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FROM SIMPLE QUESTIONS TO COMPLEX ANSWERS: A RESEARCH PROGRAM BASED ON DIET SELECTION AND WATER BALANCE OF SMALL MAMMALS

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ABSTRACT

Information on key biological traits is fundamental to understand complex ecological processes, and to develop mechanistic models of geographic distributions and community structure based on functional attributes. These ideas were the main motivation behind pioneer studies on food habits, diet selection, and ecophysiology of small mammals coordinated by Dr. Rui Cerqueira at the Laboratório de Vertebrados (LABVERT) of Universidade Federal do Rio de Janeiro (UFRJ). Here we review his research program and his most important contributions on diet selection and water balance, which were studied to understand community structure, biogeography, and species distribution. Studies of diet selection varied from fecal content analyzes to comparative morphometric and anatomical studies of digestive organs, and its relations to diet digestibility. One of the main contributions was the development of a method to experimentally establish diet selection and food preference in laboratory. Previously, most Neotropical marsupials were simply described as omnivorous, but using this method it was possible to detect that species are distributed along a gradient of nutrient and food consumption, from frugivory to carnivory. A study of the water balance and urine concentration by the marsupial *Philander frenatus* supported the hypothesis that it is dependent on mesic habitats because of its limited ability to concentrate urine. This study also set the experimental apparatus used later in intra and interspecific comparisons, successfully determining local adaptation to different habitats in populations of the same species, and the physiological limitations of different species to occupy more xeric habitats. The experiments to determine diet selection and water balance by small mammals allowed unique inferences on intrinsic characteristics of populations and species, important aspects of their fundamental niche. They also provided the basis to characterize the function that these species may provide in communities and ecosystems.

Keywords: digestive morphology; ecophysiology; food habits; nutrition; trophic niche; water balance.

INTRODUCTION

The progress of Ecology as a science depends on the development of models and theories, a particularly important enterprise to provide answers to current environmental issues (Scheiner and Willig 2011). These advances, however, depend on basic information about the organisms involved, which in many cases are completely unknown. Taking small mammals as a study group, basic biological information is fundamental to understand their ecology and evolution, as well as develop mechanistic models of geographic distributions and community structure. These ideas only recently are being incorporated in geographic distribution modeling (Kearney and Porter 2009), and in a trait-based understanding of community structure (Webb *et al.* 2010). However, they were the main motivation behind studies on food habits, diet selection, and ecophysiology coordinated by Dr. Rui Cerqueira at the Laboratório de Vertebrados (LABVERT) of the Universidade Federal do Rio de Janeiro (UFRJ), since its foundation in 1982. “Scientific knowledge begins with simple questions” as Dr. Cerqueira uses to say. Before trying to elaborate complex questions about population ecology, community structure, and biogeography, we have to answer questions as simple as those made by zoo visitors: “What does this animal eat?”, “How many puppies does it have?”, “Where does it live?” Many studies and research projects fostered by Dr. Cerqueira tried to answer those simple questions, generating new and valuable scientific knowledge on small mammal’s biology and ecology, using this information to investigate more complex issues in ecology.

Here we review the most important contributions of Dr. Cerqueira’s pioneer scientific research program on diet selection and water balance. We also discuss how this basic information may allow new insights on events occurring at large spatial scales, involving community structure, biogeography, and species distribution modeling. Valle and Lorini (this volume) reviewed his contribution in these areas. Studies of diet selection and water balance focused on didelphid marsupials and small rodents, the “small mammals” in most of the Neotropical region. Studies on food habits varied from fecal content analyses (Santori *et al.* 1995a, Santori *et al.* 1997, Ceotto *et al.* 2009) to comparative morphometric and anatomical studies of digestive organs (Santori *et al.* 1995b, Santori *et al.* 2004, Finotti *et al.* 2012), and their relations to diet digestibility (Santori *et al.* 1995b) and diet choice (Périssé *et al.* 1988, Perissé *et al.* 1989, Cerqueira *et al.* 1994, Santori *et al.*, this volume). One of the main contributions, over which most of these studies were built, was the development of a method to experimentally establish food preference in laboratory conditions (Perissé *et al.* 1988, Perissé *et al.* 1989).

