

WATER CONSERVATION ABILITY OF THREE SPECIES OF THE GENUS *THRICHOMYS* (RODENTIA, HYSTRICOMORPHA)

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ABSTRACT

We tested the water conservation ability of three species of the genus *Trichomys* that occur in localities with very different climatic regimes, *T. fosteri* (Pantanal – seasonal wetlands), *T. aff. laurentius* (Cerrado - savanna) and *T. laurentius* (Caatinga – shrub land). Individuals were submitted to laboratory urinary concentration experiments using two treatments: one where food and water *ad libitum* were offered (control experiment - I) and the other of food and water deprivation (test experiment - II). Experiments were conducted during 24 hours and urine volume was collected and measured every 6 hours. We compared the differences in body mass, body mass loss (BML), urine volume (UV), relative urine volume (UVr) and urine osmolality (UO) between treatments for each species and between species for the test experiment (II). The patterns of temporal variation in urine concentration were also analyzed during the experiments. *T. fosteri* has significantly higher body mass than the other species. Significant differences were found in UV, UVr and UO but not in BML when experiments I and II were compared. Interspecific comparisons showed no differences between species, except for UV, which was correlated with body mass and was higher for *T. fosteri*. All species presented low mean urine concentration values (*T. aff. Laurentius* = 1226.14±608.03 mOsmol/kg, *T. laurentius* = 1210.02±662.68 mOsmol/kg, *T. fosteri* = 1301±541 mOsmol/kg) compared to other South American rodents. All species showed high intraspecific variability. Some individuals of *T. laurentius* reached values of UO higher than 3000mOsmol/Kg. The temporal patterns of urine concentration from experiments I and II were very similar for all species. Changes in the pattern of urine concentration over time were not observed when comparing experiments I and II. The *Trichomys* species studied here seem not to have efficient mechanisms for urine concentration. However, based on the high individual variability and the lack of changes in the short-term temporal variation, this question has to be better analyzed.

Keywords: adaptation, body mass loss, semi-arid, urine concentration, water conservation.

INTRODUCTION

Species of the genus *Thrichomys* (Trouessart, 1880) have a complex taxonomic history. It was originally believed to be a monospecific genus (*T. apereoides* (Lund, 1839)), but in the 1950s and 60s, Moojen (1952), Vieira (1955) and Cabrera (1961) described some subspecies of *T. apereoides* and named the genus *Cercomys*. More recent studies based on geometric morphometric (Bandouk and Reis 1995, Reis *et al.* 2002a, 2002b, Pessôa *et al.* 2004, Neves and Pessôa 2011), chromosomal (Bonvicino *et al.*, 2002, Pessôa *et al.* 2004), molecular (Braggio and Bonvicino 2004) and bionomic (Teixeira *et al.* 2005) traits have demonstrated differences between geographically separate populations. Thus, currently, *Thrichomys* is considered a complex of eight species (Nascimento *et al.* 2013). These species are distributed along the open dry and semi-arid vegetational formations of Cerrado, Pantanal and Caatinga, spanning a diagonal from eastern Brazil to Paraguay (Favaroni-Mendes *et al.* 2004).

Among these species, *T. aff. laurentius* (Thomas, 1904), *T. laurentius* (Thomas, 1904) and *T. fosteri* (Thomas, 1903) have quite distinct geographical distribution and habitat characteristics. *Thrichomys laurentius* occurs in semi-arid areas (Caatinga), associated with mesic refuges and rocky habitats (slopes of mountain chains and “lajedo” formations), where they find suitable microhabitats with more moderate temperature and humidity levels. *Thrichomys aff. laurentius* can be found

throughout the Brazilian northeast, above the São Francisco River, in open shrub land areas. *Thrichomys fosteri* is found in open areas of Pantanal in Mato Grosso do Sul state, where there is marked seasonality in water availability (Nascimento *et al.* 2013). Its habitats vary from open vegetation areas and grasslands with isolated trees to typical Cerrado formations with high tree density in forest fragments (Streilen 1982b, Basile 2003).

