Water economy in rodents: evaporative water loss and metabolic water production

Economía del agua en roedores: relación entre pérdida de agua evaporativa y producción de agua metabolica

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ABSTRACT

Studies on water balance in desert-dwelling granivorous rodents use evaporative water loss (EWL) and metabolic water production (MWP) to evaluate the efficiency of water regulation, expressed by the model Ta @ MWP = EWL, defined by an ambient temperature (Ta) value at (@) which MWP/EWL = 1. Here we evaluate and apply this model $(1 - r^2)$ determining water regulation efficiency, based on the energetic cost (MR) to maintain water balance (WB), that is MR-WB. To test the model, EWL was measured and MWP estimated in nine species of rodents from different localities of northern and north-central Chile (II and IV Regions): *Octodon degus* (Od) and *O. lunatus* (Olu) (Octodontidae), *Abrothrix olivaceus* (Ao), *A. longipilis* (Al), *A. andinus* (Ad), *Phyllotis darwini* (Pd), *P. rupestris* (Pr), *P. magister* (Pm), *Oligoryzomys longicaudatus* (Ol) (Muridae) and *Chinchilla lanigera* (Cl) (Chinchillidae). Literature information on rodents from xeric and mesic habitats was also analyzed. Results indicate that: 1) Cl has the lowest EWL (0.58 mg H_2O/g h), followed by Od < Olu < Ao < Pd < Pm < Pr < Ad < Al < Ol. 2) EWL and body mass (M) are related through independent equations considering two distinctive habitats: EWL (xeric)= 5.968 $M^{-0.416}$ (r = -0.89; P < 0.001) and EWL (mesic) = 17.272 $M^{-0.532}$ (r = -0.85; P < 0.001). 3) MWP and M are related through the equation: MWP = 14.256 $M^{-0.539}$ (r = -0.98; P< 0.001). 4) At the intraspecific level, MWP/EWL and Ta are related through a negative exponential equation: MWP/EWL=a 10^{-bTa} (r = -0.95; P< 0.001). 5) Ta @ MWP = EWL and M are related through the equation: T @ (MWP = EWL) = 26.799 $M^{-0.142}$, (r = -0.49, P < 0.02). 6) MR-WB and M, are related through independent equations according to the prevailing animal's habitat : MR - WB (xeric) = 34.627 $M^{-0.339}$ (r = -0.93; P < 0.001) and MR-WB (mesic) = 68.132 $M^{-0.381}$ (r = -0.86; P < 0.001). These last two equations have comparative advantages to the previous ones because they include rodents with different dietary habits, are able to discriminate patterns in the water regulation efficiency as a function of different habitats (xeric and mesic), and enable to evaluate the energetic cost of water balance.

Key words: rodents, water economy, arid habitats, Chile.

RESUMEN

Para evaluar la eficiencia en la regulación hídrica de roedores granívoros desertícolas se usa la pérdida de agua por evaporación (EWL) y la producción de agua metabólica (MWP), estando esta expresada por el modelo Ta @ MWP = EWL, que representa el valor de una temperatura ambiente (Ta) al cual (@) MWP/EWL = 1. En este trabajo se evalua este modelo $(1 - r^2)$ y se estima la eficiencia en la regulación de agua basados en el costo energético (MR) de mantención del balance hídrico (WB), es decir MR-WB. Se midió EWL y se estimó MWP en las siguientes nueve especies de roedores de diferente localidades del norte y centro de Chile (Regiones II y IV): *Octodon degus* (Od) y *O. lunatus* (Olu) (Octodontidae), *Abrothrix olivaceus* (Ao), *A. longipilis* (Al), *A. andinus* (Ad), *Phyllotis darwini* (Pd), *P. rupestris* (Pr), *P. magister* (Pm), *Oligoryzomys longicaudatus* (Ol) (Muridae) and *Chinchilla lanigera* (Cl) (Chinchillidae). Se analizó además información de la literatura de roedores de hábitats xericos y mesicos. Los resultados indican que: 1) Cl posee la menor EWL (0,58 mg H_2O/g h), seguido por Od < Olu < Ao < Pd < Pm < Pr < Ad < Al < Ol. 2) EWL y masa corporal (M) se relacionan a través de ecuaciones independientes que consideran dos hábitats distintos: EWL (xérico)= 5,968 $M^{-0.416}$ (r = -0,89; P < 0,001) y EWL (mésico) = 17,272 $M^{-0.532}$ (r = -0,85; P < 0,001). 3) MWP and M se relacionan por la ecuación: MWP = 14,256 $M^{-0.539}$ (r = -0,98; P < 0,001). 4) A un nivel intraespecífico, MWP/EWL y Ta se relacionan a través de una ecuación exponencial negativa: MWP/EWL=a 10^{-bTa} (r = -0,95; P < 0,001). 5) Ta @ MWP = EWL y

M se relacionan a través de la ecuación: Ta @ (MWP = EWL) = 26,799 $M^{-0,142}$, (r = - 0,49, P < 0,02). 6) MR-WB y M, se relacionan por ecuaciones hábitats-dependientes y son: MR - WB (xérico) = 34,627 $M^{-0,339}$ (r = - 0,93; P < 0,001) y MR-WB (mésico) = 68,132 $M^{-0,381}$ (r = -0,86; P < 0,001). Estas dos últimas ecuaciones poseen ventajas comparativas con respecto a las anteriores pues incluyen roedores con diferentes hábitos dietarios, son capaces de discriminar patrones de regulación hídrica en función del hábitat (xérico y mésico), y son capaces de evaluar el costo energético del balance hídrico.

Palabras clave: roedores, economía hídrica, habitats áridos, Chile.

INTRODUCTION

Adaptations of rodents to life in deserts may include different combinations of morphological, physiological, behavioral, and ecological characteristics (Bozinovic & Contreras 1990). Traditionally, 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 & MacMillen 1985). Granivorous desert rodents display physiological features that favor body water conservation, such as an efficient kidney function, low fecal water content, and comparatively lower evaporative water loss (EWL) (MacMillen & Lee 1967, MacMillen 1972, Schmidt-Nielsen 1979, 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 & Contreras 1990). Desert colonization and survival in xeric habitats of rodents lacking physiological specialization to desert life are based on behavioral strategies such as nocturnal and/or crepuscular activity, and selection of favorable microhabitats (MacMillen 1972, Schmidt-Nielsen 1979, MacMillen & Hinds 1983, Degen et al. 1986).

