PHYSIOLOGICAL FLEXIBILITY IN FIELD URINE OSMOLALITY OF RODENTS FROM SEMI-ARID CHILE

FLEXIBILIDAD FISIOLÓGICA EN LA OSMOLARIDAD URINARIA DE CAMPO EN ROEDORES DE CHILE SEMI-ÁRIDO

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ABSTRACT

We assessed long-term physiological responses in field urine osmolality (Uosm) of 4 murid rodents from semi-arid Chile, as a function of the El Niño Southern Oscillation. In general, all of the rodent species studied showed important temporal fluctuations in their Uosm-values, indicating both seasonal and annual patterns of physiological variability characterized by high Uosm-values during the Austral spring-summer and low Uosm-values during autumn-winter. This pattern was clearly observed during wet years (1991-1992), while during dry years there was an increase in Uosm-values during autumn-winter but not spring-summer. We observed significant effects of year and season on Uosm-values, with a year x season interaction. We demonstrate how flexibility of physiological mechanisms allows small mammals in arid or semi-arid regions to cope with long-term seasonal and annual water variability in their semi-arid habitat. The trends of seasonal water balance during contrasting years (i.e., El Niño vs. dry years) likely is a consequence of plant cover, since this is the principal food and water source for rodents at Fray Jorge.

Key words: El Niño, long-term physiology, water economy, urine concentration, semiarid ecosystems, small mammals, Chile

RESUMEN

Estudiamos las respuestas fisiológicas de largo plazo en la osmolaridad de la orina (Uosm) de cuatro especies de roedores muridos de ambientes semi áridos de Chile en función del fenómeno climático El Niño. En general las cuatro especies muestran importantes fluctuaciones temporales en Uosm, indicando un patrón de variabilidad

[1] Deceased

fisiológica anual y estacional caracterizado por valores de Uosm altos durante la primavera-verano austral y valores de Uosm bajos durante otoño-invierno. Este patrón se observó claramente durante los años lluviosos (1991-1992), mientras que durante los años secos se observó un aumento en los valores de Uosm durante otoño-invierno pero no en primavera-verano. Observamos además un efecto significativo de la interacción año y estación sobre Uosm. Finalmente demostramos como la flexibilidad en los mecanismos fisiológicos les permite a los pequeños mamíferos de regiones áridas o semi-áridas tolerar la variabilidad anual y estacional de largo plazo en la disponibilidad de agua en sus habitats semi-áridos. La tendencia de balance de agua estacional durante años contrastantes (i.e., El Niño vs. años secos) parece ser consecuencia de cambios en la cubierta de plantas pues es la fuente de alimento y agua principal para los roedores de Fray Jorge.

Palabras claves: El Niño, fisiologia de largo plazo, economía de agua, concentración de orino, ecosistemas semi-áridas, mamíferos pequeños, Chile

INTRODUCTION

The study of phenotypic flexibility has been a central issue in ecological and evolutionary physiology (Willmer et al., 2000). Indeed, the environmental tuning of an organism's physiology in the field often is hypothesized to be responsible for allowing it to adjust to changing biotic and abiotic conditions, through increases in biological performance (Huey and Berrigan, 1996). This is well-exemplified by desert-dwelling rodents for whom maintaining water homeostasis is challenging (Walsberg, 2000). Rodents from arid and semiarid habitats are faced with the problem of water conservation in conditions where the temporal availability of free water is limited or scarce (Degen, 1997; Bozinovic and Gallardo, 2006). Nevertheless, the physiology of water regulation among desert rodent appears to show remarkable flexibility. The response of small mammals to water deficits and unproductive desert have been investigated intensively (e.g., Schmidt-Nielsen, 1964). However, studies of water economy generally rely heavily on short-term laboratory-oriented experiments (Bozinovic et al., 2003)

