

## Variability in urine concentration and fecal water content of bats in a tropical deciduous forest

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We examined seasonal variation in urine concentration and fecal water content (FWC) of free-ranging bats inhabiting the tropical deciduous forest of the Chamela-Cuixmala Biosphere Reserve, Mexico, which is characterized by marked dry and rainy seasons. We tested the hypothesis that bats inhabiting this forest would exhibit seasonal physiological changes to maintain water balance. We predicted that bats would have higher urine concentrations and reduced FWC during the dry season. Our results were consistent with the 1st prediction for the insectivore, Parnell's mustached bat (*Pteronotus parnellii*), but not for the Jamaican fruit bat (*Artibeus jamaicensis*). Our data were consistent with our 2nd prediction for *P. parnellii* and the facultative nectarivore Pallas' long-tongued bat (*Glossophaga soricina*), but not for *A. jamaicensis*. Our findings indicate that for the bats we studied, the 2 routes by which water is lost were affected differently by seasonal changes in water availability as a function of feeding habits. DOI: 10.1644/09-MAMM-A-370.1.

Key words: bats, fecal water loss, seasonality, urine concentration

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The water balance of terrestrial mammals inhabiting highly seasonal biomes is challenged during periods with reduced water availability. In addition to changing their behavior to cope with these conditions (Schmidt-Nielsen 1964), mammals also can adjust their physiology to maintain water balance. For instance, South American desert mouse opossums (*Thylamys pusillus*—Diaz et al. 2001) and degus (*Octodon degus*—Bozinovic et al. 2003) reduce water losses by producing low volumes of hyperosmotic urine during the dry season. In the springhare (*Pedetes capensis*) water loss is reduced by producing concentrated urine and dry feces (Peinke and Brown 1999). In contrast, Merriam's kangaroo rat (*Dipodomys merriami*) conserves water by decreasing losses due to evaporation rather than in urine or feces (Schmidt-Nielsen and Schmidt-Nielsen 1950; Tracy and Walsberg 2001).

Like rodents, bats inhabiting seasonal environments can adjust their physiology to cope with conditions that could affect water balance and compromise survival (Buffenstein et al. 1999). For example, the insectivorous Angolan free-tailed bat (*Mops condylurus*, Molossidae) had higher urine concentration before leaving the day roost in summer than in autumn (Buffenstein et al. 1999). Similarly, Jamaican fruit bats (*Artibeus jamaicensis*, Phyllostomidae) had higher urine

concentrations in the dry season than in the wet season in a tropical rain forest in Panama (Studier et al. 1983a).

Tropical dry forests experience extremely seasonal levels of precipitation (Marco and Páez 2002; McLaren and McDonald 2005; Singh and Kushwaha 2005), with dry seasons usually extending for about 8 months of the year. More than 90% of the annual rain falls during the remaining months (García-Oliva et al. 2002). Therefore, bats inhabiting these forests may be water-stressed during the dry season, and we hypothesized that such bats will exhibit seasonal physiological adjustments to maintain water balance. A previous experimental study showed that urine was more concentrated and feces were drier in water-deprived than in hydrated individuals of Egyptian fruit bats (*Rousettus aegyptiacus*, Pteropodidae—Arad and Korine 1993). Accordingly, we predicted that bats would reduce water losses by producing more-concentrated urine and drier feces during the months of limited precipitation.

We tested these predictions on 3 species of bats with different feeding habits in a highly seasonal dry forest in Mexico: the frugivorous *A. jamaicensis*, the facultative



nectarivorous Pallas' long-tongued bat (*Glossophaga soricina*, Phyllostomidae), and the insectivorous Parnell's mustached bat (*Pteronotus parnellii*, Mormoopidae). In contrast to plant-eating bats that base their diet on items with high water content (floral nectar and fruit pulp—Roces et al. 1993; Wendeln et al. 2000), the water balance of insectivorous bats is probably compromised more significantly during periods of low availability of sources of free water. Therefore, we expected that seasonal changes in urine concentration and fecal water content (FWC) would be more pronounced in *P. parnellii* than in *G. soricina* and *A. jamaicensis*. Virtually nothing is known about FWC in bats and its relation to diet. We expected that content of water in feces of *G. soricina* and *A. jamaicensis* would be higher than in *P. parnellii* in both seasons.