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 an array of adaptive traits to life in deserts comparable to that found in other continents. Several authors pointed out that South American desert rodents lack physiological and energetic specialization for energy and water conservation, postulating that their success essentially owes to behavioral and ecological strategies (Mares 1975, Meserve 1978, Streilein 1982). Nevertheless, McNab (1982) noted that such lack of adaptations may, to some extent, be more apparent than real, because only few studies have been conducted in South American desert environments. In fact, Bozinovic et al. (1995), and Cortés et al. (1988, 1990) reported several energetic, renal and pulmocutaneous features favoring water conservation in some species of north-central Chile,

resembling those previously described for "typical" desert rodents (e.g. Schmidt-Nielsen 1979). Cortés et al. (1988, 1990) reported maximum urine concentration capabilities over 4,000 mOsm/kg, similar to those found among desert rodents of North America and Australia (Schmidt-Nielsen & O'Dell 1961, MacMillen & Lee 1967, 1969, Abbott 1971, Maxon & Morton 1974, Schmidt-Nielsen 1979). Also, Cortés et al. (1988, 1990) documented species-specific variability in EWL and differences in nasal passages that account for variations in the dependency to free water among sympatric species in north-central Chile. In addition, Bozinovic & Rosenmann (1988a,1988b), Caviedes-Vidal et al. (1990), Bozinovic & Marquet (1991) reported mechanisms of energy conservation such as torpor in South American rodents.

Kidney morphology and its maximum capacity to concentrate urine have been traditionally used to explain and predict water regulation efficiency by small mammals (Sperber 1944, Vimtrup & Schmidt-Nielsen 1952, Schmidt-Nielsen & O'Dell 1961, Dantzler 1970, 1982, MacMillen & Lee 1967, MacMillen 1972, MacMillen & Christopher 1975, Hewit 1981). Subsequent studies used EWL and metabolic water production (MWP) as physiological indicators to evaluate the efficiency of water regulation in rodents. MacMillen & Hinds (1983) proposed the index Ta @ MWP = EWL for a particular ambient temperature (Ta), requirement that is fulfilled when MWP/EWL = 1. Theoretically, some Ta exists at which a rodent can survive exclusively on a dry diet and be independent of exogenous water (MacMillen & Hinds 1983). By analyzing the amount of common variation between two variables (r^2), here we evaluate MacMillen and Hinds' model and introduce new indices to assess water regulation efficiency. We search for the energetic cost (MR) necessary to maintain water balance (WB), which is expressed by MR-WB, condition that is met when MWP/EWL = 1. To test our model, we measured EWL and estimated MWP (at different Ta's) at intra- and inter-specific levels among rodents differing in food habits and inhabiting different localities of northern and north-central Chile (Regions II and IV). We also used literature information on EWL and Ta @ MWP = EWL of

rodents from xeric and mesic habitats (MacMillen & Hinds 1983, Hinds & MacMillen 1985). To eliminate potential methodological distortions, we restricted our analysis to original data and published information in which all variables were studied with similar methods.

MATERIALS AND METHODS

Animals and Maintenance

Species studied were the rodents: *Octodon degus* (Molina 1782), *O. lunatus* (Osgood 1943) (Octodontidae), *Chinchilla lanigera* (Molina 1782) (Chinchillidae), *Abrothrix olivaceus* (Waterhouse 1837), *A. longipilis* (Waterhouse 1837), *A. andinus,*(Philippi 1858), *Phyllotis darwini* (Waterhouse 1837),, *P. rupestris* (Waterhouse 1837), *P. magister* (Thomas 1912), and *Oligoryzomys longicaudatus* (Bennett 1832) (Muridae). Individuals were captured with Sherman and National traps, during winter and summer seasons of consecutive years (1994 - 1996) in different localities of northern (II Region) and north-central Chile (IV Region); see Table 1. After capture, individuals were trans-

ported to the laboratory and maintained in individual cages with water and food ad libitum. For comparative purposes and following international standard, we used barley seeds as food source (9.7% protein, 75.4% carbohydrate, and 9.7% lipid, see Schmidt-Nielsen 1979). In the animal room, rodents were maintained during one or two weeks under a photoperiod L:D = 12:12, Ta = $21.0 \pm 3°C$ and a relative humidity of 60%.

Evaporative Water Loss, Metabolic Water Production and Water Regulation Efficiency

Evaporative water loss was measured at different ambient temperatures (Ta) in an open-flow system (Cortés et al. 1990). Air flow passed through the system at a constant rate of 3 L/min. Moisture in the air was removed by columns of silica gel and Drierite desiccants. To avoid temperature changes dried air was admitted through copper coils submerged in a thermoregulated bath. After passage through a flowmeter (La Motte), air was introduced into a glass chamber containing the animal. This chamber was equipped with a 25 mm mesh wire floor placed above 2.5 inch of mineral oil to prevent evaporation from urine and feces.

TABLE 1

Number of individuals (n), body mass (mean ± SD) and collection sites (habitats in Table 2)

Número de individuos (n), masa corporal (promedio ± DE) y sitios de captura (habitats en Tabla 2)

Family Species	N	Body mass (g)	Collection sites
Chinchillidae			
Chinchilla lanigera	6	365.0 ± 37.9	RN Las Chinchillas 30°38'S, 71°40'W
Octodontidae			
Octodon degus	5	136.4 ± 28.4	PN Fray Jorge (FJ) 31°30'S, 71°06'W
Octodon lunatus	3	165.4 ± 24.5	RN Las Chinchillas
Muridae			
Abrothrix olivaceus	5	36.6 ± 6.5	PN Fray Jorge
Abrothrix olivaceus	3	21.1 ± 0.6	Ojo Opache (OO) 22°29'S, 69°00'W
Abrothrix andinus	5	26.6 ± 5.3	Talabre (T) 23°22'S, 67°49'W
Abrothrix longipilis	5	52.6 ± 25.3	PN Fray Jorge
Phyllotis darwini	5	78.0 ± 21.9	PN Fray Jorge
Phyllotis rupestris	5	63.6 ± 12.0	Quebrada Jerez 23°21'S, 67°49'W
Phyllotis rupestris	5	64.6 ± 9.5	Talabre
Phyllotis magister	3	53.5 ± 9.3	Ojo Opache
Oligoryzomys longicaudatus	5	27.5 ± 4.3	PN Fray Jorge

PN = Parque Nacional (National park); RN = Reserva Nacional (National reserve)

To monitor the ambient temperature, a stainless steel thermistor probe was inserted into the chamber. Evaporative water loss in the airstream leaving the animal chamber was recovered in a preweighed ($\pm$ 0.1 mg) glass U-tube containing Drierite. All EWL measurements were carried out after reaching thermal equilibrium (45 min). Measurements were conducted every 5 min during 2-3 h. Metabolic water production was estimated from oxygen consumption values, assuming that in average, 1 ml of O_2 yields 0.62 mg of metabolic water (Schmidt-Nielsen 1979). Oxygen consumption was calculated from the equations (metabolic rates versus Ta) reported by Rosenmann (1977) and Bozinovic & Rosenmann (1988a). Finally, water regulation efficiency was estimated according to Hinds & MacMillen (1985) and also by the proposed efficiency index MR-WB.