The ability to conserve body water is one of the most important physiological strategies that enable a small mammal species to live in xeric environments and can help explain the differences in habitat and geographical distribution (Prosser 1973, Mares 1977, Kan and Degen 1988, Beauchat 1990, Beauchat 1996, Schmidt-Nielsen 1996, Ivanova *et al.* 2000). This characteristic has been studied in small mammals that inhabit xeric environments in South America (Cortés *et al.* 1990, Cortés *et al.* 1994, Díaz and Ojeda 1999, Shanas *et al.* 2003, Al-Kahtani *et al.* 2004, Bozinovic and Gallardo 2006, Díaz *et al.* 2006) but there are few studies of Brazilian species and its importance in their evolution and geographical distribution (Meserve 1978, Streilein 1982a, Mares *et al.* 1985, Fonseca and Cerqueira 1991, Cerqueira *et al.* 2003, Favaroni-Mendes *et al.* 2004, Ribeiro *et al.* 2004).

Mammals of the semi-arid Brazilian Caatinga biome supposedly lack water conservation abilities (Mares *et al.* 1981, Ribeiro *et al.* 2004). In fact, mean urine osmolality found for species captured in Caatinga sites are usually lower (2193 mOsmol for *T. inermis*,

2649 mOsmol.kg⁻¹ for *Oligoryzomys nigripes* and 2450 mOsmol.kg⁻¹ for *Necromys lasiurus*) compared to other South American desert rodents, e.g. *Spalacopus cyanus* - 3300 mOsmol.kg⁻¹, *Octogon degus* - 4338 mOsm/kg, *Phyllotis darwini*-4500 mOsmol.kg⁻¹ (Cortes et al. 1998, Bozinovic 1995, Favaroni-Mendes et al., 2004, Ribeiro et al. 2004) and North American and Australian desert species (*Notomys alexis* – 9.370 mOsmol/Kg, *Dipodomys merriane* – 5.500 mOsmol/Kg and *Jaculus jacullus* - 6.500 mOsmol/Kg) (MacMillen and Lee 1967).

However, data on the ability to survive on dry seeds for long periods and on intraspecific differences of body mass loss and urine volume decrease for *Thrichomys* species can provide an indication of some degree of adaptation to arid conditions, and even being small, they can be significant for habitat and geographical differentiation. Streilein (1982b) found that individuals of *T. apereoides* can live up to 18 days under water deprivation, feeding only on dry grain and losing only 12% of their body mass. Favaroni-Mendes et al. (2004) compared the ingestive balance of two Caatinga populations of *T. apereoides* (now *T. inermis* (Nascimento et al. 2013)) with different rainfall regimes, in trials with 18 h food and water *ad libitum* and water and food deprivation. They found that individuals of the more mesic area have higher body mass, water intake and urine volume excretion than individuals from more xeric ones, but did not find differences in urine concentration. This lack of high urine osmolality values is generally viewed as

a consequence of the low evolutionary time that these species have had to adapt to arid conditions (Mares 1977, Streilein 1982b, Ribeiro et al. 2004).

Some studies have shown that in laboratory rats, changes in urine concentration correlate with circadian cycles. When water and food are available, rats have higher urine flow and more diluted urine during activity periods (at night), and lower urine flow in higher concentrations during inactive periods (during the day) (Christensen and Agner 1982). Moreover, they also observed a daily urine concentration variation under normal conditions that still occurs when animals are water deprived.

Here we analyzed the differences in body mass loss, urine excretion and concentration among three *Thrichomys* species (*T. fosteri*, *T. aff. laurentius* and *T. laurentius*), using water deprivation experiments in the laboratory. We expected they could have different abilities to cope with water deprivation since they occur at regions with very different aridity conditions. We also analyzed and compared the variations in urine osmolality under conditions of food and water *ad libitum* and food and water deprivation.

