Ecological physiology examines how animals cope with changing environmental demands. In low-productivity desert habitats, small mammals should consume low-quality, high-fiber food as a consequence of necessity rather than by choice. Diet quality of populations can differ at both spatial and temporal scales. Nevertheless, spatial and temporal variation in the digestive system has not been extensively studied in the field. We captured individuals from 4 populations of *Microcavia australis* and measured their digestive morphological traits. Fieldwork was carried out in 4 localities belonging to arid and semiarid regions, in dry and wet seasons. We also estimated diet quality for each population and season. We found significant effects of sex, season, and site on the size of digestive organs. The concentration of fiber and nitrogen in the plants consumed differed between populations and varied seasonally: dietary fiber was higher in the dry season and nitrogen concentration was higher in the wet season. As predicted by theory, the cecum, the organ most closely related to cellulose fermentation, was significantly larger in animals facing the lowest quality diet. The other organs also were affected by reproductive state and water requirements. Intraspecific variation in the digestive morphology of *M. australis* probably helps this species cope with remarkable seasonal and geographical variability.

Key words: digestive traits, environment variation, intraspecific variation, low-quality food, *Microcavia australis*, nutritional requirements

Food selection, intake, and digestive efficiency of small herbivores present trade-offs between competing factors (Chilcott and Hume 1985; Sibly 1981; Weiner 1992). Nutrient turnover and extraction are directly related to energy metabolism and the amount of food transported through the digestive tract (Bozinovic 1993). In addition to food quality, digestibility and resource availability also affect the rate of energy metabolism (Batzli 1985; McNab 1986). An increase in dietary fiber diminishes with food preferences and digestibility (Hume et al. 1993), thereby affecting rates of energy metabolism and allocation (Van Soest 1982) and, finally, influencing energy budgets and fitness.

Theoretically, small endotherms should show decreased energy expenditures and faster gut turnover time because they have a relative digestive-tract size similar to that of larger animals, but higher relative metabolic rates (Demment and Van Soest 1985). Despite these physiological and allometric constraints on digestion and metabolism, several studies have reported that small mammals compensate for low-quality diets through a combination of digestive mechanisms such as rapid turnover time of fibrous food, changes in gut capacity, increased nutrient uptake by the small intestine, and the use of fermentation chambers (Bozinovic et al. 1988, 1990; Caughley and Sinclair 1994; Foley and Cork 1992; Gross et al. 1985; Hammond and Wunder 1991; Karasov 1986; Sibly 1981; Veloso and Bozinovic 1993).

During nutritional bottlenecks, for example during a summer drought or in habitats with low productivity, small herbivorous mammals are expected to consume low-quality, high-fiber food (Bozinovic 1995). In the field, some species often include fibrous plant tissues as a major dietary item most likely because they are able to obtain a considerable amount of energy from fiber to satisfy their maintenance energy requirements during the
In diets containing lignin, hemicelluloses, and cellulose, animals obtain energy by daily production of short-chain fatty acids through fermentation (Holtenius and Björnåeg 1985). According to Hume (1989), the catalytic digestion of plant cell contents in the small intestine, coupled with fiber fermentation and the production of fatty acids in the cecum or rumen, allow an increase in digestible energy. The cecum and colon in herbivorous rodents are relatively larger and more complex than in omnivorous ones (Vorontsov 1962).

According to optimal digestion theory, the digestive strategy that maximizes fitness is favored (Sibly 1981). The net rate of obtaining energy is a direct function of the mass of food carried by the digestive system, food ingestion, and food turnover time. Thus, the prediction would be an increase in the size of digestive organs, in order to increase the amount of food ingested and optimize absorption and fermentation processes, resulting in higher energy yields. Previous studies, cited above, support these predictions, at least for animals maintained in captivity. Nevertheless, spatial and temporal variation in the digestive system has been poorly assessed in the field. Diet quality in populations can show spatial and temporal differences. The ability for acclimatization is certainly adaptive in an evolutionary sense and can be genetically sustained (Garland and Adolph 1991). In order to assess such variability, comparisons among populations exposed to different degrees of plant quality are useful. In this case, the phenotypic plasticity of the digestive tract could determine dietary diversity and trophic niche breadth (Bozinovic and Martínez del Río 1996).