Here we examine long-term flexibility in field urine osmolality in an assemblage of arid-zone rodents in temperate South America. To the best of our knowledge, this is the first such study to include dry as well as rainy years associated with the El Niño Southern Oscillation (ENSO) phenomenon. When El Niño occurs, coastal waters warm up during winter months, thereby breaking down thermal inversion, and allowing the intrusion of moist Pacific air masses (Aceituno, 1992; Trenberth, 1997). The ecological effects of ENSO on terrestrial ecosystems of western South America are intense (Jaksic, 2001; Meserve et al., 2003). Indeed, long-term ecological studies have documented that periodic El Niño events have caused several changes in ecological processes and patterns, both at population (Lima et al., 1999, 2002) and community levels (Meserve et al., 1995, 2003; Jaksic, 2001). Since the period of ENSO oscillation is around 6.4 years, long-term studies are essential for understanding such effects across a range of organizational levels, from individuals to communities (Meserve et al., 2003).

Urine osmolality (Uosm in mOsm/kg) reflects the capacity of the kidney for water conservation efficiency by small mammals (e.g., Bozinovic et al., 2003; Gallardo et al., 2005). This capacity has traditionally been used as an estimator of the efficiency of the kidneys for conserving body water, especially in laboratory studies (McNab, 2002). However, this measure has seldom been used as a tool for assessing the water balance stages of small mammals in their natural environments (Cortés et al., 1994). Laboratory studies on water regulation and conservation in small mammals from the arid Mediterranean habitat of north-central Chile, show that the majority of species have maximum concentration capacity > 4,000 mOsm/kg (Bozinovic et al., 1995).

We studied seasonal and yearly long-term acclimatization in the urine osmolality of 4 nocturnal murid rodents, *Abrothrix olivaceus*, *A. longipilis*, *Oligoryzomys longicaudatus*, and *Phyllotis darwini* (for the generic attribution of the former 2 species see Pearson and Smith (1999) and Smith and Patton (1993), respectively). All of these species occur sympatrically at our study site in northern Chile. This site has a semi-arid climate, with highly variable precipitation (Meserve et al., 2003). Although Fray Jorge has a long-term mean of ca. 110 mm of precipitation annually (Meserve et al., 2003), precipitation patterns in the region present large inter-annual variability (e.g., a high rainfall year typically is followed by an intervening 2-3 year period of low or average rainfall). During this study an ENSO event in 1991-1992 resulted in annual rainfall of 233 mm and 229 mm, respectively. In 1993 and 1994 annual rainfall was below average (77 mm and 35 mm, respectively). Consequently, this study was carried out during 2 rainy (1991-1992) and 2 dry (1993-1994) years. Because many arid zone small mammals obtain much or most of their water from plant foods, and precipitation leads to increased green plant growth, which increases environmental water availability to consumers, we predict that: 1) during rainy years, the water economy of rodents in the field will have a marked, seasonal rhythm, presenting moderate Uosm values during the dry seasons (late spring and summer); 2) during dry years, the seasonal, cyclic rhythm will tend to disappear and/or will show evidence of higher levels of water economy (i.e., comparably higher Uosm-values) year round (Cortés et al., 2000) and finally, 3) water balance will be modulated and synchronized by rainfall and consequently primary production, associated with cycles of ENSO events.

MATERIAL AND METHODS

We conducted our study in the Quebrada de Las Vacas (30°38′ S, 71°40′ W, 240 m elevation), in Fray Jorge National Park; Fray Jorge is located along the coast of north-central Chile, 100 km south of La Serena and 400 km north of Santiago. The climate is Mediterranean, and the plant community is characterized by spiny drought-deciduous and evergreen shrubs, 2-3 m in height, with a herbaceous understory. This community has been termed the *Porlieria chilensis-Adesmia bedwellii-Proustia pungens* association (Muñoz and Pisano, 1947). A complete account of the biotic and abiotic conditions of study site is provided by Meserve et al. (2003).