MATERIAL AND METHODS

Individuals were collected from regions with different climatic regimes (Table 1). We used 32 individuals, captured near Parque Nacional da Serra da Capivara, southeast Piauí state; eighteen individuals, collected from the Rio Negro ranch, municipality of

Aquidauna, Mato Grosso do Sul state (20°28'29" S / 55°47'10" W) (Pantanal) 16 *T. aff. laurentius* individuals, caught in the municipality of Caetité, Bahia state (14°03'45" S - 42°29'10" W) (transition between Caatinga and Cerrado biomes).

The animals were brought to the Vertebrates Laboratory of Rio de Janeiro Federal University and placed in plastic cages (414 x 344 x 168 mm) cages and maintained under standard laboratory conditions of temperature (22 – 27°C), humidity (50 - 70%) and natural photoperiod (Rio de Janeiro city, Brazil). The animals were fed with commercial food pellets (Nuvilab CR1, 12.5% moisture, 22% protein, 8% fiber and 4% fat) and water *ad libitum*. They were tested after a period of acclimation of about 40 days in the laboratory. Pregnant and lactating females were not used.

Urinary concentration experiment

We used modified experimental design from that developed by Fonseca and Cerqueira (1991). The animals were weighed and placed in metabolic cages

with collectors containing mineral oil (Nujol). The collector's funnel in each cage was also covered with mineral oil to avoid the urine retention. Urine was collected and its volume was registered every 6 hours in 24-hour trials. The urine collected was stored in a freezer at -4°C in a sealed vial to avoid sample water loss. Urinary osmolality was measured with a freezing point osmometer (Osmomat® 030 - Gonotec).

The animals were visually checked for health conditions during every urine collection period. If some change in an individual's movements and behavior was noted, it was immediately removed from the metabolic cages and put back into a plastic cage with water and food available *ad libitum*. The animals were housed in metabolic cages for 3 hours during the experiment and the urine excreted during these 3 hours was discarded to prevent possible changes in urine volume and concentrations due to stress. This period was considered the period of metabolic cage acclimation. After 24 hours, the animals were removed from

Table 1. State/biome, minimum (Min) and maximum (Max) monthly absolute temperature (°C), minimum (Min) and maximum (Max) mean monthly precipitation (mm), aridity index (AI) and climatic classes of the localities where each species was collected.

Species	State/ biome	Min-Max T(°C)	Min-Max Prec. (mm)	AI	Climatic class
<i>Thrichomys aff. laurentius</i>	BA/Cerrado	19-35	5-290	0.56	Dry Sub-humid
<i>Thrichomys laurentius</i>	PI/Caatinga	13-31	5-180	0.32	Semi-Arid
<i>Thrichomys fosteri</i>	MS/Pantanal	13-31	0-240	0.84	Humid

the metabolic cages, weighed again and placed in plastic cages with food and water *ad libitum*. During the first experiments, funnels were checked for urine retention and urine retention was found to be negligible compared to total urine excreted (0.2 ± 0.04 mL). Afterward, this was only checked but not measured.

Each individual was subjected to two types of experiment, namely: Control Experiment (I) – when the animals had access to food and water *ad libitum* during 24 hours; and Test Experiment (II) – when the individuals were deprived of food and water for 24 hours.

Data were tested for normality using the Komolgorov-Smirnov (D) test (Zar 1996). Body mass, body mass loss (BML), urine volume (UV) (mL/day), relative urine volume (UVr) ($\mu\text{l}\cdot\text{h}^{-1}\cdot 100\text{g}^{-1}$) and urine osmolality (UO) (mOsmol/kg) were calculated. The BML was calculated as the ratio between the final body mass and the initial body mass, UV was the sum of urine excreted by an individual during all the experimental periods. These parameters and UVr were converted using the arcsine square root to achieve normality. Body mass and UO were natural log-transformed to achieve normality. Body mass, BML, UV, UVr, UO were compared between experiments for each species using repeated measures ANOVA. Urine osmolality temporal variation for each species in each experiment (I and II) was analyzed by testing the differences between the experiment hours also using repeated measures ANOVA. All data were analyzed using the Statistica

package (StatSoft Inc. Statistica 7.0.).

