Canadian Journal of Zoology

A comprehensive review of dietary strategies of sigmodontine rodents of central-eastern Argentina: linking diet, body mass and stomach morphology

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2021-0042.R1
Manuscript Type:	Article
Date Submitted by the Author:	22-Apr-2021
Complete List of Authors:	Barbero, Sofía; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Mastozoología; Consejo Nacional de Investigaciones Científicas y Técnicas Teta, Pablo; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Mastozoología; Consejo Nacional de Investigaciones Científicas y Técnicas Cassini, Guillermo; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Mastozoología; Universidad Nacional de Luján, Departamento de Ciencias Básicas; Consejo Nacional de Investigaciones Científicas y Técnicas
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	small mammals, feeding ecology, SIZE < Discipline, DIGESTIVE SYSTEM < Organ System, Neotropics, Pampas, Rodentia

SCHOLARONE™
Manuscripts

A comprehensive review of dietary strategies of sigmodontine rodents of central-eastern Argentina: linking diet, body mass and stomach morphology

Sofía Barbero (1, 2), Pablo Teta (1, 2), Guillermo H. Cassini (1, 2, 3)

(1) División Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina.

(2) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Argentina.

(3) Departamento de Ciencias Básicas, Universidad Nacional de Luján, Ruta 5 y Av. Constitución s/n, Luján (6700), Buenos Aires, Argentina.

Corresponding author: Sofía Barbero (sofibarbero@gmail.com)

Running title: **Dietary strategies of central-eastern Argentine sigmodontines**

Competing interests: The authors declare there are no competing interests.

Abstract

Information on dietary ecology plays a key role in a wide array of biological research and conservation decisions, but its availability is biased towards large and charismatic taxa, whereas small mammals are underrepresented. Of the scarce publications on the Neotropical sigmodontine rodents, most are concentrated in central-eastern Argentina, and, up until now, no revision of the totality of these data has been made available. In this work, we performed a thorough review of the dietary information from over 50 publications on 22 species, finding omissions and errors propagated up to the present time. This resulted in a robust database, the proposal of *a posteriori* dietary categories, and a list of the species that have been neglected in feeding ecology research. In turn, we used that database to test whether the patterns which associate diet and morphology in medium and large mammals could be replicated in these small rodents, despite their overall generalist habits and the restrictions characteristic to their size. We found that larger species tend towards a low-protein diet. Additionally, we identified some stomach types which are restricted to specific diets. These results are consistent with the observations for larger species and shed light on the biology of small mammals.

Keywords: small mammals, feeding ecology, size, digestive system, Neotropics, Pampas, Rodentia

Introduction

Dietary information plays a key role in a varied array of biological studies. As morphological, physiological and behavioral traits are influenced by diet, this kind of data is useful in estimating functional diversity and evolution, inferring the diets of extinct or poorly known species, examining habitat use and resource partitioning, and directing management and conservation efforts (Verde Arregoitia and D'Elía 2020). However, detailed information is scarce for over half of the mammalian species (Kissling et al 2014), with the available studies are not randomly distributed, but focused on charismatic large, long-lived and widely distributed taxa such as ungulates and carnivores (González-Suárez et al. 2012).

One of the most neglected orders in ecological research are rodents, despite accounting for the majority of the taxonomic diversity of Mammalia (Fleming and Bateman 2016; Jarić et al. 2019). Sigmodontines (Rodentia, Cricetidae), which constitute one of the most abundant and diverse groups of mammals in the Neotropics, are not an exception. Information on their diet is scattered across their range and covers mostly a few well-known species, resulting in an incomplete depiction of the relationship to their environment (Patton et al. 2015; Shaley et al. 2015). The largest concentration of research on the dietary ecology of these rodents can be found in central-eastern Argentina: in no other region of the Neotropics these studies are as abundant, covering the vast majority of the species present and even counting for some of them with detailed information (such as seasonal data) (*cf.* Patton et al. 2015). Some of the 22 species present there are representatives of some of the most speciose genera of this subfamily (e.g., *Akodon*, *Calomys*, *Oligoryzomys*) (Patton et al. 2015). Furthermore, the different assemblages occurring across this

region have been severely impacted by the recent transformation of the native landscape into agroecosystems (Crespo et al. 1970; Polop et al. 1982, 1985; Pardiñas et al. 2010a, 2010b; Teta et al. 2014), thus, their dietary information is relevant to research focusing on the anthropic effect on biodiversity (*e.g.*, Barbero et al. 2020). To date, no comprehensive synthesis of the feeding ecology of this group of sigmodontines is available, and qualitative information (constituting a large portion of the published data) is often referenced as a precedent, and not in a manner allowing for its integration with modern quantitative studies (*e.g.*, Rosi 1983). The deeper understanding of sigmodontine diets that would arise from a thorough compilation of the studies from central-eastern Argentina would also make it possible to approach those species as a case study where the relationship between diet and other aspects of their biology, such as body mass and morphology, can be explored, shedding light on the ecophysiology of small mammals.

Consistent with their richness and diversity, the dietary habits of central-eastern Argentine sigmodontines show considerable diversification. Their diets have been documented to include invertebrates, seeds, leaves and grasses (*e.g.*, Kravetz 1972; Bilenca et al. 1992; Ellis et al. 1998; Castellarini et al. 2003), but reports attempting to describe them present a wide variety of detail, using ecological categories that are often broad and non-standardized (see below). This is a common problem, which also has been documented in other clades (see Bournaud et al. 1992 for 12 environmental and three physioecological variables of aquatic beetles; Olsen 2015, 2017 for dietary habits of birds; Gagnon and Chew 2000 for diet of African bovids; Cassini and Toledo 2021 for feeding ecology of Neotropical deer). The amount and type of primary data on diet ranges from nonexistent to meticulous quantitative studies. For a handful of well-known species, diet variation has been documented for different reproductive states, seasons, regions, and even for a variety of microhabitats of the same locality (*e.g.*, crop fields and their borders; a review on diet variation of five sigmodontine species of central-eastern Argentina, comparing quantitative data

from seven studies, can be found in Dellafiore and Polop 2010). As for the rest of them, most of the information available is based on qualitative descriptions from a small number of individuals or even a single organism, while sometimes only the items relevant to the author's search are noted (*e.g.*, Massoia 1961; Hershkovitz 1966). Moreover, in some cases, all that is known of a species is that it is considered responsible for crops damage, despite the lack of direct evidence (*e.g.*, Massoia 1971).

Sigmodontines dietary classifications generally follow the same categories used for rodents. They are typically described as "omnivores" (*e.g.*, Gómez Villafañe et al. 2005; Chebez et al. 2014; Pineda-Munoz and Alroy 2014; Patton et al. 2015). Even though this class can imply a simplification of a species' ecology, it may be the best option available to summarize reports of heterogeneous nature and variable quality, especially when more refined information is unavailable (Leiser-Miller and Santana 2020; Verde Arregoitia and D'Elía 2020). This is often the case for rodents, where poor or no data at all has been published for a significant number of species (Kissling et al. 2014). However, in spite of its usefulness, this category has been questioned due to the ambiguity it involves, as it can mean either that no elements compose the majority of a species' diet, that it includes both plant and animal matter, or that the information available is ambiguous or incomplete. In a recent review on classification of rodent diets for comparative research, it was proposed to replace it for categories that can reduce its ambivalence, such as "generalist" or "unknown" (Pineda-Munoz and Alroy 2014; Verde Arregoitia and D'Elía, 2020).

Other traditional classifications include insectivores, granivores and folivores (Ellis et al. 1994; Michaux et al. 2007; Maestri et al. 2016b). General terms of this kind are based on a simplification of dietary strategies that defines a species by the food type that constitutes the majority of its diet (*e.g.*, Kerley and Whitford 1994). Some authors have proposed more detailed categories, subdividing invertebrates in adult hard-shelled arthropods and soft-bodied larvae and worms

(Martin et al. 2016; Barbero et al. 2020; Verde Arregoitia and D'Elía 2020), or distinguishing among plant matter between grass, leaves, roots and fruits (Giannoni et al. 2005; Croft et al. 2011; Hautier et al. 2012; Polop et al. 2015; a review of rodent diet classifications can be found in Verde Arregoitia and D'Elía 2020). However, even the most specific classifications are insufficient at accounting for the complexity of sigmodontine dietary habits: in literature of varied detail, descriptions of sigmodontine diets using traditional terms are most times found accompanied by clarifications of items that cannot fit in any strict food type (*e.g.*, Massoia and Fornes 1965; Barlow 1969; Kravetz 1972). This issue has been proposed to be expected upon using any *a priori* categorization (Wright et al. 2006), but may be especially true for a clade deemed for its omnivory, as sigmodontines are. The lack of consensus regarding dietary categories in these rodents complicates drawing comparisons amongst different publications, in turn, undermining the basis of studies that depend on ecological information.

Reliable sources of dietary information are crucial in researching the correspondence between diet and body mass, anatomy of skulls, stomachs, and intestines (Vorontsov 1967, 1979; Carleton 1973; Samuels 2009; Maestri et al. 2016b; Vizcaíno et al. 2016; Barbero et al. 2020). Differences in dietary composition have been linked to variations in body mass and stomach morphology across Mammalia. Low-protein or high-fiber diets have been associated to larger body sizes, and often specific stomach types, in research focusing on medium and large sized mammals (*e.g.*, Chivers and Hladik 1980; Eisenberg 1981; Peters 1983; Demment and Van Soest 1985; Gagnon and Chew 2000; Vizcaíno et al. 2012; Schiaffini and Prevosti 2014; Price and Hopkins 2015; Pineda-Munoz et al. 2016). This relationship remains to be elucidated in smaller-sized taxa (Langer and Clauss 2018), where fewer studies have explored it, presenting mainly speculative arguments and species-level evidence (*e.g.*, Carleton 1983; Ellis et al. 1994; Hume 1994). Given the specific characteristics of the biology of small mammals, which imply restrictions to their alimentary physiology and body

size variations (Eisenberg 1981; Langer 2002; Merritt 2010), we wonder if similar patterns to those reported for larger species can be observed in sigmodontine rodents. Particularly, two main questions arose: i) does body mass respond to protein content in diet?, and ii) is dietary composition associated to different stomach types?

Regarding their stomach morphology, precedents in sigmodontines have shown considerable variation between genera, although anatomical diversity among species of the same genus has been reported only for *Thomasomys* (Carleton 1973; Pardiñas et al. 2020 found differences in the thickness of the glandular epithelium between *Akodon* species, but no intra-generic stomach type variability was reported). The general anatomy of this organ was described by Carleton as “unilocular” (formed by a single cavity), divided in two parts by the esophageal opening: the antrum, that follows the linear projection of the digestive tract, and the corpus (or forestomach), a saccular protrusion towards the left side of the animal (Carleton 1973; Gärtner 2001). With respect to stomach histology, the Sigmodontinae exhibit an inner lining formed by cornified and glandular epithelia, separated by a ridge. The area covered by these epithelia varies between different genera and species. In the most common character state, called unilocular-hemiglandular, the cornified and glandular epithelia are in approximate correspondence with the corpus and antrum; though there is also variation in the relative size of each part and its associated epithelium. In some genera, the glandular epithelium is highly reduced and restricted to a small region in the fundus of the stomach (*e.g.*, forming a disc in *Scapteromys*, and a pouch in *Oxymycterus*; Carleton 1973). In his work, Carleton made an attempt at associating stomach types to dietary strategies, concluding that the existing ecological information at the time was insufficient to lead to robust results (Carleton 1973). More recent contributions have provided results supporting the association between a constrained glandular epithelium and insectivory, and between majorly cornified stomachs and folivory (with a tendency towards omnivory),

although pointing that the relation between stomach morphology and diet is weak, and that caecum morphology should be addressed instead (Hume 1994; Gärtner 2001; Langer 2002; Pardiñas et al. 2020). A synthesis of the dietary data currently available could enable a revision of that comparison, making it possible to infer the diet of species that count with stomach descriptions but no dietary data.

In this work, we present a thorough review of publications on the diet of sigmodontine rodents from central-eastern Argentina. In addition to a compilation of the raw information, we include a dataset where these data are converted to numeric magnitudes, enabling meta-analyses that comprise the diverse array of studies. Finally, we perform three analyses based on all of their published dietary information: cluster analyses of dietary preference, which result in *a posteriori* dietary categories, and an exploration of the relationship between body mass, stomach morphology, and diet.

Materials and methods

Study region and taxonomy

The region under study was in central-eastern Argentina, comprehending the entire ecoregion of the Humid Pampas and adjoining parts of the ecoregions of Espinal, Low Monte and Parana Flooded Savannas (Olson et al. 2001). With a flat to undulating relief, it is mainly comprised of modified grasslands, with patches of different environments, such as wetlands, salt marshes, swamps, gallery and xeric forests (Soriano et al. 1991; Baldi and Paruelo 2008; Morello et al. 2012). With grasslands having been predominant since at least the Neogene (Prieto 2000), the area is

currently converted to a large agroecosystem, including crop fields, pastures and implanted forestations (e.g., Rapoport 1996; Zalba and Villamil 2002; Alberio and Comparatore 2014). A characterization of its climate and flora can be found in Burgos (1968); Cabrera (1968); Soriano et al. (1991); Murphy (2008).

We chose this region due to the following: (i) sigmodontine rodents from this area are relatively well known taxonomically; (ii) their dietary habits are also very well known in comparison with other parts of southern South America; (iii) this area has been subject to severe anthropic alterations during the last centuries, which has profoundly affected their small mammal communities (Teta et al. 2014).