Statistical analyses

Results are reported as mean $\pm$ 1 standard deviation for each species. Regression equations were calculated by the least-square method. Slopes of the regression equations were compared with the equality test for two slopes. Statistical analyses were performed using STATISTICA® (1997) statistical package for Windows, 95 program.

RESULTS AND DISCUSSION

Evaporative water loss

Evaporative water loss has often been ignored in the comparative analysis of South American desert rodents. This variable has fundamental implications on thermoregulatory mechanisms, but it is also an important factor in the maintenance of water balance (Blackwell & Pivorun 1979). Our measured values of EWL obtained at Ta below the lower critical temperature were relatively constant at the intraspecific level. However, significant differences were observed between some species (Table 2). The two larger species studied, *Chinchilla lanigera* and *O. degus* had the lowest rates of EWL (0.58 and 0.89 mg $H_2O/$g h, respectively).

The rate of EWL in *C. lanigera* was equivalent to 2/3 of that in *O. degus*, 1/2 of that in *O. lunatus*, 1/3 of the rates in both *A. olivaceus* (IV Region) and *P. darwini*, 1/4 of those shown by *A. olivaceus* (II Region), *A. andinus, A. longipilis, P. rupestris* and *P. magister*, and only 1/5 of that in *O. longicaudatus* (Table 2).

The relationship between EWL ($mgH_2O/$g h) and body mass (M in g) for all species of rodents examined (current data and literature sources) inhabiting xeric habitats (see Table 2) is shown in Fig. 1, and is represented by the following allometric equation:
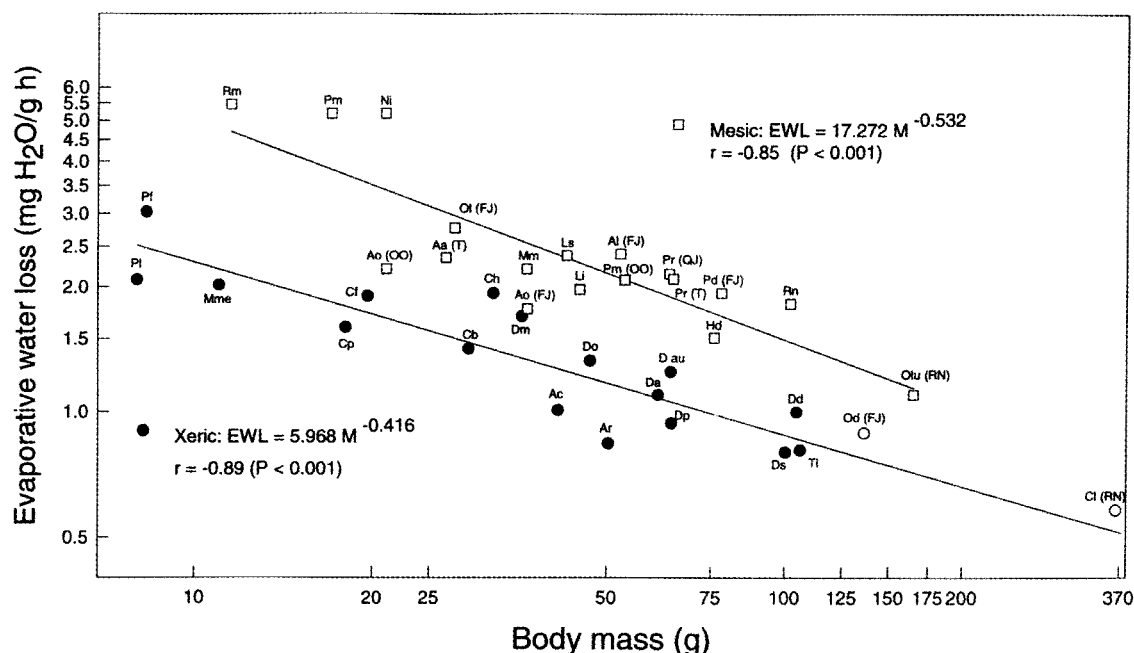

Fig. 1. Double logarithmic relationships between evaporative water loss and body mass in rodents from xeric and mesic habitats (see Table 2 for species identification).

Relación doble logarítmica entre pérdida de agua evaporativa y masa corporal en roedores de hábitats xéricos y mésicos (véase Tabla 2 para la identificación de las especies).

$$EWL = 5.968 \ M^{-0.416} \quad (1)$$
$$r = -0.89, \ P < 0.001$$

relationship between EWL and M for mesic-dwelling rodents (Table 2) was:

which is similar to that reported by Hinds & MacMillen (1985) for seed-eating rodents. The

$$EWL = 17.258 \ M^{-0.532} \ (2)$$
$$r = -0.85, \ P < 0.001$$

TABLE 2

Body mass, evaporative water loss (EWL), range of ambient temperature (Ta) at which EWL was measured, and habitat used by rodent species

Masa corporal, pérdida de agua evaporativa (EWL), rango de temperatura ambiente (Ta) al cual se midió EWL, y hábitat usado por las especies de roedores

