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Review

The water economy of South American desert rodents: From integrative to molecular physiological ecology ☆

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Abstract

Rodents from arid and semi-arid habitats live under conditions where the spatial and temporal availability of free water is limited, or scarce, thus forcing these rodents to deal 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. In addition, studies in small South American mammals are scarce. Indeed xeric habitats have existed in South America for a long time and it is intriguing why present day South American desert rodents do not show the wide array of adaptive traits to desert life observed for rodents on other continents. Several authors have pointed out that South American desert rodents lack physiological and energetic specialization for energy and water conservation, hypothesizing that their success is based more on behavioral and ecological strategies. We review phenotypic flexibility and physiological diversity in water flux rate, urine osmolality, and expression of water channels in South American desert-dwelling rodents. As far as we know, this is the first review of integrative studies at cellular, systemic and organismal levels. Our main conclusion is that South American desert rodents possess structural as well as physiological systems for water conservation, which are as remarkable as those found in "classical" rodents inhabiting other desert areas of the world.

Keywords: Water economy; Desert; South American rodents; Urine osmolality; Evaporative water loss; Metabolic water production; Aquaporins

Contents

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1. Introduction

The study of physiological adaptation and diversity has been a central issue in ecological and evolutionary physiology (Willmer et al., 2000). For example, the environmental tuning of an organism's physiology is often hypothesized to be responsible for allowing an organism 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 a significant challenge (Walsberg, 2000).

Rodents from arid and semi-arid habitats are faced with the problem of water conservation, where conditions cause the temporal availability of free water to be limited or scarce (Degen, 1997). The response of small mammals to unproductive deserts and water deficits have been intensively investigated (e.g., Schmidt-Nielsen, 1964). However, present understanding of the cellular, systemic and organismal physiology of water economy relies heavily on short-term, laboratory-oriented experiments that usually focus on isolated levels of biological organization (Bozinovic et al., 2003; Gallardo et al., 2005). Furthermore, few studies deal with the evolutionary and comparative physiological ecology of South American rodents. In South America xeric habitats have existed since the late Tertiary (Montgomery et al., 2001; Hinojosa and Villagrán, 1997), and it is intriguing why present day South American desert rodents appear not to have the wide array of adaptive traits for life in deserts, as compared to desert rodents found on other continents. Several authors have pointed out that South American desert rodents lack physiological and energetic specializations for energy and water conservation, postulating that their success is essentially due to behavioral and ecological strategies (Mares, 1975; Meserve, 1978 but see Koford, 1968). Nevertheless, McNab (1982) noted that such a lack of physiological adaptations may, to some extent, be more apparent than real, because (comparatively) only a small amount of studies have been conducted in South American desert environments. In fact studies published by Koford (1968), Bozinovic and Rosenmann (1988a,b), Bozinovic et al. (2003), Gallardo et al. (2005), Bozinovic and Marquet (1991), Cortés et al. (1990, 2000), Caviedes-Vidal et al. (1990), Diaz and Ojeda (1999), and Al-kahtani et al. (2004) all seem to support McNab's (1982) proposal. Here we examine and critically review the physiological mechanisms of water economy in South American desert-dwelling rodents, from a comparative perspective. As far as we know, this is the first review that incorporates integrative studies at the cellular, systemic and organismal levels.

2. The integrative physiological ecology of South American desert rodents

2.1. Foraging behavior and diet selection

Rodent adaptations to life in deserts includes different combinations of morphological, physiological, behavioral, and ecological characteristics (Bozinovic and Contreras, 1990). In addition, low energy expenditure linked to dietary specialization on seeds is considered adaptive for energy and water conservation in xeric environments because it results in lower food requirements and reduced water turnover in variable and unproductive habitats (Hinds and MacMillen, 1985). Granivorous desert rodents display physiological features that favor body water conservation, such as efficient kidney function, low fecal water content, and comparatively lower evaporative water loss (MacMillen and Lee, 1967; MacMillen, 1972; Schmidt-Nielsen, 1964; Christian, 1979; Withers et al., 1982). In contrast, omnivorous, herbivorous, and insectivorous desert rodents are unable to survive under the same conditions because they depend on exogenous water (Bozinovic and Contreras, 1990). Apparently, desert colonization and survival in xeric habitats by rodents lacking physiological specialization to desert life is accomplished through behavioral strategies such as nocturnal and/or crepuscular activity, and selection of favorable microhabitats (MacMillen, 1972; Schmidt-Nielsen, 1964; MacMillen and Hinds, 1983; Degen et al., 1986). In this regard, rates of water flux in the field (which represent the loss of water via excretion and evaporative water loss, and the simultaneous input of water via metabolic water production, and preformed water via food and drink (Nagy and Costa, 1980; Nagy and Peterson, 1988)) can be used to understand how herbivorous desert rodent inhabit xeric ecosystems.

Bozinovic et al. (2003) demonstrated that the herbivorous degus (*Octodon degus*), which inhabit arid and semi-arid localities in Chile, feed primarily on shrub foliage, seeds, and conductive tissue. In Mediterranean environments degus feed primarily on forb and grass foliage and on seeds. In addition they also experience geographical and seasonal changes in the availability of water as well as the nutrients in their food (Meserve, 1981; Meserve et al., 1983, 1998). Although small mammals may select sparsely distributed, high quality plants, or can use coprophagy to recycle water and nutrients (Kenagy et al., 1999), during nutritional-water bottlenecks they must consume low-quality food out of necessity rather than choice (Bozinovic, 1995, 1997, Bozinovic et al., 1997; Torres-Contreras and Bozinovic, 1997). Through the use of stable isotopes, Bozinovic et al. (2003) indicated that differences in the seasonal water flux of *O. degus* in the field are likely a product of differences in the