Digestive morphology of two species of *Abrothrix* (Rodentia, Cricetidae): comparison of populations from contrasting environments

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The digestive system is one of the most reactive physiological systems to changes in environmental conditions as a result of a trade-off between functional benefits and maintenance costs. Empirical studies indicate that high-fiber diets promote an increase in the rate of food intake, and, thus, an increase in the size of the digestive organs. Here, we investigated variation in the size of digestive organs in 4 populations of *Abrothrix olivacea* and *A. longipilis*, both inhabiting 2 contrasting habitats. Based on published data on diet composition, we predicted that individuals from the more-productive forest habitat should show larger digestive organs than individuals from the less-productive steppe habitat. As expected, we found that individuals from the forest had significantly larger small and large intestines (relative to body mass) than individuals from the steppe. In addition, we found that individuals from the forest had a larger body size than individuals from the steppe, suggesting that habitat productivity has an important effect on body size.

Key words: digestive system, forest, gut size, interpopulational analysis, Sigmodontinae, steppe

The digestive system comprises the functional link between ingested food and the energy and nutrients needed to meet all vital functions, including survival, growth, and reproduction (Secor 2001). However, the digestive system also represents one of the most expensive physiological systems in terms of energy and protein metabolism (Cant et al. 1996). This trade-off between functional benefits and maintenance costs determines that a close match between the demands imposed upon the system (e.g., related to food availability and quality, and internal energy needs) and the system attributes (e.g., organ size, and enzyme and transporter activities) should be expected at any time. Accordingly, digestive adjustments to cope with changes in environmental conditions have been observed at different temporal scales, including those affecting individual organisms over a few days (i.e., phenotypic flexibility), those established by individual organisms through their ontogeny (i.e., developmental plasticity), those occurring in different populations of 1 species (i.e., interpopulational changes), and, finally, those occurring in different species separated by thousands or millions of years of evolution (i.e., interspecific changes—Starck and Wang 2005).

To date, however, the study of phenotypic variation in digestive traits has been mainly conducted at 2 levels of biological organization. On one hand, classical comparative studies, which can be traced back as far as the early 19th century (e.g., de Cuvier 1835), used the species as the unit of the analysis. These studies clearly demonstrate the existence of a relationship between food habits of species and gut morphology, in such a way that digestive system size and complexity increase with the amount of undigestible material in the diet (Stevens and Hume 1995; Karasov and Martínez del Rio 2007). On the other hand, studies on digestive flexibility have used the individual as the unit of the analysis, evaluating the effect of different internal (e.g., reproduction) and external (e.g., diet and temperature) factors on digestive attributes (Piersma and Lindstrom 1997; Pennisi 2005; Karasov and Martínez del Rio 2007). Even though these studies can be traced back to the beginning of the 20th century (e.g., Jackson
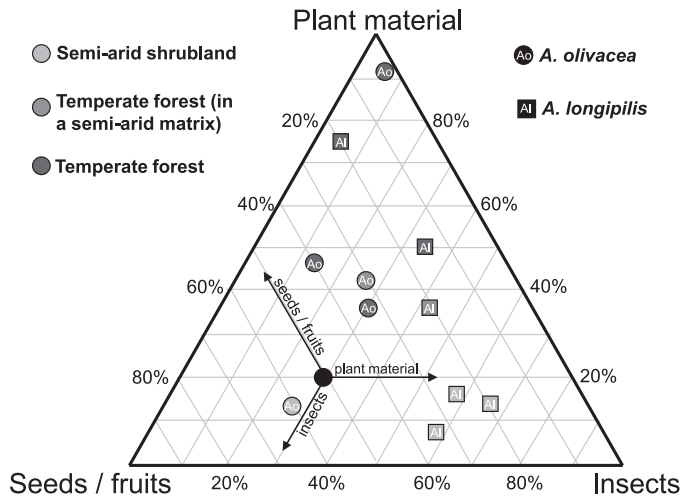
Fig. 1.—Food habits of different populations of the South American olive mouse (*Abrothrix olivacea*) and the long-haired grass mouse (*A. longipilis*) inhabiting low-productivity (i.e., semiarid shrublands) and high-productivity (e.g., temperate forests) habitats (modified from Silva 2005).