FEEDING HABITS IN NATURE AND FOOD PREFERENCE IN LABORATORY

Studies on food habits of didelphid marsupials conducted by Dr. Cerqueira were the starting point for other studies developed between the late 1980s and mid-1990s. At that time, French researchers in Guyana performed most of the studies on Neotropical mammal feeding habits in nature (Charles-Dominique *et al.* 1981, Atramentowicz 1988, Julien-Laferrière and Atramentowicz 1990). In the 1990s, studies on natural diet of didelphid marsupials answered some basic questions, including the identification of most common food items in the wild, diet seasonality, and interspecific differences in diet between sympatric species of marsupials (Santori *et al.* 1995a, Santori *et al.* 1997). These studies started to cast light on the subject, generating new questions to deepen the understanding of diet selection by animals with a broad range of food habits. Until then, didelphid marsupials were frequently characterized generally as small solitary mammals, nocturnal and omnivorous.

The methodological limitations of the analysis of fecal samples in the field to identify and quantify dietary items, together with the need to raise animals in captivity for reproduction and ecophysiological studies, led Dr. Cerqueira and his students to develop an experimental method capable of elucidating not only species' diet, but also diet selection or preference, and consumption of macronutrients (Périssé *et al.* 1989), based on cafeteria experiments (review in Meier *et al.* 2015). Experimental diet determination consisted in simultaneously offering 26 kinds of foods in known amounts, varying from animal to vegetal matter, recording the amount consumed, and calculating a food preference index for each food item consumed. The method, through the free choice of food items, addressed several difficulties: (1) it can be done anywhere at any time of the year, (2) it allows the identification and quantification of any food item used, and (3) it experimentally standardized food availability. Thus, the study of diet selection in captivity reveals the intrinsic aspects of each species responsible for the differential use of food. Because the method gives the animal unlimited access to the different food items, the actual selection based on preference can be determined. Fecal and stomach content analyses have provided an estimate of food resources used in nature (realized niche), but not the selection or preference of food items (the actual diet selection), since estimating availability of such itens in the field as well as identifying digested items found in stomach content and feces of small mammals is rather difficult. In addition, the variation in food availability in nature, and species' plasticity in resource use has resulted in the classification of all species of didelphids as omnivores, *i.e.,* all consume items of animal (mainly arthropods) and plant (fruits) origin (Santori *et al.* 1995a, Santori *et al.* 1997). The diet selection experiment conducted in the laboratory enables different species to select preferred food items, an estimate of their fundamental niche, even if commercially produced foods are used. Because the supply of resources is standardized, the experiment allows inter- and intraspecific comparisons (Périssé *et al.* 1988, Cerqueira *et al.* 1994, Santori *et al.* 1997, Cerqueira *et al*. 2003), eliminating the effect of varying food availability.

In general, critics to the experimental procedure of Perissé *et al.* (1989) and to cafeteria experiments are related to the use of commercial food items that are not found in nature, or that are found in nature but not in the way offered at the experiment. However, only cafeteria experiments allow inference on the intrinsic factors that drives food choice, such as dentition, digestive tract anatomy and physiology, food recognition and selective food intake (Finotti *et al.* 2012, Meier *et al.* 2015), hence to infer the ability of an organism to identify, find, obtain and process food resources (for details see Santori *et al.*, this volume). This kind of inference is impossible in field studies using fecal or stomach analyses, with large variety of potential food items, of unknown availability, and inaccurate estimates of consumption and absorption. However, the use stable isotopes is allowing detailed information on assimilation efficiencies of plant and animal material of different origins (review in Crawford *et al.* 2008).

Using the experimental procedure of Perissé *et al.* (1989), Astúa de Moraes *et al.* (2003) demonstrated that 12 didelphids previously considered omnivorous are actually distributed along a gradient of nutrient consumption (Figure 1). At one extreme are more carnivorous species, with high protein intake, such as *Chironectes minimus* (Zimmermann 1780), *Lutreolina crassicaudata* (Desmarest 1804), *Monodelphis americana* (Müller 1776) and *Philander frenatus* (Olfers 1818); at the intermediate position, consuming equivalent amounts of carbohydrates, proteins and fats, are *Didelphis albiventris* Lund 1840, and *Didelphis aurita* Wied-Neuwied 1826; at the other extreme, with a high carbohydrate intake, is *Caluromys philander* Linnnaeus 1758. Although species' omnivorous status has not changed, the diet selection experiment allowed an estimate of macronutrients intake, which revealed subtleties, ordering species in a gradient that goes from omnivorous species with a tendency to carnivory, to omnivorous species tending to frugivory. In some cases, the laboratory diet selection experiment corroborated field data, as is the case of the omnivory of the genus *Didelphis*, the carnivory of *Lutreolina* and *Chironectes*, and the omnivorism-frugivory of *Caluromys* spp. For *Philander frenatus*, experimental results strengthened the hypothesis of omnivory with a tendency to carnivory, as had been advocated by Santori *et al.* (1995b), based on anatomical and digestive efficiency analysis. Additionally, the experiments provided information on dietary habits for poorly known species such as *Monodelphis americana*, *Marmosa demerarae* (Thomas 1905), *Gracilinanus agilis* (Burmeister 1854), and *Marmosops incanus* (Lund 1841), the last three being closer to *Caluromys philander* in terms of nutrient intake (Astúa de Moraes *et al.* 2003).