Differences between species were analyzed by ANOVA and the Tukey post-hoc test for unequal N (HSD). The urine volumes excreted at each time period were correlated with the respective urine osmolality (UO) in both experiments by linear regression for each species (Zar 1996).

RESULTS

No significant differences were found between gender for *T. laurentius*, *T. fosteri* and *T. aff. laurentius* for BML ($n = 2$, $F = 0.73$, $p = 0.54$, $n = 2$, $F = 0.45$, $p = 0.25$, $n = 2$, $F = 0.55$, $p = 0.32$, respectively), UVr ($n = 2$, $F = 0.44$, $p = 0.35$, $n = 2$, $F = 1.35$, $p = 0.14$, $n = 2$, $F = 2.33$, $p = 0.11$, respectively) and UO ($n = 2$, $F = 1.75$, $p = 0.22$, $n = 2$, $F = 0.35$, $p = 0.23$, $n = 2$, $F = 1.23$, $p = 0.13$, respectively), so data were grouped.

All the variables analyzed showed high intraspecific variation (Table 2). Individuals of *T. fosteri* showed significantly greater body mass than individuals of other species ($n = 3$, $F = 37.67$, $p < 0.01$), being about 1.62 times larger than those of *T. aff. laurentius* ($H = 2.98$, $p < 0.01$), and about 1.64 times bigger than *T. laurentius* ($H = 3.62$, $p < 0.01$) (Table 2). *Trichomys aff. laurentius* and *T. laurentius* did not differ significantly considering body mass ($H = 8.95$, $p = 0.35$). Total urine volume excreted was significantly correlated with body mass in both experiments (I: $r = 0.50$, $p < 0.01$ and II: $r = 0.53$, $p < 0.01$).

None of the species showed significant body mass loss between

experiments I and II (Wilks lambda = 0.70, $F(40) = 0.30$, $p = 0.59$ for *T. aff. laurentius*; Wilks lambda = 0.53, $F(62) = 2.53$, $p = 0.12$ for *T. laurentius* and Wilks lambda = 0.84, $F(34) = 0.93$, $p = 0.34$ for *T. fosteri*) (Table 2). Mean UV and UVr were significantly greater in experiments I for the three species (for UV: Wilks lambda = 0.65, $F(32) = 11.2$, $p = 0.02$ for *T. aff. laurentius*; Wilks lambda = 0.83, $F(64) = 19.69$, $p < 0.001$ for *T. laurentius* and Wilks lambda = 0.75, $F(36) = 13.21$, $p < 0.01$ for *T. fosteri*; for UVr: Wilks lambda = 15.5, $F(137) = 21.29$, $p < 0.01$ for *T. aff. laurentius*; Wilks lambda = 13.9, $F(164) = 18.37$, $p < 0.01$ for *T. laurentius* and Wilks lambda = 10.4, $F(86) = 4.78$, $p = 0.03$ for *T. fosteri*) (Table 2). Mean UO was also significantly greater in experiment II for the three species (Wilks lambda = 12, $F(83) = 8.81$, $p < 0.01$ for *T. aff. laurentius*; Wilks lambda = 17.3, $F(161) = 22.03$, $p < 0.01$ for *T. laurentius* and Wilks lambda = 8.89, $F(132) = 6.75$, $p < 0.01$ for *T. fosteri*). Urine volume and concentration presented a significant negative relationship for all species in both experiments (Figure 1).

Significant differences were found for urine volume in experiment I ($F = 22.38$, $p < 0.01$) and experiment II ($F = 11.05$, $p < 0.01$). *T. fosteri* produced greater urine volume than *T. laurentius* ($p < 0.01$) and *T. aff. laurentius* ($p = 0.01$), respectively. However, UVr did not differ between species in experiment I ($F = 2.58$, $p = 0.07$) and experiment II ($F = 0.33$, $p = 0.72$) (Table 2). Also, no significant differences were found in UO between species in experiment I (F

= 1.32, $p = 0.27$) and experiment II ($n = 174$, $M = 0.52$, $p = 0.59$). Mean UO in experiment II varied from 1210 for *T. laurentius* to 1328 mOsmol/Kg for *T. fosteri* (Table 2).