1915), they became common only after the publication of the Optimal Digestion Theory (Sibly 1981; see also Naya 2008). One of the most pervasive results of these studies is that when animals consume high-fiber, low-quality diets to meet their energy and nutrient requirements, they eat and process more food per unit of time (Gross et al. 1985; Castle and Wunder 1995; Young Owl and Batzli 1998; Liu and Wang 2007). As a consequence, hypertrophy of digestive organs occurs (Gross et al. 1985; Castle and Wunder 1995; Young Owl and Batzli 1998; Liu and Wang 2007; Naya et al. 2007). In other words, animals that enlarge their guts when consuming a bulky diet are capable of maintaining nearly constant food digestion at increased levels of food consumption, and thus, are capable of maintaining energy and nutrient assimilation (Zaldúa and Naya 2014).

Studies aimed at assessing phenotypic variation in digestive traits at intermediate levels of analysis between species and individuals, such as variation among populations of a given species, are still scarce (e.g., Hansson 1985; Corp et al. 1997; Tracy and Diamond 2005; Naya et al. 2009). Nevertheless, these studies are crucial for understanding how physiological variables are affected by environmental conditions, and consequently, how they evolve (Spicer and Gaston 1999; Chown and Nicolson 2004). This is because each population consists of a set of individuals exposed to similar environmental conditions, which might differ, if appropriately selected, in only a few major environmental factors of interest from those experienced by individuals in other populations. In addition, the problem of phylogenetic dependence among the units of analysis is certainly minimized at this intraspecific scale (Garland et al. 2005). In this way, interpopulational analyses represent a straightforward approach to explore the proximal role of different environmental factors on phenotypic variation for a given physiological trait.

Within this general context, here we evaluate the digestive morphology of 4 populations of 2 widespread sigmodontine species of the genus *Abrothrix*, the South American olive mouse (*A. olivacea*) and the long-haired grass mouse (*A. longipilis*), both of which inhabit 2 highly contrasting habitats, the Valdivian and Magellanic forests and the Patagonian steppe. Diet data for our focal species indicate that populations inhabiting highly productive habitats (e.g., temperate forests) have a more herbivorous diet than populations inhabiting less-productive habitats (e.g., semiarid shrublands), where they tend to have a more insectivorous (in *A. longipilis*) or omnivorous–frugivorous (in *A. olivacea*) diet (Silva 2005, and references therein; Fig. 1). Thus, based on the abovementioned relationship between diet quality and gut size—repeatedly reported in rodents at the individual (e.g., Piersma and Lindstrom 1997; Pennisi 2005; Karasov and Martínez del Rio 2007) and interspecific (e.g., Lovegrove 2010; Naya et al. 2013) levels—we predicted that populations inhabiting the Valdivian and Magellanic forests should have larger digestive (and associated) organs than populations inhabiting the Patagonian steppe. In addition, based on recent studies that indicate geographic variation in habitat primary productivity—a measure of, among other things, food availability at the basal level—is the major cause of clinal variation in body size (e.g., Medina et al. 2007; Greve et al. 2008; Gur and Gur 2012), we predicted that populations of both species of *Abrothrix* inhabiting more-productive habitats (e.g., forests) should have a greater body mass than populations inhabiting less-productive habitats (e.g., steppe).

Materials and Methods

Species and study area.—The South American olive mouse is distributed in diverse habitats of Chile and Argentina, from 18°S to 56°S latitude (Fig. 2). This species inhabits a great variety of environments, such as coastal deserts in the north, Mediterranean scrubs in central Chile, Valdivian and Magellanic forests through the south of Chile and Argentina, and Patagonian steppe toward the Atlantic coast (Pardiñas et al. 2011). The long-haired grass mouse is distributed from 33°S to 54°S latitude (Fig. 2), and also inhabits Mediterranean scrubs in central Chile, Valdivian and Magellanic forests through the south of Chile, and Patagonian steppe in southern Argentina and Chile (Palma et al. 2010; Pardiñas et al. 2011). Thus, both species must withstand the arid Patagonia steppe (which over large areas receives approximately 300 mm of annual rainfall) and also the Valdivian rain forest (which receives approximately 2,700 mm of annual rainfall), and thus provide an excellent model to evaluate the effect of some climatic (e.g., rainfall) and ecological (e.g., habitat productivity) factors on intraspecific phenotypic variability.