In terms of intraspecific variation, the diet selection experiment enabled the study of the overlap in trophic niche, diet breadth and nutritional needs of individuals of distinct sex, age and reproductive stage (Perissé *et al.* 1989, Santori *et al.* 1997). These experiments confirmed the existence of intraspecific variation in food preference and diet selection, hardly detectable from fecal or stomach content analyses. Individual variation has been recently recognized as an important issue in ecological theory (Bolnick *et al.* 2003), and the diet selection method combined with

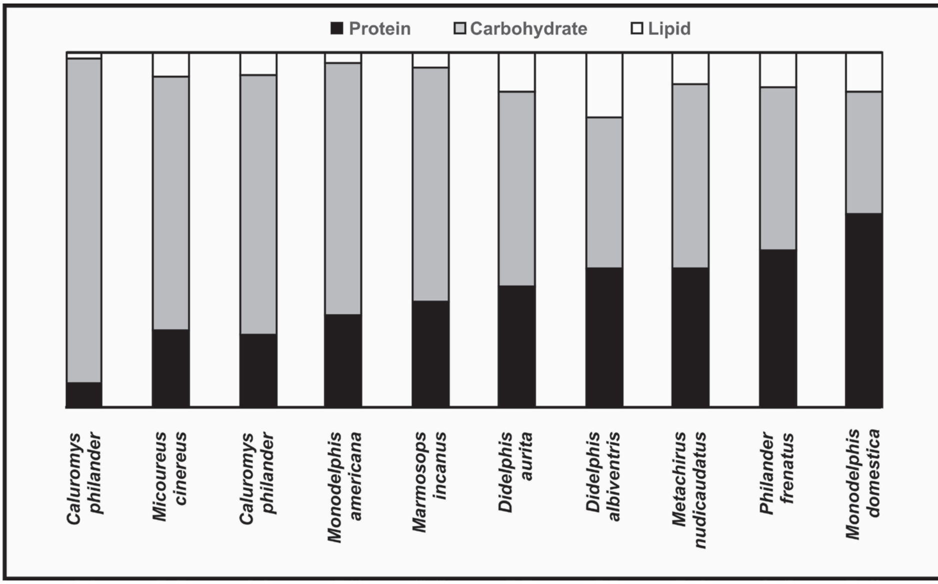

Figure 1. Relative proportions of protein, carbohydrates and lipids on 12 Neotropical marsupial species diets. Note the increasing gradient in proportion of protein (from left to right), and the proportional decrease in carbohydrates (modified from Astúa de Moraes *et al.* 2003).

isotopic analyses (Crawford *et al.* 2008) are tools that allow the quantification of individual variation in diet selection.

Understanding these different aspects of small mammal dietary habits in the wild can provide important insights on how small mammal communities are structured. However, as stated above, limitations of fecal and stomach content analysis, and variation in food availability in nature provide an imprecise and biased picture of trophic niche. Thus, diet selection experiments could also be used to study trophic structure of an assemblage of small mammals based on food preference gathered experimentally. Indeed, Cerqueira *et al.* (1994) detected segregation between species after combining food preference indices obtained from trials with didelphid marsupials, rodents and a lagomorph species, with data on population and microhabitat characteristics. This segregation between species was only detected because of the more accurate and precise characterization of diet provided by the diet selection experiment.

DIGESTIVE MORPHOLOGY

As diet selection experiments allowed an advance in accuracy and precision in estimation of composition and nutritional content of diets, it was also possible to investigate hypotheses of the relationship between feeding habits and digestive tract measurements at inter and intraspecific levels (Santori *et al.* 2012, Finotti *et al.* 2012) (Figure 2).

Thus, studies of digestive tract characteristics of small terrestrial mammals conducted under supervision of Dr. Cerqueira focused on understanding differences in diet among species in terms of digestive tract features in an adaptive context. The principal contribution in this area was to elucidate the parallel between differences found in digestive tract of ten didelphid species and their feeding habits according to field and laboratory studies. Considering the distribution of didelphid species on the omnivory gradient mentioned earlier, the digestive tract characteristics of *C. philander* are consonant with a diet with higher content of fiber from fruits (complex caecum), *P. frenatus* and *L. crassicaudata* agree with their high protein content diet (simple stomach morphology and long intestine), and *Didelphis* species with their generalized feeding habits (long posterior digestive tract) (Figure 3).