Family Species	Body mass (g)	EWL (mg/g h)	Ta (°C)	Habitat	Reference
Chinchillidae					
C. lanigera (Cl-RN)	365.0	0.58	5-20	Xeric	(1)
Octodontidae					
O. degus (Od-FJ)	136.4	0.89	10-20	Xeric	(1)
O. lunatus (Olu-RN)	165.2	1.10	5-20	Mesic	(1)
Muridae					
A. olivaceus (Ao-FJ)	36.6	1.77	10-25	Mesic	(1)
A. olivaceus (Ao-OO)	21.1	2.21	5-25	Mesic	(1)
A. andinus (Aa-T)	26.6	2.35	5-25	Mesic	(1)
A. longipilis (Al-FJ)	52.6	2.40	10-25	Mesic	(1)
P. darwini (Pd-FJ)	78.0	1.93	10-25	Mesic	(1)
P. magister (Pm-OO)	53.5	2.08	5-25	Mesic	(1)
P. rupestris (Pr-QJ)	63.6	2.15	10-25	Mesic	(1)
P. rupestris (Pr-T)	64.6	2.09	10-25	Mesic	(1)
O. longicaudatus (Ol-FJ)	27.5	2.77	10-25	Mesic	(1)
Rattus norvegicus (Rn)	102.0	1.82	—	Mesic	(8)
Mus musculus (Mm)	36.5	2.21	—	Mesic	(5)
Peromyscus maniculatus (Pm)	17.0	5.20	29	Mesic	(3)
Reinthrodontomys megalotis (Rm)	11.5	5.47	25	Mesic	(9)
Acomys cahirinus (Ac)	41.3	1.01	30	Xeric	(5)
A. russatus (Ar)	50.3	0.84	30	Xeric	(5)
Tatera leucogaster (Tl)	106.2	0.81	15-32	Xeric	(4)
Desmodillus auricularis (Da)	64.0	1.25	23	Xeric	(7)
Zapodidae Napaeozapus insignis (Ni)	21.0	5.20	29	Mesic	(3)
Heteromiydae					
Dipodomys merriami (Dm)	35.8	1.70	5-25	Xeric	(2)
D. deserti (Dd)	104.7	1.00	5-25	Xeric	(2)
D. ordii (Do)	46.8	1.33	5-25	Xeric	(2)
D. panamintinus (Dp)	64.2	0.94	5-25	Xeric	(2)
D. spectabilis (Ds)	100.1	0.80	5-25	Xeric	(2)
D. agilis (Da)	61.0	1.10	5-25	Xeric	(2)
Perognathus longimembris (Pl)	8.0	2.08	5-25	Xeric	(2)
P. flavus (Pf)	8.3	3.03	5-25	Xeric	(2)
Chaetopidus baileyi (Cb)	29.1	1.42	5-25	Xeric	(2)
C. fallax (Cf)	19.6	1.90	5-25	Xeric	(2)
C. hispidus (Ch)	32.0	1.93	5-25	Xeric	(2)
C. penicillatus (Cp)	18.0	1.60	29	Xeric	(3)
Microdipodops megacephalus (Mme)	11.0	2.02	5-25	Xeric	(2)
Heteromys desmarestianus (Hd)	75.8	1.51	10-25	Mesic	(2)
Liomys irroratus (Li)	44.9	1.97	5-30	Mesic	(2)
L. salvani (Ls)	42.7	2.38	5-30	Mesic	(2)

References: (1) This study; (2) Hinds & MacMillen (1985); (3) Brower & Cade (1966); (4) Webb & Skinner (1996); (5) Shkolnik & Borut (1969); (6) Buffenstein & Jarvis (1985); (7) Christian (1978); (8) Schmidt-Nielsen & Schmidt-Nielsen (1950); (9) Coulombe (1970).

Metabolic Water Production

Estimated values of MWP are shown in Table 3. Same as in the EWL comparison, *C. lanigera* showed the lowest MWP value (0.54 mg H_2O/g h), followed by the Octodontids *O. degus* and *O. lunatus* (0.98 and 0.97 mg H_2O /g h, respectively). Marked differences were found when comparing these three low values with the much higher MWP rates of the murids. Nevertheless, the observed variations in MWP may be explained by differences in body size (Fig. 2). Equation 3 expresses this relationship:

$$MWP = 14.256\ M^{-0.539}\ (3)$$
$$r = -0.98,\ P < 0.001$$

On the basis of equation 1 it may be expected that differences in EWL among species should partly be explained by the effects of body size. Nevertheless, comparing measured values of EWL of the nine species against those expected from equation 1 ($\pm$ Syx 0.272), only *C. lanigera* and *O. degus* present values that fall within the range predicted by this equation. In contrast, the rest of the examined species (*O. lunatus, P. darwini, A. olivaceus, A. longipilis, O. longicaudatus, P.*

TABLE 3

Body mass and metabolic water production (MWP) calculated at 15°C for rodents inhabiting Chilean mesic and xeric habitats

Masa corporal y producción de agua metabólica (MWP) calculada a 15 °C Para roedores de hábitats mésicos y xéricos en Chile

Species	Body mass (g)	MWP (mg/g h)
Chinchilla lanigera (Cl-RN)	344.1	0.54
Octodon degus (Od-FJ)	129.8	0.98
Octodon lunatus (Olu-FJ)	164.5	0.97
Abrothrix olivaceus (Ao-FJ)	36.7	2.21
Abrothrix olivaceus (Ao-OO)	21.8	2.21
Abrothrix andinus (Aa-T)	28.3	2.23
Abrothrix longipilis (Al-FJ)	51.4	1.79
Phyllotis darwini (Pd-FJ)	78.1	1.83
Phyllotis magister (Pm-OO)	54.9	1.70
Phyllotis rupestris (Pr-QJ)	64.1	1.70
Phyllotis rupestris (Pr-T)	57.5	1.70
Oligoryzomys longicaudatus (Ol-FJ)	26.8	2.45

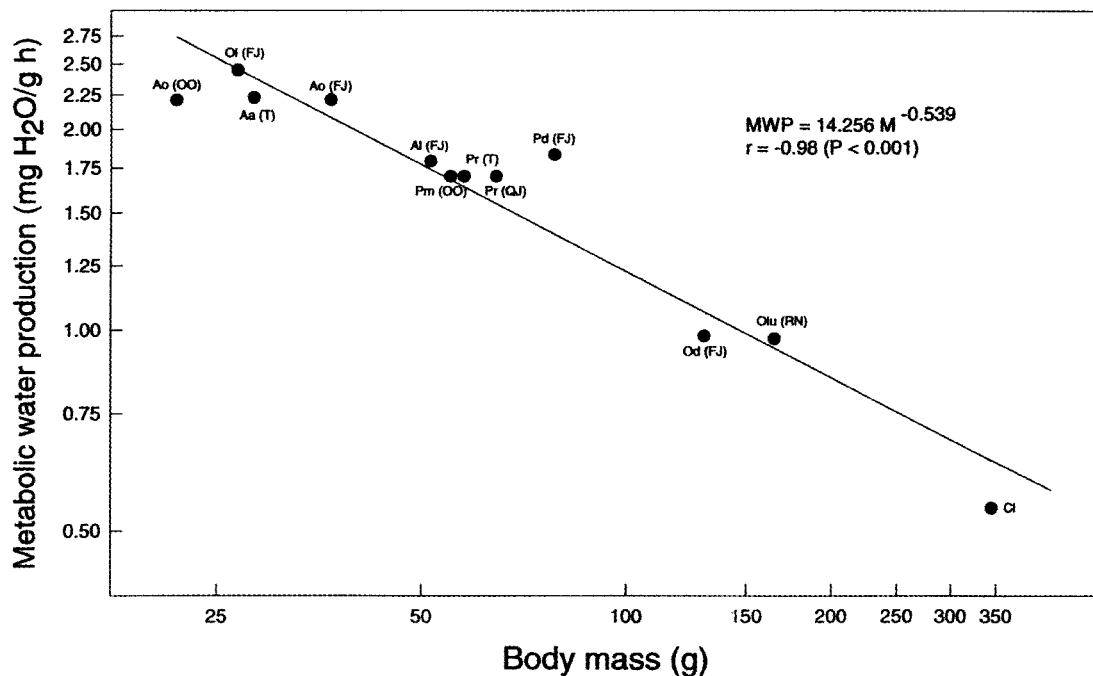*Fig. 2.* Double logarithmic relationship between metabolic water production estimated at Ta = 15°C and body mass of rodents inhabiting Chilean habitats (see Table 2 for species identification).

