Comparative lengths of digestive tracts of seven didelphid marsupials (Mammalia) in relation to diet

Nilton C. Cáceres

ABSTRACT. The relative proportions of the digestive tract were rarely explored to understand the behaviour and the ecology of neotropical marsupials. In this study, proportions of the digestive tract and diet were compared in seven opossum species. The animals studied were Didelphis albiventris Lund, 1840, D. aurita Wied-Neuwied, 1826, Metachirus nudicaudatus (Desmarest, 1817), Philander frenatus (Olfers, 1818), Lutreolina crassicaudata Desmarest, 1804, Monodelphis sox (Hensel, 1872) and Caluromys lanatus (Olfers, 1818). Segments of digestive tracts of marsupials were measured and differences were statistically tested by Analysis of Variance and Covariance. Caecum and hard guts were responsible for the main differences among opossums, although all segments differed significantly. Caluromys lanatus was the most specialised species, with a large hard gut and caecum, small stomach and shorter small gut. The large caecum of M. nudicaudatus and the shortest hard gut of M. sox were also noticed. The arboreal C. lanatus has a well different feeding habit and life style regarding other marsupials studied, such as M. sox and M. nudicaudatus which are terrestrial, corroborating the results reached.

KEY WORDS. Caecum, Caluromys lanatus, digestive tract proportions, hard gut, Metachirus nudicaudatus.

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MATERIAL AND METHODS

The digestive tracts of seven species of didelphid marsupials (N = 29 individuals, family Didelphidae) were obtained from adult individuals collected in the Paraná and Santa Catarina States. Species used were the white-eared opossum Didelphis albiventris Lund, 1840 (1500 g, N = 5 individuals), the southern black-eared opossum D. aurita Wied-Neuwied, 1826 (1200 g, N = 4), the grey four-eyed opossum Philander frenata (Ollers, 1818) (250 g, N = 3), the brown four-eyed opossum Metachirus nudicaudatus (Desmarest, 1817) (290 g, N = 5), the short-tailed opossum Monodelphis oreas (Hensel, 1872) (45 g, N = 6), the woolly opossum Caluromys lanatus (Ollers, 1818) (300 g, N = 3) and the thick-tailed opossum Lutreolina crassicaudata (Desmarest, 1804) (600 g, N = 3). All animals used were deposited in the Capão da Imbuia Museum of Natural History (MHNCP) collection, in Curitiba, Brazil. Nomenclature follows Fonseca et al. (1996).

The complete digestive tract of fresh individuals, from pharynx to anus, was removed through a longitudinal section from the abdomen (beginning at the anus) to the throat. Latter, each digestive tract was extended on a salver with flat surface and the caecum, hard gut, small gut, stomach and oesophagus were measured with a 1 mm precision ruler. The length of each segment was measured after removing all mesenteric attachments but only when the tissue stopped contraction after its distension on the salver. For stomachs, after emptying all food material through a small incision, their areas were estimated by measuring their length on the longer stomach axis, and width on the shorter axis, perpendicularly.

The relative dimension of each portion of the digestive tract was obtained by dividing each measure (e.g. the caecum length) by the total length of the respective digestive tract. For comparison to other measures, the stomach area was transformed to its square root (Medellín 1991).

The coefficient of variation of each segment of the digestive tract was calculated based on arithmetic means and standard deviation for each species (CV = standard deviation / mean x 100). Differences observed in digestive tracts of species were analysed statistically by two-way Analysis of Variance (ANOVA) and the Analysis of Covariance (ANCOVA), using the total digestive length as covariate, in order to increase the statistical power. Species that contributed more to differences in proportions of digestive tracts were tested by the post-hoc HSD Tukey test for samples of different sizes (Zar 1984, Statistica 1993). To avoid the variance heterogeneity associated with percentages (Zar 1984), arcsin transformations were performed on relative proportions (Crowe & Hume 1997).

RESULTS

The caecum was the segment of the digestive tract that varied more among species (average CV = 36%), followed by the hard gut (23%). The longer segment in all species, the small gut, was the one that varied less (8%). Stomach and oesophagus lengths varied at percentages of 16% and 20%, respectively. However, the Covariance analysis, a more robust analysis, showed that hard gut (F = 74.7; g.l. 6, 21; p < 0.0001) and small gut (F = 70.3; g.l. 6, 21; p < 0.0001) were the most important for general variations (see F values), although all segments differed significantly among species (for caecum: F = 39.2; g.l. 6, 21; p < 0.0001; for oesophagus: F = 27.0; g.l. 6, 21; p < 0.0001, and for stomach: F = 22.3; g.l. 6, 21; p < 0.0001).

