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# Intra and interspecific allometric scaling of intestinal dimensions in phyllotine rodents

## Alometría intra e interespecífica en las dimensiones intestinales en roedores filotinos

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## ABSTRACT

We compared the scaling of small intestine morphology (length, area and calculated volume) to body mass, in rodents (*Phyllotis xanthopygus rupestris* and *P. magister*) from northern Chile. *Phyllotis magister* feeds primarily on grasses whilst *Phyllotis x. rupestris* is mainly omnivorous. Significant differences between residuals of scaling relationships of small intestine area and volume between species were observed. Intestinal area in *P. magister* was 40.9% higher than in *P. x. rupestris* whilst intestinal volume was 53.4% higher in *P. magister* than in *P. x. rupestris.* Apparently modifications in mass-independent intestinal surface area is the mechanistic basis for differences in food habits of these species.

**Key words:** allometry, intestinal dimensions, food habits, rodents.

## RESUMEN

Comparamos la relación entre la morfología del intestino delgado (largo, área y volumen) y la masa corporal en roedores (*Phyllotis xanthopygus rupestris* y *P. magister*) del norte de Chile. *Phyllotis magister* se alimenta preferentemente de gramineas mientras que *Phyllotis x. rupestris* es principalmente omnívoro. Observamos diferencias significativas entre los residuos de las relaciones alométricas de área y volumen intestinal. El área intestinal de *P. magister* fue 40,9% mayor que en *P. x. rupestris* mientras que el volumen fue 53,4% mayor en *P. magister* que en *P. x. rupestris.* Al parecer, los cambios en area intestinal masa-independiente son las bases mecanicistas para las diferencias en hábitos alimentarios en estos roedores.

**Palabras clave:** alometría, dimensiones intestinales, hábitos alimentarios, roedores.

## INTRODUCTION

The balance between acquisition and expenditure of energy depends on the interplay among digestive processing and metabolic rates. Adaptations to food processing include variations in intestinal morphology, enzyme activity and nutrient absorption (e.g. Karasov 1996). Changes in the size of the intestine among endotherms in response to variation in dietary chemistry have been demonstrated under field and laboratory conditions. For instance, some species of small mammals respond to diets quality by a combination of digestive mechanisms that include: rapid transit time, changes in gut morphology and capacity, and increased nutrient uptake (see Bozinovic et al. 1988, 1990, Foley & Cork 1992, Green & Millar 1987, Gross et al. 1985, Hammond & Wunder 1991, Myrcha 1964, 1965). Thus, a pattern of energy intake, use and expenditure, could be greatly influenced by morphological and physiological design and constraints of the digestive system and viceversa.

Scaling deals with the structural and functional consequences of changes in scale among otherwise similar organisms. In birds, the small intestine (SI) absorptive

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area scales about the same as metabolic rate, suggesting that intestinal morphology is the variable responding to changes in food intake and assimilation (Ricklefs 1996). To test for allometric adaptations in SI dimensions at the species level, the relationships between SI gross morphology and body mass as a function of dietary habits in two species of the *Phyllotis* genus (Rodentia: Muridae) are examined. We compared the scaling of SI morphology (length, area and volume) to body mass ($m_b$) between *Phyllotis xanthopygus rupestris* and *P. magister* in northern Chile. Both species are nocturnal and inhabit the semiarid habitats and Andean slopes in northern Chile. According to Pizzimenti & De Salle (1980), *P. magister* feeds primarily on grasses (60% of stomach contents) whilst *Phyllotis x. rupestris* is omnivorous, feeding on seeds, insects and grasses (1/3 of stomach contents).

