Journal of Arid Environments 72 (2008) 2011–2016

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

ENSO-associated response of field urine osmolality in the insectivorous marsupial *Thylamys elegans*

C. Tirado[a], A. Cortés[a,b], F.M. Jaksic[c], F. Bozinovic[c,*]

[a] Departamento de Biología, Facultad de Ciencias, Universidad de La Serena, Casilla 599, Chile
[b] Centro de Estudios Avanzados en Zonas Áridas (CEAZA), La Serena, Chile
[c] Departmento de Ecología, Facultad de Ciencias Biológicas, Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

ARTICLE INFO

Article history:
Received 12 February 2008
Received in revised form
8 April 2008
Accepted 24 June 2008
Available online 30 July 2008

Keywords:
Climate change
El Niño
Field physiology
La Niña

ABSTRACT

From 1991 to 1994, we assessed physiological responses in field urine osmolality (Uosm) of an insectivorous marsupial (*Thylamys elegans*) of semiarid Chile faced with a complete cycle of El Niño Southern Oscillation (ENSO). El Niño phase of ENSO determined the initial 2 wet years at the study site, while La Niña phase determined the 2 subsequent dry years. The marsupial showed marked temporal fluctuations in field Uosm values, with both seasonal and between-year patterns of physiological variability. Indeed, Uosm values during wet years were: 2.719 ± 405 mOsm/kg in summer versus 2.246 ± 209 mOsm/kg in winter. During dry years in summer, Uosm values were: 3.340 ± 384 mOsm/kg versus 2.481 ± 293 mOsm/kg during winter. There were significant effects of dry versus wet years and between dry and wet seasons on Uosm values, as well as a statistical interaction year $\times$ season. We discuss how the integration of flexible physiological mechanisms enable an insectivorous marsupial to cope with seasonal and yearly water variability in a semidesert, and also the importance of using ENSO climate effects as a proxy for the study of future climate change in natural communities and its subsequent impact on field physiological performance of desert mammals.

1. Introduction

Fluctuations in the tropical and subtropical Pacific sea surface temperature are related to the occurrence of El Niño Southern Oscillation (ENSO), during which the equatorial surface waters warm up, from the International Date Line to the western coast of South America (Aceituno, 1992). Recently, ENSO has been associated with large-scale climate and ecological changes that occur every few years on the western fringe of South America (Jaksic, 2001). When the warm phase of ENSO occurs, coastal waters warm up considerably during winter months, and the Pacific anticyclone weakens, thereby allowing the intrusion of moist Pacific air masses onto the western fringe of South America, thus bringing rain to that desert area (Jaksic, 2001; Meserve et al., 2003). The ecological effects of ENSO in terrestrial ecosystems of western South America are intense. Indeed, long-term ecological studies have documented that periodic ENSO events cause multiple changes in ecological processes and patterns both at the population (Lima et al., 1999b, 2002) and community levels

* Corresponding author. Tel.: +562 686 2618.
E-mail address: fbozinovic@bio.puc.cl (F. Bozinovic).

0140-1963/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2008.06.012

(Jaksic et al., 1997; Meserve et al., 1995, 1999, 2003). These changes occur because ENSO cycles between El Niño and La Niña phases, which determine the existence of wet and dry years, respectively (Lima et al., 1999a, b).

Bozinovic et al. (2007a) assessed the putative effects of ENSO at the physiological level among five rodent species of semiarid Chile. They live under conditions where the spatial and temporal availability of free water is limited, thus facing water conservation problems (Degen, 1997; McNab, 2002; Schmidt-Nielsen, 1979; Walsberg, 2000). The physiology of water regulation among those rodents shows remarkable flexibility in both time and space (Bozinovic and Gallardo, 2006; Bozinovic et al., 2003; Cortés et al., 1994). Nevertheless, current understanding of the physiological variability of water economy relies heavily on short-term, laboratory-oriented experiments. Indeed, multi-year physiological studies under field conditions are scarce, mostly on rodents, and restricted to a few species from Northern hemisphere deserts (Bozinovic and Gallardo, 2006).