WATER BALANCE

In the 1950's and 1960's, studies on the water balance of North American desert rodents demonstrated that some species had the ability to produce a highly concentrated urine (Schmidt -Nielsen and Schmidt -Nielsen 1952), and in 1970's and 1980's similar ability was demonstrated in Australian marsupials (Kinnear *et al.* 1968, Dawson and Denny 1969, Barker 1971, Morton 1980). By the end of 1980's, many studies on urine concentration, kidney morphometry and evaporative water loss (EWL) were developed (Christian 1983). Therefore, this physiological ability was considered very important to explain species' habitat differentiation at distinct geographic scales (MacNab 1982).

During that time, Michael A. Mares and Brian McNab studied body mass loss

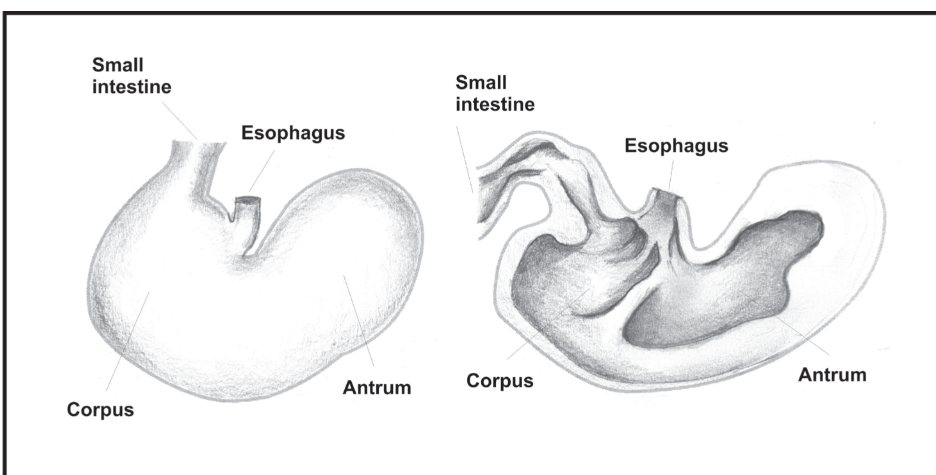

Figure 2. Stomach morphological characteristics (modified from Finotti *et al.* 2012).