## MATERIALS AND METHODS

**Study site.**—Our study was conducted in Chamela-Cuixmala Biosphere Reserve (~13,200 ha), in Jalisco, on the Pacific coast of Mexico (19°29'N, 105°01'W) between May and September 2008. The predominant vegetation in the area is tropical deciduous forest, with small evergreen riparian bands of vegetation (Noguera et al. 2002). The mean annual temperature in the area is 24.9°C, and mean annual rainfall is 750 mm. Climate is characterized by 2 marked seasons, a dry season from November to May and a rainy season from June to October (Bullock 1995).

During our study, the dry season lasted between 1 May and 30 June, whereas the rainy season lasted between 1 July and 6 September. Water vapor deficit was significantly higher in the dry season than in the rainy season (dry: 0.652 kPa  $\pm$  0.021 SE,  $n = 61$ ; rainy: 0.493  $\pm$  0.02 kPa,  $n = 71$ ;  $t_{130} = 5.42$ ,  $P < 0.0001$ ). Additionally, a total of 713 mm of rainfall was recorded, >97% from 2 July through 6 September (González del Castillo Aranda, University of California, Davis, pers. comm.).

**Capture of bats.**—We caught bats in mist nets at least twice a week (except 8–24 August). We kept bats in individual cloth bags until processing and released them immediately after processing. We recorded sex, reproductive status (nonreproductive, pregnant, or lactating), and age class of each individual processed. We measured body mass to  $\pm 0.5$  g with a spring balance (model 20100; Pesola, Baar, Switzerland) and forearm length to  $\pm 0.01$  mm using digital calipers (Mitutoyo, Kawasaki, Japan) in the field. All protocols were approved and performed under Scientific Collector License FAUT-0069 granted to LGHM by the Secretaría de Medio Ambiente y Recursos Naturales, Mexico, and followed the guidelines for research on wild mammals approved by the American Society of Mammalogists (Gannon et al. 2007).

**Sample collection and processing.**—In addition to our focal species we also collected urine or feces samples, or both, from 14 species of bats, but due to small sample sizes they were not used to test our predictions. In total, we collected 235 urine samples (66 in the dry season and 169 in the rainy season;

Table 1). Urine samples were collected with capillary tubes (310  $\mu$ l; Marienfeld, Lauda-Königshofen, Germany) directly from the urethral orifice in 57% of the cases. If bats did not urinate while handled they were placed in plastic jars (1.87 liters, 12 cm in diameter) for 0.5–1 h. The bottom of the jar was replaced with a metal net from which a bat could hang. The jar with the bat inside was placed upside down, allowing collection of urine and feces from the lid. Urine and feces were collected immediately upon voiding or defecating, minimizing evaporation of water from samples. We did not collect feces contaminated with urine or vice versa, and jars were cleaned thoroughly once bats were released. Urine was kept in 0.5-ml vials sealed with Parafilm (American Can Company, Greenwich, Connecticut) and cooled (0–6°C) until processing a few minutes to 4 h after collection. Feces were collected from the cloth bag or from the jars, kept in 0.5-ml vials sealed with Parafilm, and cooled (0–6°C) until processing 1–4 h after collection.

Urine osmolality ( $U_{osm}$ ) was measured with an Osmette II freezing point osmometer (Precision Systems, Natick, Massachusetts). In 35% of the samples 2 or 3 subsamples were analyzed and the values averaged. To validate the collection method we compared urine concentrations obtained directly from bats and those from the jar. We did this for 6 species (*Artibeus lituratus* [intermedius], *A. hirsutus*, *A. jamaicensis*, *G. soricina*, *P. parnellii*, and *Desmodus rotundus*). No significant differences in urine concentration were found between samples collected directly from bats versus those from jars for any species (Student's  $t$ -test,  $P > 0.06$  for all comparisons). Because time between collection and processing ranged from a few minutes to 4 h, we assessed the relationship between urine concentration values and time to analysis for the same 6 species and found no effect of time on  $U_{osm}$  ( $10^{-5} < r^2 < 0.02$ ;  $P > 0.15$  for all species).