Taxonomy follows Patton et al. (2015), who recognize for the study area 22 species, belonging to 14 different genera and four tribes. The most speciose taxon in this region is Akodontini, counting with nine species of the genera *Akodon*, *Deltamys*, *Necomys*, *Oxymycterus*, and *Scapteromys*. It is followed by Phyllotini, with seven species distributed among the genera *Calomys*, *Eligmodontia*, *Graomys*, and *Phyllotis*. Oryzomyini encompasses two genera: *Holochilus* and *Oligoryzomys*, with a total of five species. Finally, Reithrodontini is represented by a single species of the genus *Reithrodon*. The species studied were *Akodon azarae* (Fischer, 1829); *Akodon dolores* Thomas, 1916; *Akodon iniscatus* Thomas, 1919; *Bibimys torresi* Massoia, 1979; *Calomys laucha* (Fischer, 1814); *Calomys musculus* (Thomas, 1913); *Calomys venustus* (Thomas, 1894); *Deltamys kemp* (Thomas, 1917); *Eligmodontia typus* (F. Cuvier, 1837); *Graomys griseoflavus* (Waterhouse, 1837); *Holochilus chacarius* (Thomas, 1906); *Holochilus vulpinus* (Brants, 1827); *Necomys lasiurus* (Lund, 1840); *Necomys obscurus* (Waterhouse, 1837); *Oligoryzomys flavescens* (Waterhouse, 1837); *Oligoryzomys longicaudatus* (Bennet, 1832); *Oligoryzomys nigripes* (Olfers, 1818); *Oxymycterus rufus* (Fischer, 1814); *Phyllotis bonariensis* Crespo, 1964; *Reithrodon auritus* (Fischer, 1814); *Scapteromys aquaticus* (Thomas, 1920).

Feeding ecology

To assess feeding ecology, we compiled the available data on diet of sigmodontine rodents of central-eastern Argentina. Our sources included 54 different publications, ranging from 1879 to 2017. Among these, 20 were comprised of quantitative dietary information, 32 provided only qualitative descriptions, and two contained both kinds of data. They accounted for 21 of the 22 sigmodontines present in the study region, although, upon further analysis, data corresponding to two of those species were determined invalid. This review covered only the natural diet of the species, excluding information on diet under captivity or experimental settings, as well as anecdotic reports on sigmodontines feeding on artificial material (such as cotton fabrics, curated leather and even the metal spout of teapots, HersHKovitz 1962). We used data from different seasons and locations, aiming primarily at research done in the region under study. We also surveyed reports from other areas, provided that they were similar environments of geographical proximity (*i.e.*, research from grasslands in Uruguay was considered, but that of Brazil or northwestern Argentina was not). Finally, publications from Argentine provinces south or west from our designated study region were included, but only for those species where no other information was available (*e.g.*, *E. typus*, *O. longicaudatus*).

Original information, either as cited text or quantitative data, was transcribed into a table (Supplementary Table S1)¹, in which the only processing made was pooling together seeds or leaves that belong to the same family. We included details on time and site of observations, study methods used, and a brief description of the statistics that accompanied quantitative data. The classification of study methods was adapted from Cassini and Toledo (2021), resulting in the

¹ Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/....>

following categories: cited in literature (CL), when the primary source was not available and we made a transcription of information from previous publications by a different author; direct observation (DO), based on descriptions or reports of the animals engaging in feeding behavior; fecal analysis (FA) and gut analysis (GA), which comprised a varied range of techniques, such as microhistology, volumetric assessments, or simple accounts of different items identified; indirect evidence (IE), when information on sigmodontine diet was inferred from studies on the dietary items alone; survey based on direct observation or popular knowledge (SDO), accounting for reports from the local communities on damages caused by the rodents on crops; and reference to personal communications or unpublished data (PCUD), which in most cases lacked details on the origin of the information. When possible, if the original source included more than one set of data, (*e.g.*, studies replicated during different seasons, quantitative assessments followed by singular observations excluded from the tables, reports from personal observations and damages observed by local community members) we treated them as separate entries, totaling 194 entries. To avoid overestimation or misassignments, we thoroughly reviewed the bulk of information presented for each species, and discarded any that met the following criteria: revision of other publications, with the exception of unavailable sources (excl1); duplicated data, repeated in different works of the same author, including mentions of unpublished data that matched works published afterwards (in the species and region considered), and different presentations of a single dataset (excl2); data presented for more than one species, when we were unable to determine with certainty if it referred to all or only one of them (excl3); and misassigned information, reported to one species but revealed to correspond to a different one upon examination of the original source (excl4).

To standardize dietary information in a simple and quantified classification, food items were summarized in nine types, based on a combination of their taxonomic identity and mechanical properties (Lucas 2004): (1) hard-shelled invertebrates, accounting for myriapods, spiders, adult

insects, pupae, and mollusks; (2) worms and larvae, including annelids, and slugs; (3) dicot leaves, representing vegetative plant parts, which covered leaves, buds, shoots, and twigs of trees, shrubs, forbs, semiaquatic plants, and nongrassy herbs; (4) monocot leaves, comprising all forms of grasses, reeds, and sedges; (5) dicot seeds, consisting on seeds, fruits, and pods; and (6) monocot seeds. For the cases where the level of detail was insufficient to classify an item in those first six types, we used a simplified set of items: (7) unidentified invertebrates, (8) unidentified leaves, and (9) unidentified seeds (which contained pollen for one study). Elements that were quantified but failed to fit in any of our nine types were discarded. These included bait, items described as “unidentified” or “unidentified plant material”, and the two single reports for this region of sigmodontine gut analyses containing vertebrate remains (Kravetz 1972; Ellis et al. 1998). Quantitative values below the level of significance of their studies were also ruled out. As a result, two datasets were generated, accounting for different degrees of detail on food items. One was comprised solely of data that fit in the first six types (“six food types dataset”, 108 entries). Subsequently, invertebrates, leaves and seeds from the nine types were totaled to generate a more inclusive dataset containing all of the available information (“three food types dataset”, 153 entries).

To use all the different types of information in statistical analyses, we generated a synthetic numerical dataset with data from quantitative and qualitative studies. For quantitative studies reporting the percentage of gut contents or percentage of stomachs containing each item, we used the raw percentages directly. To transform qualitative information into a series of numerical magnitudes, we modified Olsen’s method (Olsen 2015, 2017). We considered every mention an item or type had to be a unit. In the end, we added together all those mentions, resulting in an estimated frequency index. Single reports of items conferred a unit to each of the types those items corresponded to; if a type was referenced more than once, a unit was added for each

mention (e.g., “spiders and beetles” added two units to hard-shelled invertebrates), and we added extra units if preference was specified (e.g., “especially” or “marked predilection” added two units, “frequently” or “tending towards” added one). The most general, vague descriptions such as “varied feeding” or “omnivory” consigned one unit to the three unidentified types (invertebrates, leaves, and seeds). Information expressed as uncertain (e.g., “possibly omnivorous”) was discarded. When qualitative annotations accompanied quantitative data (Suárez 1994), we modified the original values to incorporate transformed qualitative information. Finally, all data was normalized to represent the proportions of food types as values from 0 to 1.

We adapted Gagnon and Chew’s information reliability index (Gagnon and Chew 2000) to be more inclusive of qualitative studies. After classifying all data in quantitative or qualitative, we assigned each row an index, representing the reliability of its information. Quantitative data was considered the most reliable (A), followed by qualitative data that explicitly mentioned more than one item and quantitative data restricted to only a fraction of the food types (B), while the lowest reliability coefficient was reserved for quantitative reports of a single item, surveys based on popular knowledge, and information from indirect evidence (C). The main purpose of the reliability index was to facilitate interpretation of the datasets. Additionally, we explored if assignment of different weighting coefficients to the indexes affected the results of our statistical analyses. The final numerical dataset, and the two sub-sets we used for the three food types and six food types datasets, are available as Supplementary Table S2¹.

A posteriori dietary categories

All statistical analyses were carried out under R environment version 3.6.3 (R Core Team 2020). We used different R packages to perform cluster analyses of dietary information and identify *a*

posteriori dietary categories. Considering that distance measures are fundamental in clustering algorithms (Rokach and Maimon 2005), we calculated four distance metrics for continuous-valued attributes with the *dist* R function: Minkowski ($p = 4$), Euclidean (same as Minkowski, with $p = 2$), Manhattan (same as Minkowski, with $p = 1$), and Chebyshev (or maximum metric). We performed hierarchical clustering methods by calculating six similarity measures, using the *hclust* function of *vegan* package v2.5-6 (Oksanen et al. 2019): single-link, complete-link, average-link (=UPGMA), median-link (=WPGMC), centroid-link (=UPGMC), and Ward's. Using the *cutree* function of that same package, we explored different cutting points to identify dietary categories. The 24 resulting dendrograms were transformed to a tree of class phylog using the *as.phylo* function of *ape* package v5.5 R (Paradis and Schliep 2018), to obtain a strict consensus and a 50% majority consensus of the different clustering methods used. Lastly, we compared the groups generated by different distance metrics and methodologies.

Dietary categories originating from cluster analyses were evaluated for the more inclusive three food types dataset, by means of a ternary diagram, using the Ternary package v1.1.4 (Smith 2017). We plotted in the three axes the relative proportions of leaves, seeds and invertebrates of the 19 species for which dietary information was available. Additionally, with the intent of accounting for phylogenetic covariance when predicting group membership, we performed a Phylogenetic Flexible Discriminant Analysis (pFDA). This analysis was developed by Motani and Schmitz (2011), combining the protocols by Hastie et al. (1994) with a phylogenetic GLS regression by Martins and Hansen (1997). In contrast to standard discriminant analyses (which do not take into account the evolutionary relationships between the taxa), pFDA aims at considering phylogenetic bias by incorporating a phylogenetic covariance matrix to continuous (in our case: proportions of food items) and class (in our case: dietary categories) variables. After building a phylogenetic tree of the species under study using the time-scaled supertree by Upham *et al.*

(2019), with the following task ID: tree-pruner-7adc17a8-12fe-4e37-a085-8b43f6f76886, we carried out the pFDA using the function *phylo.fda* from the *phylo.fda* package v0.2.R.

Body mass and diet

We assessed the relationship between body mass and diet. Following Gagnon and Chew (2000), we used single body mass estimates to minimize computational difficulties that would arise from considering sex dimorphism, annual or geographic variation. Body mass information was derived from six sources, in which values respecting size relationships between the species were chosen (Leveau et al. 2006; Chebez et al. 2014; Maestri et al. 2016a; Pardiñas et al. 2017a, 2017b; Coda et al. 2019). Body mass normality was analyzed using the Shapiro-Wilk test (Shapiro and Wilk 1965). Differences between dietary categories and body mass were contrasted by means of a non-parametrical Kruskal-Wallis rank sum test using the *kruskal* function of *agricolae* package v1.3-2 (de Mendiburu 2020). Following Cassini et al. (2012), we assessed the extent and significance of the association between body mass and food type proportion variables via Spearman rank non-parametric correlations. This procedure tests how monotonically the variables are related, even if their relationship is non-linear (Zar 1999); therefore, we used the original untransformed data.

Stomach morphology

Finally, we surveyed the stomach types of the species under study following Carleton (1973). Descriptions and illustrations of this organ were obtained from genus-level characterizations in his work, and complemented with Teta et al. (2007) for *D. kempfi* (which was revised by Pardiñas et al.

2020, who presented a different description of anatomical details not affecting type designation). Four different stomachs were reported for our sample: unilocular-discoglandular, unilocular with glandular pouch, and two variations of the unilocular-hemiglandular type. Particularly, most representatives had more coverage of the cornified epithelium (“unilocular-hemiglandular majorly cornified”), whereas the remainder had more abundant glandular epithelium (“unilocular-hemiglandular majorly glandular”).

To assess the correspondence between stomach morphology and dietary composition, we used the list of stomach types and both continuous food type datasets (*i.e.*, three and six food types datasets) to calculate an intraclass correlation coefficient (ICC). The ICC differs from others correlation measures in that it operates on data structured in groups, rather than data structured as paired observations. We used the ICC 2.3.0 package (Wolak et al. 2012) to calculate the ICC between the three and six food types variables with stomach morphology, and interpreted these results following Chicchetti’s criteria (Cicchetti 1994). Interdependence between stomach anatomy and *a posteriori* dietary categories obtained from cluster analyses was evaluated performing Fisher’s exact test in a contingency table, using the *fisher.test* R function.

No new data was collected in the course of this research. Datasets were derived from publications referenced throughout the text, and have been included as Supplementary data accompanying this paper.

Results

Synthesis of dietary information

Not all the dietary information we reviewed has been included in our final dataset. Two entries documented the lack of information for two species (*B. torresi* and *G. chacoensis*). 39 entries, corresponding to 15 different publications, met our exclusion criteria and were discarded (Supplementary Table S1)¹. From a total of 153 valid entries, 114 were quantitative and 39 were qualitative. In respect to information quality, most of the entries had the highest index ($A = 114$), a small fraction was of low quality ($C = 26$), and the least frequent data were of intermediate quality ($B = 13$). A synthesis of the dietary information compiled for the 22 sigmodontine rodent species of central-eastern Argentina is available in Table 1, including body mass, averaged percentage of food items consumed, the list of sources for diet data and their reliability index. Dietary information was either nonexistent or null for three species (*B. torresi*, *G. chacoensis*, *N. obscurus*). Only qualitative data has been presented for five species (*A. iniscatus*, *D. kempi*, *H. chacarius*, *H. vulpinus*, *P. bonariensis*), of which three relied exclusively on the lowest quality information (*A. iniscatus*, *H. chacarius*, *P. bonariensis*). For the remaining 14 species (*A. azarae*, *A. dolores*, *C. laucha*, *C. musculus*, *C. venustus*, *E. typus*, *G. griseoflavus*, *N. lasiurus*, *O. flavescens*, *O. longicaudatus*, *O. nigripes*, *O. rufus*, *R. auritus*, *S. aquaticus*), quantitative data has been reported at least once. Consequently, analyses exploring dietary strategies and their relationship with body mass and stomach types were performed on the subset of species with valid dietary information ($n = 19$).