To evaluate this variability, it is useful to compare populations exposed to different degrees of environmental productivity. The Monte Desert includes environments with different vegetation and productivity, and may therefore exert different selective pressures on the nutritional ecology of consumers.

Laboratory-oriented studies conducted on small mammals have demonstrated that low diet quality results in higher rates of food intake, and in hypertrophy of food-processing organs (Bozinovic et al. 1988, 1990; Gross et al. 1985). The use of experimental laboratory settings does not allow the reconstruction of natural conditions experienced by these animals or the dynamics of the digestive response of animals as they cope with moderate demands along a gradient of natural environmental conditions. Our study subject was Microcavia australis, one of the smallest caviomorph rodents (250 g). It is a strict herbivore (Campos et al. 2001) widely distributed throughout a variety of habitats in arid regions of western Argentina (Tognelli et al. 2001). We examined responses of digestive morphology to spatial and temporal variation in the availability and quality of trophic resources. For this purpose, we measured digestive morphological traits in individuals from 4 populations of M. australis, in 2 seasons, and analyzed chemical changes in available food items among the studied sites. We hypothesized, following the economy principle of Sibly (1981), that digestive organs would increase in size when M. australis faced diets of poor nutritional quality (i.e., high fiber, low nitrogen content, or both). We predicted that populations inhabiting low-productivity localities would have to cope with lower-quality diets than populations in more productive habitats. In consequence, digestive organs of M. australis would show larger sizes in seasons and localities in which ingested plants were of comparatively lower quality.

**MATERIALS AND METHODS**

Fieldwork was carried out during wet and dry seasons in 4 localities in arid and semiarid regions: Man and Biosphere Reserve of Ñacuñán, Private Reserve of Villavicencio, Matagusanos, and National Park El Leoncito. Each locality occurs within the range of distribution of M. australis (Fig. 1), and, because they are all separated by at least 200 km, we considered them as 4 different populations of M. australis. Furthermore, the different sites are characterized by different temperature and rainfall regimes.

**Study sites.**—The Man and Biosphere Reserve of Ñacuñán is located in the Central Monte Desert (34°02’S, 67°58’W), 700 m above sea level, 200 km southeast of Mendoza, Argentina (Ojeda et al. 1998). The climate is semiarid with an average annual rainfall of 322 mm, concentrated in the summer months (November–March). Mean temperatures are 22.1°C in summer
and 8.7°C in winter. The vegetation consists of open woodland dominated by Prosopis flexuosa, a shrub layer of Larrea divaricata, Larrea cuneifolia, Atriplex lampa, and a species-rich herbaceous layer.

The Private Reserve of Villavicencio is located northwest of Mendoza (32°30’S, 69°0.2’W). It presents different vegetation belts, from which we chose Cardonal mainly occurring on sunny slopes between 1,600 and 2,700 m above sea level (Dalmasso et al. 1999), where humidity is trapped within the gulches. Vegetation is dominated by Schinus barbatus, Larrea nitida, Junellia scoparia, Proustia cuneifolia, and Trichocereus, with a high plant cover dominated by shrubs. At 1,750 m above sea level, mean temperatures are 17°C in summer and 5°C in winter and rainfall reaches 309 mm, occurring mainly during the summer months (Dalmasso et al. 1999). The great variability in climate is related to differences in altitude, irradiation, and topography, which provide sites with higher relative humidity.

Matagusanos (31°20’S, 68°30’W) belongs to the arid extreme of the Monte Desert. Rainfall does not surpass 70 mm annually and occurs primarily during summer. Mean temperatures are 33°C in summer and 18°C in winter. The Matagusanos region is a flat plain (700 m above sea level) surrounded by mountain ranges on east and west. Vegetation is xerophytic with very low plant cover. The dominant tree is mesquite (P. flexuosa), and the shrub stratum is comprised of creosotebush, retamo, and some grasses.