No significant differences were found for the temporal variation of urine excreted at each time period and the pattern found for each species between experiments was the same (for *T. aff. laurentius*: Wilks lambda = 0.72, $F(58) = 1.71$, $p = 0.13$; for *T. fosteri*: Wilks lambda = 0.82, $F(6.120) = 2.14$, $p = 0.054$, and for *T. laurentius*., Wilks lambda = 0.93, $F(132) = 0.81$, $p = 0.56$) (Figure 2). The maximum osmolality value found was 3226 mOsmol/Kg for an individual of *T. laurentius* in experiment II after 24 h. Except for this individual, and two individuals of this same species that reached 3153,5 mOsmol/Kg and 3224,5 mOsmol/Kg in the same experiment and period, respectively, and a *T. fosteri* individual that reached 3055 mOsmol/Kg in experiment II after 6 h, no other individual of the three species studied here reached or passed 3000 mOsmol/Kg.

DISCUSSION

All the three species studied here increased urine concentration and reduced urine flux and water loss under water and food deprivation. However, mean urine concentration values found under stressful conditions, for all the three species, were lower than those found for other South American species (2071 to 8773 mOsmol/Kg) (Bozinovic *et al.* 1995, Diaz and Ojeda 1999),

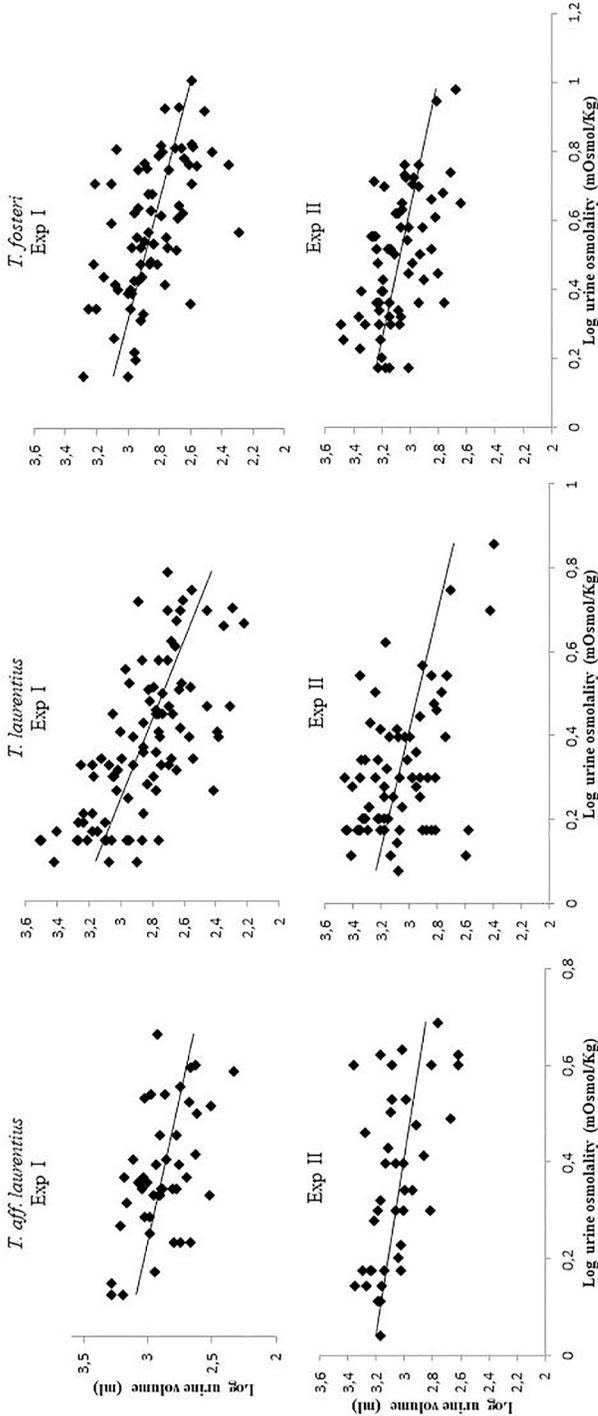


Figure 1. Linear regression between log urine volume (mL) and log urine osmolality (mOsmol/Kg) for each species in each experiment (I and II). For *T. aff. laurentius* (n = 44; Expl: $r^2 = -0.28$, $\beta = -0.53$, $F = 16.48$, $p < 0.001$, ExplII: $r^2 = -0.16$, $\beta = -0.53$, $F = 6.37$, $p = 0.0164$), for *T. fosteri* (n = 41, Expl: $r^2 = -0.27$, $\beta = -0.59$, $F = 14.08$, $p < 0.001$, ExplII: $r^2 = -0.22$, $\beta = -0.48$, $F = 9.10$, $p = 0.005$) and for *T. laurentius* (n=79, Expl: $r^2 = -0.48$, $\beta = -0.40$, $F = 10.98$, $p < 0.001$, ExplII: $r^2 = -0.16$, $\beta = -0.69$, $F = 71.89$, $p = 0.002$).