We collected 255 fecal samples (67 in the dry season and 188 in the rainy season; Table 2). Feces were weighed to  $\pm 0.0001$  g using an electronic scale (model BL210; Sartorius AG, Göttingen, Germany) and then dried at 80°C for 24 h to constant mass in a convection oven. Samples were reweighed after drying, and FWC was calculated as the percent (%) of total feces mass composed of water mass. We could not measure the amount of water that evaporated from feces from the moment of collection until processing, and our values probably underestimate the real FWC. However, because we collected feces immediately upon defecating and conserved them in sealed vials in a cool environment, evaporation probably was negligible.

**Statistical analysis.**—Data are presented as means  $\pm$  SE. When samples were homoscedastic, the  $t$ -test was used for pairwise comparisons. When data were not homoscedastic even when transformed, we used Mann–Whitney  $U$ -tests for pairwise comparisons. When comparisons were among more than 2 independent groups we used nonparametric Kruskal–Wallis ( $H$ ) tests (Zar 1999). We used the sequential Bonferroni correction (Rice 1989) to control for group-wide type I error rates among comparisons. All tests were 2-tailed, and type I

**TABLE 1.**—Mean  $\pm$  SE urine concentration (mOsmol/kg H<sub>2</sub>O) for several bat species during the dry and the rainy seasons of 2008 in Chamela-Cuixmala Biosphere Reserve, Mexico. Mean values between seasons were compared for those species with  $n \geq 19$  in each season using Mann–Whitney *U*-tests. Critical values ( $P = 0.05$ ) were adjusted using sequential Bonferroni correction ( $P_B$ —Rice 1989). Significant differences were considered when  $P \leq P_B$ .

Species and guild	Mean urine concentration		<i>n</i> (dry/rainy)	Range (minimum– maximum) (dry/rainy)	Statistical comparison		
	Dry	Rainy			<i>U</i>	<i>P</i>	<i>P<sub>B</sub></i>
<b>Vampires</b>							
<i>Desmodus rotundus</i>	2,021.6 $\pm$ 231.8	1,850.3 $\pm$ 184.3	8/6	944–3,180/1,239–2,546			
<b>Insectivorous</b>							
<i>Lasiurus intermedius</i>		2,065	—/1				
<i>Peropteryx macrotis</i>	2,248		1/—				
<i>Pteronotus parnellii</i>	2,129.6 $\pm$ 122.1	1,730.6 $\pm$ 72.2	24/42	109–2,813/309–2,813	224	0.0002	0.025
<i>Pteronotus personatus</i>		1,734	—/1				
<b>Frugivorous</b>							
<i>Artibeus hirsutus</i>	614.5 $\pm$ 150.7	576.8 $\pm$ 63.4	4/12	259–934/163–805			
<i>Artibeus lituratus (intermedius)</i>	675.1 $\pm$ 38.4	541.8 $\pm$ 51.8	4/17	573–752/125–857			
<i>Artibeus jamaicensis</i>	592.2 $\pm$ 47.2	517.5 $\pm$ 23.4	19/80	189–846/41–909	565.5	0.08	0.05
<i>Artibeus (Dermanura) phaeotis</i>		712	—/1				
<i>Artibeus (Dermanura) watsoni</i>	892.5		1/—				
<i>Sturnira lilium</i>	874	342.5	1/1				
<b>Nectarivorous</b>							
<i>Glossophaga soricina</i>	293.2 $\pm$ 132.2	442.7 $\pm$ 106.7	3/7	105–548/45–864			
<i>Leptonycteris yerbabuenae</i>	402	65	1/1				

error level in all tests was  $\alpha = 0.05$ . The sequential Bonferroni correction *P*-level is indicated as *P<sub>B</sub>*. Significant differences were considered when  $P \leq P_B$ . All calculations were done using Statistica (version 9; StatSoft, Inc., Tulsa, Oklahoma).