Individuals of both species of *Abrothrix* were captured with RodentTrap Special-S traps (Formal Ltda, Santiago, Chile) at 2 different latitudinal bands in the Valdivian and Magellanic forests and the Patagonian steppe (Fig. 2). In our system annual accumulated rainfall ranged between 167 and 2,211 mm, net
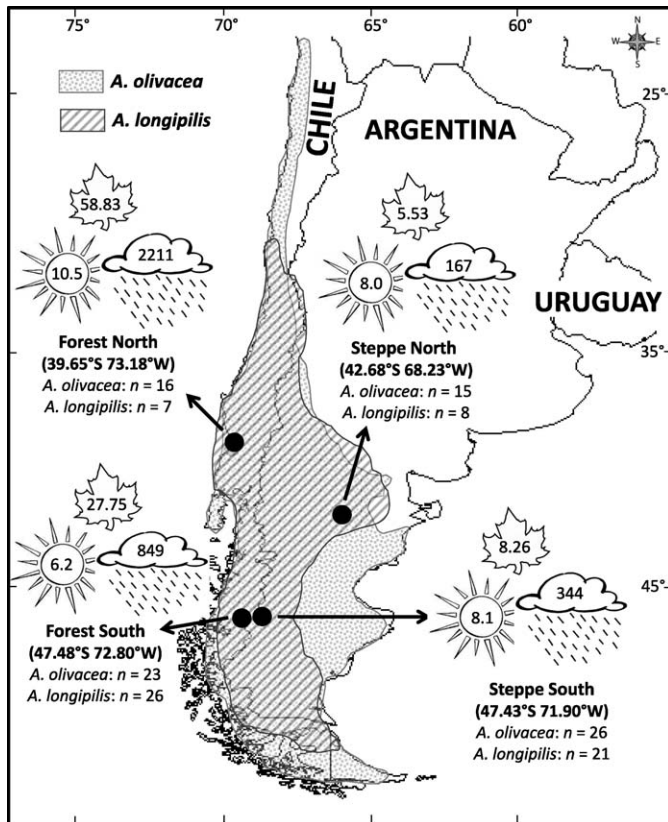
FIG. 2.—Distributional ranges of the South American olive mouse (*Abrothrix olivacea*) and the long-haired grass mouse (*A. longipilis*) and values of annual accumulated precipitation (inside cloud symbols, in mm), annual mean temperature (inside sun symbols, in °C), and net primary productivity (inside leaf symbols, in 1.0×10^{10} tons of carbon per 0.25-degree cell) for each population (*n* = sample size) examined within the study area in southern South America. Data on annual accumulated rainfall and annual mean temperature were downloaded from the WorldClim database (Hijmans et al. 2005), and data on net primary productivity were downloaded from the Socioeconomic Data and Application Center home page (Imhoff and Bounoua 2006).

primary productivity ranged between 5.53×10^{10} and 58.83×10^{10} tons of carbon per 0.25-degree cell, and annual mean temperature ranged between 6.2°C and 10.5°C (Fig. 2).

Morphological determinations.—After collection, animals were weighed ($\pm$ 0.1 g) and euthanized following guidelines of the American Society of Mammalogists (Sikes et al. 2011) by properly trained personnel and outside the perceptive range of the other captive individuals. Then, animals were ventrally dissected and the complete gastrointestinal tracts were quickly removed and disconnected from mesenteric attachments. The stomach, small intestine, cecum, large intestine, and liver were washed with saline solution, dried with paper towels, and weighed with an electronic balance ($\pm$ 0.001 g). *A. olivacea* and *A. longipilis* have stomachs of the unilocular–hemiglandular type (Carleton 1973), and the gross anatomy of the digestive tract is very similar in both species. Voucher specimens were housed at the Colección de Mamíferos del Centro Nacional Patagónico (Puerto Madryn, Argentina) and Colección de Mamíferos—Universidad Austral de Chile (Valdivia, Chile).