Table 2. Mean \pm standard deviation (SD), median and amplitude (minimum-maximum values) of initial and final body mass, BML (% of body weight loss), urine volume (UV), relative urine volume (UVr) and urine osmolality (UO) in the two experiments (I and II) for the three species.

	<i>T. aff laurentius</i> (n=16)		<i>T. laurentius</i> (n=32)		<i>T. fosteri</i> (n=18)		
	I	II	I	II	I	II	
Body mass	Initial	338.97 \pm 104.58	335.93 \pm 97.13	318.42 \pm 62.85	314.44 \pm 55.14	550.33 \pm 136.22	537.34 \pm 136.91
	Final	311.56 \pm 98.18	314.60 \pm 93.79	297.59 \pm 56.87	296.84 \pm 59.35	473.43 \pm 131.74	503.29 \pm 142.43
BML (%)	mean\pmSD	6.60 \pm 1.70	6.58 \pm 1.99	5.55 \pm 2.57	6.73 \pm 3.61	8.46 \pm 3.68	6.81 \pm 2.96
	median amplitude	6.91 1.89-9.35	6.01 4.21-11.07	5.60 1.01-10.17	7.39 1.94-15.99	8.54 2.47-16.64	6.06 1.94-15.99
UV (mL/day)	mean\pmSD	5.45 \pm 4.07	3.87 \pm 2.73	6.86 \pm 4.91	2.71 \pm 1.92	16.84 \pm 8.1	8.72 \pm 4.93
	median amplitude	4.85 0.4-12.8	3.35 0.4-11.1	5.7 0.7-20.7	2.45 0.5-8.7	15.8 1.8-33.2	8.4 1-17.2
UVr (μL h⁻¹.100g⁻¹)	mean\pmSD	100 \pm 60	70 \pm 50	120 \pm 90	70 \pm 50	140 \pm 100	70 \pm 50
	median amplitude	70 0-370	60 0.00-190	100 20-430	50 10-270	110 0-470	60 0-230
UO (mOsmol/Kg)	mean\pmSD	769.66 \pm 379.73	1226.14 \pm 608.03	854.11 \pm 412.88	1210.02 \pm 662.68	904.52 \pm 658.49	1301 \pm 541
	median amplitude	724.41 213-1907	1171 99-2291	800.50 166.5-2846	1210.50 243-3226	691 194.66-1919	1201 223-3055