Analyses using the three food types dataset

The cluster analyses performed using the most inclusive dataset (three food types) showed that distance metrics had null or little influence over group identification regardless of the clustering method used (Supplementary Figure S1)¹. In particular, Ward and complete-link presented the six

more consistent dietary groups. Furthermore, although strict consensus clustering methods maintain topology instead of cutting point distances, the same six groups were identified when using the averaged clustering methods (see Supplementary Figure S2)¹. Dendrograms generated with Ward's methodology performed on unweighted averages constituted the best summary of our results (Figure 1A). Assignment of different average weights to the indexes representing information reliability did not result in changes in the dendrogram (results not shown). The majority consensus of all the dendrograms obtained showed that 100% of trees retained the nodes grouping *R. auritus* and *P. bonariensis*; *S. aquaticus* and *O. rufus*; *O. longicaudatus* and *C. musculus*; *O. nigripes* and *H. vulpinus*; *H. chacarius* and *G. griseoflavus*; *N. lasiurus*, *A. iniscatus* and *A. azarae* (Figure 1B). Complete-link methodologies performed on unweighted averages produced dendrograms consistent with those of Ward (Figures 1C). We named the resulting dietary categories strict folivores (>90% leaves and/or grasses), strict insectivores (>80% invertebrates), non-strict granivores (>50% seeds), non-strict insectivores (>40% invertebrates), non-strict folivores (>50% leaves and/or grasses), and generalists (similar amounts of all the items).

The six dietary categories are represented in a ternary diagram in Figure 2, where average proportions of food types summarized the diets of the 19 sigmodontine species with valid information (Table 2 lists these species under their corresponding dietary strategy). The generalists were placed towards the center of the diagram, and only two corners were occupied with categories corresponding to specialist strategies (*i.e.*, due to the absence of strict granivores). Note that, among the non-strict granivores, *C. venustus* was segregated from *O. longicaudatus* and *C. musculus*, based on the invertebrate content. Additionally, the non-strict folivores were comprised of two distinct groups: species that included animal material in their diet (*H. vulpinus* and *O. nigripes*) and species that did not (*G. griseoflavus* and *H. chacarius*). Furthermore, *D. kempi*

was separated from the rest of the non-strict insectivores because of the low proportion of seeds in its diet. The pFDA showed no misclassification of cases at lambda values of zero (optimal lambda). When lambda values were increased, nine taxa were misclassified (Supplementary Figure S3)¹. Among the most representative cases, *N. lasiurus* was misclassified as generalist from lambda 0.1 to 0.7, *E. typus* was misclassified as non-strict insectivore from lambda 0.3 to 0.6, and *D. kemp*i was misclassified as non-strict folivore from lambda 0.4 to 1. The morphospace and phylomorphospace resulting from the pFDA are plotted in Supplementary Figure S3¹.

With respect to the relationship between body mass and diet, the Shapiro-Wilk test resulted in non-normal data distribution for body mass ($W = 0.63645$, $p\text{-value} < 0.0001$). The Kruskal-Wallis rank sum test showed significant differences in body mass between the dietary categories ($\chi^2 = 11.398$, $df = 5$, $p\text{-value} = 0.04403$). The *post hoc* test indicated three body mass groups: (a) strict insectivores, strict folivores and non-strict folivores were the largest; (ab) non-strict granivores had intermediate body mass; and (b) non-strict insectivores and generalists were the smallest (Figure 3). The largest size range and variance corresponded to non-strict granivores. Additionally, body mass was not correlated with proportion of leaves ($rS = 0.345$; $S = 746.83$, $p\text{-value} = 0.1482$) nor invertebrates ($rS = -0.241$; $S = 1414.2$, $p\text{-value} = 0.3212$), but it had a significant negative correlation with seed proportion ($rS = -0.497$; $S = 1706.2$, $p\text{-value} = 0.0305$).

Upon exploring stomach anatomy in relation to dietary composition, the ICC indicated, according to Cicchetti's (1994) criteria, that stomach types had a good correlation with the invertebrate proportion in diet (*ca.* 0.73), fair correlation with leaves proportion (*ca.* 0.45) and poor correlation with seeds proportion (*ca.* 0.18; Table 2). Fisher's exact test showed that stomach anatomy was not independent of proposed dietary categories ($p\text{-value} = 0.02363$). *A posteriori* dietary categories that resulted from the three food types analyses, together with the species and tribes they represent and their corresponding stomach types can be found in Table 3.

Analyses using the six food types dataset

The cluster analyses performed on the six food types dataset were restricted to 17 species (information on *A. iniscatus* and *P. bonariensis*' diet lacked the necessary level of detail to be included). Results showed that distance metrics influenced the dendrogram topology and group identification on all the clustering methods explored (Supplementary Figure S4)¹. An exception could be found using Ward's method, in which four to six consistent dietary groups were identified, similarly to the strict consensus by clustering method (Supplementary Figure S5)¹. Similar to the case of the three food types dataset, the dendrogram generated using Ward's methodology represented the best summary of our results (Figure 4A). We named the dietary categories folivores/hard-shelled insectivores ($\geq 50\%$ monocot and dicot leaves, $>30\%$ hard-shelled insects), strict dicot feeders ($>95\%$ dicot seeds and leaves), non-strict grazers ($\geq 50\%$ monocot leaves), non-strict insectivores ($>65\%$ hard-shelled invertebrates and worms and larvae), and diaspore feeders ($>40\%$ of monocot and dicot seeds, with a smaller representation of the other items). Some of the groups recovered in Ward's clustering was present in all dendrograms obtained by the majority consensus, which retained the nodes grouping *O. flavescens* and *C. venustus*; *G. griseoflavus* and *E. typus*; *S. aquaticus* and *O. rufus*; and *O. nigripes* and *H. vulpinus* (Figure 4B). Regarding assignation of weighting coefficients to the reliability indexes, the effect was similar to the case of the three food types dataset, and no significant changes were observed.

The phylogenetic flexible discriminant analysis (pFDA) showed no misclassification of cases at lambda values of zero (optimal lambda), except for *A. azarae*, which belongs to the diaspore feeder category and was, in this case, classified as a folivore/hard-shelled insectivore. When lambda values were increased, five taxa were misclassified (Supplementary Figure S3)¹. Among

them, four (*A. azarae*, *A. dolores*, *N. lasiurus* and *O. longicaudatus*) were diaspore feeders and one (*S. aquaticus*) a non-strict insectivore. In the first group, *A. azarae* was misclassified as every dietary category but non-strict grazer at different lambda values, whereas *N. lasiurus* and *O. longicaudatus* were misclassified as non-strict grazers from lambda 0.4 to 0.8. Finally, *S. aquaticus* was misclassified as a strict dicot feeder from lambda 0.7 to 0.9. Supplementary Figure S3¹ shows the resulting morphospace and phylomorphospace.

In regard to the association between body mass and diet when six food types were considered, the Kruskal-Wallis rank sum test (body mass had non-normal distribution; see above) showed non-significant differences in body mass between the proposed dietary categories ($\chi^2 = 5.9399$, $df = 4$, $p\text{-value} = 0.2037$). Furthermore, there was no correlation found between body mass and proportion of: invertebrates (values for hard-shelled were: $rS = 0.104$, $S = 731.49$, $p\text{-value} = 0.6924$ and for worms and larvae: $rS = 0.062$; $S = 765.65$, $p\text{-value} = 0.81403$), seeds (monocot: $rS = -0.242$, $S = 1013.55$, $p\text{-value} = 0.3492$; dicot: $rS = -0.363$, $S = 1111.91$, $p\text{-value} = 0.1526$) nor leaves (monocot: $rS = 0.140$, $S = 701.65$, $p\text{-value} = 0.5916$; dicot: $rS = -0.0074$, $S = 822.02$, $p\text{-value} = 0.9776$).

When six food types were considered, Cicchetti's (1994) criteria for correlation (ICC) between stomach types and proportion of food types was excellent for worms and larvae (*ca.* 0.87), good for monocot leaves proportion (*ca.* 0.69), fair for hard-shelled invertebrates (*ca.* 0.46), and poor for the remaining food items (less than 0.25; Table 2). Fisher's exact test indicated that stomach anatomy was independent of the proposed dietary categories ($p\text{-value} = 0.009502$).

Discussion

Dietary information and database

The aim of this article was to generate a thorough and critical synthesis of the available information on the diet of sigmodontine rodents of central-eastern Argentina. We were able to compile data on over 85% of the species under study, through surveying more than 50 publications. We found considerable differences in the amount and quality of dietary information between different publications, ranging from cursory notes (*e.g.*, Massoia 1964*d*; Dalby 1975; Rosi 1983) to replicated quantitative studies (*e.g.*, Bilenca et al. 1992; Ellis et al. 1998). Moreover, information quality and quantity were not equally divided among species. While for some species diet has been reported to change between seasons or habitats (see Dellafiore and Polop 2010 for a review of diet variation), several others rely only on brief superficial descriptions or anecdotic observations, and no information exists for three of them. Gaps do not seem to be randomly distributed: publications are concentrated on species that are more common and frequent (*e.g.*, *A. azarae*, *C. laucha*; Barlow 1969; Contreras 1979; Dellafiore and Polop 1998; Castellarini et al. 2003) or that happen to inhabit the surroundings of research centers (mainly north-eastern Buenos Aires province, central Córdoba and Mendoza city; *e.g.*, Bilenca 1993; Ellis et al. 1994; Campos et al. 2001; Suárez and Bonaventura 2001; Giannoni et al. 2005). This scenario of inequality may reflect a trend in ecological investigations, that focus on deep and complex descriptions of a handful of species, whereas a fraction of the assemblages is excluded (Fleming and Bateman 2016; Jarić et al. 2019). Research on less common species will be necessary to have a complete ecological map of the sigmodontines of central-eastern Argentina.

Sigmodontine dietary information was not only compiled, but also revised and compared. We were able to identify errors several decades old that have been referenced in publications up to the present. Among these, we had two patent cases of misassigned information. The single entry of *G. chacoensis*, by Brown and Patton (2015), is mistakenly based on Hershkovitz's report on *G.*

griseoflavus from 1962. As for *N. obscurus*, the only existing work on its diet is Barlow's (1969), which has since then been directly or indirectly referenced in several publications that attribute an insectivore diet to this species (e.g., Gómez Villafañe et al. 2005; González and Martínez Lafranco 2010; Pardiñas et al. 2015, 2017b). However, the taxonomical basis behind this information is questionable. In the original reference (i.e., Barlow 1969), this taxon is referred as *Akodon obscurus obscurus*, which was later synonymized with *N. obscurus* (Galliari and Pardiñas 2000). In a personal communication, E. González informed us that he had examined Barlow's series of *Akodon obscurus obscurus* at the American Museum of Natural History (AMNH 206093 through 206165), discovering that 71 of the 72 specimens were misidentified and did not correspond to this species. Particularly, only AMNH 206096 was *N. obscurus*, while the other 70 specimens were referable to *D. kempii* (AMNH 206093-206095, 206097-206102, 206104-206154, and 206156-65), except for a single individual that corresponded to *O. rufus* (AMNH 206103); additionally, the final collection number was associated to unidentifiable heterogeneous material recovered from an owl pellet (AMNH 206155) (E. González, personal communication, 2020). Barlow's report was based on the examination of seven stomachs that were not linked to individual specimens, so his description cannot be attributed with certainty to either of the three species in this series, resulting in no data on the diet of *N. obscurus*. We also found a few examples of authors modifying information when referencing previous research. Rosi (1983) claimed that de la Barrera (1939) referred to chañar fruits as *G. griseoflavus*'s "favorite food", but no information on preference or frequency is present in the original publication. Likewise, Bianchini and Delupi (1993) stated in their work on *H. vulpinus* that Ageitos de Castellanos (1965) reported freshwater clams as "an important part of its diet", while the only reference to this rat in the original text has it described as one of the clams' predators (and the majority of the data available for *H. vulpinus* describe folivore habits). In many cases, information underwent a series of citations, where the original source was not clear at first

sight (e.g., Pardiñas et al. 2015 cited González and Martínez Lafranco 2010, who referenced Barlow 1969). Some publications made it difficult to locate the original source by providing a single list of bibliography at the end, instead of attributing each piece of information to a paper or book (e.g., Pardiñas et al. 2017b). Citation of unseen references and dilution of authorship are fairly common practices contributing to the generation and propagation of errors, which are key in work relying on bibliographic compilation (Ball 2002; Simkin and Roychowdhury 2003; Jergas and Baethge 2015). We believe these observations stress the importance of checking original references while working with second-hand information (see Wetterer 2006 for a study on second-hand citations behind a widely spread mistake, and Simkin and Roychowdhury 2005; Goldberg et al. 2015 for models suggesting that around 80% of citations are copied from the reference list of another article). We expect that the raw data table we provide (Supplementary Table S1)¹ will function as a useful tool that facilitates future research, and serves as either a transparent synthesis, or as a basis from which original work can be tracked.

A posteriori dietary categories

We were able to generate *a posteriori* dietary categories based on the totality of the diet information available for the sigmodontine species of central-eastern Argentina. The most inclusive cluster analyses, performed on the three food types dataset, showed a high level of consistency between different methodologies; Ward's and complete-link dendrograms were the most similar to the majority consensus. Dendrograms generated using the six food types dataset showed greater variation, but Ward's was also the most representative dendrogram in this case. When considering the differences between different clustering methods, complete-link algorithms are regarded as more useful in comparison to single-link, as they generate more compact clusters.

On the other hand, the centroid method merges the clusters that have the smallest distance between centroids, carrying the disadvantage of very small clusters being lost when merged with a very large cluster. More details about clustering techniques can be found in Omran et al. (2007) and the references therein.