Statistical analysis.—Differences in organ wet masses among habitats and latitudinal bands were evaluated separately for each species through 2-way analyses of covariance (using body mass as a covariate), whereas differences in body mass among habitats and latitudinal bands were evaluated separately for each species through a 2-way analysis of variance. We used a Kolmogorov–Smirnov test to assess normality, and a Levene's test to assess homogeneity of variance. When necessary to meet assumptions, variables were log-transformed (e.g., liver wet mass in *A. longipilis*). Interactions between covariates and factors were tested using a parallelism test. In all cases, statistical significance was established at the $\alpha = 0.05$ level. Statistical analyses were performed using the package STATISTICA version 7.0 (StatSoft 2004).

RESULTS

Neither stomach nor cecum varied with habitat or latitude in either rodent species (Figs. 3A and 3B and 4A and 4B). However, wet mass of the small intestine had a significant habitat $\times$ latitude interaction for both *A. olivacea* ($F_{1,75} = 10.1$, $P = 0.002$) and *A. longipilis* ($F_{1,57} = 53.3$, $P < 0.0001$). Small intestines of both species were larger in the northern forest than in the other 3 localities (Figs. 3C and 4C). For *A. olivacea*, large intestine wet mass varied with habitat ($F_{1,75} = 4.9$, $P = 0.03$) and latitude ($F_{1,75} = 5.6$, $P = 0.02$), but not with their interaction. Large intestine was heavier in the forest than in the steppe and in the south than in the north (Fig. 3D). *A. longipilis* had a habitat $\times$ latitude interaction ($F_{1,57} = 18.2$, $P < 0.0001$), where animals in the northern forest had a heavier large intestine than those in the northern steppe and the southern forest (Fig. 4D). Finally, liver wet mass of *A. olivacea* varied only with latitude ($F_{1,75} = 89.2$, $P = 0.003$), where animals in southern locations had heavier livers than those in northern locations (Fig. 3E). Liver wet mass of *A. longipilis* had a habitat $\times$ latitude interaction ($F_{1,57} = 12.3$, $P = 0.001$), where animals in northern forests had heavier livers than those in northern and southern steppe, and those in southern forest and southern steppe had heavier livers than those in northern steppe (Fig. 4E).

Both habitat ($F_{1,76} = 16.9$, $P < 0.0001$) and latitude ($F_{1,76} = 7.8$, $P = 0.007$), but not the interaction between them ($P > 0.05$), explained the variation in body mass of *A. olivacea*. Body mass was larger in the forest than in the steppe, and in the south than in the north (Fig. 3F). In contrast, body mass of *A. longipilis* had a significant habitat $\times$ latitude interaction ($F_{1,58} = 6.6$, $P = 0.01$), where animals residing in the forests tend to be larger than those residing in the steppe ($F_{1,58} = 3.2$, $P = 0.08$; Fig. 4F).