**RESULTS**

We report urine concentration and FWC values for all the species for which we have data. However, our analysis

concentrates on *A. jamaicensis* and *P. parnellii* for  $U_{osm}$  and on *A. jamaicensis*, *G. soricina*, and *P. parnellii* for FWC.

*Urine concentration.*—Seasonal differences in urine concentration were significant for *P. parnellii*, with higher mean  $U_{osm}$  in the dry season. In contrast, *A. jamaicensis* exhibited no seasonal differences in  $U_{osm}$  (Table 1).

Given that urine samples were collected at different times of night, our comparisons may include individuals with different

**TABLE 2.**—Mean  $\pm$  SE fecal water content (%) for 14 bat species during the dry and the rainy seasons of 2008 in Chamela-Cuixmala Biosphere Reserve, Mexico. Mean values between seasons were compared for those species with  $n \geq 7$  in each season using Mann–Whitney *U*-tests. Critical values ( $P = 0.05$ ) were adjusted using sequential Bonferroni correction ( $P_B$ —Rice 1989). Significant differences were considered when  $P \leq P_B$ .

	Fecal water content		<i>n</i> (dry/rainy)	Range (minimum– maximum) (dry/rainy)	Statistical comparison		
	Dry	Rainy			<i>U</i>	<i>P</i>	<i>P<sub>B</sub></i>
<b>Insectivorous</b>							
<i>Lasiurus intermedius</i>		57.4	—/1				
<i>Mormoops megalophylla</i>		77	—/1				
<i>Natalus stramineus</i>		73.5 $\pm$ 2.6	—/2	—/70.8–76.1			
<i>Pteronotus davyi</i>		75.5	—/1				
<i>Pteronotus parnellii</i>	51.6 $\pm$ 2.3	71.1 $\pm$ 0.7	41/108	12.3–80.7/47.3–94.5	352	0.0001	0.017
<i>Pteronotus personatus</i>		61.3 $\pm$ 10.2	—/3	—/40.9–72.6			
<b>Frugivorous</b>							
<i>Artibeus hirsutus</i>		70.1 $\pm$ 4	—/6	—/56.3–81.9			
<i>Artibeus lituratus (intermedius)</i>	75.9 $\pm$ 8.2	79.6 $\pm$ 1.7	4/13	62.8–99.1/68.5–95.1			
<i>Artibeus jamaicensis</i>	72.3 $\pm$ 6.2	79 $\pm$ 2.5	12/41	10.3–100/24.5–98.9	181	0.17	0.05
<i>Sturnira lilium</i>	64.1 $\pm$ 8.1		2/—	56–72.2/—			
<i>Uroderma bilobatum</i>	66.6		1/—				
<b>Nectarivorous</b>							
<i>Glossophaga soricina</i>	45.2 $\pm$ 5.6	84.9 $\pm$ 4.3	7/11	25.9–64.8/49.1–100	3	0.0013	0.025
<i>Leptonycteris yerbabuenae</i>		72.7	—/1				

**TABLE 3.**—Interspecific comparison of fecal water content in the dry (below diagonal) and rainy (above diagonal) seasons of 2008 in Chamela-Cuixmala Biosphere Reserve, Mexico. Results shown are of Kruskal–Wallis multiple comparisons tests (dry:  $H = 18$ ,  $n = 60$ ,  $P = 0.0001$ ; rainy:  $H = 31.75$ ,  $n = 160$ ,  $P < 0.0001$ ).  $A_j = A. jamaicensis$ ;  $G_s = G. soricina$ ;  $P_p = P. parnellii$ .  $P$ -values are given in parentheses.

	<i>Artibeus jamaicensis</i>	<i>Glossophaga soricina</i>	<i>Pteronotus parnellii</i>
<i>A. jamaicensis</i>		$G_s > A_j$ (0.591)	$A_j > P_p$ (<0.0001)
<i>G. soricina</i>	$A_j > G_s$ (0.0015)		$G_s > P_p$ (0.0002)
<i>P. parnellii</i>	$A_j > P_p$ (0.0003)	$P_p > G_s$ (0.99)	