The dietary groups obtained differed between datasets, but they showed certain degree of consistency. The three food types dataset resulted in six robust groups: strict insectivores, strict folivores, non-strict insectivores, non-strict granivores, non-strict folivores, and generalists. Interestingly, neither of our dendrograms presented a strict granivores category. Groups generated with the six food types dataset were less consistent between methodologies; so, although the primary information was more precise, the majority consensus presented a high amount of polytomies, resulting in a smaller amount of *a posteriori* dietary categories. In this case, we recognized five strategies: folivores/hard-shelled insectivores, strict dicot feeders, non-strict grazers, non-strict insectivores, and diaspore feeders. This last group included the largest number of species and the most diverse dietary composition. Despite the considerable differences between the dendrograms generated with the two datasets, we observed consistency in the categorization of some species. For example, *S. aquaticus* and *O. rufus* were classified as strict insectivores when using the three food types dataset, and as non-strict insectivores when six food types were considered; likewise, all the non-strict folivore species of the first clustering analyses were grouped as folivores/hard-shelled insectivores when the information used was more detailed. Additionally, while the use of a more inclusive dataset (comprising broader food types) seemed to be more robust to the inclusion of information with different reliability levels, the more restricted dataset (of only detailed food types) required a better data quality for the analytical procedure followed here. From the 108 entries in the six food types dataset, 81 were indexed as A, but their information described exclusively 14 species (see Supplementary Material 2). Taking into

account that the three food types dataset was based on more information (153 entries vs. 108 for the six food types dataset), and that the dendrograms generated showed more consistency, we consider its results to be more robust and recommend their use in future research that should need it.

Two considerations should be taken into account regarding the certainty of the attributions of individual species to dietary groups. We noted a bias on taxonomic detail of food items, favoring arthropods in early research (*e.g.*, Barlow 1969; Contreras 1979) and plants in more recent work (*e.g.*, Martínez et al. 1990; Castellarini et al. 2003). Additionally, easily digestible worms and larvae are less likely to leave traces in the stomach than grasses or adult arthropods. These two factors are likely to impact the results of dietary research, probably causing overestimation of plant material and underestimation of soft arthropod tissue (Vavra and Holeček 1980; Holeček et al. 1982). Moreover, and taking into consideration how the amount and quality of information is variable, the cases where the number of sources is low (*e.g.*, *P. bonariensis*) or the reliability of information is minimal (*e.g.*, both species *Holochilus*) should be contemplated with more caution than those that count with a large body of quantitative data (*e.g.*, *A. azarae*). For instance, *H. vulpinus* and *H. chacarius* are species with morphological characteristics that have been linked with a highly folivorous diet (*i.e.*, robust mandibles and skulls, voluminous masseter muscles; Samuels 2009; Maestri et al. 2016b; Barbero et al. 2020), but they appear in our three food types dendrogram as non-strict folivores; a closer look to their data sources reveals they are comprised of information of low reliability with high representation of rare items (particularly, mollusks). While the integration with sources that can provide indirect information on diet is a possibility, we consider that, given that these are extant species, the ideal scenario would be to develop further research on their diets.

We would also like to remark that our analyses incorporated data from different seasons and locations, presenting an average between diverse conditions. Thus, dietary strategies of individual specimens or of specific habitats or months will most likely be less varied than the results we report for their species. There is a brief body of evidence showing diets change seasonally and geographically (sufficient information to explore diet variation is available only for a subset of the sigmodontines of central-eastern Argentina, for which an extensive review can be found in Dellafiore and Polop 2010). Additionally, whereas for the majority of the species we were able to compile dietary data from the region under study, some reports from provinces outside of it were included (*e.g.*, *E. typus*, *O. longicaudatus*). Food sources vary between different locations, so this represents the only possible approximation to their diets in the absence of region-specific research. In spite of the difficulties that arose from the deficiencies of the original sources, we were able to generate a consistent classification of dietary strategies of sigmodontines of central-eastern Argentina.

Our attempts at incorporating the complexity of the data in our statistical analyses resulted in varied outcomes. The cluster analyses made from three and six food types showed significant differences, which we could attribute to the reduction in the number of entries that six types implied in respect to the more inclusive dataset of three totaled items. The assignation of weighting coefficients to reflect data reliability when averaging it, on the other hand, generated no changes in the dendrograms, possibly because, for individual species, information usually corresponded either exclusively to low reliability sources (B and C) or counted with a majority of high reliability entries (A). Consequently, the high amount of quantitative information diluted the effect of weighting, and there were no significant differences when all the data available was qualitative. This is consistent with Olsen's (2017) method of averaging together quantitative and qualitative information, which has also been demonstrated as useful in ecomorphological studies

on deer (Cassini and Toledo 2021). While knowing the nature of the information we are working with has an intrinsic value, transcription of its specificity and reliability to the statistical analyses seems to have been unnecessary in this case, as the most robust results were derived from the simplest untransformed dataset.

Taxonomy and diet

With respect to the relationship between taxonomy and dietary strategies, a slight degree of correspondence was observed for tribes, although it was inconspicuous when analyzing at genera or species levels. In the pFDA, the estimated optimal lambda was zero, resulting in a star phylogeny for the tree turning, which is equivalent to an independency between dietary strategies and phylogeny. The sigmodontines of central-eastern Argentina represent only four tribes (Akodontini, Oryzomyini, Reithrodontini, and Phyllotini) of the 11 that comprise this subfamily. Unlike bovids (*e.g.*, frugivores Cephalopinae), or equids (*e.g.*, grazer equids), in which some clades are characterized by unique diet categories (Gagnon and Chew 2000; Mendoza and Palmqvist 2006; Cassini 2013), there are no tribes linked to a unique dietary category. Insectivores, either strict or non-strict, were composed solely of Akodontines, which were also part of the generalists (Table 2). Phyllotines were present in all the herbivore strategies (strict folivores, non-strict folivores, non-strict granivores, and generalists). Oryzomyines were characterized by not participating in any strict strategies, but instead in all the herbivore non-strict categories. Our only representative of Reithrodontini had a strict folivore strategy.

Body mass and diet

Regarding the relationship between dietary categories and body mass, we observed a significant negative correlation between seed proportion and body mass. These observations are consistent with the pattern of species of larger sizes tending to be more folivorous, which has been reported for eutherians in general and suggested for rodents (Perrin and Curtis 1980; Demment and Van Soest 1985; Langer 1994; Langer and Clauss 2018). Particularly, the analysis on the three food types dataset resulted in three groups, with generalists and non-strict insectivores as the smallest sizes, non-strict granivores at an intermediate size, and both folivore strategies as the largest. Even though we could observe a tendency towards low protein in diet as body mass increased, strict insectivores (representing the highest protein content) belonged to the large size group together with folivores, as the proportion of seeds in both these diets was small. When six food types were considered, there was no correlation between any food item proportion and body mass, and the species belonging to different dietary categories did not differ significantly in size. As for the rest of the comparisons, the three food types dataset appears to be more robust than the six food types dataset, generating, in this case, results consistent with a pattern observed for other representatives of mammalia (*e.g.*, Peters 1983; Demment and Van Soest 1985; Gagnon and Chew 2000; Vizcaíno et al. 2012; Price and Hopkins 2015; Pineda-Munoz et al. 2016).

Stomach morphology and diet

As for the correspondence between stomach anatomy and dietary strategies, we found varied degrees of correlation (ICC) between proportion of alimentary items and stomach types. Upon using the three food types dataset, the correlation for seed proportion was poor, it was fair for leaves proportion, and good for insect proportion. Moreover, when we explored the relationship between *a posteriori* dietary categories and stomach types, Fisher's exact test showed that they

were not independent. Similar results were obtained in the case of six food types; there was poor correlation between stomach types and proportion of both types of seeds and dicot leaves, but it was fair for hard-shelled invertebrates, good for monocot leaves, and excellent for worms and larvae. However, Fisher's exact test resulted in independence between stomach types and the set of *a posteriori* dietary categories originated in the more detailed dataset. While all the species classified as diaspore feeders had an unilocular-hemiglandular majorly cornified type (coincidentally with the group formed by non-strict granivores, non-strict insectivores and generalists when using the three food types dataset), the rest of the groups either included more than one stomach type or shared their stomach type with other groups. Particularly, *S. aquaticus* and *O. rufus*, two species with unique stomach types classified as strict insectivores with the three food types dataset, were grouped together with *D. kempfi* in this case, thus, creating a considerably heterogeneous group. In all, our results can be considered consistent with the existence of a relationship between dietary strategies and stomach anatomy.

Various attempts at exploring the possible connection between stomach anatomy and dietary composition in sigmodontines are present in Carleton's (1973) work. He proposed a close phylogenetic relationship between species where the glandular epithelium is limited to a small area, either as a glandular disc or glandular pouch. Additionally, he compiled different functional hypotheses to explain this phenomenon, like the proposition that restricting glandular lining could imply maintenance of the esophageal pH in the stomach, to preserve the sugar-degrading activity of the salivary amylase, instead of it being inactivated under the low pH generated by the stomach glands. This could be linked to a diet rich in sugar, or to a sequential stomach digestion, with initial amylase activity and posterior liberation of acids associated to protein catabolism. Particularly, he suggested the cases of diets with high proportions of seeds (starch) or arthropods (glycogen). On the other hand, he saw a connection between hemiglandular majorly cornified stomachs and

folivory. In this regard, he summarized two hypotheses: protection of the fragile glandular epithelium from the abrasive material that forms leaves and insects (which counts with numerous counterexamples in rodents and other mammals), and an analogy to the evolution of ruminants, where a decrease of acidification accompanied by an increase in saccularization would allow hosting of cellulolytic bacteria. No functional hypotheses concerning hemiglandular stomachs with a more extensive glandular lining are present in his work. Considering the analyses of the three food types dataset, our representatives of species with constrained glandular epithelium (*S. aquaticus* and *O. rufus*) were classified as insectivores, which supports Carleton's functional hypothesis. However, updated phylogenetic research (Salazar-Bravo et al. 2016) places *Scapteromys* and *Oxymycterus* as part of two different subclades within Akodontini; thus, we can argue that their morphological similarity is a convergence, that may be adaptive in a diet constituted primarily of invertebrates. We also observed that unilocular-hemiglandular stomachs with a more extensive glandular epithelium were only present in folivore strategies, either strict or non-strict, contrary to Carleton's proposal of cornified epithelium reduction as an adaptation for folivory. In this sense, more recent research on digestive physiology in murids has revealed that cellulose digestion does not take place in the stomach, where no cellulolytic activity has been documented for this group (Juhr and Haas 1979; Gärtner 2001; Ushakova et al. 2003), and it is in fact the caecum that plays a major role for this function (Hume 1994; Gärtner 2001; Langer 2002). We are unaware of functional hypotheses that could explain the connection between increased glandular presence and folivory, but, considering that *Phyllotis* and *Holochilus* are not closely related, a phylogenetic hypothesis would not suffice to explain their similarities. Most of the species analyzed had the stomach type that we called "majorly cornified", described by Carleton (1973) as the most common pattern in sigmodontines, where the area covered by cornified epithelium can vary between an approximate equivalence to up to twice that of the glandular

epithelium. This type was identified in all the dietary categories, with the exception of strict insectivores, and was the only one present in non-strict granivores, non-strict insectivores, and generalists. It has been suggested that the role of an extensive cornified epithelium could be related to a storage function of the forestomach, necessary to regulate the liberation of food into the rest of the digestive tract, where cellulose is digested, to attain an optimal exploitation of alimentary resources (Gärtner 2001). This would be especially adaptive in small mammals of more omnivore diets (Eisenberg 1981).

We would like to note that a recent publication on stomach morphology of the sigmodontine family Akodontini (Pardiñas et al. 2020) revised Carleton's work, and provided first hand photos and detailed descriptions of some of the species from central-eastern Argentina. Particularly, they defined three types of unilocular-hemiglandular stomachs, whereas Carleton only suggested two. We decided against using this more sensitive typification because it was restricted to Akodontines, and it differed for some species from Carleton's characterizations and figures. Therefore, we considered that a partial combination of the two sources would have affected the robustness of our database. We hope that future research will provide detailed anatomical studies for the remaining sigmodontine tribes. Regarding incorporation of morphological information on the caecum and proximal colon, no studies of these organs have been done on sigmodontines (Vorontsov 1967, 1979; Pardiñas et al. 2020).

In spite of the limitations of representing digestive system diversity exclusively with an organ that does not play a major role in food assimilation, and considering also the high degree of omnivory of the species under study, our results showed that the dietary strategies of sigmodontine rodents are to some extent related to their stomach morphology, which is consistent with observations made in larger mammal species (e.g., Chivers and Hladik 1980; Eisenberg 1981). If the tendencies observed can be extrapolated to the species for which no

dietary data is available, then we could infer their dietary habits, although those results should be treated with caution. Aside of the limited role of the stomach in digestion, Carleton remarked that no interspecific differences were observable for the same genus, and genera are not strictly linked to dietary strategies, so this would constitute only a rudimentary approach. The species that lack dietary reports, *B. torresi*, *G. chacoensis* and *N. obscurus*, belong to genera characterized by unilocular-hemiglandular majorly cornified stomachs (for a description of *Bibimys*, see Rodrigues Gonçalves et al. 2005; Pardiñas et al. 2017c). This stomach type is the most common, prevailing in non-strict dietary categories, and could potentially be linked to any strategy, except for strict insectivory. Our work responds to Carleton's (1973) call on reevaluating the relationship between stomach anatomy and dietary composition when more information was available, providing a small but solid addition to functional research on diet of small mammals. Ecomorphological studies aimed at relating diet to traits of other parts of the digestive system (such as craneomandibular morphology or characteristics of the caecum and proximal colon) can contribute to detecting correlations or patterns that could allow inference of the dietary strategies of those species for which no descriptions have been reported (*i.e.*, using the form-function correlation paradigm; see Cassini et al. 2021). However, given that these are extant species, the ideal prospect would include also quantitative dietary research for those that have not been studied, and those that only count with qualitative information.

