RESEARCH ARTICLE

Renal Intraspecific Variation Along an Aridity Gradient Detected by New Renal Indices in a Desert Herbivorous Rodent

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PATRICIA A. TEJO RIQUELME[1],
GABRIELA B. DIAZ ISENRATH[2],
NATALIA ANDINO[3,4], AND CARLOS E. BORGHI[1,3,4]*
[1]Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Rivadavia, San Juan, Argentina
[2]Instituto de Ciencias Básicas, Universidad Nacional de Cuyo, Malargüe, Mendoza, Argentina
[3]Centro de Investigaciones de la Geosfera y la Biosfera (Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional de San Juan), Rivadavia, San Juan, Argentina
[4]Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina

ABSTRACT

Mammals that live in arid and semi-arid environments in South America present physiological mechanisms that enable them to conserve water. Body water is lost through the kidneys, lungs, skin, and intestines. Regarding renal adaptation for water conservation, several indices have been used to estimate the capacity of the kidneys to produce a maximum urine concentration. Most studies were conducted at an inter-specific level, with only few performed at the intraspecific level. In this work, we compare renal function and morphology among five populations of Southern mountain cavy, *Microcavia australis*, present along an aridity gradient. We hypothesized that individuals from drier zones would present morphological and functional renal modifications that imply a greater capability to conserve body water. These features were studied considering the classical indices (RMT, PMT, PMA, and RMA) and three new indices that consider area measurements; the latter showed to be more adequate to reflect intraspecific differences. Our results suggest that the morphological modifications of kidneys, that is, the greater areas of renal inner medulla, would be related to the aridity gradient where populations of Southern mountain cavy occur. *J. Exp. Zool. 321A:348–356, 2014.* © 2014 Wiley Periodicals, Inc.

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Water balance has been one of the main research focuses in the field of ecophysiology of arid-zone mammals. In animals living in South American deserts as well as in other arid lands, water balance is a great challenge (Diaz and Ojeda, '99; Walsberg, 2000; Diaz et al., 2006) because of the high temperatures and high water-deficit rates characteristic of the environment. As a strategy to face limited exogenous water or excessive loss, numerous species present very low water loss rates through evapotranspiration, urination, and digestion (Schmidt-Nielsen, '64, '79; MacMillen and Lee, '67; Degen, '97; Cortés et al., 2000; MacNab, 2002).

Regarding the renal capacity of mammals to maintain body water balance, the efficiency of kidneys has been associated with

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*Correspondence to: Carlos E. Borghi, CIGEOBIO (UNSJ-CONICET)-INTERBIODES, Departamento de Biología y Museo de Ciencias Naturales, Universidad Nacional de San Juan, Av. Ignacio de la Roza 590 (oeste), Complejo Universitario "Islas Malvinas", Rivadavia, San Juan J5402DCS, Argentina.
E-mail: cborghi@unsj-cuim.edu.ar

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the thickness of their medulla. For species having unipapillary kidneys, their thicker medulla or longer papilla implies longer Henle loops and tubules involved in urine concentration (Sperber, '44; Schmidt-Nielsen and O'Dell, '61; Beuchat, '90a,b). The length of the papilla has been considered the structural basis of the concentrating ability (Vimtrup and Schmidt Nielsen, '52; Beuchat, '90a; Schmidt-Nielsen and Schmidt-Nielsen, 2011). Different indices were used to estimate renal performance. The most widely used renal index is the relative medullary thickness (RMT), with its magnitude being related to the dryness of the habitat and to the capability of maximum renal concentration (Sperber, '44; Schmidt-Nielsen and O'Dell, '61; Brownfield and Wunder, '76; Geluso, '78; Beuchat, '93, '96; Al-Kahtani et al., 2004). Other renal indices based on linear measurements and kidney areas have been introduced to study the structural modification of the kidney associated with the conservation of body water (Pffeifer, '68). Among those indices are the percentage of relative medulla thickness (PMT), the percentage of medullary area and the relative medullary area (RMA) (Heisinger and Breitenbach, '69; Weisser et al., '70; Schmid, '72; Blake, '77).