The environmental modification of an organism's physiology in the field, or acclimatization allows organisms to adjust to changing environmental conditions through increases in performance (Garland and Carter, 1994; Huey and Berrigan, 1996; Willmer et al., 2000). Among the physiological specializations in desert mammals is their high capacity to concentrate urine. This capacity is measured in the laboratory to determine the kidney's efficiency to conserve body water (McNab, 2002). To gauge water balance (urine osmolality = Uosm in mOsm/kg) of mammals in natural environments, it is necessary first to determine the kidney maximum capacity to concentrate urine under water deprivation and dry diets in laboratory conditions (Cortés et al., 1994). Such studies on water regulation of rodents from semiarid Chile (Bozinovic and Gallardo, 2006) show that they have morphological and physiological traits related to the renal via (maximum capacity to concentrate >4000 mOsm/kg). Thus, the capacity to concentrate urine in the laboratory may be compared with Uosm values obtained in the field.

We studied seasonal and yearly acclimatization in urine osmolality of the insectivorous marsupial *Thylamys elegans* (Didelphidae) in a semiarid Chilean locality, with large inter-annual rainfall variability, where high rainfall periods (El Niño years) are typically followed by intervening 2–3-year periods of low rainfall (La Niña years). Our field study was carried out during 2 wet and 2 consecutive dry years. The hypotheses we tested were: (1) during wet years, the water balance in the field should have a marked seasonal cyclic rhythm, showing moderate urine osmolality values during the dry seasons of the year (late spring and summer); (2) during dry years, the seasonal cyclic rhythm should disappear and/or show higher levels of water economy (higher values of urine osmolality) the year round.

2. Material and methods

2.1. Study site

The study on water economy stages of the insectivorous marsupial *T. elegans* was carried out in Quebrada de Las Vacas (30°38′S, 71°40′W, 240 m elevation), Fray Jorge National Park, north-central Chile, located 100 km south of La Serena and 400 km north of Santiago, during 2 wet (1991–1992) and 2 dry years (1993–1994). An El Niño event in 1991–1992 resulted in 233 and 229 mm rainfall, respectively. Annual rainfall during La Niña phase of 1993 and 1994 was 77 and 35 mm, respectively. The climate of the study site is Mediterranean, with hot dry summers and wetter cooler winters, with high inter-annual variability determined by oscillations of ENSO (Jaksic et al., 1997; Lima et al., 1999a, b). The plant community is characterized by spiny drought-deciduous and evergreen shrubs 2–3 m in height, with an herbaceous understory. This vegetation is called *Porlieria chilensis-Adesmia bedwellii-Proustia pungens* association (Gutiérrez et al., 1993). A complete account of the biotic and abiotic conditions of study site is provided by Meserve et al. (2003).

2.2. Live trapping and determination of urine osmolality

Live trapping of the marsupial was done using standard (75 × 85 × 240 mm) Sherman traps, in two 10 × 3 grids, two traps by station (60 traps per grid), at intervals of 10 m, encompassing an area of 0.30 ha, considering 5 m border strips. Trapping was carried out for 5 consecutive days, using oats as bait. Captured marsupials over the 4 years ($n = 70$ different individuals, mean body mass = 23.8 ± 7.9 g, range = 12.0–49.0 g) were marked with ear tags to avoid duplication of urine samples during the seasonal period. Traps were checked early in the morning and all animals were measured only once. The abdomen of each individual was gently pushed until a drop of urine was obtained, then urine samples were collected in microhematocrit tubes and measured instantly. In the urine samples, the total concentration of solids (S = g/100 g) was measured, using a field refractometer AO TS Meter/Scientific Instruments. Total solids are the fraction of solid in a liquid medium. These data allowed us to estimate the urine osmolality (Uosm) in mOsm/kg, through the equation: Uosm (mOsm/kg) = $140S^{0.984}$. For methodological details and calibration methods, see Cortés and Rosenmann (1989).

2.3. Statistical analyses

We tested the effects of year and season on Uosm values using an analysis of variance (ANOVA) model in which the years and seasons were taken as factor variables influencing the Uosm values. We used generalized linear model procedures in StatSoft (2001) with year and season as factors in a two-way ANOVA model. We also tested for interaction terms (year × season). The post-hoc Tukey's test for multiple comparisons was used to determine whether any significant difference existed between responses to the treatments (year and season). Values reported are mean ± 1 S.D. Thus, we observed high Uosm values during spring–summer and low values during autumn–winter, which was more noticeable during El Niño-driven wet years. Also, during La Niña-driven dry years there was an increase in autumn–winter and summer Uosm values.