DISCUSSION

Our study demonstrates that individuals from populations that inhabit the Valdivian and Magellanic forests in Chile have heavier small and large intestines than those from populations that inhabit the less-productive Patagonian steppe in Argentina. In addition, for 1 of the 2 species analyzed here (*A. olivacea*),
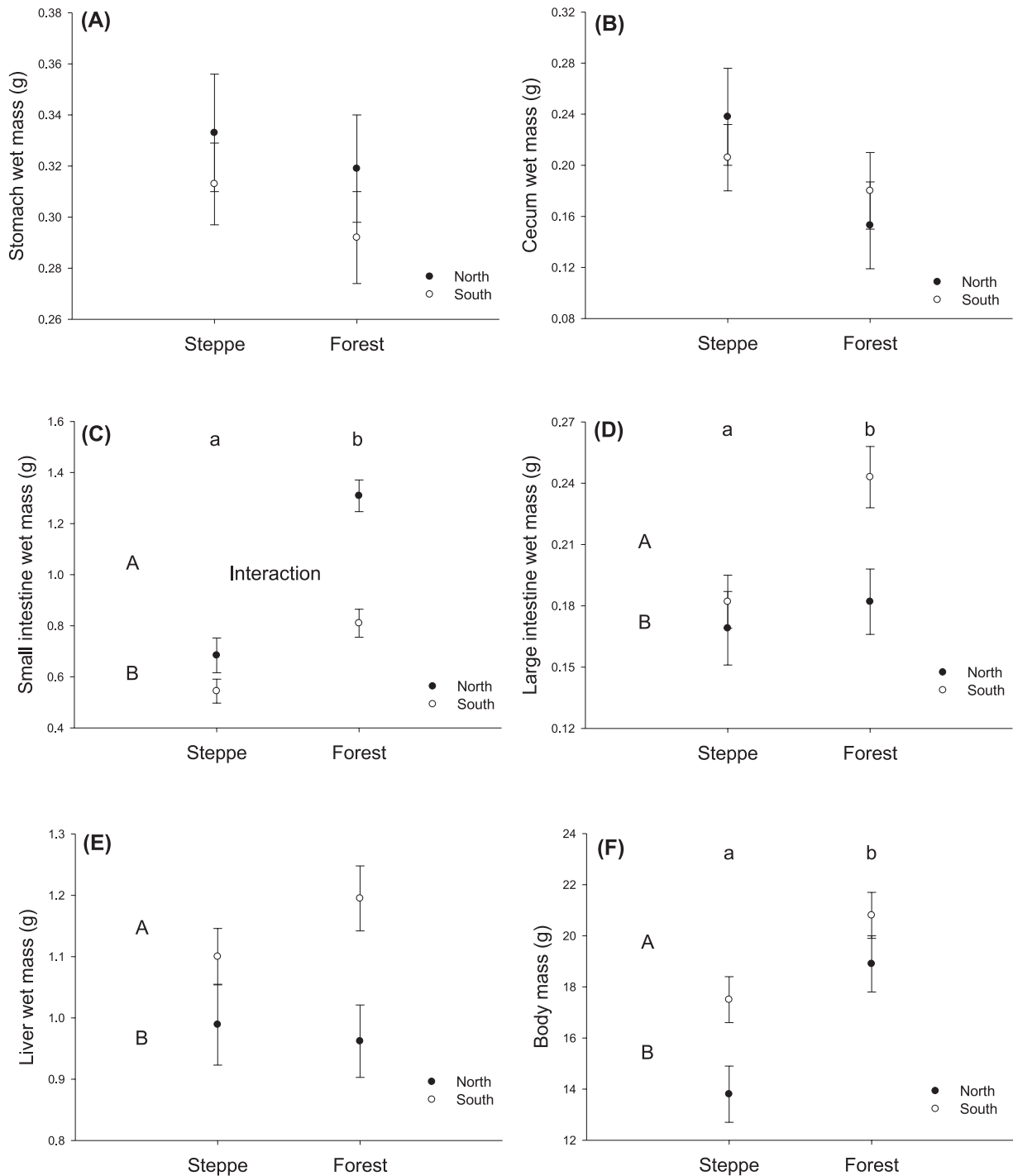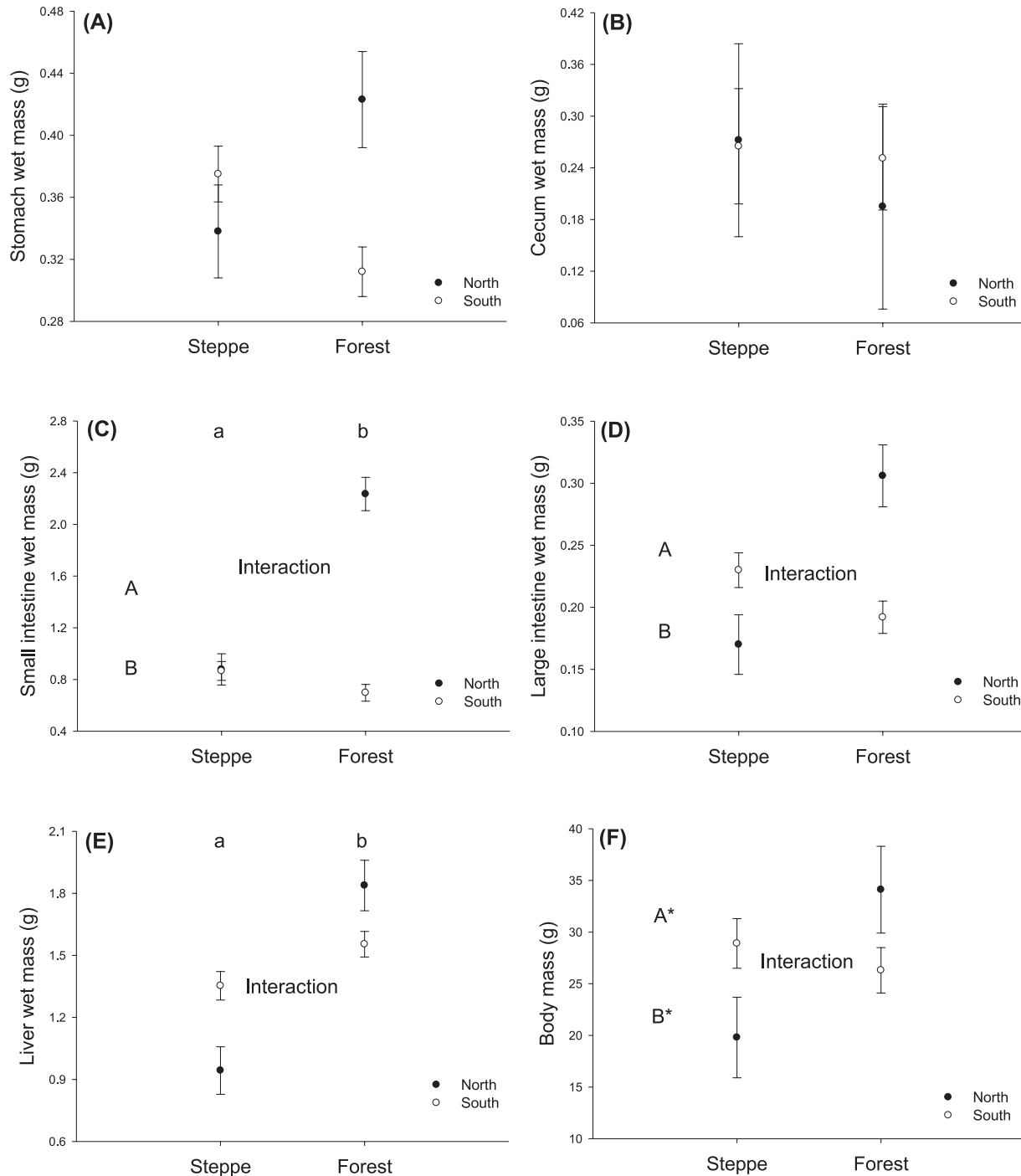
FIG. 3.—Body and organ masses for population samples of the South American olive mouse (*Abrothrix olivacea*) in the Valdivian and Magellanic forests and the Patagonian steppe, collected during April 2011 (northern populations) and May 2012 (southern populations). Values are least-squares absolute means $\pm$ 1 *SE* (for body mass) or least-squares adjusted means $\pm$ 1 *SE* (for organ wet mass). Different capital letters indicate significant differences ($P < 0.05$) between habitats, whereas different lowercase letters indicate significant differences ($P < 0.05$) between latitudinal bands (north and south).