Final remarks

This study presents for the first time a thorough synthesis of the available literature on diet of sigmodontines of central-eastern Argentina. We provide a list of species that have been most neglected in dietary characterizations, hoping to orient future investigations to fill those gaps. The

datasets presented here constitute a solid source for ecological or interdisciplinary studies on sigmodontines, as we exemplified when linking dietary categories to taxonomy, body mass and stomach morphology. We were able to observe in these rodents an association between dietary composition and body mass, with large-sized species tending to be more folivorous. We also recognized that some stomach types are restricted to specific diets. With these contributions, we hope to simplify the incorporation of diet information in future research, and particularly to increase our understanding of the biology of small mammals.

Acknowledgements:

The authors would like to thank Enrique González for selflessly providing unpublished information on *N. obscurus*, and María José Rodríguez and Juan José Martínez Lafranco for their help tracing original sources on dietary ecology. We wish to acknowledge the assistance provided by Karl Sandager, Juan Jelf, and Andrew Milton with English revisions, and by the reviewers. Our special thanks are extended to *Consejo Nacional de Investigaciones Científicas y Técnicas* (CONICET) for the PhD grant to SB that partially funded this research, to *Sociedad Argentina para el Estudio de los Mamíferos* (SAREM) for enabling the enriching discussions that originated it during the Jornadas Argentinas de Mastozoología, and to Sergio Vizcaíno for inspiring the larger plan it is part of. This is a contribution to the projects PICT 201-0537 Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) to PT, and CDD-CB 650-14 and 016/19 Universidad Nacional de Luján (UNLu) to GHC.

References

- Ageitos de Castellanos, Z.J. 1965. Contribución al estudio biológico de almejas nacaríferas del Río de la Plata. *Rev. Mus. La Plata, n.s., Secc. Zool.* **8**(60): 99–147.
- Alberio, C., and Comparatore, V. 2014. Patterns of woody plant invasion in an Argentinean coastal grassland. *Acta Oecol.* **54**: 65–71. doi:10.1016/j.actao.2013.09.003.
- Baldi, G., and Paruelo, J.M. 2008. Land-use and land cover dynamics in South American Temperate grasslands. *Ecol. Soc.* **13**(2): 6. doi:10.5751/ES-02481-130206.
- Ball, P. 2002. Paper trail reveals references go unread by citing authors. *Nature* **420**(6916): 594. doi:10.1038/420594a.
- Barbero, S., Teta, P., and Cassini, G.H. 2020. An Ecomorphological Comparative Study of Extant and Late Holocene Sigmodontinae (Rodentia, Cricetidae) Assemblages from Central-Eastern Argentina. *J. Mamm. Evol.* **27**: 697–711. doi:10.1007/s10914-020-09497-7.
- Barlow, J.C. 1969. Observations on the biology of rodents of Uruguay. *Roy. Ont. Mus., Life Sci. Contrib.* **75**: 1–59. doi:10.5962/bhl.title.52067.
- Bianchini, J.J., and Delupi, L.H. 1993. Guía de los mamíferos vinculados a los ambientes acuáticos continentales de la Argentina. Volumen 44 – Mammalia. Fascículo 2: Actualización. *In* Fauna de Agua Dulce de la República Argentina. *Edited by* Z.J. Ageitos de Castellanos. Programa de Fauna de Agua Dulce, Museo de La Plata, La Plata. pp. 1–79.
- Bilenca, D.N. 1993. Caracterización de los nichos ecológicos y organización de las comunidades de roedores cricétidos en la región pampeana. PhD in Biological Sc. thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires.

- Bilenca, D.N., and Kravetz, F.O. 1998. Seasonal variations in microhabitat use and feeding habits of the pampas mouse *Akodon azarae* in agroecosystems of central Argentina. *Acta Theriol.* **43**(2): 195–203. doi:10.4098/AT.arch.98-15.
- Bilenca, D.N., Kravetz, F.O., and Zuleta, G.A. 1992. Food habits of *Akodon azarae* and *Calomys laucha* (Cricetidae, Rodentia) in agroecosystems of central Argentina. *Mammalia* **56**(3): 371–384. doi:10.1515/mamm.1992.56.3.371.
- Bournaud, M., Richoux, P., and Usseglio-Polatera, P. 1992. An approach to the synthesis of qualitative ecological information from aquatic coleoptera communities. *Regul. Rivers: Res. Manage.* **7**(2): 165–180. doi:10.1002/rrr.3450070205.
- Brown, J.K., and Patton, J.L. 2015. Genus *Graomys* Thomas, 1916. *In* Mammals of South America, Volume 2: Rodents. *Edited by* J.L. Patton, U.F. Pardiñas, and G. D'Elía. The University of Chicago Press, Chicago. pp. 523–531.
- Burgos, J.J. 1968. Clima de la Provincia de Buenos Aires en relación con la vegetación natural y el suelo. *In* Flora de la Provincia de Buenos Aires, Parte I. *Edited by* A.L. Cabrera. Instituto Nacional de Tecnología Agropecuaria, Ciudad Autónoma de Buenos Aires. pp. 33–99.
- Burmeister, H. 1879. Animaux Vertébrés. Première Partie — Mamifères Vivants et Éteints. *In* Description Physique de la République Argentine. Imprimerie de Paul Émile Coni, Ciudad Autónoma de Buenos Aires.
- Cabrera, A.L. 1968. Vegetación de la Provincia de Buenos Aires. *In* Flora de la Provincia de Buenos Aires, Parte I. *Edited by* A.L. Cabrera. Instituto Nacional de Tecnología Agropecuaria, Ciudad Autónoma de Buenos Aires.
- Campos, C.M., Ojeda, R.A., Monge, S., and Dacar, M. 2001. Utilization of food resources by small

- and medium-sized mammals in the Monte Desert biome, Argentina. *Austral Ecol.* **26**(2): 142–149. doi:10.1046/j.1442-9993.2001.01098.x.
- Campos, C.M., Giannoni, S.M., Taraborelli, P.A., and Borghi, C.E. 2007. Removal of mesquite seeds by small rodents in the Monte desert, Argentina. *J. Arid Environ.* **69**(2): 228–236. doi:10.1016/j.jaridenv.2006.10.002.
- Carleton, M.D. 1973. A Survey of Gross Stomach Morphology in New World Cricetinae (Rodentia, Muroidea), with Comments on Functional Interpretations. *Misc. Publ. Mus. Zool. Univ. Mich.* **146**: 1–43.
- Cassini, G.H. 2013. Skull Geometric Morphometrics and Paleoecology of Santacrucian (Late Early Miocene; Patagonia) Native Ungulates (Astrapotheria, Litopterna, and Notoungulata). *Ameghiniana* **50**(2): 193–216. doi:10.5710/AMGH.7.04.2013.606.
- Cassini, G.H., and Toledo, N. 2021. An Ecomorphological Approach to Craniomandibular Integration in Neotropical Deer. *J. Mamm. Evol.* **28**: 111–124. doi:10.1007/s10914-020-09499-5.
- Cassini, G.H., Vizcaíno, S.F., and Bargo, M.S. 2012. Body mass estimation in Early Miocene native South American ungulates: a predictive equation based on 3D landmarks. *J. Zool.* **287**(1): 53–64. doi:10.1111/j.1469-7998.2011.00886.x.
- Cassini, G.H., Toledo, N., and Vizcaíno, S.F. 2021. Form-Function Correlation Paradigm in Mammalogy. A Tribute to Leonard B. Radinsky (1937–1985). *J. Mamm. Evol.* **28**(1): 1–5. doi:10.1007/s10914-020-09528-3.
- Castellarini, F., Agnelli, H.L., and Polop, J.J. 1998. Study on the diet and feeding preferences of *Calomys venustus* (Rodentia, Muridae). *Mastozool. Neotrop.* **5**(1): 5–11.

- Castellarini, F., Dellafiore, C.M., and Polop, J.J. 2003. Feeding habits of small mammals in agroecosystems of central Argentina. *Mamm. Biol.* **68**(2): 91–101. doi:10.1078/1616-5047-00067.
- Chebez, J.C., Pardiñas, U.F.J., and Teta, P. 2014. Mamíferos terrestres Patagonia sur de Argentina y Chile. Vázquez Mazzini Editores, Ciudad Autónoma de Buenos Aires.
- Chivers, D.J., Hladik, C.M. 1980. Morphology of the Gastrointestinal Tract in Primates: Comparisons With Other Mammals in Relation to Diet. *Journal of Morphology* **166**(3): 337–386. doi:10.1002/jmor.1051660306
- Cicchetti, D. V. 1994. Guidelines, Criteria, and Rules of Thumb for Evaluating Normed and Standardized Assessment Instruments in Psychology. *Psychol. Assess.* **6**(4): 284–290. doi:10.1037/1040-3590.6.4.284.
- Coda, J.A., Priotto, J.W., Provencal, M.C., Pinotti, J.D., González-Ittig, R.E., Gómez Villafañe, I.E., Formoso, A.E., Burgos, E., and Cirignoli, S. 2019. *Calomys venustus*. In: SAyDS–SAREM (eds.) Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. Available from <http://cma.sarem.org.ar/index.php/es/especie-nativa/calomys-venustus> [accessed 28 February 2020].
- Contreras, J.R. 1979. Ecología del ratón de campo *Akodon azarae* en la región semiárida del sudoeste bonaerense, Laguna Chasicó, partido de Villarino. *Deserta* **4**: 15–24.
- Crespo, J.A., Sabattini, M.S., Piantanida, M.J., and de Villafañe, G. 1970. Estudios ecológicos sobre roedores silvestres – Observaciones sobre densidad, reproducción y estructura de comunidades de roedores silvestres en el sur de Córdoba. Secretaría de Salud Pública,

División Imprenta, Ciudad Autónoma de Buenos Aires.

Croft, D.A., Niemi, K., and Franco, A. 2011. Incisor morphology reflects diet in caviomorph rodents.

J. Mammal. **92**(4): 871–879. doi:10.1644/10-MAMM-A-226.1.

Dalby, P.L. 1975. Biology of Pampa Rodents. Balcarce Area, Argentina. Publ. Mus. Mich. State Univ., Biol. Ser. **5**: 1–271.

de la Barrera, J.M. 1939. Contribución al conocimiento de la peste selvática en la Argentina. - Caracteres del brote de Mendoza en 1937. Revista del Instituto Bacteriológico del Departamento Nacional de Higiene. **8**(5): 431–454.

de Mendiburu, F. 2020. agricolae: Statistical Procedures for Agricultural Research. Available from <https://cran.r-project.org/package=agricolae>.

Dellafiore, C.M., and Polop, J.J. 1994. Feeding habits of *Calomys musculinus* in the crop fields and its borders. Mastozool. Neotrop. **1**(1): 45–50.

Dellafiore, C.M., and Polop, J.J. 1998. Dieta de *Calomys laucha* (Rodentia, Muridae) en hábitats de cultivos de la provincia de Córdoba. FACENA **14**: 25–30.

Dellafiore, C.M., and Polop, J.J. 2010. La alimentación en los sigmodontinos de la región central de Argentina. In Biología y ecología de pequeños roedores en la región pampeana de Argentina, 1st edition. Edited by J.J. Polop and M. Busch. Universidad Nacional de Córdoba, Córdoba. pp. 173–199.

Demment, M.W., and Van Soest, P.J. 1985. A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. Am. Nat. **125**(5): 641–672. doi:10.1086/284369.

Eisenberg, J.F. 1981. The Mammalian Radiations – An Analysis of Trends in Evolution, Adaptation, and Behavior. The University of Chicago Press, Chicago.

- Ellis, B.A., Mills, J.N., Kenneddy, E.J.T., Maiztegui, J.I., and Childs, J.E. 1994. The relationship among diet, alimentary tract morphology, and life history for five species of rodents from the central Argentine pampa. *Acta Theriol.* **39**(4): 345–355. doi:10.4098/AT.arch.94-40.
- Ellis, B.A., Mills, J.N., Glass, G.E., McKee, K.T.J., Enria, D.A., and Childs, J.E. 1998. Dietary Habits of the Common Rodents in an Agrecosystem in Argentina. *J. Mammal.* **79**(4): 1203–1220. doi:10.2307/1383012.
- Fleming, P.A., and Bateman, P.W. 2016. The good, the bad, and the ugly: which Australian terrestrial mammal species attract most research? *Mamm. Rev.* **46**(4): 241–254. doi:10.1111/mam.12066.
- Gagnon, M., and Chew, A.E. 2000. Dietary Preferences in Extant African Bovidae. *J. Mammal.* **81**(2): 490–511. doi:10.1644/1545-1542(2000)081<0490:dpieab>2.0.co;2.
- Galliari, C.A., and Pardiñas, U.F.J. 2000. Taxonomy and distribution of the sigmodontine rodents of genus *Necomys* in central Argentina and Uruguay. *Acta Theriol.* **45**(2): 211–232.
- Gärtner, K. 2001. The forestomach of rats and mice, an effective device supporting digestive metabolism in *muridae* (Review). *J. Exp. Anim. Sci.* **42**(1): 1–20. doi:10.1016/s0939-8600(02)80002-5.
- Giannoni, S.M., Dacar, M., Taraborelli, P.A., and Borghi, C.E. 2001. Seed hoarding by rodents of the Monte Desert, Argentina. *Austral Ecol.* **26**(3): 259–263. doi:10.1046/j.1442-9993.2001.01112.x.
- Giannoni, S.M., Borghi, C.E., Dacar, M., and Campos, C.M. 2005. Main food categories in diets of sigmodontine rodents in the Monte (Argentina). *Mastozool. Neotrop.* **12**(2): 181–187.
- Goldberg, S., Anthony, H., and Evans, T. 2015. Modelling citation networks. *Scientometrics* **105**(3):

1577–1604. doi:10.1007/s11192-015-1737-9.

Gómez Villafañe, I.E., Miño, M., Cavia, R., Hodara, K., Courtalón, P., Suárez, O. V, and Busch, M.