Live trapping of the rodents A. *olivaceus* (*N* = 285 from Autumn 1991 to Spring 1994), *A. longipilis* (*N* = 235 from Autumn 1991 to Summer 1995), *P. darwini* (*N* = 219 from Autumn 1991 to Summer 1995), and *O. longicaudatus* (*N* = 59 from Autumn 1991 to Summer 1994) was conducted using standard (75 x 85 x 240 mm) Sherman traps, placed in two 3 x 10 grids, with 2 traps per station at 10 m intervals. The entire trapping area encompassed 0.30 ha, with adjacent 5 m border strips. Trapping was carried out for 5 consecutive days, using oatmeal as bait. Traps were set near sunset, and checked approximately every 90 minutes until sunrise, minimizing the time that rodents spent in traps. We recognize that factors such as ambient temperature and moisture in the trap may influence the water budget; nonetheless, we made every feasible effort to maintain similar conditions during all our field seasons. All captured rodents were uniquely marked with an ear tag to avoid duplication of urine samples during seasonal sampling.

Urine samples were collected in microhematocrit tubes, which were sealed with parafilm and measured within one hour after collection. All measurements were taken in the field, and urine was collected directly from the genitalia. We measured the total concentration of solids (S = g/100g) in the urine samples, using a field refractometer AO TS Meter/Scientific Instruments (Scientific Instruments) following Cortés and Rosenmann (1989). These data allowed us to estimate urine osmolality as Uosm (mOsm/kg) = 140 $S^{0.984}$ (Cortés and Rosenmann, 1989). Our refractometer measurements (urine samples) were calibrated against a freezing-point osmometer (Advanced Instruments, MA, USA). Previous Uosm values over a single year were presented for *P. darwini* by Gallardo et al. (2005).

All statistical analyses were conducted using S-plus (2000). We evaluated the effects of year and season on the Uosm values of each species using a 2-way analysis of variance (ANOVA). To determine which treatments were significantly different, we utilized the post hoc Tukey test for multiple comparisons. We implemented these comparisons using the *best.fast* command in S-Plus (2000); this method uses the smallest critical point among all the valid methods. Values are listed as means ± 1 SD.

RESULTS

For all 4 species, Uosm-values were greatest in summer and during dry years, reflecting increased water economy at these times (Fig. 1). Interestingly, the magnitudes of these high Uosm-values equalled only 71.0 – 80.7% of the maximum capacity for concentration measured under laboratory conditions (Bozinovic et al., 1995).

All 4 rodent species showed important temporal fluctuations in their Uosm-values, indicating seasonal and inter-annual patterns of physiological variability (Fig. 1). Nevertheless, there were some subtle interspecific differences in seasonal water economy dynamics; specifically, *Phyllotis* retained a stronger seasonal pattern of urine osmolality during drier years than do the other murid rodents at this site, although there was some evidence for convergence after extended drought. During wet years 3 murid species (*A. olivaceus*, *O. longicaudatus*, and *A. longipilis*) exhibited clear seasonal changes in Uosm values (Fig. 1); these were low during autumn and winter (similar to values measured under standard laboratory conditions where food and water are provided *ad libitum*; Bozinovic et al., 1995), but increased in spring and summer (i.e., dry seasons), indicating an increase in water economy due to low environmental water availability (Fig. 1). The seasonal rhythm of water balance for these species tended to disappear during the dry years of 1993-1994, however, which we interpret as indicative of a higher water economy in response to more extreme physiological conditions as perceived by these species.

The seasonal pattern of *Phyllotis*, however, evidently was less markedly impacted by changes in moisture availability. During wet years (1991-1992) this species showed a clear seasonal pattern of water economy, characterized by high Uosm-values during spring-summer and low Uosm-values during autumn-winter. However, during dry