The variation in the capability of mammals to produce concentrated urine has been mostly studied at the inter-specific level (Sperber, '44; MacMillen and Lee, '69; Bridges and James, '82; ; Greenwald, '89; Beuchat, '90b; Cortés et al., '90; Brooker and Withers, '94; Diaz and Ojeda, '99; Willmer et al., 2000; MacNab, 2002). However, few works have addressed this aspect at the intraspecific level (Sahni et al., '93; Oswald, '98; Taylor, '98; Tracy and Walsberg, 2001; Laakkonen, 2002). There are no studies about differences in functional renal morphology among populations in South American desert rodents, despite the importance of local adaptation in the response of species to climate change (Bocedi et al., 2013), the predicted increases of mean annual temperature and the current area of these dry lands (Lauenroth et al., 2004).

The aim of this study is to characterize, evaluate and compare the functional renal morphology in five populations of a small desert herbivorous rodent along an aridity gradient in South America. To assess the functional morphology of the kidney, we computed the classical renal indices and designed new ones that include the area of inner medulla. In addition, we discuss the usefulness of the renal indices used. The animal model used was the Southern mountain cavy (*Microcavia australis*), a social medium-sized herbivorous desert rodent (Campos et al., 2001; Andino et al., 2011) that behaves as a facultative specialist forager when coping with heterogeneous, highly seasonal and low-quality trophic resources (Sassi et al., 2011). This species was never observed drinking free water in its natural habitat or under laboratory conditions. The species inhabits arid and semi-arid lands in an area with a wide range of precipitation, which allows us to assess the geographical variability of its functional renal morphology. We hypothesize that functional renal morphology of the Southern mountain cavy would fit spatial variations in aridity across the environment where the species occurs.

MATERIALS AND METHODS

The Southern mountain cavy is a hystricognath rodent of ca. 250–300 g, which occurs throughout a wide range of arid and semi-arid environments in the southern portion of South America, from approximately 22° S to 52° S, in a variety of habitats with different environmental conditions (Tognelli et al., 2001). The species has proved to be versatile in coping with the challenges of the arid lands it inhabits, as well as with their typical seasonal and spatial heterogeneity (Sassi et al., 2011). Accordingly, Southern mountain cavy is a good model to evaluate the influence of environmental factors on the functional renal morphology to understand their local adaptations to xeric environments.

Fieldwork was carried out in the Central Monte desert of Argentina in 2002 and 2003. Five sites of different aridity conditions (from hyper-arid through semi-arid to humid) were selected within the distribution range of Southern mountain cavy: La Laja, Matagusanos, Villavicencio, Ñacuñán, and Médano de Oro (Table 1). Médano de Oro behaves as humid because it has a shallow water table, with a high net primary productivity (see Table 1), and cavies could obtain preformed water by ingesting these plants, as reported for other desert rodents (Nagy and Peterson, '88). Therefore, we estimated a corrected precipitation value for Médano de Oro using a regression model with net primary productivity values as the independent variable and precipitation as the dependent one, in order to obtain a better estimate of the water from plant tissues available to the Southern mountain cavy.

Southern mountain cavy individuals were captured using Havahart traps during the dry season, which is characterized by low precipitation, low temperatures and low number of daylight hours (Ojeda and Tabeni, 2009; Andino et al., 2011). In the dry season, green grasses and herbaceous plants are absent and plant cover is the lowest in the year (Andino et al., 2011).

The number of individuals captured was as follows: 8 in La Laja (3 females and 5 males); 3 in Villavicencio (1 female and 2 males); 4 in Ñacuñán (1 female and 3 males); 5 in Mataguasanos (2 females and 3 males); and 7 in Médano de Oro (2 females and 5 males). None of the individuals used in the study were juveniles or pregnant females.

