ, W. 1987. Hematology of the hibernating bat: *Myotis daubentoni*. *Comp. Biochem. Physiol.* 88A: 637–639.

YAAKOBI, D. & SHKOLNIK, A. 1974. Structure and concentrating capacity in kidneys of three species of hedgehogs. *Am. J. Physiol.* 286: 948–952.