3. Results

Depending on environmental water availability, mean annual values of field Uosm in *T. elegans* ranged from 2.584 ± 376 mOsm/kg to 2.869 ± 476 mOsm/kg ($n = 70$; see Fig. 1). In summer and during dry years, this insectivorous marsupial showed higher water economy expressed by the highest Uosm values. Also during summer, Uosm values were higher in comparison to winter (wet years: 2.719 ± 405 mOsm/kg in summer versus 2.246 ± 209 mOsm/kg in winter; dry years: 3.340 ± 384 mOsm/kg in summer versus 2.481 ± 293 mOsm/kg in winter (Fig. 2). Similar results have been reported for sympatric rodents (Bozinovic and Gallardo, 2006). On the other hand, there were significant effects of year and season on Uosm values, as well as interaction year × season (Table 1). Table 2 shows the results of the *a posteriori* Tukey's pairwise comparisons test.

4. Discussion

The multitude of mechanisms by which animals regulate their water economy in face of spatial and temporal fluctuations in environmental conditions supports the importance of physiological flexibility studies in the field (McNab, 2002). Here, we illustrate the physiological responses of a desert species—the marsupial *T. elegans*—to changing environmental conditions in water availability during El Niño and La Niña events.

As Goldstein and Pinshow (2006) pointed out, quantifying organismal responses to changing environments provides a bridge between mechanistic physiology, ecology and evolutionary biology. Although uncontrolled factors in natural conditions may hinder our capacity to determine accurately causal relationships among variables, field studies provide opportunities not available under laboratory conditions. Thus, Costa and Sinervo (2004) called for a new approach to ecological physiology, denominated field physiology. These authors advocate field physiology as a discipline founded on an understanding of natural environments and natural history of organisms to develop hypotheses on the types of physiological problems faced by animals in the field. By studying organisms in this context, researchers may be able to identify the actual mechanisms necessary for survival, to evaluate the role of natural selection in determining the evolution of physiological traits, and to gauge the impacts of climate change on phenotypic traits (Bozinovic et al., 2007c; Cortés et al., 2000). Thus, an individual's physiological condition in the field can be viewed in the context of the range of responses

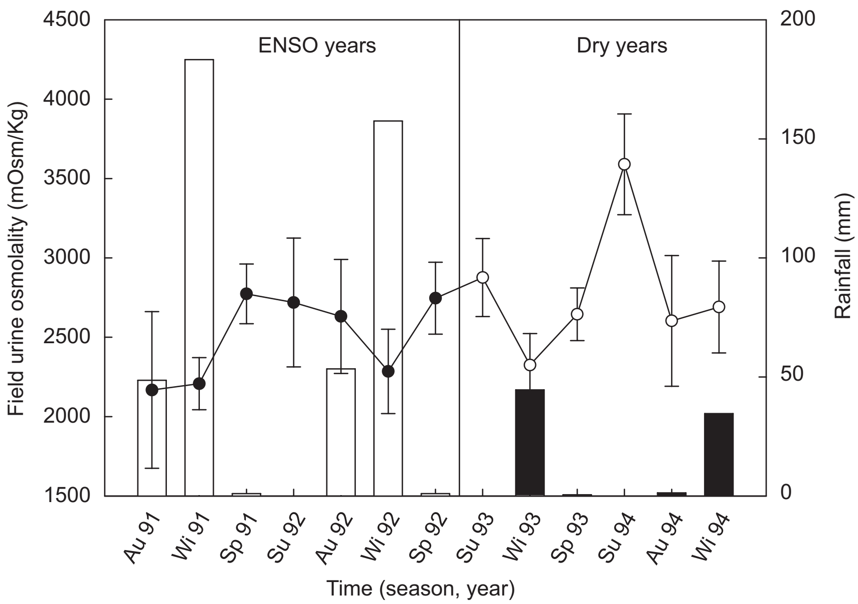

Fig. 1. Multi-annual dynamics of urine osmolality (left ordinate in mOsm/kg) of an insectivorous marsupial in semiarid Chile during consecutive El Niño wet years (closed circles) and La Niña dry years (open circles), with seasonal rainfall bars (right ordinate in mm). Au: autumn, Wi: winter, Sp: Spring, Su: summer.