The captured animals were weighed (±0.1 g) and maintained in individual cages for no longer than 24 hr. Then they were sacrificed with sodium pentobarbital in an intraperitoneal injection, following the Guidelines on Euthanasia of American Veterinary Association (AVMA, 2013). All animal procedures were approved by the Institutional Animal Care and Use Committee of the School of Exact, Physical and Natural Sciences of the National University of San Juan.

Both kidneys were removed, weighed to the nearest 0.001 g and fixed in 10% formaldehyde. Length, width, and thickness of the kidneys were measured with a dial calliper to the nearest 0.1 mm. Two sections along the frontal axis through the longest part of the renal papilla were obtained from the left kidney (Cortés et al., '90;

Table 1. Capture localities, climate classification, coordinates, mean net primary productivity (2000–2012) from the Moderate Resolution Imaging Spectroradiometer (MODIS), mean temperature in the warmest and coldest months, and mean annual precipitation.

Localities	Climate classification	Location coordinates	Mean annual precipitation	Net primary productivity (g carbon/m^2)[a]	Mean temperature Warmest month (°C)	Mean temperature Coldest month (°C)	Height (m asl)	Refs.
Matagusanos	Arid-hyperarid	31°12′57″S; 68°37′44″W	64 mm	152.7	25	8	890	De Fina et al. ('62)
La Laja	Arid-hyperarid	31°20′32″S; 68°28′05″W	80 mm	156.5	27	9	680	De Fina et al. ('62)
Villavicencio	Semi-arid	32° 31′15″S; 68° 59′02″W	309 mm	254.1	17	5	1780	Sassi et al. (2007)
Ñacuñán	Semi-arid	34° 02′44″S; 67° 54′23″W	326 mm	329.7	22	9	700	Ojeda et al. ('98)
Médano de Oro[b]	Humid	31°35′21″S; 68°26′41″W	93 mm (1,245 mm[c])	886.5	26	8	595	De Fina et al. ('62)

Temperature is expressed in °C.

[a] Data from Global MODIS NPP algorithm (Marcelo Tognelli personal communication).

[b] This site behaves as humid for plants because it has a shallow water table, and southern mountain cavies obtain preformed water by ingesting these plants.

[c] Corrected value of precipitation using a regression between NPP and precipitation ($R^2 = 0.85$), for including the effect of shallow water table available for plants.

Díaz and Ojeda, '90; Al-Kahtani et al., 2004). When it was not possible to make a complete sagittal section, the right kidney was used. Cortex thickness (CT), outer zone of the medulla, and inner zone of the medulla were distinguishable if the kidneys were freshly fixed; medulla thickness (MT) is the sum of the values of outer and inner medulla. The limit between the cortex and the medulla, and the outer and inner medulla are visible grossly. It reflects the structural differentiation between zones. The cortex is the zone that contains glomeruli and the tubules. The medulla has tubules that consist of loops of Henle and collecting ducts. The difference between the outer and inner medulla lies in the loops of Henle. The inner medulla has only thin segments of loops of Henle and the outer medulla has thin and thick segments. The edge of the outer and inner medulla can be clearly observed with a stereoscopic microscope (6×). The outline of the entire kidney, including the corticomedullary junction, and the outer and inner boundaries of the medulla, were traced on paper using a camera lucida attached to a stereoscopic microscope (Geluso, '78). The thickness of each zone was measured with a ruler (0.5 mm). Kidney zone areas were calculated from the weight of each piece of paper and the weight of a determined area of the paper. The following indices were calculated: relative medullary thickness (RMT = medullary thickness × 10/cube root of the product of kidney length, width and thickness), ratio of medulla to cortex (M/C), ratio of inner medulla to cortex (IM/C), percent medullary thickness (PMT), percent medullary area (PMA), and relative medullary area (RMA = medullary area/cortical area) (Sperber, '44; Heisinger and Breitenbach, '69; Schmid, '72; Brownfield and Wunder, '76; Geluso, '78). In addition, three new indices were proposed and calculated: IMA/CA (inner medullary area/cortical area), IMA/RA (inner medullary area/total renal area), and IMA/MA (inner medullary area/medullary area) because classical indices do not reveal kidney shape variation at the intraspecific level.