Finally, National Park El Leoncito includes a number of habitats along an altitudinal gradient. We selected the highest portion of the Monte Desert, at 31°47’S, 69°17’W and 2,552 m above sea level. It is a cold desert, annual rainfall does not exceed 100 mm, winter snow amounts to 75 mm, and summer rains average 10 mm (Le Houe´rou et al. 1999). Mean temperatures are 17°C in summer and 5°C in winter. This area shows no trees, scarce herbs, and the dominant stratum is mainly comprised of creosotebush (L. nitida).

Trophic resources.—At each locality and season we randomly set 6 line transects. Along each transect we placed 13 sample quadrats where we assessed percent cover per plant species. The total number of samples was 78 from each locality and season.

Simultaneously, we sampled fresh feces of cavies at each locality and season in order to characterize their diets. Feces and season.

Species. The total number of samples was 78 from each locality randomly set 6 line transects. Along each transect we placed a solution of 17.5% NaHCO₃ (sodium bicarbonate—Dacar and Rains average 10 mm (Le Houe´rou et al. 1999). Mean exceed 100 mm, winter snow amounts to 75 mm, and summer

RESULTS

Mean NDF and ADF in plant resources varied similarly and according to what we expected from habitat characteristics: The fiber gradient in plants consumed was El Leoncito > Matagusanos > Nacuñán > Villavicencio, although it also varied seasonally (Table 1). On the other hand, the nitrogen gradient in plants consumed was El Leoncito < Villavicencio = Nacuñán < Matagusanos (Table 1). These rank series are supported by Tukey tests between pairs of means (P < 0.05). With respect to seasonal variation, NDF and ADF varied significantly, being higher during the dry than during the wet season (factorial MANOVA, F = 4.21, df = 2, 39, P = 0.022). Furthermore, nitrogen from eaten plants was significantly higher during the wet season (factorial ANOVA, F = 77.60, df = 1, 40, P = 0.0001) and showed significant effect of site (factorial ANOVA, F = 17.59, df = 3, 40, P = 0.0001). These general patterns were significant at most of the sites studied, except for NDF and ADF in Matagusanos, and
Table 1.—Effect of sites and seasons on diet neutral detergent fiber (NDF), diet acid detergent fiber (ADF), diet nitrogen, and on the size of digestive organs in cAVies (Microcavia australis) collected from 4 locations in the Monte Desert, Argentina, during wet and dry seasons in 2003 and 2004. All values are presented as mean ± SE, plus statistical effects and interactions between factors. Number of individuals in each sample indicated by n.

<table>
<thead>
<tr>
<th>Diet quality</th>
<th>Villavicencio</th>
<th>Nacúñan</th>
<th>Matagusanos</th>
<th>El Leoncito</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wet (n = 5)</td>
<td>Dry (n = 6)</td>
<td>Wet (n = 5)</td>
<td>Dry (n = 6)</td>
</tr>
<tr>
<td>ADF (%)</td>
<td>0.15 ± 0.06</td>
<td>0.18 ± 0.07</td>
<td>0.21 ± 0.03</td>
<td>0.22 ± 0.01</td>
</tr>
<tr>
<td>Effects (P)</td>
<td>Site = 0.0001</td>
<td>Season = 0.009</td>
<td>Site × season = 0.25</td>
<td></td>
</tr>
<tr>
<td>NDF (%)</td>
<td>0.25 ± 0.07</td>
<td>0.28 ± 0.07</td>
<td>0.28 ± 0.06</td>
<td>0.32 ± 0.04</td>
</tr>
<tr>
<td>Effects (P)</td>
<td>Site = 0.0001</td>
<td>Season = 0.008</td>
<td>Site × season = 0.0003</td>
<td></td>
</tr>
<tr>
<td>Nitrogen (%)</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.01</td>
</tr>
<tr>
<td>Effects (P)</td>
<td>Site = 0.0001</td>
<td>Season = 0.0001</td>
<td>Site × season = 0.02</td>
<td></td>
</tr>
</tbody>
</table>