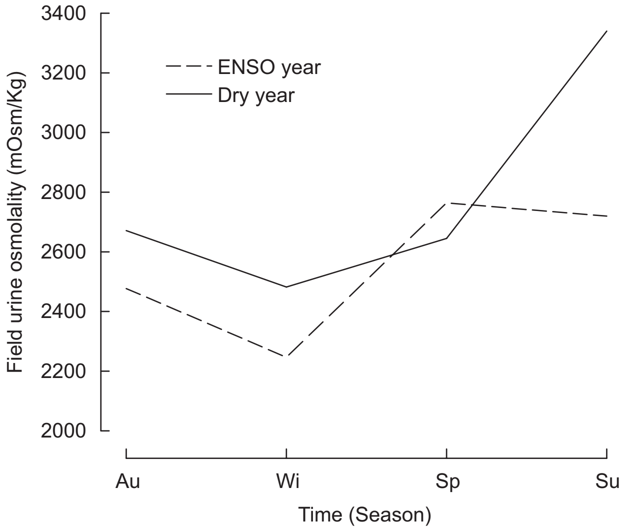

Fig. 2. Interaction plots between seasons and years for urine osmolality (mOsm/kg) of an insectivorous marsupial in semiarid Chile. Segmented line = El Niño wet years, solid line: La Niña dry years, Au: autumn, Wi: winter, Sp: Spring, Su: summer.

Table 1
Two-way model analysis of variance of field urine osmolality of an insectivorous marsupial in semiarid Chile

Effects	d.f.	*F*	*P*
Year	1	8.16	0.006
Season	1	13.88	<0.0001
Season × year	3	3.69	0.002
Residuals	62		

Table 2
Tukey's pairwise comparisons test of urine osmolality (Uosm) for wet and dry conditions by season and year

Variables	Uosm (mOsm/kg)	Homogeneous groups
Condition/season		
Dry/summer	3.340±384	a
Wet/spring	2.764±388	b
Wet/summer	2.719±405	b
Dry/autumn	2.671±365	bc
Dry/spring	2.645±277	bc
Dry/winter	2.481±293	bc
Wet/autumn	2.476±211	bc
Wet/winter	2.246±209	c
Condition/year		
Dry year	2.784±338	a
Wet year	2.551±307	b
Season		
Summer	3.029±251	a
Spring	2.704±276	b
Autumn	2.573±344	bc
Winter	2.364±306	c

Same letters indicate that means are not significantly different.

established under controlled laboratory conditions. Here, we illustrate the physiological responses of animals to changing environmental conditions in water availability.

The insectivorous marsupial studied showed important temporal fluctuations in its field Uosm values, demonstrating seasonal and between-year patterns of physiological variability (Fig. 1; see also Diaz et al., 2001, 2006). There was a clear seasonal pattern of water economy characterized by high Uosm values during spring–summer and low values during autumn–winter, which was more marked during El Niño-driven wet years. During La Niña-driven dry years, there was an increase in autumn–winter and summer Uosm values. Bozinovic et al. (2007a) assessed physiological responses in Uosm of five rodent species in the same study area and they all showed similar seasonal and between-year patterns of physiological variability. The seasonal rhythm of water economy of these Chilean mammals during wet years is consistent with that observed among North American desert heteromyds (MacMillen, 1972; MacMillen and Grubbs, 1976), but differs from that of Indian desert gerbils (Goyal, 1988).

The trends of seasonal Uosm values during contrasting years (wet and dry years) may be a consequence of associated changes in abundance of plants and insects, because they constitute the major sources of food and water for mammals in the study site (Bozinovic et al., 2003; Meserve, 1981). The productivity of plants and insects there is determined by the amount of rainfall (Gutiérrez, 2001; Gutiérrez et al., 1993). The insectivorous habits of *T. elegans* allow a larger water intake during wet seasons or years but it also implicates a higher excretion of nitrogen products such as urea. This increases osmotic diuresis, which can be compensated by an increase in Uosm. In addition, this species is able to compensate for low water availability by the use of torpor. Bozinovic et al. (2005, 2007b) showed that the frequency and depth of torpor in *T. elegans* varies with food availability: food amounts exceeding daily energy requirements resulted in individuals rarely becoming torpid as opposed to those confronting lower food availability. We hypothesize the same pattern with changes in water availability, with individuals likely minimizing water deficits by becoming torpid.