We used an analysis of variance to assess the variation of renal linear indices among localities and its statistical significance. The variables fit the requirements of ANCOVA and ANOVA. We used renal indices as response variables, and localities as the explanatory variable. Firstly, we used body weight as a covariable in comparisons; however, as it did not show any significant effect, we used only ANOVA analysis. When there were differences between localities among renal indices, an a posteriori Newman–Keuls test was performed. Results are expressed as mean ± SD, and in all statistical tests, $\alpha = 0.05$ was considered. Spearman correlations were performed between mean renal indices and mean annual precipitation of each study site only for renal indices that were significantly different from the ANOVA (RMT, PMA, IMA/CA, IMA/RA, and IMA/MA).

A generalized linear model (GLM), with Normal distribution, provided in R 3.0.1 (R Development Core Team 2013) software was used to identify the factors that affect renal indices in the Southern mountain cavy. We used precipitation, mean minimum temperature of the coldest month (T min) and mean maximum temperature of the warmest month (T max) as fixed factors. We previously performed a correlation analysis to identify multicollinearity in order to remove correlated variables (Neter et al., '90). However, we included all variables in the analysis because the coefficients were $r < 0.8$.

We used the Kullback–Leibler information–theoretic approach as the distance between the various candidate models and full reality (Anderson et al., 2001; Johnson and Omland, 2004). We computed the Akaike Information Criterion corrected for small samples (AICc) for each of the candidate models and selected the models with the lowest AICc value (Burnham and Anderson, 2002). We ranked the remaining competing models according to their AICc value and subsequently estimated their Akaike differences (Δ_i) with respect to the best model (lowest AICc), the Akaike weight ($w_{i,}$) of each model and the relative importance (RI) of the exploratory variables (Burnham and Anderson, 2002). In the comparison among models we considered all combinations of factors mentioned earlier.

RESULTS

For each site, the kidneys examined were unilobular, had a single papilla, did not present extra-renal extension, and had a two-zone medulla (Fig. 1). The KW/BW ratio (kidney weight/body weight) showed significant differences among sites ($P < 0.05$). The morphology of kidneys and the renal indices of each study locality are shown in Table 2.

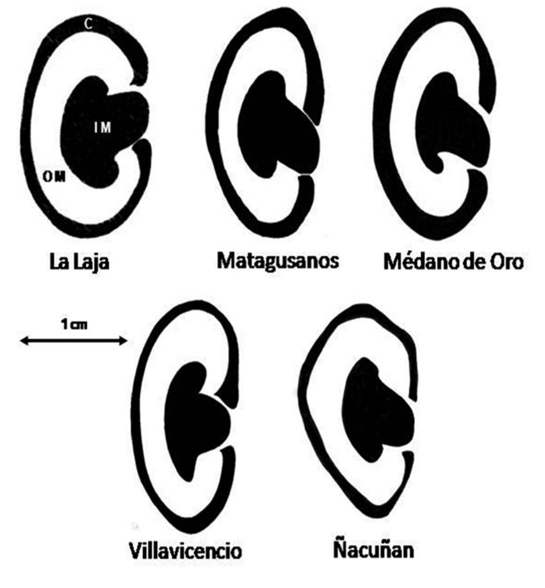

Figure 1. Renal morphology of the Southern mountain cavy (*Microcavia australis*) for individuals of the five study sites (La Laja, Matagusanos, Médano de Oro, Ñacuñán, and Villavicencio). C, cortex; OM, outer medulla; IM, inner medulla.

