

## COMPARATIVE WATER ECONOMY OF SYMPATRIC RODENTS IN A CHILEAN SEMI-ARID HABITAT

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**Abstract**—1. Water requirements, water balance components and dependence on exogenous water were estimated in four species of sympatric rodents inhabiting a Chilean semi-arid region.

2. A significant increase in free water drinking was observed in all rodents when the diet composition was changed from 14 to 20% protein.

3. Under water balance conditions the cricetid species (*Phyllotis darwini*, *Oryzomys longicaudatus* and *Akodon olivaceus*) showed 1.66 to 1.88 times the weight-specific daily water gain of *Octodon degus*.

4. In the three cricetid rodents, evaporation was the largest water loss component (2/3 to 3/4 of total loss), while in *O. degus* evaporative water loss amounted to only 38% of the total.

5. Survival time during water deprivation ranged from 13.4 days in *O. degus* to only 4 days in *O. longicaudatus*.

6. All water variables combined indicate that water dependence of *O. longicaudatus* > *P. darwini* > *A. olivaceus* > *O. degus*.

### INTRODUCTION

In contrast to many field and laboratory studies evaluating capabilities and mechanisms for water conservation of small mammals inhabiting arid and semi-arid regions in Africa, Australia and North America, far less is known about species that live in similarly arid South American environments (McNab, 1982). Some observations have been made on a few rodents from Argentina (Mares, 1977a,b,c,d), from Peru (Koford, 1968), Brazil (Streilein, 1982) and Chile (Meserve, 1978); but due to the great diversification of South American rodents, further studies are needed to get a better insight into their water economy and to uncover possible shared specific features in their physiological responses to the water shortage that characterizes their arid habitats. With this purpose we have chosen to examine four of the most common rodent species inhabiting the Mediterranean semi-arid region of central-northern Chile, to evaluate the influence of different protein diets on their water requirements, water conservation capabilities, normal water balance and their specific responses to water deprivation.

### MATERIALS AND METHODS

Our studied species: *Phyllotis darwini*, *Oryzomys longicaudatus*, *Akodon (Abrothrix) olivaceus* (Cricetidae) and *Octodon degus* (Octodontidae) were captured live during the spring and summer seasons in Quebrada Monardez, 10 km south-east of La Serena (29°55'S; 71°22'W). This locality is characterized by a typical xerophytic vegetation, scarce and irregular annual precipitation (less than 130 mm), and a mean annual temperature of 14.8°C (Di Castri and Hajek, 1976). All rodents were transported to the laboratory in La Serena and maintained individually caged at 21 ± 3°C, with

natural photoperiod and with food (commercial pellets) and water *ad libitum*. Body weight (±0.1 g) was recorded daily and measurements of water intake, water balance and water deprivation were initiated when body weight showed insignificant changes (usually 1 to 2 weeks after capture). Measurements of *ad libitum* free water intake were conducted following the procedures of Abbott (1971) and Mares (1977a). To test the effects of diet composition on rates of water ingestion, pellets of different protein concentration (14 and 20%), but of equal water content (9 ± 1%) were given to paired groups of each of the examined species. In water balance evaluations the low protein diet was given, using metabolic chambers and separating urine from feces according to Hulbert and Dawson (1974). Water gain was estimated from the daily volume of ingested water (±0.2 ml) plus the calculated metabolic water, based on the oxidation water equivalents for various foodstuffs (Schmidt-Nielsen, 1979). Water loss was evaluated from the daily water loss in feces and urine (dried to constant weight at 105°C), plus body surface and respiratory evaporation, calculated from the difference between water gained and lost during steady state conditions. Direct measurements of evaporative water loss (EWL) conducted in some animals, following the method described by Heinsworth (1968), gave very similar values to the calculated ones, except *P. darwini* that showed almost no activity during the experiments. In this species EWL was lower than that calculated by subtraction.

The high protein diet was used in water deprivation experiments. Changes in weight were recorded daily and the slopes of the regression equations describing loss of weight vs days of water deprivation were submitted to a covariance analysis and to a *t*-test for paired slopes (Dagnelie, 1970). Unless otherwise stated all values are given as means ± SD.