Small intestine

| Fresh mass (g)        | 6.4 ± 1.92          | 5.11 ± 0.48      | 4.74 ± 0.79      | 4 ± 0.21          | 3.13 ± 0.33      | 2.89 ± 0.29     | 4.11 ± 0.50     | 3.83 ± 0.15     |
| Effects (P)           | Site = 0.0008       | Season = 0.06    | Site × season = 0.35 |
| Dry mass (g)          | 0.67 ± 0.20         | 0.46 ± 0.06      | 0.5 ± 0.08       | 0.38 ± 0.03       | 0.26 ± 0.03      | 0.21 ± 0.02     | 0.39 ± 0.05     | 0.34 ± 0.01     |
| Effects (P)           | Site = 0.0003       | Season = 0.006   | Site × season = 0.31 |
| Area (cm²)            | 151.08 ± 14.55      | 100.39 ± 5.59    | 133.47 ± 10.23   | 101.94 ± 4.43     | 117.79 ± 7.48    | 115.77 ± 4.20   | 106.28 ± 6.46   | 156.22 ± 2.80   |
| Effects (P)           | Site = 0.0002       | Season = 0.07    | Site × season = 0.0001 |

Cecum

| Fresh mass (g)        | 2.96 ± 0.30         | 3.42 ± 0.11      | 2.47 ± 0.36      | 3.46 ± 0.29       | 2.28 ± 0.20      | 2.49 ± 0.13     | 3.50 ± 0.16     | 3.25 ± 0.23     |
| Effects (P)           | Site = 0.004        | Season = 0.04    | Site × season = 0.04 |
| Dry mass (g)          | 0.31 ± 0.01         | 0.29 ± 0.02      | 0.24 ± 0.02      | 0.34 ± 0.03       | 0.23 ± 0.02      | 0.23 ± 0.01     | 0.35 ± 0.02     | 0.32 ± 0.01     |
| Effects (P)           | Site = 0.0003       | Season = 0.22    | Site × season = 0.004 |
| Area (cm²)            | 87.86 ± 2.84        | 71.18 ± 3.19     | 80.05 ± 6.72     | 76.39 ± 5.46      | 87.39 ± 2.96     | 87.14 ± 3.58    | 90.29 ± 5.59    | 115.68 ± 7.35   |
| Effects (P)           | Site = 0.0003       | Season = 0.8     | Site × season = 0.01 |

Large intestine

| Fresh mass (g)        | 2.55 ± 0.12         | 2.67 ± 0.18      | 2.92 ± 0.34      | 3.24 ± 0.13       | 2.80 ± 0.15      | 3.09 ± 0.12     | 2.71 ± 0.26     | 2.77 ± 0.11     |
| Effects (P)           | Site = 0.03         | Season = 0.007   | Site × season = 0.03 |
| Dry mass (g)          | 0.33 ± 0.01         | 0.42 ± 0.06      | 0.50 ± 0.07      | 0.45 ± 0.03       | 0.38 ± 0.04      | 0.38 ± 0.03     | 0.41 ± 0.05     | 0.38 ± 0.01     |
| Effects (P)           | Site = 0.002        | Season = 0.03    | Site × season = 0.004 |
| Area (cm²)            | 58.01 ± 5.08        | 44.47 ± 1.46     | 75.75 ± 7.67     | 58.51 ± 1.60      | 81.37 ± 2.3      | 77.84 ± 3.75    | 53.95 ± 4.26    | 74.98 ± 2.34    |
| Effects (P)           | Site = 0.02         | Season = 0.61    | Site × season = 0.04 |

Total gut

| Fresh mass (g)        | 14.06 ± 2.05        | 13.35 ± 0.63     | 12.51 ± 1.62     | 12.49 ± 0.61      | 10.51 ± 0.79     | 11.25 ± 0.63    | 12.13 ± 0.74    | 12.46 ± 0.40    |
| Effects (P)           | Site = 0.0006       | Season = 0.96    | Site × season = 0.16 |
| Dry mass (g)          | 1.68 ± 0.19         | 1.55 ± 0.14      | 1.63 ± 0.16      | 1.51 ± 0.12       | 1.26 ± 0.10      | 1.29 ± 0.06     | 1.52 ± 0.12     | 1.51 ± 0.01     |
| Effects (P)           | Site = 0.0004       | Season = 0.54    | Site × season = 0.37 |
| Area (cm²)            | 319.83 ± 20.25      | 235.89 ± 7.17    | 321.23 ± 22.73   | 259.28 ± 6.58     | 323.10 ± 12.52   | 312.66 ± 9.39   | 270.35 ± 0.43   | 382.76 ± 8.46   |
| Effects (P)           | Site = 0.01         | Season = 0.27    | Site × season = 0.0001 |

Nitrogen in El Leoncito, which showed no seasonal changes (Table 1).