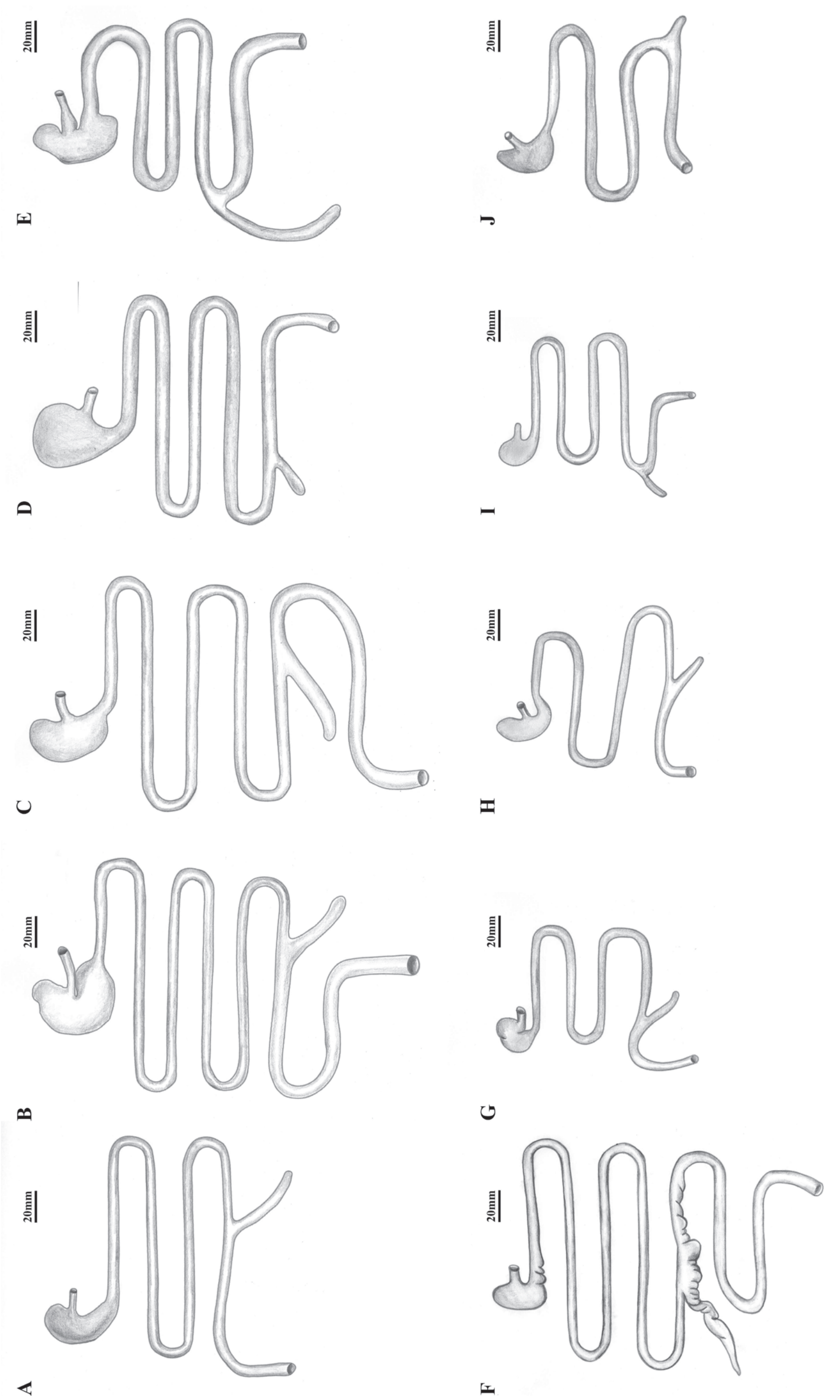

Figure 3. Gastrointestinal tract of ten didelphid marsupials. A. *Philander frenatus*, B. *Didelphis albiventris*, C. *Didelphis aurita*, D. *Lutreolina crassicaudata*, E. *Metachirus nudicaudatus*, F. *Caluromys philander*, G. *Monodelphis domestica*, H. *Marmosa paraguayanus*, I. *Gracilinanus agilis*, J. *Marmosops incanus* (modified from Santori *et al.* 2004).

by South American desert rodents under water deprivation regimes and found clear differences between species related to differences in habitat use (Mares 1977a, b). These studies showed that the ability to produce highly concentrated urine should be determinant of the occupation of environments with water deficit and drought periods, and that the geographic distribution of small mammals in these environments could be influenced by their ability to concentrate urine. The first study developed by Dr. Cerqueira and his student, Carlos R. S. D. Fonseca (Fonseca and Cerqueira 1991), evaluated the ability of a widely distributed marsupial, *Philander frenatus* (at that time, *Philander opossum*), to concentrate sodium and potassine under different diets and NaCl solution concentrations (Figure 4). Species of this genus occur in mesic environments, or close to water streams (Hershkovitz 1997). The hypothesis that *P. frenatus* did not have the ability to produce a highly concentrate urine was confirmed by the experiments, explaining the species' dependence on mesic habitats. They also showed the importance of diet composition on the maintenance of body mass, and its implications to the evolution of the group. This was one of the first studies of urine concentration ability on a Brazilian small mammal species. At that time, only Streilen (1982) had studied body mass loss associated with water deficit in small mammals of the Caatinga, and Christian (1983) studied EWL and urine concentration of *Monodelphis domestica* Burnett 1829.

Using the same procedure, diet choice and urine concentration were also studied on a small spatial scale to test the influence of feeding habits and water physiology on intraspecific habitat differences (Cerqueira *et al.* 2003). The preferred diet items and urine concentration ability were compared between two populations of *Akodon cursor* (Winge 1888) inhabiting a Brazilian *restinga*, but occupying habitats with different flood regimes, vegetation and soil cover. There was a clear relationship between habitat occupancy and diet choice (but not urine concentration) on a local scale, highlighting the importance of ecological processes on intraspecific niche partitioning. Diet of the *restinga* scrub population was composed by fruits, roots, seeds items and arthropods (shrimps), whereas marsh populations preferred only roots and fruits items (Figure 5). These studies exemplify Dr. Cerqueira's view, using informative physiological and life history traits to understand evolutionary processes occurring at small and large spatial scales, determining intraspecific variation in habitat preference and geographic distribution.