the size of the liver also was greater in the Valdivian and Magellanic forests than in the Patagonian steppe. Even though data on diet composition for our focal species in the Patagonian steppe are not available, previous studies conducted in different regions of Chile indicate that populations of both species of *Abrothrix* inhabiting temperate forests have a more herbivorous diet than populations inhabiting less-productive habits, such as semiarid shrubland (Silva 2005, and references therein). In addition, Bozinovic et al. (2010) analyzed digestive organ size of 2 populations of *A. olivacea* that consumed 2 different experimental diets for 6 months. Even though their study only compared the amount of digestive flexibility (i.e., changes

FIG. 4.—Body and organ masses for population samples of the long-haired grass mouse (*Abrothrix longipilis*) in the Valdivian and Magellanic forests and the Patagonian steppe, collected during April 2011 (northern populations) and May 2012 (southern populations). Values are least-squares absolute means $\pm$ 1 *SE* (for body mass) or least-squares adjusted means $\pm$ 1 *SE* (for organ wet mass). Different capital letters indicate significant differences ($P < 0.05$) between habitats, whereas different lowercase letters indicate significant differences ($P < 0.05$) between latitudinal bands (north and south). Asterisks (*) denote a marginal probability value ($P < 0.10$).

between experimental diets) among populations, examination of their data indicated that the population from the temperate forest had larger digestive organs than the population from the semiarid shrubland (Bozinovic et al. 2010:375, table 2). Thus, the data obtained in the present study, as well as previously published evidence for *A. olivacea*, support the prediction that

populations of animals consuming low-quality diets (e.g., plant material) have larger gastrointestinal tracts than populations of animals consuming high-quality diets (e.g., animal material).