Finally, this study illustrates that longer-term (multi-year) physiological studies are necessary to elucidate the relationship between physiological conditions and climatic fluctuations, and to determine the acclimatization responses over more meaningful time spans. Our results contribute to understand the sensibility of semidesert ecosystems and their inhabitants to climate change, considering that El Niño and La Niña phases of ENSO determine the existence of wet and dry years, respectively (Lima et al., 1999a, b). More advantage should be taken of this climatic oscillatory phenomenon to predict the physiological responses and adaptability of animals facing future drier conditions (Jaksic, 2001).

Acknowledgments

We are grateful to CONAF-IV Region and the collaboration of C. Pino and E. Miranda. This study was supported by Grants FONDECYT-92-0797, DIULS 120-2-63 to AC and FONDAP 1501-0001 (Programs 1 and 2) to FB and FMJ, respectively. Two referrers provided useful comments.

References

Aceituno, P., 1992. El Niño, the Southern Oscillation, and ENSO: confusing names for a complex ocean–atmosphere interaction. Bulletin of the American Meteorological Society 73, 483–485.

Bozinovic, F., Gallardo, P., 2006. The water economy of South American desert rodents: from integrative to molecular physiological ecology. Comparative Biochemistry and Physiology 142C, 163–172.

Bozinovic, F., Gallardo, P.A., Visser, R.H., Cortés, A., 2003. Seasonal acclimatization in water flux rate, urine osmolality and kidney water channels in free-living degus: molecular mechanisms, physiological processes and ecological implications. Journal of Experimental Biology 206, 2959–2966.

Bozinovic, F., Ruiz, G., Rosenmann., M., 2005. Energetics, thermoregulation and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae). Revista Chilena de Historia Natural 78, 199–206.

Bozinovic, F., Lima, M., Bacigalupe, L.D., Gutierrez, J.R., Rosenmann, M., Cortés, A., 2007a. Physiological flexibility in field urine osmolality of rodents from semiarid Chile. In: Kelt, D.A., Lessa, E.P., Salazar-Bravo, J.A., Patton, J.L. (Eds.), The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publication in Zoology 134, pp. 165–176.

Bozinovic, F., Muñoz, J.L.P., Naya, D.E., Cruz-Neto, A.P., 2007b. Adjusting energy expenditure to energy supply: food availability regulates torpor use and organ size in the Chilean mouse-opossum *Thylamys elegans*. Journal of Comparative Physiology B 177, 393–400.

Bozinovic, F., Cruz-Neto, A.P., Cortés, A., Diaz, G.B., Ojeda, R.A., Giannoni, S.M., 2007c. Physiological diversity in tolerance to water deprivation among species of South American rodents. Journal of Arid Environments 70, 427–442.

Cortés, A., Rosenmann, M., 1989. A field lab method to determine urine concentration in small mammals. Comparative Biochemistry and Physiology 94A, 261–262.

Cortés, A., Pino, C., Rosenmann, M., 1994. Balance hídrico del ensamble de micromamíferos de dos localidades de la región mediterránea árida del norte de Chile central: un estudio de campo. Revista Chilena de Historia Natural 67, 65–77.

Cortés, A., Rosenmann, M., Bozinovic, F., 2000. Water economy in rodents: evaporative water loss and metabolic water production. Revista Chilena de Historia Natural 73, 311–321.

Costa, D.P., Sinervo, B., 2004. Field physiology: physiological insights from animals in nature. Annual Review of Physiology 66, 209–238.

Degen, A.A., 1997. Ecophysiology of Small Desert Mammals. Springer, Berlin.

Diaz, G.B., Ojeda, R.A., Dacar, M., 2001. Water conservation in the South American desert mouse opossum *Thylamys pusilla* (Didelphimorphia, Didelphidae). Comparative Biochemistry and Physiology 130A, 323–330.