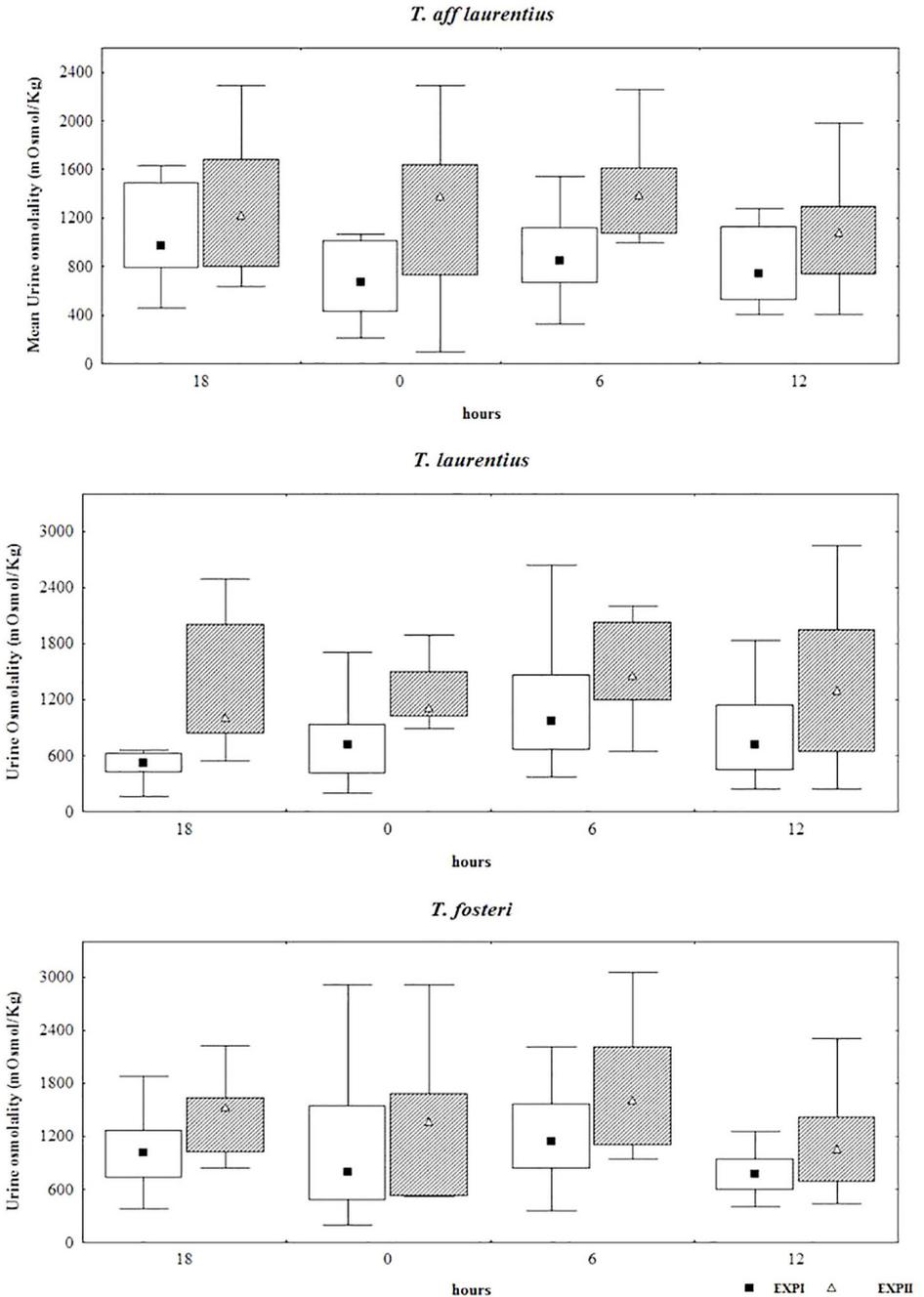


Figure 2. Temporal variation of urine osmolality with *ad libitum* food and water experiments (I) and water and food deprivation experiments (II) for the three *Thrichomys* species. Points represent means and bars represent 95% confidence limits.

including populations of *Thrichomys inermis*, a species that inhabits dry areas and can reach mean urine concentration of 2193 ± 340 mOsmol after 18 h of water and food deprivation (Favaroni-Mendes *et al.* 2004). High individual variability was noted in all parameters analyzed except BML. The coefficient of variation for UV, UVR and UO varied from 41% to 71.42% for all species considering the two experiments. Three individuals of *T. laurentius* (Caatinga) and one of *T. aff. laurentius* reached values as high as 3000 mOsm/Kg after 24 h of water and food deprivation. Such high phenotypic plasticity is probably related to some degree of adaptation to xeric conditions, at least for *T. laurentius*, and there is potential for the development of these characteristics during periods of water shortage for the other *Thrichomys* species (Ribeiro *et al.* 2004, Bozinovic and Gallardo 2006).