Of the classical linear renal indices, PMT, M/C, and IM/C did not detect significant differences among the populations compared (Table 2). Only PMA showed a significant difference among sites (Table 2). All the new renal area indices proposed (IMA/CA, IMA/RA, and IMA/MA), however, revealed statistical significant differences among sites (Table 2). Among the renal area indices that detected differences among Southern mountain cavy populations from different sites with different climate conditions (RMT, PMA, IMA/CA, IMA/RA, and IMA/MA), only IMA/RA and IMA/MA showed a statistical negative Spearman rank correlation with precipitation ($r_S = -0.56$; $n = 27$; $P = 0.002$; $r_S = -0.67$; $n = 27$; $P < 0.0002$, respectively), which was stronger when we used the corrected precipitation value ($r_S = -0.69$; $n = 27$; $P < 0.0001$; $r_S = -0.69$; $n = 27$; $P < 0.0001$, respectively).

We built GLM models to evaluate the effect of precipitation and maximum and minimum temperature on renal linear indices (RMT, PMT, M/C, IM/C) and renal area indices (RMA, PMA, IMA/CA, IMA/RA, IMA/MA). We also calculated the models with a corrected precipitation value estimated for Médano de Oro. For renal linear indices, only best models for M/C and IM/C indices included precipitation as a predictor, and the RI of precipitation was 0.81 and 0.68, respectively; however, when we used the corrected precipitation value, precipitation was not included in the models. The percentage of the total deviance explained by these models was low (<32%).

Among the classical renal area indices, precipitation was included in the best models only for RMA with the corrected precipitation values (Table 3), but the percentage of the deviance explained was low (14.1%). With respect to the new area renal indices, the best models for IMA/RA and IMA/MA included precipitation (IMA/CA only when corrected precipitation values were used in the analysis). In all cases, when the GLM analyses were made with the corrected precipitation values, the percentage of the total variance explained increased (from 33 to 67 for IMA/RA and from 40 to 60 for IMA/MA). The RI of precipitation in the models also increased (from 0.65 to 1.00 for IMA/RA, and from 0.95 to 0.99 form IMA/MA) when we used the corrected precipitation value for Médano de Oro (Table 3). The RI of maximum temperature of the warmest month was also high for IMA/RA and IMA/RA indices (Table 3).

DISCUSSION

Most classical linear renal indices (PMT, M/C, and IM/C) were not able to detect statistical differences among Southern mountain cavy populations from sites with different aridity conditions (from hyper-arid through semi-arid to humid). The means of the index that detected statistical differences among populations (RMT) did not reflect the studied rainfall gradient. Nevertheless, the values of the indices estimated for Southern mountain cavy populations were similar to those reported for other species in arid zones (Rickart, '88; Cortés et al., '90; Brooker and Withers, '94; Diaz and Ojeda, '99).

Table 2. Linear and areal renal indices for the Southern mountain cavy (*Microcavia australis*) from different localities (mean ± SE).