Relación doble logarítmica entre producción de agua metabólica estimada a Ta = 15 °C y masa corporal en roedores de diferentes hábitats en Chile (véase Tabla 2 para la identificación de las especies).

rupestris, P. magister, A. olivaceus and *A. andinus*) had higher EWL values. Consequently, *C. lanigera* and *O. degus* appear as the only two species (thus far reported) with EWL rates similar to those of "typical" desert rodents.

Phyllotis rupestris, P. magister and *A. andinus*, had relatively higher rates of EWL as compared to rodents from xeric habitats. This physiological trait was unexpected, considering that they live at 2,300 to 3,360 m above sea level, in arid high-Andean environments of the Atacama desert, where extreme climatic conditions prevail. In spite of the stressful environmental condition, these rodents maintain moderate water balance, judging from their summer urine concentrations ranging between 2,500 to 3,000 mOsm/kg (A. Cortés unpublished data). On the other hand, we have observed that *P. rupestris* and *P. magister* are chiefly nocturnal, while *A. andinus* is mostly crepuscular. Further, they select microhabitats where shrub vegetation is relatively abundant, along to water courses, and with rock piles. Consequently, the observed physiological constraint on water conservation by the pulmocutaneous route, appears to be compensated by behavioral traits, as happens among desert rodents of North America such as *Neotoma lepida* (MacMillen 1972).

Slopes of equations 1 and 2 are significantly different (t = 4.86 , P < 0.001). Thus, the magnitude of EWL of the species studied (Table 2), is not only affected by body size, but it is also related to the type of microhabitat used. Consequently, EWL appears as an important variable to evaluate the degree of specialization of the pulmocutaneous route in species that occupy different habitats (xeric versus mesic). Equation 3 indicates that the magnitude of the MWP of the species studied depends only on the body size, suggesting that the ratio MWP/ EWL may be a variable that reflects the efficiency in water regulation of rodents as a function of the habitat in which they live.

The relationship between MWP/EWL and Ta is described by exponential equations with negative slopes (Fig. 3), similar to those reported by MacMillen & Hinds (1983). These relationships are highly significant (r = 0.97; P << 0.01). Regression equations and Ta @ MWP = EWL for rodents in Chile and for North American heteromyids as reported in the literature (MacMillen & Hinds 1983) are listed in Table 4. Regarding the values of the index Ta @ MWP = EWL, *A. olivaceus* and *O. degus* are the Chilean rodents that had the highest values (18.6 and 16.6°C, respectively). Based on the model of MacMillen & Hinds (1983), *A. olivaceus* could be said to have a greater efficiency in water economy than that of *O. degus*. Nevertheless, studies of
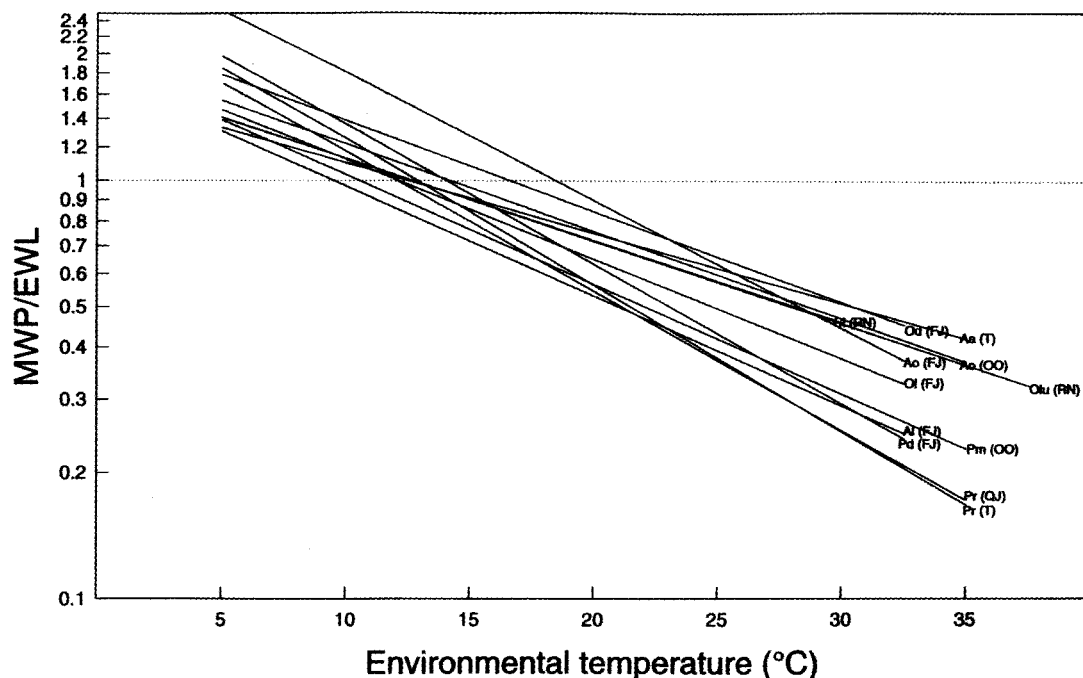

Fig. 3. Relationship between the ratio of metabolic water production to evaporative water loss (MWP/ EWL) and environmental temperature in rodents from Chilean habitats.

Relación entre la razón producción de agua metabólica y evaporación de agua (MWP/EWL) y temperatura ambiental en roedores de hábitats chilenos.