2005. Roedores: Guía de la Provincia de Buenos Aires. L.O.L.A., Ciudad Autónoma de Buenos Aires.

González, E.M., and Martínez Lafranco, J.A. 2010. Ratón Oscuro *Necromys obscurus* (Waterhouse, 1837). *In* Mamíferos del Uruguay – Guía de campo e introducción a su estudio y conservación, 1st edition. *Edited by* E.M. González and J.A. Martínez Lafranco. Banda Oriental, Montevideo. pp. 104–105.

González, E.M., and Pardiñas, U.F.J. 2002. *Deltamys kempi*. Mamm. Species (711): 1–4. doi:10.1644/0.711.1.

González-Suárez, M., Lucas, P.M., and Revilla, E. 2012. Biases in comparative analyses of extinction risk: mind the gap. J. Anim. Ecol. **81**: 1211–1222. doi:10.1111/j.1365-2656.2012.01999.x

Hastie, T., Tibshirani, R., and Buja, A. 1994. Flexible Discriminant Analysis by Optimal Scoring. J. Am. Stat. Assoc. **89**(428): 1255–1270. doi:10.1080/01621459.1994.10476866.

Hautier, L., Lebrun, R., and Cox, P.G. 2012. Patterns of Covariation in the Masticatory Apparatus of Hystricognathous Rodents: Implications for Evolution and Diversification. J. Morphol. **273**(12): 1319–1337. doi:10.1002/jmor.20061.

Hershkovitz, P. 1955. South American Marsh Rats, Genus *Holochilus*, With a Summary of Sigmodont Rodents. Fieldiana Zool. **37**(24): 639–673. doi:10.5962/bhl.title.2902.

Hershkovitz, P. 1962. Evolution of neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. **46**: 1–524. doi:10.5962/bhl.title.2781.

Hershkovitz, P. 1966. South American Swamp and Fossorial Rats of the Scapteromyine Group

- (*Cricetinae*, *Muridae*) with Comments on the Glans Penis in Murid Taxonomy. *Z. für Säugetierkd.* **31**: 81–149.
- Holechek, J.L., Gross, B., Dabo, S.M., and Stephenson, T. 1982. Effects of Sample Preparation, Growth Stage, and Observer on Microhistological Analysis of Herbivore Diets. *J. Wildl. Manag.* **46**(2): 502–505. doi:10.2307/3808666.
- Hume, I.D. 1994. Gut morphology, body size and digestive performance in rodents. *In* The Digestive System in Mammals: Food, Form and Function. *Edited by* D.J. Chivers and P. Langer. Cambridge University Press, Cambridge. pp. 315–323.
- Jarić, I., Correia, R.A., Roberts, D.L., Gessner, J., Meinard, Y., and Courchamp, F. 2019. On the overlap between scientific and societal taxonomic attentions — Insights for conservation. *Sci. Total Environ.* **648**: 772–778. doi:10.1016/j.scitotenv.2018.08.198.
- Jergas, H., and Baethge, C. 2015. Quotation accuracy in medical journal articles—a systematic review and meta-analysis. *PeerJ* **3**:e1364: 1–20. doi:10.7717/peerj.1364.
- Juhr, N.C., and Haas, A. 1979. Substrate-specific selective culture of cellulose splitting intestinal bacteria of small laboratory rodents. *Vet. Sci. Commun.* **2**(1978/1979): 323–329.
- Kerley, G.I.H., and Whitford, W.G. 1994. Desert-dwelling Small Mammals as Granivores: Intercontinental Variations. *Aust. J. Zool.* **42**(4): 543–555. doi:10.1071/ZO9940543.
- Kissling, W. D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K., and Svenning, J.-C. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecol. Evol.* **4**(14):2913–2930. doi:10.1002/ece3.1136
- Kravetz, F.O. 1972. Estudio del régimen alimentario, períodos de actividad y otros rasgos

- ecológicos en una población de “ratón hocicudo” (*Oxymycterus rufus platensis* Thomas) de Punta Lara. *Acta Zool. Lilloana* **29**: 201–212.
- Landry, S.O.J. 1970. The Rodentia as Omnivores. *Q. Rev. Biol.* **45**(4): 351–372. doi:10.1086/406647.
- Langer, P. 1994. Food and digestion of Cenozoic mammals in Europe. *In* The digestive system in mammals: Food, form and function. *Edited by* D.J. Chivers and P. Langer. Cambridge University Press, Cambridge. pp. 9–24.
- Langer, P. 2002. The digestive tract and life history of small mammals. *Mamm. Rev.* **32**(2): 107–131. doi:10.1046/j.1365-2907.2002.00101.x.
- Langer, P., and Clauss, M. 2018. Morphological adaptation of the eutherian gastrointestinal tract to diet. *Vertebr. Zool.* **68**(3): 237–252. doi:10.5167/uzh-157906.
- Leiser-Miller, L.B., and Santana, S.E. 2020. Morphological diversity in the sensory system of phyllostomid bats: Implications for acoustic and dietary ecology. *Funct. Ecol.* **34**(7):1416–1427. doi:10.1111/1365-2435.13561
- Leveau, L.M., Teta, P., Bogdaschewsky, R., and Pardiñas, U.F.J. 2006. Feeding habits of the Barn Owl (*Tyto alba*) along a longitudinal-latitude gradient in central Argentina. *Ornitol. Neotrop.* **17**(3): 353–362.
- Lucas, P.W. 2004. Dental Functional Morphology: How Teeth Work. Cambridge University Press, Cambridge.
- Maestri, R., Luza, A.L., de Barros, L.D., Hartz, S.M., Ferrari, A., de Freitas, T.R.O., and Duarte, L.D.S. 2016a. Geographical variation of body size in sigmodontine rodents depends on both environment and phylogenetic composition of communities. *J. Biogeogr.* **43**(6): 1192–1202. doi:10.1111/jbi.12718.

- Maestri, R., Patterson, B.D., Fornel, R., Monteiro, L.R., and de Freitas, T.R.O. 2016b. Diet, bite force and skull morphology in the generalist rodent morphotype. *J. Evol. Biol.* **29**(11): 2191–2204. doi:10.1111/jeb.12937.
- Martin, S.A., Alhajeri, B.H., and Steppan, S.J. 2016. Dietary adaptations in the teeth of murine rodents (Muridae): a test of biomechanical predictions. *Biol. J. Linn. Soc.* **119**(4): 766–784. doi:10.1111/bij.12822.
- Martínez, R.L., Bocco, M.E., Mónaco, N., and Polop, J.J. 1990. Winter Diet in *Akodon dolores* Thomas, 1916. *Mammalia* **54**(2): 197–205. doi:10.1515/mamm-1990-0204.
- Martins, E.E., and Hansen, T.F. 1997. Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information into the Analysis of Interspecific Data. *Am. Nat.* **149**(4): 646–667.
- Massoia, E. 1961. Notas sobre los Cricétidos de la selva marginal de Punta Lara (Mammalia, Rodentia). *Publicaciones del Museo Tradicional y de Ciencias Naturales de Mar del Plata* **1**(4): 115–124.
- Massoia, E. 1964a. Los roedores del Delta del Paraná – Serie descriptiva. *Noticias del Delta* **2**(3): 14–15. Campana, Argentina.
- Massoia, E. 1964b. Los roedores del Delta del Paraná – Serie descriptiva. *Noticias del Delta* **2**(6): 12–13. Campana, Argentina.
- Massoia, E. 1964c. Los roedores del Delta del Paraná – Serie descriptiva. *Noticias del Delta* **2**(5): 13–15. Campana, Argentina.
- Massoia, E. 1964d. Sistemática, distribución geográfica y rasgos etoecológicos de *Akodon (Deltamys) kempi* (Rodentia-Cricetidae). *Physis* **24**(68): 299–305.

- Massoia, E. 1964e. Los roedores del Delta del Paraná – Serie descriptiva. Noticias del Delta **2**(4): 17–20. Campana, Argentina.
- Massoia, E. 1965a. Los roedores del Delta del Paraná – Serie descriptiva. Noticias del Delta **3**(7): 1–3. Campana, Argentina.
- Massoia, E. 1965b. Los roedores del Delta del Paraná – Serie descriptiva. Noticias del Delta **3**(8–9): 1–2. Campana, Argentina.
- Massoia, E. 1971. Caracteres y rasgos bioecológicos de *Holochilus brasiliensis chacarius* Thomas (“rata nutria”) de la provincia de Formosa y comparaciones con *Holochilus brasiliensis vulpinus* (Brants) (Mammalia, Rodentia, Cricetidae). Rev. Investig. Agropecu., INTA, Ser. 1, Biol. Prod. Anim. **8**: 13–40.
- Massoia, E. 1974. Ataques graves de *Holochilus* y otros roedores a cultivos de caña de azúcar. IDIA **321**(24): 1–12.
- Massoia, E. 1976. Mammalia. In Fauna de Agua Dulce de la República Argentina. Edited by R.A. Ringuelet. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires. pp. 1–128.
- Massoia, E., and Fornes, A. 1964. Notas sobre el género *Scapteromys* (Rodentia, Cricetidae.) I. Sistemática, distribución y rasgos etoecológicos de *Scapteromys tumidus* (Waterhouse). Physis **24**(68): 279–297.
- Massoia, E., and Fornes, A. 1965. Nuevos datos sistemáticos, biológicos y etoecológicos de *Oryzomys (Oligoryzomys) delticola* Thomas (Rodentia-Cricetidae). Delta del Paraná, Investigaciones Agrícolas **4**: 34–47.
- Mendoza, M., and Palmqvist, P. 2006. Characterizing adaptive morphological patterns related to diet in Bovidae (Mammalia: Artiodactyla). Acta Zool. Sin. **52**(6): 988–1008.

- Merritt, J. F. 2010. *The Biology of Small Mammals*. The Johns Hopkins University Press, Baltimore
- Michaux, J., Chevret, P., and Renaud, S. 2007. Morphological diversity of Old World rats and mice (Rodentia, Muridae) mandible in relation with phylogeny and adaptation. *J. Zool. Syst. Evol. Res.* **45**(3): 263–279. doi:10.1111/j.1439-0469.2006.00390.x.
- Morello, J., Matteucci, S.D., Rodríguez, A.F., and Silva, M. 2012. *Ecorregiones y complejos ecosistemicos argentinos*, 1st edition. Orientación Gráfica Editora, Ciudad Autónoma de Buenos Aires.
- Motani, R., and Schmitz, L. 2011. Phylogenetic versus functional signals in the evolution of form-function relationships in terrestrial vision. *Evolution* **65**(8): 2245–2257. doi:10.1111/j.1558-5646.2011.01271.x.
- Murphy, G.M. 2008. *Atlas agroclimático de la Argentina*. Editorial Facultad de Agronomía Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H. 2019. *vegan: Community Ecology Package*. R package version 2.5-6. doi:10.4135/9781412971874.n145.
- Olsen, A.M. 2015. Exceptional avian herbivores: Multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. *Ecol. Evol.* **5**(21): 5016–5032. doi:10.1002/ece3.1787.
- Olsen, A.M. 2017. Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Funct. Ecol.* **31**(10): 1985–1995. doi:10.1111/1365-2435.12890.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H.,

- Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., and Kassem, K.R. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience* **51**(11): 933–938. doi:10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2.
- Omran, M.G.H., Engelbrecht, A.P., and Salman, A. 2007. An overview of clustering methods. *Intell. Data Anal.* **11**(6): 583–605. doi:10.3233/ida-2007-11602.
- Paradis, E., and Schliep, K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**(3): 526–528. doi:10.1093/bioinformatics/bty633.
- Pardiñas, U.F.J., and Galliari, C.A. 2001. *Reithrodon auritus*. *Mamm. Species* (664): 1–8. doi:10.2307/0.664.1.
- Pardiñas, U.F.J., Teta, P., and Bilenca, D.N. 2010a. Análisis biogeográfico de los roedores sigmodontinos de la provincia de Buenos Aires. *In* *Biología y ecología de pequeños roedores en la región pampeana de Argentina*, 1st edition. *Edited by* J.J. Polop and M. Busch. Universidad Nacional de Córdoba, Córdoba. pp. 37–57.
- Pardiñas, U.F.J., Teta, P., and D'Elía, G. 2010b. Roedores sigmodontinos en la región pampeana: historia evolutiva, sistemática y taxonomía. *In* *Biología y ecología de pequeños roedores en la región pampeana de Argentina*, 1st edition. *Edited by* J.J. Polop and M. Busch. Universidad Nacional de Córdoba, Córdoba. pp. 9–36.
- Pardiñas, U.F.J., Teta, P., Ortiz, P.E., Jayat, J.P., and Salazar-Bravo, J. 2015. Genus *Necomys* Ameghino, 1889. *In* *Mammals of South America, Volume 2: Rodents*, 1st edition. *Edited by* J.L. Patton, U.F. Pardiñas, and G. D'Elía. The University of Chicago Press, Chicago. pp. 232–247.