Biomass	Matagusanos (n = 5)	La Laja (n = 8)	Villavicencio (n = 3)	Ñacuñán (n = 4)	Médano de Oro (n = 7)	ANOVA $F_{4.22}$	ANOVA *P*
Body weight (g)	202 ± 18^{a,b}	199 ± 14^{a,b}	172 ± 24^{b}	196 ± 20^{a,b}	252 ± 15^{a}	2.826	**0.049**
Kidney weight (g)	1.64 ± 0.16	1.54 ± 0.13	1.50 ± 0.21	1.51 ± 0.18	1.30 ± 0.14	0.703	0.598
(KW/BW) × 100	0.82 ± 0.084^{a,b}	0.78 ± 0.066^{a,b}	0.91 ± 0.109^{b}	0.79 ± 0.094^{a,b}	0.52 ± 0.071^{a}	3.431	**0.025**
Renal linear indices							
RMT	8.91 ± 0.26^{a}	8.96 ± 0.21^{a}	7.82 ± 0.34^{b}	9.33 ± 0.30^{a}	9.09 ± 0.22^{a}	3.220	**0.032**
PMT	87.79 ± 0.92	88.9 ± 0.72	88.27 ± 1.18	88.53 ± 1.02	89.77 ± 0.77	0.771	0.555
M/C	2.13 ± 0.22	2.33 ± 0.17	2.66 ± 0.28	3.00 ± 0.25	2.53 ± 0.19	2.081	0.118
IM/C	5.12 ± 0.48	5.96 ± 0.38	5.31 ± 0.62	7.18 ± 0.54	5.26 ± 0.41	2.723	0.056
Renal area indices							
RMA	2.22 ± 0.23	2.62 ± 0.18	2.31 ± 0.29	2.75 ± 0.25	2.00 ± 0.19	2.108	0.114
PMA	68.29 ± 1.95^{b}	71.94 ± 1.54^{a,b}	68.60 ± 2.52^{b}	76.74 ± 2.18^{a}	66.24 ± 1.65^{b}	4.335	**0.009**
IMA/CA	0.89 ± 0.09^{a,b}	1.03 ± 0.07^{a}	0.80 ± 0.11^{a,b}	1.09 ± 0.10^{a}	0.67 ± 0.07^{b}	4.449	**0.009**
IMA/RA	0.28 ± 0.01^{a}	0.28 ± 0.01^{a}	0.24 ± 0.02^{a,b}	0.25 ± 0.01^{a,b}	0.22 ± 0.01^{b}	6.175	**0.002**
IMA/MA	0.41 ± 0.02^{a}	0.40 ± 0.01^{a}	0.34 ± 0.02^{b}	0.33 ± 0.02^{b}	0.34 ± 0.01^{b}	6.406	**0.001**

Results of the ANOVAs comparing indices among localities.
BW, body weight; KW, kidney weight; RMT, relative medullary thickness; PMT, percent medullary thickness; M/C, ratio of medulla to cortex; IM/C, ratio of inner medulla to cortex; RMA, relative medullary area; PMA, percent medullary area; IMA/CA, inner medullary area/cortical area; IMA/RA, inner medullary area/total renal area; IMA/MA, inner medullary area/medullary area.
Bold indicates significance at 0.05% or lower.
Letters (a, b, c) indicate the result of an a posteriori Tukey test for unequal N among means ($P < 0.05$).

With respect to the classical area indices, only PMA detected differences among cavy populations; however, as in RMT, means did not reflect the studied precipitation gradient. The highest RMA value obtained for an individual of Southern mountain cavy (2.75) was higher than the ones reported for South American desert rodents: *Muridae*, between 0.96 and 1.69; *Octodontidae*, between 0.75 and 1.73 (Cortés et al., '90; Diaz and Ojeda, '99; Diaz et al., 2006), but similar to those reported for other desert rodents, such as *Dipodomys merriami* and *D. odii* (Sperber, '44; Brownfield and Wunder, '76). The highest RMA value documented for a desert rodent corresponds to the Australian hopping-mouse *Notomys alexis* (4.26, MacMillen and Lee, '67), a smaller species than Southern mountain cavy.