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TABLE 4

Body mass, Ta @ MWP=EWL, regression equations of MWP/EWL versus Ta, and the maintenance energetic of the water balance (MR-WB) for Chilean rodents and North-American heteromyids

Masa corporal, Ta @ MWP=EWL, ecuaciones de regresión de MWP/EWL versus Ta, y costo energético de mantención del balance hídrico (MR-WB) para roedores Chilenos y heterómidos Norteamericanos

Habitat and Species	Body mass (g)	Ta @ MWP=EWL (°C)	Equation	MR-WB (cal/g h)
Mesic				
O. lunatus (Olu-FJ)	165.2	12.6	MWP/EWL=1.774(0.956)$_{Ta}$	8.3
A.olivaceus (Ao-FJ)	36.6	18.6	MWP/EWL=3.469(0.934)$_{Ta}$	14.5
A.olivaceus (Ao-OO)	21.6	14.1	MWP/EWL=1.957(0.953)$_{Ta}$	17.8
A. andinus (Aa-T)	26.6	12.5	MWP/EWL=1.619(0.962)$_{Ta}$	19.1
A. longipilis (Al-FJ)	52.6	9.5	MWP/EWL=1.769(0.941)$_{Ta}$	17.5
P. darwini (Pd-FJ)	78.0	14.0	MWP/EWL=2.923(0.926)$_{Ta}$	14.8
P. magister (Pr-OO)	53.5	10.5	MWP/EWL=1.880(0.942)$_{Ta}$	15.8
P. rupestris (Pr-QJ)	63.6	12.1	MWP/EWL=2.517(0.926)^{Ta}	14.9
P. rupestris (Pr-T)	64.6	12.8	MWP/EWL=2.812(0.923)$_{Ta}$	14.4
O. longicaudatus (Ol-FJ)	27.5	12.1	MWP/EWL=1.938(0.947)$_{Ta}$	21.2
H. desmarestianus (Hd)	75.8	18.0	MWP/EWL=2.691(0.947)$_{Ta}$	11.9
Liomys irroratus (Li)	44.9	16.1	MWP/EWL=1.659(0.969)$_{Ta}$	15.2
L. salvani (Ls)	42.7	14.4	MWP/EWL=2.021(0.952)$_{Ta}$	19.0
Xeric				
C. lanigera (Cl-RN)	365.0	12.7	MWP/EWL=1.764(0.956)$_{Ta}$	4.6
O. degus (Od-FJ)	136.4	16.6	MWP/EWL=2.278(0.951)$_{Ta}$	7.1
Dipodomys deserti (Dd)	104.7	16.2	MWP/EWL=2.150(0.954)$_{Ta}$	7.1
D. merriami (Dm)	35.8	17.0	MWP/EWL=2.451(0.946)$_{Ta}$	12.3
D. ordii (Do)	46.8	18.7	MWP/EWL=2.143(0.960)$_{Ta}$	9.5
D. panamintinus (Dp)	64.2	20.7	MWP/EWL=2.504(0.957)$_{Ta}$	6.9
M. megacephalus (Mm)	11.0	26.3	MWP/EWL=3.351(0.955)$_{Ta}$	13.2
Chaetopidus baileyi (Cb)	29.2	20.8	MWP/EWL=2.243(0.962)$_{Ta}$	9.0
C. flavus (Cf)	8.4	18.9	MWP/EWL=2.493(0.954)$_{Ta}$	20.9
C. hispidus (Ch)	32.1	16.0	MWP/EWL=2.084(0.956)$_{Ta}$	13.0
Perognathus fallax (Pf)	19.6	17.3	MWP/EWL=2.097(0.957)$_{Ta}$	13.1
P. longimembris (Pl)	8.0	25.8	MWP/EWL=4.521(0.942)$_{Ta}$	15.0

Note: MR-WB values for heteromyid rodents were estimated from the literature (MacMillen & Hinds 1983, Hinds & MacMillen 1985).

tolerance to water deprivation, maximum urine concentration and EWL show the opposite (Cortés et al. 1990). The relationships between T@ MWP = EWL and M for the species listed in Table 4 is described by the following allometric equation (Fig. 4):

$$Ta @ MWP = EWL = 26.799 \ M^{-0.142} \quad (4)$$
$$r = -0.49; P < 0.02$$

Non-explained variance $(1 - r^2)$ of the model (4) was 76%, suggesting that the index Ta @ MWP = EWL had low ability to detect differences in water regulation efficiency of species with regard to the habitat type used.

Assesment of the "new model"

Table 4 shows the average values of water regulation efficiency expressed by the index MR-WB for the rodents studied and for heteromyids of North America. The relationship between MR-WB and M, values taking into account the type of habitat (Table 2), yields two allometric equations (see Fig. 5). The equation for rodents in xeric habitats is:

$$MR\text{-}WB = 34.627 \ M^{-0.339} \quad (5)$$
$$r = -0.934; P < 0.001$$

and for rodents from mesic habitats is:

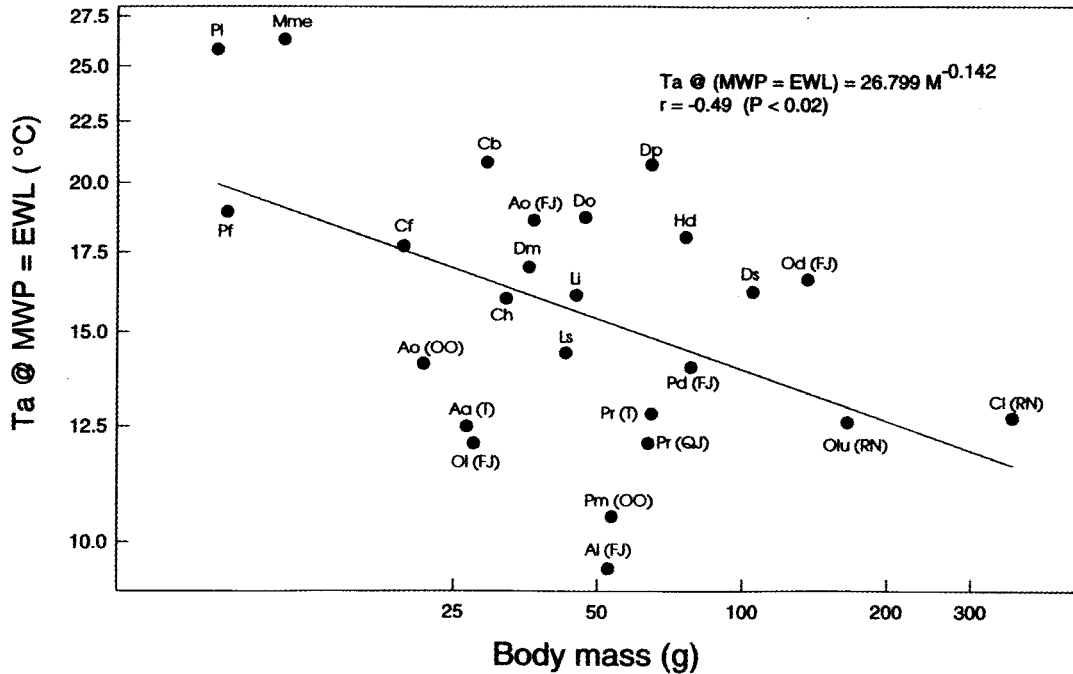$$MR\text{-}WB = 68.132 \ M^{-0.381} \quad (6)$$
$$r = -0.860; P < 0.001$$

Fig. 4. Double logarithmic relationship between the index Ta @ MWP/EWL and body mass of Chilean and North-American heteromyid rodents.