Extending this approach of urine concentration ability to interspecific comparisons posed new problems. How to compare urine concentrating ability between individuals of different species if they are raised and exposed to quite different conditions and environments? How to sort out local environmental effects and aspects of the realized niche from inherent and fundamental niche differences (*sensu* Hutchinson 1957)? This is essential to relate urine concentration

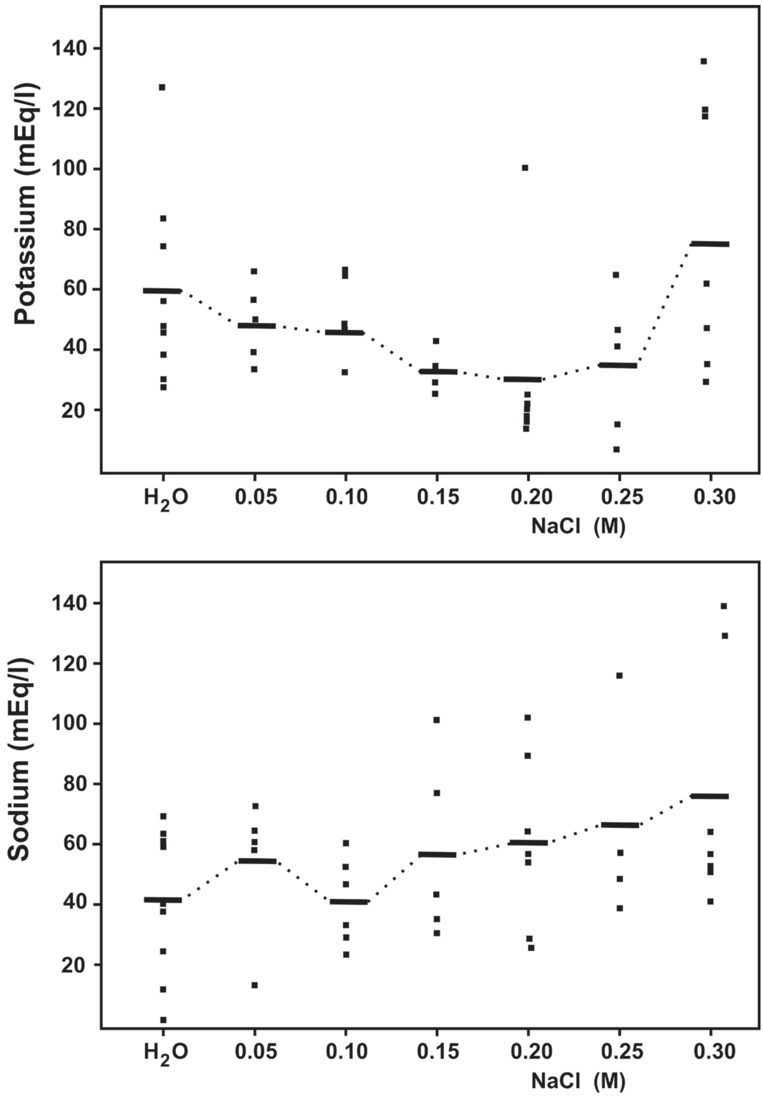

Figure 4. Concentration of potassium and sodium in the urine of *Philander frenatus* under increasing saline solution concentrations (modified from Fonseca and Cerqueira 1991).

ability to geographical distribution and habitat occupancy. To deal with this issue and based on kidney function knowledge, a new approach was developed to evaluate species' maximum concentration ability under standard laboratory conditions.

The kidney counter-current mechanism increases urine concentration by increasing water reabsorption