The high values of the indices RMT and RMA obtained in this work highlight the morphological kidney variation of all Southern mountain populations from the studied arid environments, with a high efficiency of urine concentration associated with the elongation of the papilla (Sperber, '44; Schmidt-Nielsen and O'Dell, '61; MacMillen and Lee, '67, '69; Purohit, '74; Calder and Braun, '83; Bankir and de Rouffignac, '85; Cortés et al., '90; Beuchat, 1990a,b, '96; Diaz and Ojeda, '99). The length of the loops of Henle, that is, an elongated renal papilla, increases the capacity to concentrate urine. The renal medulla in the Southern mountain cavy represents a great portion of the kidney, but does not have a notorious extra-renal papilla (Fig. 1), as observed in other small arid-zone species (Beuchat, '90b; Brooker and Withers, '94; Diaz and Ojeda, '99). The RMT of the Southern mountain cavy is higher than that of other Caviidae (Al-Kahtani et al., 2004), probably due to the presence of a large medulla and a thin cortex. Previous studies have been focused on total medulla indices to test the degree of adaptation of a species to aridity conditions (Calder and Braun, '83; Beuchat, '96; Al-Kahtani et al., 2004). The relationship of the inner medulla to cortex thickness (Geluso, '78) is the only classical ratio that takes into account the inner medulla separated from the entire medulla. Nevertheless, Bankir and de Rouffignac ('85) proposed not considering the medulla as a whole but, instead, analyzing the role of each zone in the renal medulla (outer medulla, inner space and inner medulla) to evaluate the urine concentration capacity and the adaptation of species to water stress. The length of the loops of Henle, the arrangement of the tubules and vascular bundles in the inner medulla, and the presence of extensions of the renal pelvis in contact with the inner medulla may all contribute to the urine concentration capability of the kidneys (Beuchat, '90b; Schmidt-Nielsen, '95; Schmidt-Nielsen and Schmidt-Nielsen, 2011), and to explain why only the IMA/RA and IMA/MA indices, which use the inner medulla area information, show a statistical significant correlation with precipitation. Furthermore, urea molecules are continuously cycling back to the inner medulla (Yang and Bankir, 2005), and then a large inner medulla would provide a greater ability to accumulate urea, a key process in the mechanism of urine concentration.

Table 3. The relationship between renal indices in the Southern mountain cavy and climatic variables pre (precipitation), T min (mean minimum temperature of the coldest month), and T max (mean maximum temperature of the warmest month) were examined by Generalized Linear Models with a Gaussian distribution.

				Relative importance of variables		
Renal Indices	Best model	Akaike weight	% of the total deviance explained	Precipitation	T max	T min
Renal linear indices						
RMT	T min	0.50	30	0.29	0.33	0.81
W/corrected precipitation	T min + T max	0.65	30	0.32	0.92	0.95
PMT	Null model	–	–	–	–	–
W/corrected precipitation	Null model	–	–	–	–	–
M/C	Pre	0.41	20.8	0.81	0.37	0.27
W/corrected precipitation	Null model	–	–	–	–	–
IM/C	Pre + T min	0.35	32.1	0.68	0.56	0.71
W/corrected precipitation	T min + T max	0.65	30.6	0.20	0.82	0.88
Renal area indices						
RMA	Null model	–	–	–	–	–
w/corrected precipitation	Pre	0.31	14.1	0.60	0.33	0.43
PMA	T min + T max	0.50	38.9	0.47	0.68	0.91
w/corrected precipitation	T min + T max	0.50	38.9	0.32	0.92	0.95
IMA/CA	T min + T max	0.37	27.1	0.41	0.62	0.85
w/corrected precipitation	Pre + T min	0.34	37.6	0.93	0.36	0.64
IMA/RA	Pre + T min + T max	0.53	33.3	0.65	0.65	0.78
w/corrected precipitation	Pre + T max	0.74	66.6	1.00	0.70	0.31
IMA/MA	Pre + T min + T max	0.71	40	0.95	0.79	0.76
w/corrected precipitation	Pre + T min + T max	0.74	60	0.99	0.95	0.76

The best model exhibited minimum AIC_c (Akaike's Information Criterion corrected for small sample size); Akaike weight; % of the total deviance explained by the best model; and the relative importance of the climatic variables in adjusting the renal indices.

In the Southern mountain cavy, the new indices that take into account the inner medullary area, IMA/CA, IMA/RA, and IMA/MA, differed significantly among localities (Table 2), becoming lower with increasing precipitation. The only exception was the humid area Médano de Oro, which behaves as humid because it has a shallow water table, with high plant productivity, and cavies could obtain preformed water by ingesting these plants, as other desert rodents do (Nagy and Peterson, '88).

These indices (IMA/MA and IMA/RA), which include information about the inner medulla, clearly correlate with the precipitation gradient. This result is not true for relative medullary thickness (RMT). Although RMT index is commonly used as an indicator of renal efficiency in inter-specific studies in arid zones (Calder and Braun, '83; Beuchat, '96; Al-kahtani et al., 2004), it has not been efficient in the study of the functional morphology of the kidney at intraspecific level, as previously observed by Laakkonen (2002).