Relación doble logarítmica entre el índice Ta @ MWP/EWL y masa corporal de roedores Chilenos y heterómidos Norteamericanos.
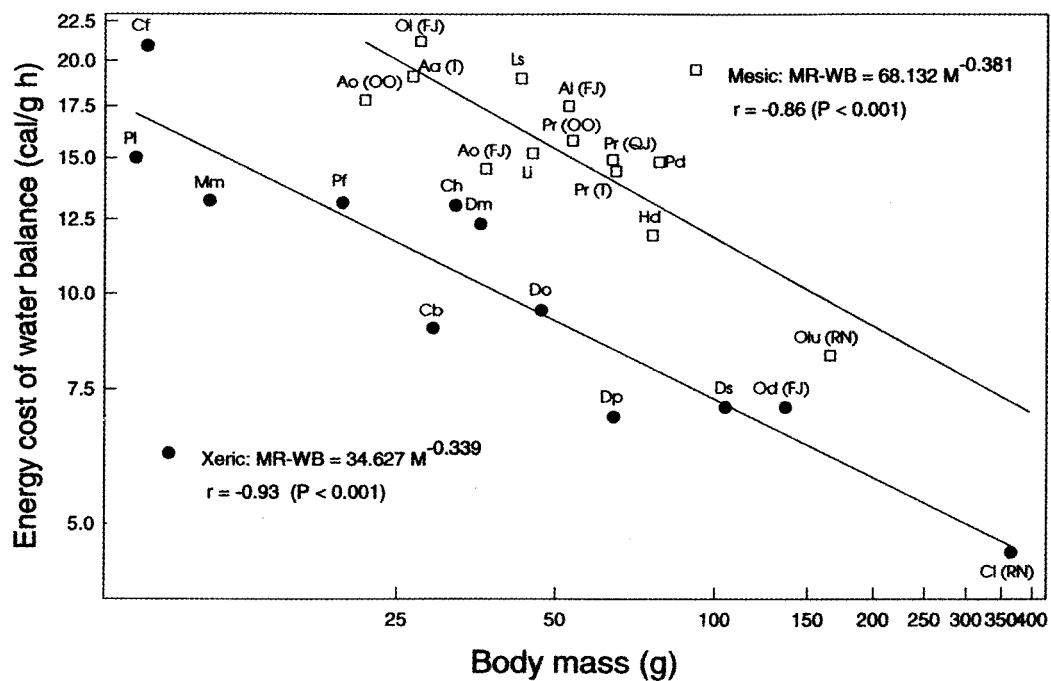

Fig. 5. Double logarithmic relationships between the energy cost of water balance (MR-WB) and body mass of rodents from xeric and mesic habitats.

Relación doble logarítmica entre el costo energético de balance hídrico (MR-WB) y masa corporal en roedores de hábitats xéricos y mésicos.

Equations 5 and 6 have similar slopes, but different intercepts, indicating that when body size effects are considered, variations in MR-WB are basically explained by the type of habitat that the species are using (Fig. 5). Out of all species of north- central Chile that we studied, only *C. lanigera* and *O. degus* resembled the pattern of MR-WB observed among heteromyid rodents of xeric habitats of North America (MacMillen & Hinds 1983, Hinds & MacMillen 1985). The remainder of the species studied are similar to heteromyids inhabiting mesic habitats, such as *Liomys salvani, L. irroratus* or *Heteromys desmarestianus* (Hinds & MacMillen 1983, MacMillen & Hinds 1985). As expected, energy cost to maintain water balance in rodents inhabiting xeric habitats was lower than that of rodents from mesic habitats. The lower energy cost may be adaptive for energy and water conservation because it permits a reduced water turnover in a variable, unpredictable, or unproductive environment.

The rodents we studied have different food habits: *O. degus, O. lunatus* and *C. lanigera* are herbivorous (Meserve 1981, A. Cortés, unpublished data), *A. olivaceus, A. andinus* and *A. longipilis* are insectivorous/omnivorous (Meserve 1978, Meserve 1981, Contreras & Rosi 1981), *P. darwini* and *O. longicaudatus* are frugivorous/granivorous (Meserve 1978, 1981) and *P. magister* is herbivorous/insectivorous (Pizzimenti & DeSalle 1980). In contrast, the 13 species of North American heteromyids in the present study are highly granivorous (MacMillen & Hinds 1983, Hinds & MacMillen 1985). Thus, 1) different food habits of Chilean and North American rodents do not seems to be important in the validation of the water regulation efficiency model, — i.e. the index of MR-WB, or 2) because we maintained rodents with the same diet, they responded in a similar way; however, this last aspect seems unlikely since rodents were maintained in the lab for a short time. In contrast, one of the assumptions in the model of MacMillen & Hinds (1983) is that granivory is associated with the aridity and seasonality of precipitations in arid environments, a major factor in the evolutionary history of the family Heteromyidae. Consequently, the water regulation efficiency (Ta @ MWP = EWL) of heteromyids is negatively related to body mass, apparently because these rodents depend on seeds, which sustain both their energetic and hydric requirements. However, we found a low r-value when the MacMillen & Hinds relationship, log Ta @ MWP = EWL, was plotted against log M. An additional inconvenient of this approach is that,

at present, it does not enable for a clear discrimination between different patterns of habitat use.

Finally, we think that our new model has some advantages, because it is able to discriminate patterns of water regulation efficiency as a function of the habitat (xeric versus mesic), independent of dietary habits and allows to evaluate variations in the energetic cost of water balance.

LITERATURE CITED

ABBOTT K (1971) Water economy of the canyon mouse *Peromyscus crinitus stephensis.* Comparative Biochemistry and Physiology 38: 37-52.

BLACKWELL TL & E PIVORUN (1979) Influence of temperature on the water balance of three parapatric species of *Peromyscus.* Journal of Mammalogy 60: 70-75.

BOZINOVIC F & M ROSENMANN (1988a) Comparative energetics of South American cricetid rodents. Comparative Biochemistry and Physiology 91: 195-202.