### RESULTS

The *ad libitum* daily water intake measured in all rodents while maintained for several days with low and high protein diets is shown in Table 1. Significant differences ( $P < 0.01$ ) were found in the daily water ingested by the groups. An increase in water require-

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Table 1. Effects of diets with different protein content on daily free water drinking in four rodent species from central-northern Chile

Species	14% protein		20% protein	
	Body weight (g)	Free water drinking	Body weight (g)	Free water drinking
<i>O. degus</i>	128.0 ± 10.8 (7)	10.3 ± 2.1	127.5 ± 20.8 (5)	16.1 ± 3.2
<i>P. darwini</i>	47.6 ± 9.8 (5)	17.9 ± 2.1	44.8 ± 8.2 (6)	23.0 ± 1.8
<i>A. olivaceus</i>	24.0 ± 1.9 (6)	17.2 ± 2.6	24.1 ± 1.1 (6)	22.9 ± 1.0
<i>O. longicaudatus</i>	23.9 ± 3.8 (6)	19.7 ± 2.2	27.6 ± 3.5 (7)	26.7 ± 1.6

Volumes for free water drinking are given in ml H<sub>2</sub>O/100 g of body weight per day. Values represent means ± SD. Numbers in parentheses indicate number of animals used.

ments was common to all species fed with the high protein diet. The increment in water consumption ranged from 28.5% in *P. darwini* to 56.3% in *O. degus*. Intermediate values (33.1 and 39.1%) were found for *A. olivaceus* and *O. longicaudatus*, respectively. Under both diets *O. degus* required 30 to 48% less water per unit of body weight than the three cricetid species. Gain and loss components under water-balanced conditions and with low protein diet are shown in Table 2. In the four species total water gained per unit of body weight was chiefly represented by drinking water (89.2 ± 0.9%). Metabolic water accounted for 12% of the total water gained in *O. degus* and for 10.5 ± 0.7% in the cricetids. Total water gained basically followed the relations found for *ad libitum* water intake, thus the cricetid rodents showed 1.66–1.88 times the daily weight specific water gain of *O. degus*.

In the cricetid species EWL was the largest water loss component (2/3 to 3/4 of total loss), significantly different ( $P < 0.05$ ) from the evaporative loss of *O. degus* that amounted to only 38% of the total water loss. The opposite situation occurred when comparing interspecific renal water losses; *O. degus* showed the largest figure with about 50% of the total water loss, and the cricetids 16 ± 6.5%.

Fecal water loss was in general a minor water loss component. Nevertheless, *O. longicaudatus* lost through this route significantly more water ( $P < 0.05$ ) than *O. degus* and *P. darwini* (14% vs 5–8%). Results from water deprivation experiments in 5–7 animals per species are shown in Fig. 1. Least squares regression equations comparing loss of weight per day show that under these conditions none of the rodents was able to maintain body weight. Limits for irreversible body weight losses were observed in few animals and are shown with dotted lines in Fig. 1. These values were not included in the regression analysis. Statistical null hypothesis tests for similarity of slopes indicated that each species shows characteristic weight loss kinetics significantly

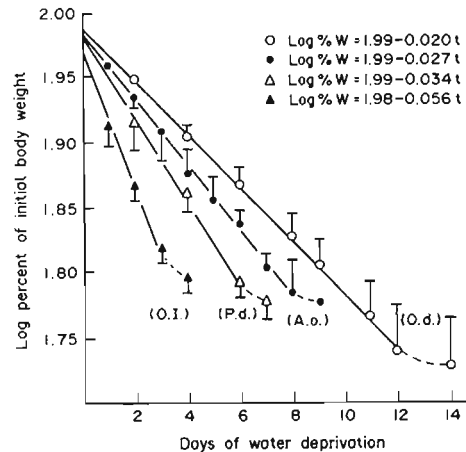


Fig. 1. Time course effects of water deprivation on body weights of seven *Octodon degus* (*O.d.*), six *Akodon olivaceus* (*A.o.*), six *Phyllotis darwini* (*P.d.*) and five *Oryzomys longicaudatus* (*O.l.*). Dotted lines indicate irreversible weight losses. Correlation coefficients for all regressions are between  $-0.97$  and  $-0.99$  ( $P < 0.001$ ). Vertical lines indicate 1 SD.

different from all others ( $P < 0.01$ ). *O. degus* showed the smallest % reduction in weight (4.3% per day), while the cricetids ranged between 5.5 and 10% per day. Maximum weight loss in the three cricetid species was found to be of similar magnitude (37 ± 2%;  $P > 0.05$ ) but significantly lower than the weight loss endured by *O. degus* (45.5 ± 4%;  $P < 0.05$ ). Survival time during water deprivation varied from 13.4 days in *O. degus* to only 4 days in *O. longicaudatus*.