- Pardiñas, U.F.J., Cañón Valenzuela, C., and Salazar-Bravo, J. 2017a. A matter of weight: Critical comments on the basic data analysed by Maestri et al. (2016) in *Journal of Biogeography*, 43, 1192–1202. *J. Biogeogr.* **44**(11): 2673–2677. doi:10.1111/jbi.13098.
- Pardiñas, U.F.J., Myers, P., León-Paniagua, L., Ordóñez Garza, N., Cook, J., Kryštufek, B., Haslauer, R., Bradley, R., Shenbrot, G., and Patton, J.L. 2017b. Family Cricetidae (True Hamsters, Voles, Lemmings and New World Rats and Mice). *In Handbook of the Mammals of the World*, 1st edition. *Edited by* D.E. Wilson, R.A. Mittermeier, and T.E.J. Lacher. Editions, Lynx, Barcelona. pp. 204–535.
- Pardiñas, U.F.J., Voglino, D., and Galliari, C.A. 2017c. Miscellany on *Bibimys* (Rodentia, sigmodontinae), a unique akodontine cricetid. *Mastozool. Neotrop.* **24**(1): 241–250.
- Pardiñas, U.F.J., Cañón Valenzuela, C., Galliari, C.A., Brito, J., Hoverud, N.B., Lessa, G., and Alves de Oliveira, J. 2020. Gross stomach morphology in akodontine rodents (Cricetidae: Sigmodontinae: Akodontini): a reappraisal of its significance in a phylogenetic context. *J. Mammal.* **101**(3): 835–857. doi:10.1093/jmammal/gyaa023.
- Patton, J.L., Pardiñas, U.F.J., and D'Elía, G. 2015. *Mammals of South America, Volume 2: Rodents*, 1st edition. *Edited by* J.L. Patton, U.F. Pardiñas, and G. D'Elía. The University of Chicago Press, Chicago. doi:10.7208/chicago/9780226169606.001.0001.
- Pearson, O.P. 1988. Biology and feeding dynamics of a South American Herbivorous rodent, *Reithrodon*. *Stud. Neotrop. Fauna Environ.* **23**(1): 25–39. doi:10.1080/01650528809360741.
- Perrin, M.R., and Curtis, B.A. 1980. Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. *S. Afr. J. Zool.* **15**(1): 22–33. doi:10.1080/02541858.1980.11447680.

- Peters, R.H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge, United Kingdom.
- Pineda-Munoz, S., and Alroy, J. 2014. Dietary characterization of terrestrial mammals. *Proc. Royal Soc. B.* **281**(20141173):1–7. doi: 10.1098/rspb.2014.1173
- Pineda-Munoz, S., Evans, A. R., and Alroy, J. 2016. The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42**(4):659–669. doi: 10.1017/pab.2016.6
- Polop, F., Sepúlveda, L., Pelliza Sbriller, A., Polop, J.J., and Provencal, M.C. 2015. Estructura de la dieta de roedores sigmodontinos en arbustales del ecotono bosque-estepa del suroeste de Argentina. *Mastozool. Neotrop.* **22**(1): 85–95.
- Polop, J.J., Gardenal, C.N., and Sabattini, M.S. 1982. Comunidad de roedores de cultivos de sorgo en la provincia de Córdoba y su posible vinculación con la fiebre hemorrágica Argentina. *ECOSUR* **9**: 107–116.
- Polop, J.J., Martínez, R.L., and Torres, M.P. 1985. Distribución y abundancia de poblaciones de pequeños roedores en la zona del embalse de Río Tercero, Córdoba. *Hist. Nat.* **5**(5): 33–44.
- Price, S A; Hopkins, S S B (2015) The macroevolutionary relationship between diet and body mass across mammals. *Biological Journal of the Linnean Society* **115**:173–184.
- Prieto, A.R. 2000. Vegetational history of the Late glacial-Holocene transition in the grasslands of eastern Argentina. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **157**(3–4): 167–188. doi:10.1016/S0031-0182(99)00163-7.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from <https://www.r-project.org/>.
- Rapoport, E.H. 1996. The flora of Buenos Aires: low richness or mass extinction? *Int. J. Ecol.*

Environ. Sci. **22**: 217–241.

Rodrigues Gonçalves, P., Alves de Oliveira, J., Oliveira Corrêa, M., and Pessôa, L.M. 2005. Morphological and Cytogenetic Analyses of *Bibimys labiosus* (Winge, 1887) (Rodentia, Sigmodontinae): Implications for its Affinities with the Scapteromyine Group. In Mammalian Diversification in the Neotropics: From Chromosomes to Phylogeography (A Celebration of the Career James L. Patton). Edited by E.A. Lacey and P. Myers. Univ. Calif. Publ. Zool. **133**: 175–209.

Rokach, L., and Maimon, O. 2005. Clustering Methods. In Data Mining and Knowledge Discovery Handbook, 1st edition. Edited by L. Rokach and O. Maimon. Springer, Tel-Aviv. pp. 321–352. doi:10.1007/978-1-4471-6735-8_6.

Rosi, M.I. 1983. Notas sobre la ecología, distribución y sistemática de *Graomys griseoflavus griseoflavus* (Waterhouse, 1837) (Rodentia, Cricetidae) en la provincia de Mendoza. Hist. Nat. **3**(17): 161–167.

Salazar-Bravo, J., Pardiñas, U.F.J., Zeballos, H., and Teta, P. 2016. Description of a New Tribe of Sigmodontine Rodents (Cricetidae: Sigmodontinae) with an Updated Summary of Valid Tribes and Their Generic Contents. Occas. Pap. Mus. Texas Tech. Univ. (338): 1–23.

Samuels, J.X. 2009. Cranial morphology and dietary habits of rodents. Zool. J. Linn. Soc. **156**(4): 864–888. doi:10.1111/j.1096-3642.2009.00502.x.

Scaglia, O.A., Velázquez, C.A., and Cauhépé, M.A. 1982. Plant Composition of Coney Rat's (*Reithrodon auritus*) Diet. Acta Theriol. **27**(24): 350–353. doi:10.4098/at.arch.82-29.

Schiaffini, M.I., and Prevosti, F.J. 2014. Trophic Segregation of Small Carnivorans (Carnivora: Mustelidae and Mephitidae) from the Southern Cone of South America. J. Mamm. Evol.

21(4): 407–416. doi:10.1007/s10914-013-9240-7

Shaley, C.T., Cervantes, K., Pacheco, V., Salas, E., Paredes, D., and Alonso, A. 2015. Diet of a sigmodontine rodent assemblage in a Peruvian montane forest. *J. Mammal.* **96**(5):1071–1080. doi:10.1093/jmammal/gyv112

Shapiro, A.S.S., and Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). *Biometrika* **52**(3/4): 591–611. doi:10.2307/2333709.

Simkin, M., and Roychowdhury, V. 2003. Read Before You Cite! *Complex Syst.* **14**(3): 269–274.

Simkin, M., and Roychowdhury, V. 2005. Stochastic modeling of citation slips. *Scientometrics* **62**(3): 367–384. doi:10.1007/s11192-005-0028-2.

Smith, M.R. 2017. Ternary: An R Package for Creating Ternary Plots. Zenodo. doi:10.5281/zenodo.1068996.

Soriano, A., León, R.J.C., Sala, O.E., Lavado, R.S., Deregibus, V.A., Cauhépé, M.A., Scaglia, O.A., Velázquez, C.A., and Lemcoff, J.H. 1991. Río de La Plata grasslands. *In* *Ecosystems of the world 8A - Natural Grasslands: Introduction and Western Hemisphere*. Elsevier, New York.

Suárez, O. V. 1994. Diet and habitat selection of *Oxymycterus rutilans* (Rodentia, Cricetidae). *Mammalia* **58**(2): 225–234. doi:10.1515/mamm.1994.58.2.225.

Suárez, O. V, and Bonaventura, S.M. 2001. Habitat use and diet in sympatric species of rodents of the low Paraná delta, Argentina. *Mammalia* **65**(2): 167–176. doi:10.1515/mamm.2001.65.2.167.

Taraborelli, P.A., Dacar, M., and Giannoni, S.M. 2003. Effect of plant cover on seed removal by rodents in the Monte Desert (Mendoza, Argentina). *Austral Ecol.* **28**(6): 651–657. doi:10.1046/j.1442-9993.2003.01326.x.

- Taraborelli, P.A., Borruel, N., and Mangeaud, A. 2009. Ability of Murid Rodents to Find Buried Seeds in the Monte Desert. *Ethology* **115**(3): 201–209. doi:10.1111/j.1439-0310.2008.01605.x.
- Teta, P., Cueto, G.R., and Suárez, O. V. 2007. New data on morphology and natural history of *Deltamys kemp* Thomas, 1919 (Cricetidae, Sigmodontinae) from central-eastern Argentina. *Zootaxa* **51**(1665): 43–51. doi:10.11646/zootaxa.1665.1.4.
- Teta, P., Formoso, A., Tammone, M.N., de Tommaso, D.C., Fernández, F.J., Torres Monges, J.C., and Pardiñas, U.F.J. 2014. Micromamíferos, cambio climático e impacto antrópico: ¿Cuánto han cambiado las comunidades del sur de América del Sur en los últimos 500 años? *Therya* **5**(1): 7–38. doi:10.12933/therya-14-183.
- Upham, N.S., Esselstyn, J.A., and Jetz, W. 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**(12): e3000494. doi:10.1371/journal.pbio.3000494.
- Ushakova, N.A., Belov, L.P., Varshavski, A.A., Kozlova, A.A., Kolganova, T. V, Boulygina, E.S., and Tourova, T.P. 2003. Cellulose Decomposition under Nitrogen Deficiency by Bacteria Isolated from the Intestines of Phytophagous Vertebrates. *Microbiology* **72**(3): 356–362. doi:10.1023/A:1024264419393.
- Vavra, M., and Holechek, J.L. 1980. Factors Influencing Microhistological Analysis of Herbivore Diets. *J. Range Manag.* **33**(5): 371. doi:10.2307/3897886.
- Verde Arregoitia, L.D., and D'Elía, G. 2020. Classifying rodent diets for comparative research. *Mamm. Rev.*: 1–15. doi:10.1111/mam.12214.
- Vizcaíno, S.F., Cassini, G.H., Toledo, N., and Bargo, M.S. 2012. On the Evolution of Large Size in

- Mammalian Herbivores of Cenozoic Faunas of Southern South America. *In*: Bones, clones, and biomes: the history and geography of recent Neotropical mammals. *Edited by*: B. Patterson and L. Costa. 1st edition. University of Chicago Press, Chicago. 76–101
- Vizcaíno, S.F., Bargo, M.S., Cassini, G.H., and Toledo, N. 2016. Forma y función en paleobiología de vertebrados, 1st edition. EDULP, La Plata. Available from <http://hdl.handle.net/10915/55101>.
- Vorontsov, N.N. 1959. The system of the hamster (Cricetinae) in the sphere of the world fauna and their phylogenetic relations. Byulleten' Moskovskovo Obschestva Ispytatelei Prirody, Otdel Biologicheskii **64**: 134–137. (*non vide*)
- Vorontsov, N.N. 1967. Evolution of the alimentary system myomorph rodents. Nauka, Siberian Branch, Novosibirsk.
- Vorontsov, N.N. 1979. Evolution of the alimentary system in myomorph rodents. Indian National Scientific Documentation Centre, New Dehli.
- Wetterer, J.K. 2006. Quotation error, citation copying, and ant extinctions in Madeira. Scientometrics **67**(3): 351–372. doi:10.1556/Scient.67.2006.3.2.
- Williamson, J. 1940. Plaga poco conocida entre los agricultores, “el ratón conejo.” Granos **4**(78): 31. (*non vide*)
- Wolak, M.E., Fairbairn, D.J., and Paulsen, Y.R. 2012. Guidelines for estimating repeatability. Methods Ecol. Evol. **3**(1): 129–137. doi:10.1111/j.2041-210X.2011.00125.x.
- Wright, J.P., Naeem, S., Hector, A., Lehman, C.L., Reich, P.B., Schmid, B., and Tilman, D. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. Ecol. Lett. **9**(2): 111–120. doi:10.1111/j.1461-0248.2005.00850.x.
- Zalba, S.M., and Villamil, C.B. 2002. Woody plant invasion in relictual grasslands. Biol. Invasions

4(1–2): 55–72. doi:10.1023/A:1020532609792.

Zar, J.H. 1999. Biostatistical Analysis, 4th edition. Prentice Hall, New Jersey.

Draft

Fig. 1. Dendrograms of cluster analyses performed on the 19 sigmodontine rodent species of central-eastern Argentina with valid dietary information, using the three food types dataset. **A.** Strict consensus of different distance metrics for Ward's method, showing the resulting dietary groups and invertebrates (inv), seeds (see) and leaves (lea) proportions for each species. **B.** Majority consensus between all methodologies, **C.** Strict consensus of different distance metrics for complete-link method, both showing the dietary groups identified with numbers in A.

Fig. 2. Ternary diagram of relative proportions of total leaves, seeds and invertebrates of the 19 species where dietary information was available. Different symbols represent each species' average dietary composition: Aa: *Akodon azarae*, Ad: *Akodon dolores*, Ai: *Akodon iniscatus*, Cl: *Calomys laucha*, Cm: *Calomys musculus*, Cv: *Calomys venustus*, Dk: *Deltamys kempi*, Et: *Eligmodontia typus*, Gg: *Graomys griseoflavus*, Hc: *Holochilus chacarius*, Hv: *Holochilus vulpinus*, Nl: *Necomys lasiurus*, Of: *Oligoryzomys flavescens*, Ol: *Oligoryzomys longicaudatus*, On: *Oligoryzomys nigripes*, Or: *Oxymycterus rufus*, Pb: *Phyllotis bonariensis*, Ra: *Reithrodon auritus*, Sa: *Scapteromys aquaticus*. Dietary categories are indicated with the following symbols: white squares: strict insectivores, dark grey triangles: non-strict insectivores, white triangles: strict folivores, dark grey triangles: non-strict folivores, dark grey circles: non-strict granivores, white diamonds: generalists.

Fig. 3. Box plot of body mass in relation to dietary category. The *post hoc* test indicated statistical differences between three body mass groups: large (a), medium sized (ab) and small (b). sFol: strict folivores; nsFol: non-strict folivores; nsGra: non-strict granivores; Gen: generalists; nsIns: non-strict insectivores; sIns: strict insectivores.

Fig. 4. Dendrograms of cluster analyses performed on the 17 sigmodontine rodent species of central-eastern Argentina with detailed dietary information, using the six food types dataset. **A.** Strict consensus of different distance metrics for Ward's method, showing the resulting dietary groups and hard-shelled invertebrates

(i_hs), worms and larvae (i_wl), monocot seeds (s_m), dicot seeds (s_di), monocot leaves (l_m) and dicot leaves (l_di) proportions next to the species' names (hs: hard-shelled). **B.** Majority consensus between all methodologies.