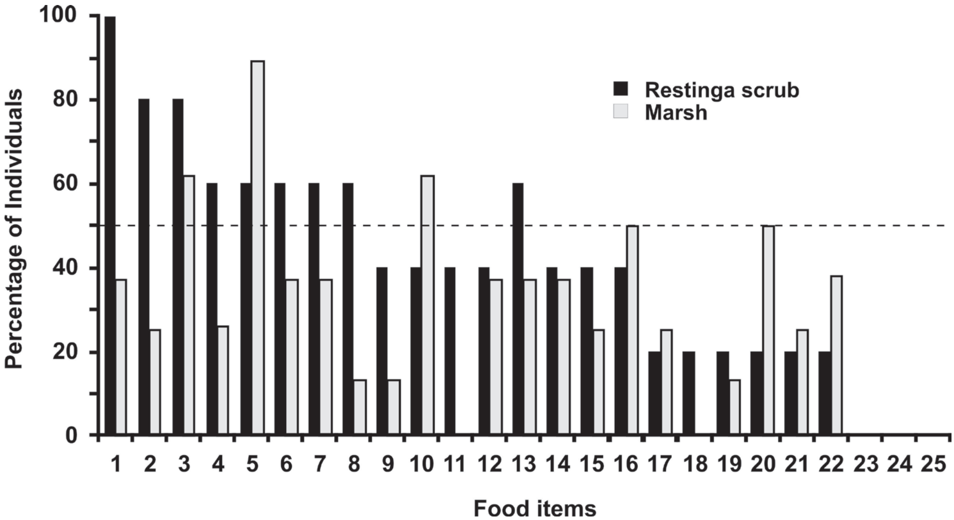

Figure 5. Food items and food preferences of two *Akodon cursor* populations in restinga de Maricá, Rio de Janeiro state, Brazil. Bars shows percentage of individuals from each group that preferred each food item offered at food choice trials. Items preferred by 50% or more individuals differ between the two groups (1: peanuts, 2: shrimp, 3: orange, 4: carrot, 5: banana, 6: pumpkin, 7: cucumber, 8: corn, 9: sweet potato, 10: manioc, 11: beet root, 12: lettuce, 13: cabbage, 14: zucchini, 15: gambo, 16: pea, 17: turnip, 18: yam, 19: spinach, 20: tomato, 21: pimento, 22: fruit of the eggplant, 23: quail egg, 24: chayot, 25: green husk (modified from Cerqueira *et al*. 2003).

and, consequently, decreasing water excretion in a gradual manner, where water concentration decreases and salt and urea concentration increases (Schmidt-Nielsen 1996). Many physiological pathways are possibly responsible for this mechanism. Species' differences in concentration ability can be related to a variety of mechanisms, from molecular pathways (*e.g.* quantity and quality of aquaporin channels) to anatomical features (*e.g.* collector duct length) (Bozinovic and Gallardo 2006). Regardless of the mechanism involved, the final result under persisting hydric stress is the production in the maximum concentration possible, taking individuals to reach their osmotic ceiling. Therefore, new experiments were devised to calculate the maximum theoretical concentration ability by inducing individuals to hydric stress, and monitoring the increase in urine concentration with time until the animals reach osmotic ceiling (Schmidt-Nielsen 1996).

Water deprivation experiments consisted of measuring temporal variation of urine concentration, body mass loss and urine volume excreted at trials of 30 hours, when urine was collected on six hour periods. In a study that compared three phylogenetically close rodent species with distinct habitat characteristics (Finotti *et al.* unpublished data), more xeric habitat species not only had the highest urine concentration, but also achieved osmotic ceiling in a shorter time, with less variation in the frequency of achieving it (*Akodon cursor* (Winge 1887) - more mesic habitats, against *Akodon lindberghi* Hershkovitz 1990 and *Necromys lasiurus* (Lund, 1841) - more xeric habitats). Xeric habitat species also had lower body mass loss, and a reduced urine excretion than species from mesic habitats. Therefore, these results supported the idea that physiological limitations linked to water availability are important to understand habitat differences. Another result from these experiments is that there may be specific differences not only in maximum urine concentration ability but also in the physiological ways that species achieve it (Finotti *et al.* unpublished data) (Figure 6). Control treatments are better fit by sine functions, while test treatments by logistic functions. These two types of functions demonstrate a circadian variation in urine concentration in control treatments, while in test treatments concentration increases with time until achieving a high osmolarity ceiling.

Many other techniques were developed since the 70's that are capable of measuring global water flux, such as the use of tritiate water to measure water turnover rates (WTR) (Muleen 1971, Yousef *et al.* 1974, Hewitt *et al.* 1981, Cortés *et al.* 2000, Zhu *et al.* 2008) and field metabolic rate (FMR) (Cooper *et al.* 2003). However, South American small mammals studies still focus mainly on urine concentration capacity (Cortés *et al.* 1988, Carvalhães *et al.* this volume), ingestive balance (Mendes *et al.* 2004), and kidney morphology and morphometry (Diaz and Ojeda 1999, Al-kahtany *et al.* 2004). These studies demonstrate that, although South American small mammals do not achieve urine concentrations as high as that achieved by Australian and North American species, they "possess structural as well as physiological systems for water conservation, which are as remarkable as those found in ''classical'' rodents inhabiting other desert areas of the world" (Bozinovic and Gallardo 2006). The studies of Dr. Cerqueira's group on Brazilian small mammals, in addition to other research groups in South America, form the baseline to understand this great physiological diversity, and to start the integrative and mechanistic approaches of molecular physiological ecology (Bozinovic and Gallardo 2006).