Diaz, G.B., Ojeda, R.A., Rezende, E.L., 2006. Renal morphology, phylogenetic history and desert adaptation of South American hystricognath rodent. Functional Ecology 20, 609–620.

Garland, T., Carter, P., 1994. Evolutionary physiology. Annual Review of Ecology and Systematics 56, 579–621.

Goldstein, D.L., Pinshow, B., 2006. Taking physiology to the field: using physiological approaches to answer questions about animals in their environments. Physiological and Biochemical Zoology 79, 237–241.

Goyal, S.P., 1988. Field urine concentration in two Indian desert gerbils. Journal of Mammalogy 69, 418–421.

Gutiérrez, J.R., 2001. Dynamics of ephemeral plants in the coastal desert of north-central Chile. In: Prakash, I. (Ed.), Ecology of Desert Environments. Desert Regional Station, Zoological Survey of India, Jodhpur, India, pp. 105–124.

Gutiérrez, J.R., Meserve, P.L., Jaksic, F.M., Contreras, L.C., Herrera, S., Vásquez, H., 1993. Structure and dynamics of vegetation in a Chilean semiarid thorn-scrub community. Acta Oecologia 14, 271–285.

Huey, R.B., Berrigan, D., 1996. Testing evolutionary hypotheses of acclimation. In: Johnston, I.A., Bennett, A.F. (Eds.), Animals and Temperature. Phenotypic and Evolutionary Adaptation. Society for Experimental Biology, Seminar Series 59. Cambridge University Press, Cambridge, pp. 205–237.

Jaksic, F.M., 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24, 241–250.
Jaksic, F.M., Silva, S.I., Meserve, P.L., Gutiérrez, J.R., 1997. A long term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South American. Oikos 78, 341–354.
Lima, M., Marquet, P.A., Jaksic, F.M., 1999a. El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22, 213–218.
Lima, M., Keymer, J.E., Jaksic, F.M., 1999b. ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America: from demography to population dynamics. American Naturalist 153, 476–491.
Lima, M., Stenseth, N.C., Jaksic, F.M., 2002. Food web structure and climate effects in the dynamics of small mammals and owls in semiarid Chile. Ecology Letters 5, 273–284.
MacMillen, R.E., 1972. Water economy of nocturnal desert rodents. In: Maloiy, G.M.O. (Ed.), Comparative Physiology of Desert Animals. Symposium of the Zoological Society of London, pp. 147–174.
MacMillen, R.E., Grubbs, D.E., 1976. The effects of temperature on water metabolism of rodents. In: Johnson, H.D. (Ed.), Progress in Animal Biometeorology. Swets and Zeitlinger, The Netherlands, pp. 63–69.
McNab, B.K., 2002. The Physiological Ecology of Vertebrates. A View from Energetics. Cornell University Press, Cornell.
Meserve, P.L., 1981. Trophic relationships among small mammals in Chilean semiarid thorn scrub community. Journal of Mammalogy 62, 304–314.
Meserve, P.L., Yunger, J.A., Gutiérrez, J.R., Contreras, L.C., Milstead, W.B., Lang, B.K., Cramer, K.L., Herrera, S., Lagos, V.O., Silva, S.I., Tabilo, E.L., Torrealba, M.A., Jaksic, F.M., 1995. Heterogeneous responses of small mammals to an El Niño southern oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76, 580–595.
Meserve, P.L., Milstead, W.B., Gutiérrez, J.R., Jaksic, F.M., 1999. The interplay of biotic and abiotic factors in semiarid Chilean mammal assemblage: results of a long-term experiment. Oikos 85, 362–372.
Meserve, P.L., Kelt, D.A., Milstead, W.B., Gutiérrez, J.R., 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53, 633–646.
Schmidt-Nielsen, K., 1979. Desert Animals: Physiological Problems of Heat and Water. Dover Publications, Inc., New York.
StatSoft, Inc., 2001. STATISTICA (Data Analysis Software System), Version 6. Tulsa, Oklahoma.
Walsberg, G., 2000. Small mammals in hot deserts: some generalizations revisited. BioScience 50, 109–120.
Willmer, P., Stone, G., Johnston, I., 2000. Environmental Physiology of Animals. Blackwell Science, Oxford.