In line with our findings, a handful of studies conducted in rodents also have found a negative correlation between gut size and diet quality at the interpopulational level. For instance,

individuals of *Myodes glareolus* and *Microtus agrestis* from populations that consume greater amounts of plant material have a larger gut than individuals from populations that mainly feed on seeds (Hansson 1985; Hansson and Jaarola 1989). Also, specimens of *Apodemus sylvaticus* from a seed-eating population had larger small intestines than specimens from a population that largely preyed on invertebrates (Corp et al. 1997). More recently, Sassi et al. (2007) found that, during the dry (nonreproductive) season, specimens of a strictly herbivorous species (*Microcavia australis*) have a larger small intestine area and cecum mass in poor-quality environments (i.e., those where available plants have high-fiber and low-nitrogen contents) than in richer ones.

As for our 2nd prediction, we found that body mass of both species of *Abrothrix* was strongly affected by habitat type, with those animals from forested areas being larger than those from the steppe. In line with this, similar results were recently obtained for cranial measurements of several populations of *A. longipilis* (Teta 2013). Moreover, a previous study explicitly suggests that habitat productivity could be the main factor explaining the observed variation in body size displayed by specimens of *A. longipilis* in central and southern Chile (Yañez et al. 1978). Specifically, these authors recorded a fairly constant body-size value between 32°S and 40°S and then a noticeable decrease in body size, in parallel with habitat productivity, toward higher latitudes. Thus, examination of the data obtained in the present study, as well as existing data for *A. longipilis*, suggests that habitat productivity has an important effect on the patterns of body-size variation of at least 2 *Abrothrix* species. However, we note that forests and steppes, in addition to primary productivity, also differ in many attributes (e.g., species of plants and insects, and vegetative coverage), which also could be related with the differences in body size recorded here.

The relationship between gut size and diet quality is one of the few cases where theoretical models of diet selection and physiology are well in agreement with a large amount of empirical evidence at the organismic (flexibility studies) and the species (comparative studies) levels (see Naya et al. 2008; Piersma and van Gils 2010). However, at present, only minor efforts have been conducted at intermediate levels of analysis, such as the evaluation of digestive trait variation among populations of one species occurring in contrasting environments. From this perspective, the present contribution is an attempt to fill this gap in our current knowledge.

Resumen

El sistema digestivo es uno de los sistemas fisiológicos más reactivos frente a cambios en las condiciones ambientales, lo que se relaciona con el compromiso existente entre los beneficios funcionales y el costo energético de su mantenimiento. Diversos trabajos empíricos realizados a distintos niveles de organización biológica, desde individuos hasta especies, han demostrado que las dietas de baja calidad (e.g., con un alto contenido de fibra) promueven un incremento en las tasas de consumo de alimento (para cubrir sus requerimientos diarios de energía y nutrientes), y por tanto, un aumento en el tamaño de los órganos digestivos. En el presente trabajo investigamos la variación en el tamaño de los órganos digestivos al nivel interpoblacional, evaluando la variación existente entre 4 poblaciones de 2 especies del género *Abrothrix* (*A. olivacea* y *A. longipilis*) que habitan 2 ambientes contrastantes (el bosque templado Valdiviano y Magallánico y la estepa Patagónica). Basados en información existente sobre la dieta de estas especies, predecimos que los individuos provenientes de los ambientes más productivos (bosque)—los cuales tienen una dieta más herbívora—deberían presentar órganos digestivos más grandes que los individuos provenientes de ambientes menos productivos (estepa)—los cuales presentan una dieta más insectívora u omnívora. En efecto, los resultados obtenidos indican que los individuos que habitan el bosque Valdiviano y Magallánico tienen intestinos delgado y grueso significativamente mayores (respecto al tamaño corporal) que los individuos que habitan la estepa Patagónica. Además, se encontró que los individuos que provienen del bosque tienen un mayor tamaño corporal que los individuos que proviene de la estepa, sugiriendo que—al menos para nuestro sistema—la productividad primaria del hábitat tiene un efecto importante sobre el tamaño.

Acknowledgments

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