## MATERIALS AND METHODS

### *Animals and maintenance*

Rodents were captured with Sherman traps in several localities of northern Chile, from approximately sea level to 3000 meters above sea level. Localities for *P. magister*

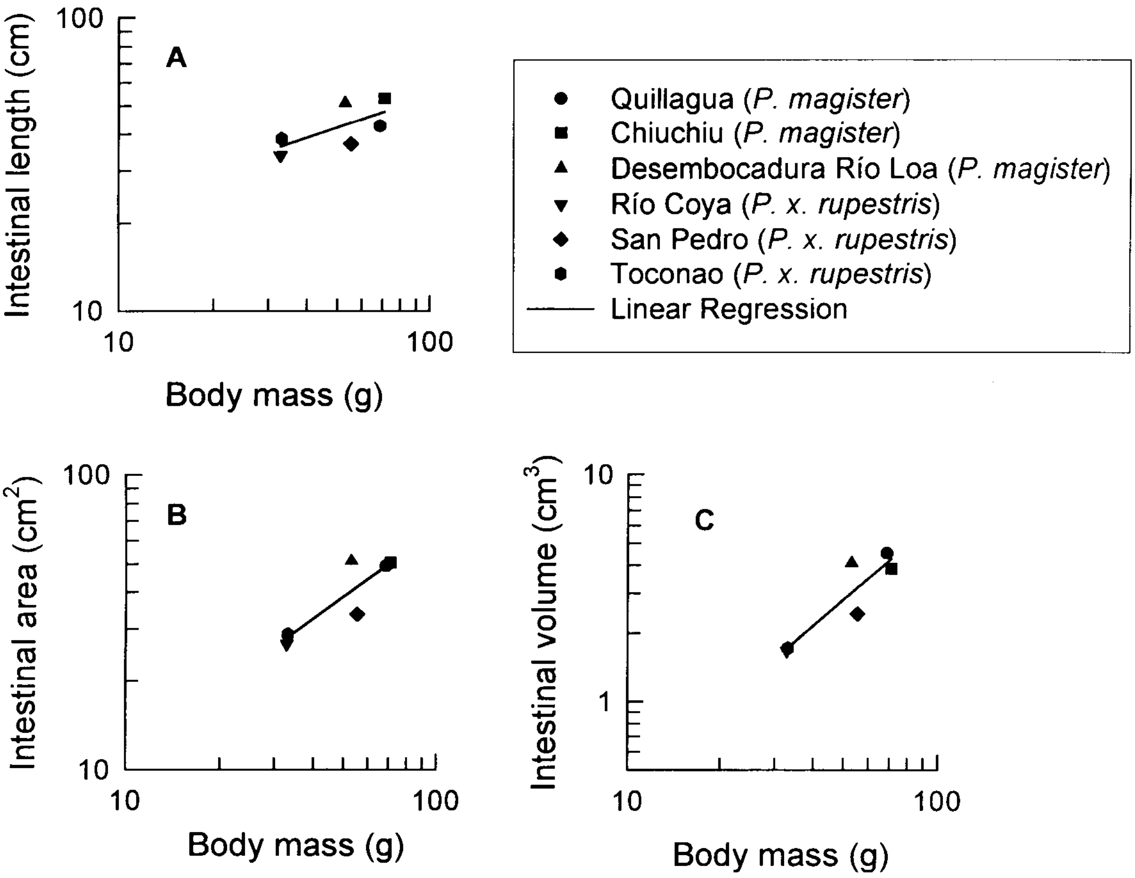

*Fig. 1.-* Double logarithmic relationships between: A) small intestinal length and body mass, B) small intestinal area and body mass, and C) small intestinal volume and body mass in *Phyllotis xanthopygus rupestris* and *Phyllotis magister* from different localities in northern Chile. The line is fitted by linear least-squared regression. Each point represent the mean value for each population.