Regarding gross morphology of the digestive tract, we observed that each organ responded differently. We detected significant effects of sex, season, site, and the covariable body mass on digestive organs (MANCOVA; Table 2).

Means, standard errors, and P-values for each digestive organ and total gastrointestinal tract are shown in Table 1. The fresh mass of the small intestine was greater in the samples from Villavicencio and Nacúñan than Matagusanos, whereas El Leoncito samples were intermediate between both habitats. No significant differences were observed among seasons. Dry mass values followed a tendency similar to fresh mass regarding differences among sites, but also were significantly affected by season. The nominal surface area of the small intestine was unaffected by season, even though there were significant
effects of site and in the site \times \text{season} interaction. Higher values were during the wet season in individuals from Nacuñá and Villavicencio, and smaller values during the same season in El Leoncito.

Fresh mass of the cecum changed between sites, being smaller in Matagusanos. There were seasonal changes in Nacuñá samples, where fresh mass was greater in the dry season. Dry mass showed similar effects of site, and did not change between seasons. Mean nominal surface area of the cecum for El Leoncito in the dry season was higher than for all the other sites and seasons.

Fresh and dry mass of the colon were affected by site and season and the highest means were for the Nacuñá and Matagusanos populations. Nominal surface area of the colon at El Leoncito and Matagusanos was greater than at the other sites during the dry season. Nominal surface area of the colon of cavies from Matagusanos did not change between seasons. In Nacuñá and Villavicencio, nominal surface area of the colon was greater in the wet season, whereas in El Leoncito, it was greater in the dry season.

Finally, size of the total gastrointestinal tract changed between sites and showed no effect of season. Total dry and fresh masses were lower for the Matagusanos population and total nominal surface area was greatest in the El Leoncito and Matagusanos populations.

**DISCUSSION**

A major area of interest in comparative ecological physiology has been understanding how animals cope with changing environmental demands in time and space. Our study related environmental variables associated with habitat food quality to responses by the digestive tract. We found effects of site and season on every organ tested. In selecting predictor and dependent variables in the field, we followed the guidelines of a great number of controlled experimental studies regarding different models, conditions, and consequences (Bozinovic 1995; Starck and Rahmaan 2003).

A strict herbivore such as *M. australis* might indeed be affected by changes in its trophic environment, and the different ways of responding to these changes probably include modulation at morphological, physiological, and behavioral levels. We focused on form, which has traditionally been related to function (Brown and Lasiewski 1972; Martínez del Río et al. 1994), treated theoretically (Alexander 1993, 1994), and usually not assessed in field studies. Furthermore, the issue has been treated interspecifically (i.e., comparing different species or genera within a family, often specialists on different types of food—Ellis et al. 1994; Langer 1991) and intraspecifically in controlled laboratory experiments (Gross et al. 1985; Hammond and Wunder 1991).

An important digestive response is an increase in mass of digestive organs, a result that has been recorded experimentally (Bozinovic et al. 1988; Green and Millar 1987; Sabat and Bozinovic 2000; Schwaibold and Pillay 2003; Toloza et al. 1991). In this sense, increased gut size in response to variation in nutritional quality can yield several benefits to an animal. By increasing the total number of transporters in the gut lining or by allowing food retention time to remain constant with increased food intake, a greater amount of energy will be made available to the animal (Hammond and Wunder 1991).

In the field it is not possible to discriminate among the effects of environmental factors such as temperature, diet quality, and plant secondary compounds. Furthermore, reproductive state may combine with these environmental factors and create a complex scenario that is temporally and spatially heterogeneous. There is probably a whole set of characteristics enabling this species to have such a broad geographic range. Our study aimed not only to test predictions from theory, but also to detect intraspecific variation and how much of this variation can be explained by habitat factors under natural conditions. Accordingly, we selected heterogeneous conditions to examine changes temporally, considering the marked seasonality of arid lands, and spatially, considering the geographic versatility of *M. australis*.