levels of hydration. A seasonal comparison between urine samples of *P. parnellii* collected within 1.5 h after leaving day roosts revealed the same pattern as when time of collection was not considered. That is,  $U_{osm}$  was significantly higher in the dry season than in the rainy season (dry:  $2,144.1 \pm 117.8$  mOsmol/kg  $H_2O$ ,  $n = 15$ ; rainy:  $1,732.6 \pm 81.7$  mOsmol/kg  $H_2O$ ,  $n = 29$ ;  $t_{42} = 2.9$ ,  $P = 0.006$ ). We did a similar analysis for *A. jamaicensis* and found no significant seasonal differences (dry:  $590.2 \pm 153.3$  mOsmol/kg  $H_2O$ ,  $n = 3$ ; rainy:  $455.3 \pm 54.6$  mOsmol/kg  $H_2O$ ,  $n = 16$ ;  $t_{17} = 0.95$ ,  $P = 0.35$ ).

*Within-species seasonal variation in FWC.*—Differences in FWC between seasons were not significant in the frugivorous *A. jamaicensis*, but we found significantly higher FWC in the rainy season in the facultative nectarivorous *G. soricina* and in the insectivorous *P. parnellii* (Table 2).

*Interspecific seasonal differences in FWC.*—We tested interspecific differences in FWC in both seasons for *A. jamaicensis*, *G. soricina*, and *P. parnellii*. We found significant differences in dry and rainy seasons (Table 3). A posteriori multiple comparison tests revealed that for the dry season no significant differences in FWC existed between *G. soricina* and *P. parnellii*, and both had significantly drier feces than *A. jamaicensis*. In contrast, in the rainy season *P. parnellii* produced significantly drier feces than *G. soricina* and *A. jamaicensis*, but no significant differences in FWC were found between the 2 plant-feeding species (Table 3).

## DISCUSSION

This study has shown that frugivorous and insectivorous bats differ in their seasonal  $U_{osm}$  and FWC patterns. Our prediction that  $U_{osm}$  would vary seasonally was supported only for *P. parnellii*, which had higher mean  $U_{osm}$  value in the dry season. We suggest that lack of seasonal changes in  $U_{osm}$  values in *A. jamaicensis* is due to feeding on fruit with high water content throughout the year. Even during the dry season, when fruit availability is lower (Bullock and Solís-Magallanes 1990), *A. jamaicensis* likely increases foraging range in search of these food items. Bats have high mobility compared to other small mammals, and this allows them to extend foraging areas (Bassett 1982; Heithaus and Fleming 1978; Horner et al. 1998). Moreover, the kidney of *A. jamaicensis* cannot produce

highly concentrated urine (Studier et al. 1983b), thus precluding significant increases in  $U_{osm}$  values even in drier environments or seasons. In contrast to our study, Studier et al. (1983a) found significant seasonal differences in  $U_{osm}$  values in urine samples of *A. jamaicensis* collected within 1.5 h after sunset in a tropical rain forest in Panama (dry:  $699 \pm 19$  mOsmol/kg  $H_2O$ ; rainy:  $411 \pm 33$  mOsmol/kg  $H_2O$ ). When we compared samples collected in Chamela within 1.5 h after sunset we found the same pattern as that of Studier et al. (1983a), but the difference was not significant, probably due to the small sample size in the dry season ( $n = 3$ ).

In contrast, *P. parnellii* is an insectivore that feeds mainly on Lepidoptera and Coleoptera (Herd 1983). In Chamela, populations of these insect orders undergo seasonal fluctuations, with a sharp decrease in abundance during the dry season (Lister and García 1992). Because *P. parnellii* does not use night roosts and forages continuously over large distances (Bateman and Vaughan 1974; Herd 1983), it is likely that foraging time is extended in the dry season. This would entail an increase in pulmocutaneous evaporative water loss due to the increased water vapor deficit in the dry season (see ‘‘Materials and Methods’’). In addition, assuming that water content of prey is constant year-round, the seasonal differences we found in  $U_{osm}$  suggest lower levels of water intake or higher levels of water loss, or both, in the dry season. By increasing  $U_{osm}$  *P. parnellii* is able to cope with low water and food availability in the dry season. In fact, Studier et al. (1983b) suggested, based on renal morphology, that *P. parnellii* should be tolerant of dry habitats.