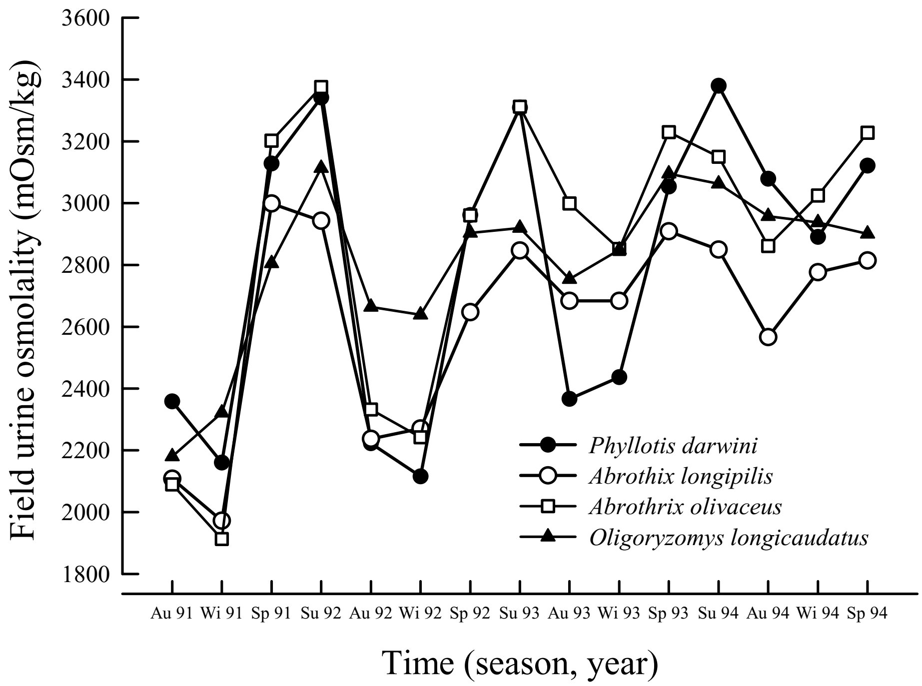

Figure 1. Long term dynamics of field urine osmolality of murid rodents at the semi-arid Fray Jorge National Park. This field study was carried out during 2 rainy, ENSO years (1991-1992) and 2 dry years (1993-1994). Au = autumn, Wi = winter, Sp = spring, and Su = summer.

years (1993-1994) there was an increase in the Uosm-values for autumn-winter, while spring-summer values remained similar to previous years (Fig. 1). Interestingly, however, in winter 1994, after over a year of relative drought, *Phyllotis* appeared to converge on the other rodent species, exhibiting higher urine osmolality even during the more mesic winter season (Fig. 1).

While we observed significant effects of year and season on Uosm-values in *P. darwini*, the year x season interaction was only marginally significant (Table 1). Multiple comparisons showed that spring had significantly higher Uosm-values than autumn and winter ($p < 0.01$), and summer Uosm-values were higher than all other seasons ($p < 0.001$). During 1994 Uosm-values for this species were significantly higher than during other years (1991-1993; $p < 0.01$). The interaction plot (Fig. 2A) shows that Uosm-values were very similar in autumn and winter. Summer values declined from 1991 to 1993, but then increased in 1994, while spring values declined greatly from 1991 to 1992, followed by an increase in 1993, and a slight decline in 1994.

As seen for *P. darwini*, we also observed a significant effect of year, season, and the year x season interaction on Uosm-values for *A. olivaceus* (Table 1). *A posteriori* multiple comparisons showed that spring Uosm-values were significantly higher than both autumn and winter Uosm-values (both $p < 0.01$), and significantly lower than summer values ($p < 0.01$). Furthermore, during 1993 and 1994 Uosm-values for this species were significantly higher ($p < 0.001$) than during other years (1991-1992). The interaction plot

Table 1. Results from the 2-way ANOVA of field urine osmolality for different rodent species inhabiting the semi-arid habitat of Fray Jorge National Park, northern Chile. The residuals serve as expected mean square for all analyses.

Effects/Source of Variation	*d.f.*	*F*-value	*p*
Phyllotis darwini			
Season	3	158.55	< 0.0001
Year	3	3.98	0.0093
Season x year	9	3.49	0.0600
Residuals	134		
Abrothrix olivaceus			
Season	3	76.77	<0.0001
Year	3	14.10	<0.0001
Season x year	8	6.81	<0.0001
Residuals	270		
Oligoryzomys longicaudatus			
Season	3	8.47	0.0002
Year	3	9.39	0.0007
Season x year	8	2.65	0.0180
Residuals	204		
Abrothrix longipilis			
Season	3	38.39	<0.0001
Year	3	20.33	<0.0001
Season x year	9	7.12	<0.0001
Residuals	219		

(Fig. 2B) indicates that autumn and winter Uosm-values tended to increase in parallel throughout the study. In contrast, spring values showed a significant increase during only the driest year (1994), and summer values declined from 1991 to 1993 (we failed to capture any of this species in summer 1994).