Draft

Table 1. Dietary information available for the 22 sigmodontine rodent species of central-eastern Argentina.

Species	Body mass (gr)	Source of body mass	% of invertebrates				% of seeds				% of leaves				n of valid entries			Source of diet
			Hard-shelled	Worms and larvae	Unid.	Total	Mono.	Dicot	Unid.	Total	Mono.	Dicot	Unid.	Total	Quant.	Qual.	Total	
<i>Akodon azarae</i>	28	Leveau et al. 2006	4.50	0.46	39.07	44.03	2.00	5.91	19.72	27.62	1.04	5.00	22.31	28.35	17 A	2 B 2 C	21	A: Barlow 1969; Bilenca et al. 1992; Bilenca 1993; Ellis et al. 1994, 1998; Suárez and Bonaventura 2001 B: Massoia 1964a, 1964b; Contreras 1979 C: Massoia 1964a, 1964b; Dalby 1975 Excl: Bilenca and Kravetz 1998; Dellafiore and Polop 2010
<i>Akodon dolores</i>	37	Chebez et al. 2014	0.97	0.32	32.31	33.59	8.08	13.74	7.62	29.41	5.36	25.76	5.88	37.00	10 A	1 B	11	A: Martínez et al. 1990; Campos et al. 2001; Castellarini et al. 2003; Giannoni et al. 2005 B: Contreras 1979 Excl: Campos et al. 2007; Dellafiore and Polop 2010
<i>Akodon iniscatus</i>	20	Chebez et al. 2014	0.00	0.00	50.00	50.00	0.00	0.00	25.00	25.00	0.00	0.00	25.00	25.00	0	1 C	1	C: Pardiñas et al. 2017b
<i>Bibimys torresi</i>	28	Maestri et al. 2016a	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	No information available: Pardiñas et al. 2017c
<i>Calomys laucha</i>	14	Maestri et al. 2016a	0.83	0.00	24.78	25.61	16.85	6.72	24.06	47.62	0.78	1.46	24.53	26.77	23 A	1 B	24	A: Bilenca et al. 1992; Bilenca 1993; Ellis et al. 1994, 1998; Dellafiore and Polop 1998; Castellarini et al. 2003 B: Barlow 1969 Excl: Dellafiore and Polop 2010
<i>Calomys musculus</i>	16	Chebez et al. 2014	0.00	0.00	18.50	18.50	19.91	37.74	11.21	68.86	1.72	7.89	3.02	12.64	16 A	0	16	A: Dellafiore and Polop 1994; Ellis et al. 1994, 1998; Campos et al. 2001; Castellarini et al. 2003; Giannoni et al. 2005

																		Excl: Campos et al. 2007
<i>Calomys venustus</i>	38	Coda et al. 2019	0.00	0.00	3.56	3.56	31.33	26.18	3.95	61.45	2.03	27.37	5.59	34.99	11 A	0	11	A: Castellarini et al. 1998, 2003 Excl: Dellafiore and Polop 2010
<i>Deltamys kempi</i>	24	Pardiñas et al. 2017a	29.17	12.50	14.29	55.95	0.00	0.00	11.31	11.31	25.00	0.00	7.74	32.74	0	2 B 2 C	4	B: Massoia 1964a, 1964c; González and Pardiñas 2002 C: Massoia 1964a, 1964c, 1964d Excl: Barlow 1969
<i>Eligmodontia typus</i>	19	Chebez et al. 2014	0.00	0.00	23.99	23.99	0.00	15.77	16.44	32.21	1.27	30.70	11.83	43.8	3 A	0	3	A: Campos et al. (2001); Giannoni et al. (2005) Excl: Giannoni et al. 2001, 2005; Taraborelli et al. 2003, 2009; Campos et al. 2007
<i>Graomys chacoensis</i>	75	Pardiñas et al. 2017b	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	No information available: Pardiñas et al. 2017b Excl: Brown and Patton 2015
<i>Graomys griseoflavus</i>	67.5	Maestri et al. 2016a	0.00	0.00	0.46	0.46	0.00	22.14	4.90	27.04	0.04	41.32	31.14	72.50	3 A	2 C	5	A: Campos et al. 2001; Giannoni et al. 2005 C: de la Barrera 1939 (with taxonomic annotations by Hershkovitz 1962); Rosi 1983 Excl: Hershkovitz 1962; Giannoni et al. 2001; Taraborelli et al. 2003; Campos et al. 2007
<i>Holochilus chacarius</i>	165.5	Pardiñas et al. 2017a	0.00	0.00	0.00	0.00	11.25	19.58	0.00	30.83	49.58	19.58	0.00	69.17	0	4 C	4	C: Massoia 1971, 1974, 1976
<i>Holochilus vulpinus</i>	301	Chebez et al. 2014	21.43	0.00	4.90	26.33	5.36	1.79	11.33	18.47	15.05	27.30	12.86	55.20	0	3 B 4 C	7	B: Burmeister 1879 (with geographic annotations by Hershkovitz 1955); Massoia 1976 C: Massoia 1964a, 1964e; Ageitos de Castellanos 1965; Barlow 1969 Excl: Massoia 1974; Bianchini and Delupi 1993
<i>Necomys lasiurus</i>	31	Leveau et al. 2006	0.00	0.00	40.53	40.53	13.68	15.19	6.97	35.84	11.14	5.53	6.97	23.64	5 A	0	5	A: Ellis et al. 1994, 1998

<i>Necromys obscurus</i>	43	Leveau et al. 2006	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	Excl: Barlow 1969
<i>Oligoryzomys flavescens</i>	24	Pardiñas et al. 2017a	0.00	0.00	26.80	26.80	9.48	11.44	17.63	38.55	1.32	14.84	18.49	34.65	7 A	2 C	9	A: Barlow 1969; Bilenca 1993; Ellis et al. 1994, 1998
<i>Oligoryzomys longicaudatus</i>	33	Pardiñas et al. 2017a	0.00	0.00	16.93	16.93	5.96	69.55	0.00	75.50	4.27	0.50	2.80	7.57	1 A	0	1	A: Polop et al. 2015
<i>Oligoryzomys nigripes</i>	29.4	Maestri et al. 2016a	1.67	0.56	16.10	18.32	0.00	0.00	22.25	22.25	0.00	20.00	39.43	59.43	3 A	2 C	5	A: Barlow 1969; Suárez and Bonaventura 2001 C: Massoia 1964a, 1965a Excl: Massoia and Fornes 1965
<i>Oxymycterus rufus</i>	55	Pardiñas et al. 2017a	41.05	36.16	8.33	85.53	0.00	0.00	8.25	8.25	0.00	0.00	6.21	6.21	8 A	2 B 2 C	12	A: Kravetz 1972; Suárez 1994 B: Massoia 1961; Kravetz 1972 C: Vorontsov 1959 (<i>non vide</i> in Massoia 1961); Massoia 1964a, 1965b Excl: Barlow 1969
<i>Phyllotis bonariensis</i>	42	Pardiñas et al. 2017a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0	1 C	1	C: Pardiñas et al. 2017b
<i>Reithrodon auritus</i>	80	Chebez et al. 2014; Pardiñas et al. 2017a	0.00	0.00	0.65	0.65	0.085	0.006	0.000	0.09	77.86	4.63	16.77	99.26	4 A	2 C	6	A: Scaglia et al. 1982; Polop et al. 2015 C: Williamson 1940 (<i>non vide</i> in Pardiñas and Galliari 2001); Pearson 1988
<i>Scapteromys aquaticus</i>	112	Maestri et al. 2016a	21.77	23.47	37.92	83.16	0.28	0.85	6.18	7.32	0.00	0.00	9.52	9.52	3 A	2 B 2 C	7	A: Barlow 1969; Suárez and Bonaventura 2001 B: Hershkovitz 1966; Barlow 1969 C: Massoia 1961; Massoia and Fornes 1964 Excl: Massoia 1964a, 1965b

Note: Numbers represent the average percentage of each food type in a species’ diet. Unid.: unidentified; Mono.: monocot. *n* of valid entries: total sets of data from all included publications; Quant.: quantitative; Qual.: qualitative. Diet composition sources are indexed based on their reliability in A: quantitative data; B: qualitative data that explicitly

mentioned more than one item and quantitative data restricted to only a fraction of the categories; C: quantitative reports of one item only, surveys based on popular knowledge, and information from indirect evidence; Excl: publications excluded for containing invalid or duplicated data.

Draft

Table 2. Values of intraclass correlation coefficient (ICC) between stomach types and proportion of invertebrates, seeds and leaves in the diet of the sigmodontine species under study.

Dataset	Variable	ICC	Variance within	Variance between
Three food types dataset (19 species)	inv_tot	0.7281	0.0303	0.0812
	seeds_tot	0.1815	0.0422	0.0094
	leaves_tot	0.4529	0.0583	0.04828
Six food types dataset (17 species)	inv_hs	0.4633	0.0263	0.0227
	inv_wl	0.8711	0.0050	0.0334
	seeds_mono	-0.1440	0.03419	-0.0043
	seeds_di	0.2272	0.0460	0.0135
	leaves_mono	0.6898	0.0292	0.0649
	leaves_di	0.0272	0.0417	0.0012

Note: Variable names indicate proportion of food types: inv_tot: total of invertebrates, seeds_tot: total of seeds, leaves_tot: total of leaves, inv_hs: hard-shelled invertebrates, inv_wl: worms and larvae; seeds_mono: monocot seeds, seeds_di: dicot seeds, leaves_mono: monocot leaves, leaves_di: dicot leaves. Excellent and good correlations are shown in bold in the ICC column.

Table 3. *A posteriori* dietary categories proposed for the sigmodontines of central-eastern Argentina, based on the most inclusive dataset (three food types).

	Strict folivores (>90% leaves and/or grasses)	Strict insectivores (>80% invertebrates)	Non-strict folivores (>50% leaves and/or grasses)	Non-strict granivores (>50% seeds)	Non-strict insectivores (>40% invertebrates)	Generalists (~30% of all food types)	Unavailable dietary information
Species	<i>Phyllotis bonariensis</i> <i>Reithrodon auritus</i>	<i>Oxymycterus rufus</i> <i>Scapteromys aquaticus</i>	<i>Graomys griseoflavus</i> <i>Holochilus chacarius</i> <i>Holochilus vulpinus</i> <i>Oligoryzomys nigripes</i>	<i>Calomys musculinus</i> <i>Calomys venustus</i> <i>Oligoryzomys longicaudatus</i>	<i>Akodon azarae</i> <i>Akodon iniscatus</i> <i>Deltamys kemp</i> <i>Necomys lasiurus</i>	<i>Akodon dolores</i> <i>Calomys laucha</i> <i>Eligmodontia typus</i> <i>Oligoryzomys flavescens</i>	<i>Bibimys torresi</i> <i>Graomys chacoensis</i> <i>Necomys obscurus</i>
Tribes	Phyllotini Reithrodontini	Akodontini	Oryzomyini Phyllotini	Oryzomyini Phyllotini	Akodontini	Akodontini Oryzomyini Phyllotini	Akodontini Phyllotini
Stomach types	Unilocular- hemiglandular majorly cornified Unilocular- hemiglandular majorly glandular	Unilocular with glandular pouch Unilocular-discoglandular	Unilocular- hemiglandular majorly cornified Unilocular- hemiglandular majorly glandular	Unilocular-hemiglandular majorly cornified	Unilocular- hemiglandular majorly cornified	Unilocular- hemiglandular majorly cornified	Unilocular- hemiglandular majorly cornified

Note: Species and tribes that represent each diet, and Carleton's (1973) stomach types associated with them.

Fig. 1. Dendrograms of cluster analyses performed on the 19 sigmodontine rodent species of central-eastern Argentina with valid dietary information, using the three food types dataset. A: strict consensus of different distance metrics for Ward's method, showing the resulting dietary groups and invertebrates (inv), seeds (see) and leaves (lea) proportions for each species. B: majority consensus between all methodologies, C: strict consensus of different distance metrics for complete-link method, both showing the dietary groups identified with numbers in A.

173x233mm (600 x 600 DPI)

Fig. 2. Ternary diagram of relative proportions of total leaves, seeds and invertebrates of the 19 species where dietary information was available. Circles represent each species' average dietary composition: Aa: *Akodon azarae*, Ad: *Akodon dolores*, Ai: *Akodon iniscatus*, Cl: *Calomys laucha*, Cm: *Calomys musculus*, Cv: *Calomys venustus*, Dk: *Deltamys kempi*, Et: *Eligmodontia typus*, Gg: *Graomys griseoflavus*, Hc: *Holochilus chacarius*, Hv: *Holochilus vulpinus*, NI: *Necomys lasiurus*, Of: *Oligoryzomys flavescens*, Ol: *Oligoryzomys longicaudatus*, On: *Oligoryzomys nigripes*, Or: *Oxymycterus rufus*, Pb: *Phyllotis bonariensis*, Ra: *Reithrodon auritus*, Sa: *Scapteromys aquaticus*. Dietary categories are indicated with the following symbols: white triangles: strict insectivores, dark grey triangles: non-strict insectivores, white triangles: strict folivores, dark grey triangles: non-strict folivores, dark grey circles: non-strict granivores, white diamonds: generalists.

85x80mm (600 x 600 DPI)

Fig. 3. Box plot of body mass in relation to dietary category. Correspondence to three different groups is indicated above the boxes. sFol: strict folivores; nsFol: non-strict folivores; nsGra: non-strict granivores; Gen: generalists; nsIns: non-strict insectivores; sIns: strict insectivores.

83x87mm (600 x 600 DPI)

Fig. 4. Dendrograms of cluster analyses performed on the 17 sigmodontine rodent species of central-eastern Argentina with detailed dietary information, using the six food types dataset. A: strict consensus of different distance metrics for Ward's method, showing the resulting dietary groups next to the species' names (hs: hard-shelled). B: majority consensus between all methodologies.

179x168mm (600 x 600 DPI)