No reports exist on drinking by *P. parnellii* in the wild. However, this species requires drinking water in captivity (Herd 1983). Additionally, it is associated with water bodies (cenotes) in the Yucatan peninsula from which it may drink (MacSwiney G. et al. 2009). This species could resort to drinking from ponds and creeks in addition to gaining water from food to maintain water balance. Reduced availability of open water in Chamela during the dry season would increase the need to conserve water.

As for urine concentration, our prediction that FWC would change seasonally was partly supported. FWC was significantly different between seasons for *P. parnellii* and *G. soricina* but not for *A. jamaicensis*. *A. jamaicensis* feeds on fig fruits throughout the year in Chamela (Herrera M. et al. 2001), thus maintaining similar levels of dietary hydration in the dry and rainy seasons. The production of drier feces during the dry season by *G. soricina* might be caused by increased efficiency in absorption of nutrients (McWhorter et al. 2003) or by lower levels of hydration (Arad and Korine 1993). We have no basis to draw conclusions on seasonal changes in efficiency of nutrient digestion in *G. soricina*, and our findings probably reflect a diet with lower water content in the dry season due to a higher use of insects as food during this period (Herrera M. et al. 2001).

The lower FWC in the dry season found for *P. parnellii* is consistent with the seasonal pattern found in  $U_{osm}$  for this species and probably explained by the same argument; that

is, lower levels of hydration in the dry season due to reduced availability of drinking water, high pulmocutaneous evaporative water loss during that period, or both. Average water content in feces of *P. parnellii* (52%) and *G. soricina* (45%) during the dry season was slightly above the water content of feces in other mammals with restricted access to drinking water (35–43%—Peinke and Brown 1999). Reducing FWC may thus conserve body water in bats when water is limited in the environment. Little is known about fecal water-saving mechanisms in bats, and further experiments are needed to evaluate its relative importance in conservation of body water.

Our prediction that plant-eating bats would produce feces with higher water content than insectivores was partly supported. *A. jamaicensis* produced feces with higher water content than *P. parnellii* in the rainy and dry seasons, presumably due to higher water content in diet in both seasons. However, FWC in *G. soricina* was higher than in *P. parnellii* only in the rainy season, probably due to the use of insects during the dry season by *G. soricina* (Herrera M. et al. 2001).

We found that plant-eating bats were affected differently than insectivorous bats by seasonal fluctuations in water availability. Urine concentration and FWC of frugivorous bats did not seem to be affected by low precipitation levels in the dry season because their food is rich in water year-round. The facultative nectarivorous species tested produced drier feces in the dry season probably due to increased insect consumption during this period. The insectivorous species had higher urine concentrations and lower FWC in the dry season, suggesting increased water loss or decreased hydration levels, or both. Our results indicate that in plant-eating and insectivorous bats, 2 routes ( $U_{\text{osm}}$  and FWC) by which water is lost are affected in different ways by the extreme seasonality of the Chamela-Cuixmala tropical deciduous forest.

## RESUMEN

Examinamos la variación estacional en concentración de orina y contenido de agua en las heces de murciélagos silvestres residentes en el bosque seco tropical de la reserva de la biósfera Chamela-Cuixmala, México, caracterizado por una diferencia marcada entre estación seca y lluviosa. Para ello pusimos a prueba la hipótesis que los murciélagos residentes en este bosque tendrían cambios fisiológicos estacionales para mantener su balance de agua. Predijimos que los murciélagos tendrían una mayor concentración de orina y menor contenido de agua en las heces durante la época seca. Nuestra primera predicción fue confirmada para el insectívoro *Pteronotus parnellii*, pero no para el frugívoro *Artibeus jamaicensis*. Nuestra segunda predicción fue confirmada para *P. parnellii* y para el nectarívoro facultativo *Glossophaga soricina*, pero no para *A. jamaicensis*. Nuestros datos indican que en los murciélagos que investigamos, las vías de pérdida de agua fueron afectadas en diferentes maneras por los cambios estacionales en la disponibilidad de agua en el ambiente según la dieta de los murciélagos.

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