## DISCUSSION

In the four studied rodents, free water drinking was the main water gain component when maintained on

Table 2. Water balance components in four rodent species from central-northern Chile

	<i>O. degus</i> (7)	<i>P. darwini</i> (5)	<i>A. olivaceus</i> (6)	<i>O. longicaudatus</i> (6)
Body weight (g)	128.8 ± 10.3	47.6 ± 9.8	24.0 ± 1.9	23.9 ± 3.8
Free water drinking	10.3 ± 2.1	17.9 ± 2.1	17.2 ± 2.6	19.7 ± 2.2
Metabolic water	1.4 ± 0.1	1.9 ± 0.1	2.2 ± 0.1	2.3 ± 0.1
Total water gains	11.7 ± 2.2	19.8 ± 2.3	19.4 ± 2.7	22.0 ± 2.3
Urine water loss	6.3 ± 1.7	3.3 ± 1.4	4.3 ± 0.9	2.4 ± 0.7
Fecal water loss	0.9 ± 0.5	0.9 ± 0.4	2.3 ± 0.6	3.1 ± 0.7
Evaporative water loss	4.5 ± 1.1	15.6 ± 2.8	12.9 ± 2.1	16.5 ± 2.8

Water variables are given in ml H<sub>2</sub>O/100 g of body weight, per day. Values represent means ± SD. Numbers in parentheses indicate number of animals used.

dry diets ( $9 \pm 1\%$  water and 14–20% protein). Natural diets reported for some of these species include diverse proportions of grasses, seeds, arthropods, flowers and even pollen (Meserve, 1981). Being different from our experimental diets, natural food consumption should basically cope with the energy and water needed by xeric rodents (Morton and MacMillen, 1981). Thus, although our data on free water drinking (Table 1) may not fully represent natural conditions, they nevertheless give an estimation of the range of daily water requirements that should be satisfied. Comparison of these values with data on other mesic and xeric rodents should also take into account the variety of experimental diets utilized. For example, in *Microtus ochrogaster* a free water ingestion of 20.6 ml/100 g per day was reported (Getz, 1963), but a value 40% higher was also given for this species (Dupré, 1983). The higher water intake was measured using a 25% protein diet, while the lower figure was obtained with a diet containing 8% protein. Our values in Table 1 show a similar diet effect. Under these considerations, just making gross comparative estimations may place our free water drinking values within the ranges given for other mesic and xeric rodents (Hudson and Rummel, 1966; Mares, 1977c). Under water balance conditions, calculated metabolic water represents the minimum production of oxidation water (about 10% of total gains), so although somewhat larger amounts may be produced in natural conditions, substantial changes in total water gained are not expected to occur.

Partitioning of total water loss reveals that EWL is the main water loss component in the three cricetid rodents, while in *O. degus* the largest water loss is from urine. Granivorous-omnivorous food habits of the examined cricetids (Glanz, 1977; Meserve, 1981) may result in a negative water balance by increasing the excreted nitrogen load (Schmidt-Nielsen, 1948). However, these rodents (and also *O. degus*) are able to produce highly concentrated urine ( $>4000$  mosM/kg), thus even during dry seasons renal water loss may not be greatly affected (Cortés, 1985).

Fecal water loss averaged about 10% of total water loss (4.5–14%). Water content of feces ranged from 39.8% in *O. degus* up to 52.7% in *O. longicaudatus*. Intermediate values were found for *P. darwini* (45.8%) and *A. olivaceus* (46.6%). These values compare well with data on other desert rodents which are around 46% (MacMillen and Lee, 1967; Blackwell and Pivorun, 1979).

EWL is an obligatory water loss component that, except in extreme conditions is basically stable. Thus, relations of metabolic water to EWL may partially explain the differences observed in the four species when subjected to water deprivation. In *O. degus* metabolic water represents about 1/3 of EWL while in the cricetids metabolic water is equivalent to only 1/6 of EWL. The different magnitude of these relations is explained by the low EWL values shown by *O. degus* which, in turn, may well be associated with morphological adaptations of nasal passages, as has been reported in other species (Schmid, 1976).

Taking *O. degus* values as a reference (1.0) for the rates of reduction in body weight under water deprivation, we find that the losses in body weight are

equivalent to 1.3 in *A. olivaceus*, to 1.5 in *P. darwini* and 2.2 in *O. longicaudatus*. Rates of weight loss in these species did not appear to be related to their body sizes. For example, *A. olivaceus*, which is about one half the size of *P. darwini*, lost weight significantly more slowly than the larger species. Furthermore, *O. longicaudatus* and *A. olivaceus*, with almost identical body weight, show significantly different slopes (Fig. 1). During water deprivation, survival times for *P. darwini* and *A. olivaceus* are shorter than those reported for these species (Meserve, 1978). Differences in diet composition may account for this variation. Finally, although the four species clearly depend on exogenous water, the combined effects of different rates in weight loss, survival time, maximum weight loss during dehydration, EWL, fecal water loss and free water intake, indicate a specific succession of water dependences graded from more to less dependent: *O. longicaudatus* > *P. darwini* > *A. olivaceus* > *O. degus*. This hierarchy explains the observed association of *O. longicaudatus* and *P. darwini* with environments of denser vegetation, while *A. olivaceus* and *O. degus* have been reported to be associated with drier and more variable habitats (Mares, 1977b; Jacksic *et al.*, 1981; Meserve, 1981).

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