With regard to nutritional quality for the populations studied, chemical analysis of vegetation indicated that the lowest nutritional quality corresponded to El Leoncito, whereas the Matagusanos population was exposed to a highly fibrous but also nitrogen-rich diet. The population from Nacuñá showed a diet similar to that of cavies from Matagusanos, but with a lower concentration of fiber in the diet during the wet season and also a lower concentration of nitrogen. Finally, cavies from Villavicencio presented the lowest fiber level in their diet, but also the lowest values of nitrogen. The gradient of fiber in plant resources is at least in agreement with what we expected from the climate characteristics at each locality. The nitrogen gradient is apparently dependent on the availability of plant species, because, for instance, when nitrogen-rich *Prosopis* were present, they were highly selected over other species (P. L. Sassi, in litt.). As reported by different studies, plants with high nitrogen content are preferred by mammals (Bozinovic 1997; Lindroth and Batzli 1984; Marquis and Batzli 1989). Plant fiber and nitrogen content varied differently among sites, implying a gradient of nutritional conditions to cavies, and their diet selection ultimately defined the quality of ingested food.

In relating morphological digestive responses to environmental characteristics, there were almost no differences

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**Table 2.** Multivariate analysis of covariance table showing the effects of mass, sex, season, and site on digestive organ sizes in cavies (*Microcavia australis*) collected from 4 locations in the Monte Desert, Argentina, during wet and dry seasons in 2003 and 2004.

<table>
<thead>
<tr>
<th></th>
<th>Wilks’ value</th>
<th>F</th>
<th>Effect d.f.</th>
<th>Error d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass</td>
<td>0.31</td>
<td>4.58</td>
<td>9</td>
<td>19.00</td>
<td>0.003</td>
</tr>
<tr>
<td>Sex</td>
<td>0.44</td>
<td>2.59</td>
<td>9</td>
<td>19.00</td>
<td>0.038</td>
</tr>
<tr>
<td>Season</td>
<td>0.32</td>
<td>4.29</td>
<td>9</td>
<td>19.00</td>
<td>0.004</td>
</tr>
<tr>
<td>Site</td>
<td>0.04</td>
<td>4.22</td>
<td>27</td>
<td>56.13</td>
<td>0.001</td>
</tr>
<tr>
<td>Sex \times season</td>
<td>0.46</td>
<td>2.41</td>
<td>9</td>
<td>19.00</td>
<td>0.050</td>
</tr>
<tr>
<td>Sex \times site</td>
<td>0.33</td>
<td>0.94</td>
<td>27</td>
<td>56.13</td>
<td>0.555</td>
</tr>
<tr>
<td>Season \times site</td>
<td>0.06</td>
<td>3.13</td>
<td>27</td>
<td>56.13</td>
<td>0.000</td>
</tr>
<tr>
<td>Sex \times season \times site</td>
<td>0.43</td>
<td>0.69</td>
<td>27</td>
<td>56.13</td>
<td>0.847</td>
</tr>
</tbody>
</table>
between the information recorded for fresh and dry mass. Therefore, we conclude that the proportion of water in tissues was approximately equal in all organs assessed. On the other hand, the nominal surface area yielded complementary information pertaining to the size of digestive organs.