The three *Thrichomys* species studied here differed in body mass. Small body mass has been considered a strategy to deal with water restrictions (Lindstedt and Swain 1988, Nevo 1989, Degen 1997). However, they presented very similar physiological responses under water and food deprivation and did not differ in the parameters analyzed (except for UV, which was correlated with body mass). This result was not expected, as the species are from regions with very different aridity conditions.

It is possible that Caatinga species posses no “extraordinary physiological mechanisms for water conservation”, as stated by Ribeiro *et al.* (2004) and hypothesized by Mares *et al.* (1981) and Streilein (1982b) for South American

species. However, Favaroni-Mendes *et al.* (2004) showed that even individuals of the same species can present differences in urine concentration ability. They compared the ingestive balance, e.g. the balance between the water and food intake and excretion with water and food *ad libitum* (I) and water deprivation (II) in 18-hour experiments involving two geographically distant populations of *Thrichomys inermis* under different climatic regimes, and showed that body mass was smaller and urine concentration was greater for the dry habitat population, although the two populations did not differ regarding the other parameters analyzed (UV and UVR). They also showed that these parameters did not change in populations from the dry locale between the two treatments, showing no significant stress during water restriction. Therefore, it is possible that *Thrichomys* species need to undergo more severe conditions to achieve their maximum urine concentration capacity.

We conducted food and water deprivation experiments during 24h and it is possible that individuals were not subjected to stressful conditions during this period, since they did not had significant body mass loss or change in urine concentration with time. So, we can also hypothesize that species were not submitted to conditions necessary to achieve the greatest urine concentration and maybe can withstand this regime for a longer period. It is possible that water and food deprivation periods longer than 24 hours are needed to induce more acute responses in these species.

The data presented here are representative of the great physiological variability also found in other small South American rodents (Al-Katahni *et al.* 2004, Bozinovic *et al.* 1995, Bozinovic and Gallardo, 2006) and also indicate selective forces acting mainly on intra and interspecific variability found in a set of characteristics ranging from body mass to urine concentration physiology. Caatinga is a quite recent vegetation form and presents a highly unpredictable climatic regime, with alternating dry and wet years (Mares *et al.* 1985, Coimbra-Filho and Câmara 1996). In this scenario, allele frequencies that favor phenotypes adapted to dry and wet conditions can be preserved in *Thrichomys* populations (Weiner 2006).

We stress the need to analyze not only the urine concentration capacity but also the physiological mechanisms in action when animals are deprived of water (temporal variation in urine concentration at a diversity of organizational levels) (Bozinovic and Gallardo 2006) to understand all the physiological diversity found in small South American mammal species.

ACKNOWLEDGEMENTS

We are grateful to Nelio P. Barros and Rosana Juazeiro for assistance with the laboratory experiments and general assistance. We also thank two anonymous referees that made substantial comments to help improve. This work was supported by PPBIO/CNPq/MMA process no. 457524/2012-0, PROBIO/MMA, FUIB, CAPES, PIE/CNPq, FIOCRUZ and FAPERJ. Licenses for collection, maintenance and experimental procedures were Proc. 02001.000384/00-12 (137/2002 – CGFAU/LIC - 16/12/2002 a 16/12/2003, Proc. 02001.000228/00-99 – 122/2002 - CGFAU/LIC - 02/12/2002 a 01/12/2003, Proc. 02001.007437/2002-60 – 0124/002 – CGFAU/LIC - 28/10/2002 a 27/10/2003 and 02022.002062/01-04.

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Submetido em 16/07/2014

Aceito em 14/04/2015