Renal hypertrophy and greater urine concentration were reported in environments where habitat aridity increases during the dry season (Blount and Blount, '68; Bakko, '75; Csuti, '79; Hewitt, '81; Cortés et al., '94). The physiological changes of an organism as a response to environmental changes are very often considered the processes responsible for promoting the adjustments of those organs to biotic and non-biotic changes in environmental conditions as a strategy to improve their biological performance (Garland and Carter, '94; Huey and Berrigan, '96; Bozinovic et al., 2003). The renal area is not modified by a change in environmental humidity, but the inner medullary area is, which increases while the outer medulla decreases. IMA/RA and IMA/MA were among the renal indices that showed significant differences among the studied Southern mountain cavy populations from different localities along an aridity gradient, and had the highest correlation coefficient with corrected precipitation values ($r_S = -0.69$ and $rs = -0.69$) and uncorrected precipitation ($r_S = -0.56$ and $rs = -0.67$). Although there is no reason to assume that these indices will behave differently with other desert mammals, further research is needed to assess their efficiency in order to characterize the adaptation of renal morphology to an arid environment. Therefore, a long and broad renal papilla and a large inner medulla would be important to produce a high urine concentration (Diaz, 2001; Yang and Bankir, 2005). Finally, the GLM showed that the relative importance of precipitation was higher for IMA/MA and IMA/RA than for the other indices. IMA/MA is mainly related to precipitation > T max > T min (all of them factors related to aridity) for uncorrected and corrected precipitation values. IMA/RA was associated with the same variables; the RI of the variables was similar to IMA/MA for corrected precipitation values, but was T min > T max > precipitation for uncorrected precipitation values (Table 3). These abiotic variables may contain climate-related information that also affects renal morphology.

Phenotypic variation among populations subjected to seasonal and geographical changes that impose constraints, such as the availability of water or food (Meserve, '81; Sassi et al., 2011), might develop phenotypical plasticity (Nespolo et al., 2001; Tracy and Walsberg, 2001; Bozinovic et al., 2003; Piersman and Drent, 2003; Sassi et al., 2007), or genetically fixed variation when plasticity cost increases (DeWitt et al., '98). Plasticity could explain the intraspecific variation in time and space of a widespread species (Tracy and Walsberg, 2001), such as the Southern mountain cavy, but it could also account for genetically fixed variations (DeWitt et al., '98), or stabilizing selection models (Polechová et al., 2009); however, these processes are not mutually exclusive (Olsson, 2006). The mechanism of the interpopulation variation remains to be studied, and both processes could be a response to aridity (Stearns, '89; Sahni et al., '93; Schlichting and Pigliucci, '98).

CONCLUSIONS

Functional renal morphology of populations of the Southern mountain cavy fits a spatial aridity gradient. Renal area indices revealed more kidney shape variation in the Southern mountain cavy than that reported at the inter-specific level. Nevertheless, the classical linear renal indices used for these cavies did not show significant differences among the populations of arid, semi-arid and humid zones. These indices were formerly designed to indicate inter-specific differences. The present results highlight the high local acclimation of this desert rodent at the level of renal morphology.

The Southern mountain cavy populations from arid zones showed an increase in the inner renal medullary area with respect to the renal and total medullary area, this relationship decreasing with mean precipitation (from hyper-arid through arid to semi-arid populations). These intraspecific modifications in the kidneys of the Southern mountain cavy populations, probably associated with the capacity to preserve body water volume, were detected by two of the renal indices proposed (IMA/RA and IMA/MA). These results highlight the importance of intraspecific variation in renal morphology of desert species. Further research work is needed to elucidate this aspect. Finally, as for other studied organisms, such as ectotherms, local adaptation and phenotypic variation of mammals will allow researchers to build predictive models to understand the effects of climate change on biodiversity in South American dry lands.

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