Size of the small intestine is one of the most studied variables in experiments on responses of mammals to energetic and nutritional conditions (Buret et al. 1993; Stain et al. 2005; Starck and Rahmaan 2003). There have been numerous laboratory studies describing increases in size of the small intestine and interpreting its functional significance. We found a significant effect of sex on the size of the small intestine. Generally mean intestinal size was significantly greater in females, which could be related to energy demands for pregnancy or lactation, particularly during the reproductive season in summer (Bozinovic et al. 1990). Therefore, by using sex as a factor in the analysis, we controlled for the effects of reproductive demands, preventing it from masking the effects of site and season. Intestinal mass was lowest in the Matagusanos population, which had high fiber content but also the highest nitrogen level in the diet. Intestinal mass was greatest in the Villavicencio population, which was the site with lowest plant nitrogen content, suggesting that nitrogen could be at least in part accounting for fresh and dry masses of the small intestine. Furthermore, the change in mass of one organ is limited by the change in another. In the Matagusanos population, there was probably a trade-off between selective pressures from water balance and diet quality, which is better compensated through increases in another digestive organ (i.e., colon). Morphology of the small intestine of cavies showed an important interaction between season and site, with the greatest intestinal area corresponding to samples from El Leoncito, the site with lowest plant nitrogen content, suggesting that nitrogen could be at least in part accounting for fresh and dry masses of the small intestine. During the wet season, areas of the small intestine from cavies from Villavicencio and Nacuñañ were greatest, and we suspect this difference was an effect of reproductive activity. Hammond and Wunder (1991) have reported no changes in size of the small intestine due to dietary fiber, but did report a change associated with increased energy demand by cold. During the dry season, when sex has no significant effect ($P > 0.05$), we concluded that the area of the small intestine changed according to predictions related to diet quality, being largest in the poorest quality environment, El Leoncito.

We found no effect of sex on cecum size parameters, probably because size of the cecum depends mainly on the input of fiber into fermentation (Buffenstein and Yahav 1991). Fresh and dry masses of the cecum partially responded to differences in fiber content among sites. For example, the mean cecum masses from the El Leoncito population were higher than those from other sites, as expected theoretically because this site showed the lowest-quality diet, especially during the dry season. Increases in cecum mass also were detected in Villavicencio and Nacuñañ populations, as predicted from nutritional information (Table 1).

Colon mass varied significantly among sites and seasons, with a general tendency for higher values in the dry season than in the wet season, particularly in populations from Villavicencio and Nacuñañ, where there is a marked seasonality in rainfall. Colon area, on the other hand, showed a marked gradient in the dry season: the largest colon sizes were in cavies from the Matagusanos and El Leoncito populations, followed by cavies from Nacuñañ and finally Villavicencio. According to our predictions, the nominal surface area of this organ increases with increasing levels of fiber in the diet. Nevertheless, this change also could be associated with water balance. The colon is an organ with a well-known role in water balance, particularly in species of desert rodents (Bozinovic and Gallardo 2006; Forman and Phillips 1993; Schmidt-Nielsen and Schmidt-Nielsen 1952). Water balance is probably an important factor interacting with diet quality in determining interpopulational and seasonal variations in morphological parameters (Nagy and Gruchacz 1994). Regarding the occurrence of larger colons in cavies from Villavicencio, Nacuñañ, and Matagusanos in the wet season, it is important to emphasize that although summer coincides with greater rainfall and the diet is more nutritious, evaporative losses could be higher than in winter because of high temperatures. This may turn the water balance negative, thereby imposing a higher demand for recovering water in summer (Walsberg 2000). In the El Leoncito population, there was a significant change between seasons, probably reflecting the decrease in fiber shown in Table 1.

The effect of site was significant for total gastrointestinal tract size, and could be due to marked and sustained differences in the quality of diets. The lack of effect of season (even though seasonal effects occur in individual organs) could be related to a trade-off between organs changing in response to different demands, but limited by a maximum size of the total tract.

The morphology of the digestive tract of an animal, as well as its behavior and the environmental demands it faces, determine the limits to the food resources that can be used. Although the input of energy and nutrients into the digestive tract is typically periodic, it is clear that many aspects of digestive physiology are likely to be flexible depending on the spatial and temporal environment (Naya et al. 2005). As we show here, digestive traits show a certain degree of plasticity, allowing $M. \text{australis}$ to match its performance to variations in nutrient and energy availability on both a spatial and a seasonal basis. In addition, we have demonstrated a clear intraspecific variation in $M. \text{australis}$, probably coupled with its remarkable versatility at seasonal and geographic levels. The relative importance of the different cues that allow this species to deal with energy constraints associated with its habitat use and trophic habits still need to be tested under controlled conditions.

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SASSI ET AL.—VARIATION IN DIGESTIVE TRAITS OF CAVIES


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