Relación doble logarítmica entre: A) largo del intestino delgado y masa corporal, B) área del intestino delgado y masa corporal, y C) volumen del intestino delgado y masa corporal en *Phyllotis xanthopygus rupestris* y *Phyllotis magister* de diferentes localidades en el norte de Chile. Las líneas fueron ajustadas por el método de mínimos cuadrados. Cada punto representa el valor medio de cada población.

were: Desembocadura Río Loa (21°25'S, 70°02'W, 100 m.a.s.l., n = 2), Chiuchiu (22°18'S, 68°38'W, 2250 m.a.s.l., n = 5) and Quillagua (21°38'S, 69°34'W, 800 m.a.s.l., n = 4). Specimens of *P. x. rupestris* were captured at: San Pedro de Atacama (22°56'S, 68°12'W, 2450 m.a.s.l., n = 3), Toconao (23°12'S, 68°02'W, 2475 m.a.s.l., n = 3), and Río Coya (22°25'S, 68°07'W, 3000 m.a.s.l., n = 5). After capture, animals were transported to the laboratory. In the animal room, they were maintained during three weeks before the experiments started on rabbit food pellet (energy content = 16.96 ± 0.02 kJ/g), water ad libitum and a photoperiod 12L:12D. All animals seemed healthy since they maintained body mass and were very active. After measurements were done animals were deposited and classified accordingly to collections of the National Museum of Natural History, Chile (J.C. Torres-Mura pers. comm).

### *Small intestine dimensions*

Rodents were killed by cervical dislocation, and measured length and wide (three measurements) of the SI. We calculated the nominal area and volume of SI. As pointed out by Karasov (1990), in a simple tube, volume ($V_{SI}$), length ($L_{SI}$) and area ($A_{SI}$) are related according to:

$$4\pi \cdot V_{SI} \cdot L_{SI} = A_{SI}^2$$

### *Statistics*

The allometric relationships among $L_{SI}$ (cm), Ai (cm$^2$), VSI (cm$^3$), and $m_b$ (g) were calculated by a least-square linear regression ($\log Y = \log a + b \log X$) and expressed as $Y = aX^b$, where Y = SI morphology, X = $m_b$, a = intercept at log X = 0, and b = slope. Given that $L_{SI}$, Ai and $V_{SI}$ correlates with $m_b$, analysis of residuals was applied to remove the effect of $m_b$. Using this method, we tested by a one-way ANOVA, the hypothesis of adaptation in SI dimensions as a function of food habits. The level of significance was defined as $P < 0.05$, and all values are given as mean ± SD. Statistical analyses were performed using STATISTICA® (1997) statistical package for Windows 95 program.

## RESULTS AND DISCUSSION

A significant difference in mb between but not within species was observed (F = 19.79,

TABLE 1

Statistical parameters of the double logarithmic regressions between small intestine length ($L_{SI}$ in cm), small intestine area (Ai in cm$^2$), small intestine volume ($V_{SI}$ in cm$^3$), and body mass ($m_b$ in g)

Parámetros estadísticos de la regresión doble logarítmica entre largo del intestino delgado ($L_{SI}$ in cm), área del intestino delgado (Ai in cm$^2$), volumen del intestino delgado ($V_{SI}$ in cm$^3$), y masa corporal ($m_b$ in g)

| Parameter | Estimate | SE | t-value | P-level |
|---|---|---|---|---|
| $L_{SI}$ - $m_b$ | | | | |
| Intercept | 9.77 | 1.48 | 5.89 | <<0.0001 |
| Slope | 0.37 | 0.09 | 3.74 | 0.001 |
| $A_{SI}$ - $m_b$ | | | | |
| Intercept | 2.39 | 1.54 | 2.01 | 0.05 |
| Slope | 0.71 | 0.11 | 6.42 | <<0.0001 |
| $V_{SI}$ - $m_b$ | | | | |
| Intercept | 0.05 | 1.77 | 5.30 | <<0.0001 |
| Slope | 1.05 | 0.15 | 7.11 | <<0.0001 |

df = 1,22, P = 0.0002) being, in average, *P. magister* a 37.2% larger than *P. x. rupestris* (64.3 ± 9.8 *versus* 40.4 ± 12.9 g respectively). The allometric relationships between SI dimensions and $m_b$ (Fig. 1) for individuals of both species were:

$$L_{SI} = 9.77\ m_b^{0.37} \qquad (1)$$

r = 0.62, F(1,22) = 14.02, P = 0.001, Fig 1a

$$A_{SI} = 2.39\ m_b^{0.71} \qquad (2)$$

r = 0.81, F (1,22) = 41.21, P = 0.0001, Fig. 1b

$$V_{SI} = 0.05\ m_b^{1.05} \qquad (3)$$

r = 0.84, F (1,22) = 50.57, P = 0.0001, Fig. 1c

Statistical values of the allometric equations are shown in Table 1, see also Fig. 1a,b,c. Significant differences between but again, not within species in $A_{SI}$ as well as in $V_{SI}$ were obtained after the effect of $m_b$ was removed (one-way ANOVA: F(1,22) = 6.46, P = 0.019 for $A_{SI}$ and F (1,22) = 6.62, P = 0.017 for $V_{SI}$ respectively); nevertheless, non significant differences between residuals of $L_{si}$ among species were obtained (one-way ANOVA: F (1,22) = 3.05, P = 0.095). We observed that $A_{SI}$ in *P. magister* was 40.9% higher than in *P. x. rupestris* (50.3 ± 0.9 versus 29.7 ± 3.5 $cm^2$ respectively), whilst $V_{SI}$ was 53.4% higher in *P. magister* than in *P. x. rupestris* (4.2 ± 0.34 versus 1.9 ± 0.4 $cm^3$ respectively, Fig. 1b,c). Differences in $A_{SI}$ as well as in $V_{SI}$ between species are probably a consequence of different food habits.

We have applied scaling procedures to understand how SI morphology are related to body mass and food habits. Our data validates the hypothesis of a mass-independent interspecific adaptation to food habits in SI-morphology. Since we maintained the animals during three weeks in the laboratory with the same diet, the observed differences in SI-morphology allow us to conclude that *P. magister* exhibit hard-wired digestive adaptation to herbivory (Pizzimenti & De Salle 1980). A larger SI area and volume probably allows *P. magister* to exploit poor food such as grasses. Considering that cell walls and secondary metabolites of plants interfere with digestive processes, *P. magister* appears to be able to use nutritionally poor food because of a larger gut volume. Apparently, it allows to increase food intake and digestion time, that is, to enhance digestive processing of a poor food.

On the other hand, we obtained similar allometric equations (exponents) of intestinal dimensions that the one obtained by Chivers & Hladik (1980) for the morphology of the gastrointestinal tract in primates and in other groups of mammals. At least between the range of mb here described for different populations and species of *Phyllotis* it is interesting to note that metabolic rate and SI area scales almost the same. In general, metabolic rate scale to mb with an allometric exponent of 0.75 (Kleiber 1961, Peters 1983, Calder 1984, Schmidt-Nielsen 1984). A similar result was obtained by Ricklefs (1996) for passerine birds. Apparently, SI surface-area, but not SI length and volume, is the variable that may change to meet metabolic requirements at the intraspecific level in the above mentioned groups of vertebrates.

As pointed out by Karasov (1987) the increased in metabolic rate associated with increasing in $m_b$ involve higher requirements for energy and nutrientes. This increase is met by more intestinal tissue, apparently the "simplest solution" *sensu* Karasov (1987) of absorbing all nutrientes to satisfy metabolic energy expenditure. Also, Karasov (1988) pointed out that modifications in intestinal surface area is the mechanistic basis for changes in nutrients uptake under increased metabolic rates. A similar model was proposed by Tenney & Remmers (1963) for the increase in mammalian lung capacity with increasing $m_b$. Thus, higher metabolic rates, associated to larger body masses, must be fueled by more food intake. Apparently, higher metabolic and hence ingestion rates are met by a higher surface area of the small intestine where nutrient absorption occurs, explaining the observed scaling relationships. On the other hand, since food habits affect both SI morphology (Karasov 1987) and metabolic rate (McNab 1988), it is possible that both variables may change in response to dietary habits of species. Certainly, this hypothesis needs to be tested.

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