Patterns in *O. longicaudatus* were similar to the 2 previous species, with a significant effect of year, season, and the year x season interaction on Uosm-values (Table 1). Post-hoc multiple comparisons showed that spring and summer presented significantly higher Uosm-values than autumn and winter ($p < 0.01$), and summer values were significantly higher than spring ($p < 0.001$). The effect of year appears to be the result of higher Uosm-values during 1993 than during 1991, and during 1994 Uosm-values were significantly higher than during the other years (1991-1993; $p < 0.01$). The interaction

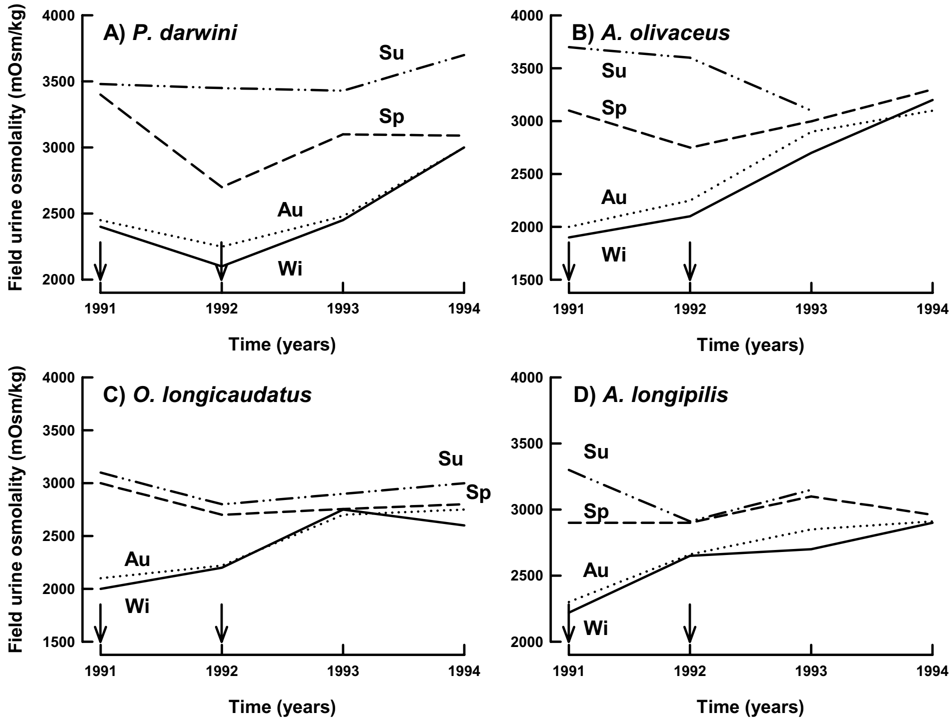

Figure 2. Interaction plots of field urine osmolality between seasons (lines) and years (x-axes) for 4 species of small mammals at the semi-arid Fray Jorge National Park. A) *Phyllotis darwini*, B) *Abrothrix olivaceus*, C) *Oligoryzomys longicaudatus*, and D) *Abrothrix longipilis*. Arrows indicate rainy years. Su = summer, Sp = spring, Au = autumn, and Wi = winter. Vertical arrows indicate rainy years (1991 and 1992)

plot (Fig. 2C) shows that Uosm-values for autumn and winter increased from 1991 to 1993, and declined in 1994. Summer and spring Uosm-values declined from 1991 to 1992 but then remained essentially stable in spring, while increasing slightly in summer.