BOZINOVIC F & M ROSENMANN (1988b) Daily torpor in *Calomys musculinus,* a South American rodent. Journal of Mammalogy 69: 150-152.

BOZINOVIC F & LC CONTRERAS (1990) Basal rate of metabolism and temperature regulation of two desert herbivorous octodontid rodents: *Octomys mimax* and *Tympanoctomys barrerae.* Oecologia 84: 567-570.

BOZINOVIC F & PA MARQUET (1991) Energetics and torpor in the Atacama desert-dwelling rodent *Phyllotis darwini rupestris.* Journal of Mammalogy 72: 734-738.

BOZINOVIC F, M ROSENMANN, FF NOVOA & RG MEDEL (1995) Mediterranean-type of climatic adaptation in the physiological ecology of rodent species. In: Kalin-Arroyo MT, PH Zedler & MD Fox (eds) Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia: 347-362. Springer-Verlag, New York.

BROWER JE & TJ CADE (1966) Ecology and physiology of *Napaeozapus insignis* (Miller) and other woodland mice. Ecology 47: 46-53.

BUFFENSTEIN R & JUM JARVIS (1985) The effect of water stress on growth and renal perfomance of juvenile Namib rodents. Journal of Arid Environments 9: 232-236.

CAVIEDES-VIDAL E, E CAVIEDES-CODELJA, V ROIG & R DOÑA (1990) Facultative torpor in the South American rodent *Calomys venustus* (Rodentia: Cricetidae). Journal of Mammalogy 71: 72-74.

CHRISTIAN DP (1978) Effects of humidity and body size on evaporative water loss in three desert rodents. Comparative Biochemistry and Physiology 60: 425-430.

CHRISTIAN DP (1979) Physiological correlates of demographic pattern in three sympatric Namib desert rodents. Physiological Zoology 52: 329-339.

CONTRERAS JR & MI ROSI (1981) Notas sobre Akodontinos argentinos (Rodentia Cricetidae). *Akodon andinus andinus* (Philippi, 1868) en la Provincia de Mendoza. Historia Natural 1: 233-236.

CORTES A, C ZULETA & M ROSENMANN (1988) Comparative water economy of sympatric rodents in Chilean semi-arid habitat. Comparative Biochemistry and Physiology 91A: 711-714.

CORTES A, M ROSENMANN & C BAEZ (1990) Función del riñón y del pasaje nasal en la conservación del agua corporal en roedores simpátridos de Chile central. Revista Chilena de Historia Natural 63: 279-291.

COULOMBE HN (1970) The role of succulent halophytes in the water balance of salt marsh rodents. Oecologia 4: 223-247.

DANTZLER W (1970) Kidney function in desert vertebrates. Memoirs of the Society of Endocrinology 18:157-190.

DANTZLER W(1982) Renal adaptation of desert vertebrates. BioScience 32:108-113.

DEGEN AA, M KAM, A HAZAN & KA NAGY (1986) Energy expenditure and water flux in three sympatric desert rodents. Journal of Animal Ecology 55: 421-429.

HEWIT S (1981) Plasticity of renal function in the Australian desert rodent *Notomys alexis*. Comparative Biochemistry and Physiology 49A: 297-304.

HINDS DE & RE MacMILLEN (1985) Scaling of energy metabolism and evaporative water loss in heteromyid rodents. Physiological Zoology 58: 282-298.

MacMILLEN RE (1972) Water economy of nocturnal desert rodents. Symposium of the Zoological Society of London 31: 147-174.

MacMILLEN RE & EA CHRISTOPHER (1975) The water relation of two population of noncaptive desert rodents. In: NF Hadley (ed) Environmental physiology of desert organisms: 117-137. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

MacMILLEN RE & AK LEE (1967) Australian desert mice: independence of exogenous water. Science 158: 383-385.

MacMILLEN RE & AK LEE (1969) Water metabolism of Australian hopping mice. Comparative Biochemistry and Physiology 28A: 493-514.

MacMILLEN RE & DS HINDS (1983) Water regulatory efficiency in heteromyid rodents: a model and its application. Ecology 64:152-164.

MARES MA (1975) South American mammal zoogeography: evidence from convergent evolution in desert rodents. Proceedings of the National Academy of Sciences 72:1702-1706.

MAXON K & MS MORTON (1974) Water and salt regulation in the antelope ground squirrel *Ammonspermophilus leucurus*. Comparative Biochemistry and Physiology 478A: 117-128.

McNAB B K (1982). The physiological ecology of South American mammals. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 187-207. Special Publication 6. Pymatuning Laboratory of Ecology. Pittsburgh, Pennsylvania.

MESERVE PL (1978) Water dependence in some Chilean arid zone rodents. Journal of Mammalogy 59: 217-219.

MESERVE PL (1981). Trophic relationship among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy 62: 304-314.

PIZZIMNTI JJ & R DESALLE (1980) Dietary and morphometric variation in some Peruvian rodent communities: The effect of feeding strategy on evolution. Biological Journal of the Linnean Society 13: 263-285.

ROSENMANN M. (1977) Regulación térmica en *Octodon degus*. Medio Ambiente 3: 127-131.

SCHMIDT-NIELSEN B & R ODELL (1961) Structure and concentrating mechanism in the mammalian kidney. American Journal of Physiology 200:1119-1124.

SCHMIDT-NIELSEN B & K SCHMIDT-NIELSEN (1950) Pulmonary water in desert rodents. American Journal of Physiology, 162: 31-36.

SCHMIDT-NIELSEN K (1979) Desert animals: Physiological problems of heat and water. Dover Publication, Inc. 277 pp.

SHKOLNIK A & A BORUT (1969) Temperature and water relations in two species of Spiny mice (*Acomys*). Journal of Mammalogy 50: 245-255.

SPERBER I (1944). Studies of the mammalian kidney. Zoologiska Bidrag fran Uppsala 22: 249-432.

STATISTICA (1997) Statistica release 5 (Quick Reference) for the Windows 95 operating system. Third Edition. StatSoft, Inc., Tulsa, Oklahoma. 238 pp.

VIMTRUP B & B SCHMIDT-NIELSEN (1952) The histology of kidney of kangaroo rats. Anatomical Record 114: 160-188.

WEBB PI & J D SKINNER (1996) Physiological adaptation to aridity in the bushveld gerbil, *Tatera leucogaster*. Journal of Zoology 238: 693-701.

WITHERS PC, N LOUW & J HENSCHEL (1982) Energetics and water relation of Namib desert rodents. South African Journal of Zoology 15: 131-137.