CONCLUSIONS

The experiments to determine diet selection and water balance by small mammals, devised and applied by Dr. Cerqueira and his students, allowed unique inferences on intrinsic characteristics of South American small mammal species, and important aspects of their fundamental niche. They also provided the basis to characterize the function that these species may provide in communities and ecosystems. Subtle differences in adaptation to frugivory and carnivory were demonstrated by these experiments (Astúa de Moraes

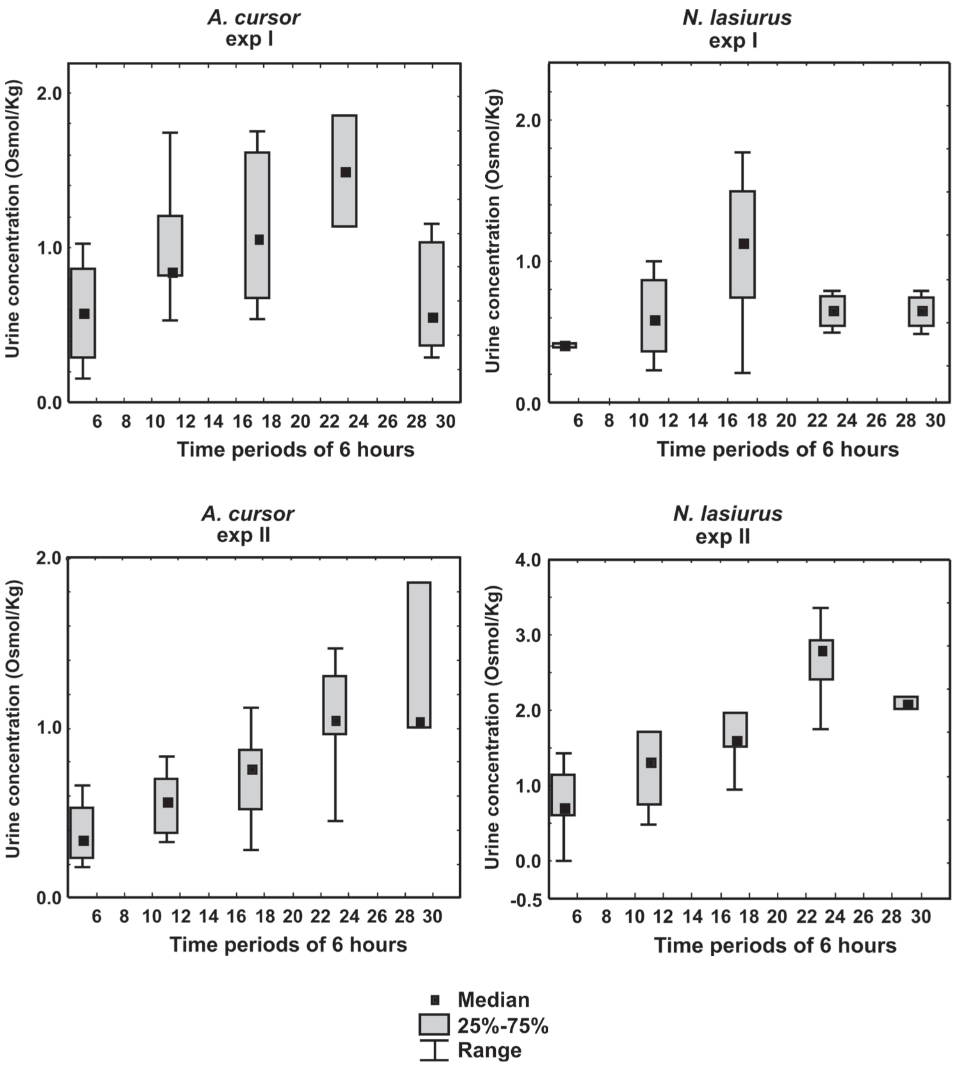

Figure 6. Temporal daily pattern of urine concentration (mOsmol/l) during 30 hours trials on water and food ad libitum conditions (expI) and on water and food deprivation (expII) of two sigmodontini species that occurs at localities with different climatic conditions. *Akodon cursor* lives at more mesic habitats and *Necromys lasiurus* lives at more xeric habitats, like *Caatinga* semi-arid localities (from Finotti *et al.* unpublished).

et al. 2003), combined with studies of the anatomy of the digestive tract (Santori *et al.* 1995b, Santori *et al.* 2004, Finotti *et al.* 2012). Still today, analyses based only on fecal or stomach contents of small omnivorous mammals find conflicting results because food availability usually cannot be evaluated and incorporated to determine actual choice of food items. Similarly, water balance experiments also allowed the determination of intrinsic abilities of species, separating environmental and phylogenetic effects. The incorporation of this information in species distribution models and biogeographic analyses can improve the accuracy of their predictions (Vale and Lorini, this volume). Dr. Cerqueira's view that basic information on intrinsic abilities of species are a fundamental information for more complex approaches may be crudely summarized by one of his metaphors, "*Escargot* is excellent, but there is nothing like a good and well-made pork chop sandwich".

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