Finally, *Abrothrix longipilis* also presented a significant effect of year, season, and the year x season interaction term on Uosm-values (Table 1). Multiple comparisons showed that Uosm-values were higher spring and summer than autumn and winter (all p values < 0.01). The significant effect of year appears to be the result of higher Uosm-values during the dry years of 1993 and 1994 than during the wet years of 1991 and 1992. The interaction plot (Fig. 2D) shows that autumn and winter Uosm-values tended to increase from 1991 to 1992 and then more gradually through 1994. In contrast, spring values fluctuated but showed no clear trajectory, and summer values declined from 1991 to 1992, then increased again in 1993; we failed to capture any of this species in summer 1994.

DISCUSSION

Rodents from arid and semi-arid habitats live under conditions where the spatial and temporal availability of free water is limited. Consequently, these species are faced with the problem of water conservation. The response of rodents to unproductive desert environments and water deficits has been intensively investigated in many deserts of the world. However, current understanding of the cellular, systemic and organismal physiology of water economy relies heavily on short-term, laboratory-oriented experiments, which usually focus on responses at isolated levels of biological organization.

Nevertheless, the mechanistic basis of these patterns likely involves seasonal variations in water flux rates as demonstrated by Bozinovic et al. (2003). In addition membrane water channels or aquaporins are more abundant in the kidney cells during summer than during winter (Bozinovic et al., 2003, Gallardo et al., 2005). Several aquaporins are involved in water reabsorption along the renal tubule. Aquaporin-1 is extremely abundant in apical and basolateral membranes of proximal tubule and thin descending loop of Henle. Recently, Gallardo et al. (2005) examined the phenotypic flexibility of field urine osmolality in response to seasonal rainfalls and the experimental expression of renal aquaporins in the leaf-eared mouse *P. darwini*. These authors reported that field urine osmolality was higher in summer than during winter. During the rainy year field urine osmolality in winter was nearly 2,100 mOsm/kg while the mean winter U value of the dry year was 2,600 mOsm/kg. During summer the mean field urine osmolality during the rainy year was 3,321 ± 71.5 mOsm/kg and 3,600 mOsm/kg during the dry year. Nevertheless, dehydration induced an increase in aquaporin protein amount compared to controls and water loaded condition. We hypothesized that the same mechanism is acting in the species of rodents studied here allowing desert rodents to cope with seasonal and yearly water availability in arid habitats.

Thus, the integration of a variety of flexible mechanisms that act at cellular, systemic, and organismal levels allow small mammals in arid regions to cope with seasonal and annual water variability in their semi-arid habitat. The seasonal, cyclic rhythm of the water economy observed in our study of rodents in semi-arid Chile during wet years is consistent with that observed for North American desert heteromyids, such as *Dipodomys merriami*, *Perognathus longimembris*, and *P*. *fallax* (MacMillen, 1972; MacMillen and Grubbs, 1976).

The seasonal trends in water balance during wet vs. dry years likely are at least partly a function of plant cover, since this is an important food and water source for rodents at Fray Jorge but also may lead to increased ambient humidity (Meserve, 1981; Bozinovic et al., 2003). The abundance and productivity of plants in the semi-arid, Mediterranean environments of north-central Chile are determined by the amount of rainfall (Gutiérrez et al., 1993; Gutiérrez, 2001), which is highly variable both between and within years (di Castri and Hajek, 1976). The response of vegetation to increased pulses of water is very fast (e.g., days to weeks), especially for annual species. In contrast, both small mammals (Meserve et al., 1995, 1999) and predators (Jaksic et al., 1997) exhibit delayed responses to pulses of primary productivity at the study site. This study (see also Bozinovic et al., 2003) demonstrates that precipitation and primary productivity influence the population dynamics of small mammals at a relatively longer temporal scale, in comparison to the more rapid responses observed in physiological acclimatization. Finally, the population dynamics and demography of small mammals and predators in semi-arid Chile is positively correlated with rainfall, which is further correlated with El Niño events (Lima et al., 1999, 2002). Indeed, in our study some species exhibited dramatic fluctuations in their water economy, which were caused by a climatic effect, which, at the same time, may be a product of physiological constraints. This study illustrates that long-term field studies are necessary to fully elucidate the relationship between physiological conditions and precipitation, and to determine the long-term acclimatization responses because of the high between- and within-year variability of rainfall.

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