Using the Analysis of Variance, all relative measures of digestive tracts differed significantly between species but with a weaker F value for the stomach (Tab. I). HSD Tukey test showed that C. lanatus differed from other species mainly because the small and hard intestines and caecum, M. nudicaudatus only because of the caecum (except in comparison with C. lanatus) and Monodelphis oreas because the hard intestine (Tab. I). Stomach, in general, did not differ between species. Thus, C. lanatus was the most different species, with a longer relative hard gut length (29%), a large relative caecum (8%), and short relative dimensions of the small intestine (51%) and stomach (3.8%) (Tab. II). Metachirus nudicaudatus had the longer relative caecum length (10%) in relation to other species. In contrast to C. lanatus, M. oreas had the shortest relative hard gut length (13%). Species of Didelphis were similar in all segments (Tabs I and II).

DISCUSSION

Caluromys lanatus and M. nudicaudatus were the species that have the larger variation observed in segments of digestive tracts, mainly regarding the caecum and hard guts. Despite of a long caecum, these two species have opposite life strategies, with M. nudicaudatus being strictly terrestrial (Malcolm 1991, Cunha & Vieira 2002). The great caecum and hard gut of C. lanatus may be related to a diet based on plant material, as occurs in other frugivorous-herbivorous mammals (Chivers & Hadler 1980, Charles-Dominique et al. 1981, for C. philander; Schick & Millar 1985). The genus Caluromys Allen, 1900 is relatively more specialized in the consumption of fruits, gums and twigs (Grand 1983, Leite et al. 1994, Julien-Laferrère 1999), similarly to some primates (Chivers & Hadler 1980, Passow 1999). A more frugivorous diet is associated to a small stomach chamber (Hilderbrand 1995), just as observed here for C. lanatus.

A large hard gut may also function in the re-absorption of water from fruits (see Atramentowicz 1988), as is probably the case of species of Caluromys that live mostly in the forest canopy, rarely descending to the ground (Malcolm 1991, Leite et al. 1994). Low levels of water deficit should occur seasonally even in tropical forests (such as the forested savannahs) during drier months (e.g. Smith 1970), and C. lanatus, a species distributed in seasonal forests in central and southern Brazil (Emons & Feer 1997), could be benefited by exploring water from fruits, as suggested for the scansorial marsupial D. albiventris in the same region (Santori et al. 2004).
According to Chivers & Hadluk (1980) and Schieck & Millar (1985), hard gut size is one of the best indicators of diet in small mammals: the greater its dimension, the more herbivorous is the diet, and in contrast, the smaller the dimension, the more carnivorous (in a strict sense, including all animal matter, sensu Vieira & Astua de Moraes 2003) is the diet. Accordingly, one could conclude that M. sorex is the more insectivore amongst the marsupials studied. Previously, Charles-Dominique et al. (1981) reached this conclusion for M. brevicaudata (Erxleben, 1777) (Didelphidae) by analysing gut proportions and contents. On the other hand, Chivers & Hadluk (1980) and Schieck & Millar (1985) also pointed out that the small gut length does not help to elucidate the actual diet of an animal.

A large caecum is utilized in the storage and fermentation of food (plant material), or in the storage of vitamins (Hildebrand 1995). Hundreds of small seeds were seen concentrated into the caecum of an individual of C. lanatus analysed (Caceres & Casella in preparation) and this could be related, possibly, to storage of fruit components or vitamin extraction from them. Anyway, the diet of Caluromys is thought to be more herbivorous than previously known (Julien-Laperriere 1999, Santori et al. 2004), based on the proportion of its caecum (Crowe & Hume 1997).

Despite the diet of M. nudicaudatus being more insectivorous (Santori et al. 1995a, Caceres 2004), its caecum had a long relative dimension, though less complex (and smaller in volume; personal observation) than that of C. lanatus (Santori et al. 2004). This could be related to the absorption of water and electrolytes, as hypothesized for insectivorous mammals (Anderson et al. 1992). Alternatively, it may be related to the metabolism of large volumes of chitin ingested, which would occur in the stomach and caecum of M. nudicaudatus, hypothetically, through specific enzymes, as in other insectivorous mammals such as bats (Webb et al. 1993). With such enzymes, bats may extract a reasonable quantity of carbohydrates from the chitinous skeleton of insects.

Revista Brasileira de Zoologia 22 (1): B1-B5, março 2005
The presence of a caecum in most didelphid marsupials is in agreement with the omnivory of the group (Astúa de Moraes et al., 2003, Santore et al. 2004). Even the more carnivorous-omnivorous marsupial *Lutreolina crassicaudata* has a relatively developed caecum when compared to other carnivorous marsupials (Santore et al. 2004, Vieira & Astúa de Moraes 2004). Material plant such as fruits could be ingested since the first months of young opossums after their independence of the mother (Cáceres 2002, 2004). Furthermore, plant-eaters herbivorous or folivorous will have greater caeca for microbial fermentation than those frugivorous animals (Crowe & Hume 1997), which will have larger caeca than more carnivorous marsupials.

The grey four-eyed opossum, *P. frenatus*, differently of the expected based on its more carnivorous diet (Santore et al. 1995b, 1997, 2004, Cáceres 2004), did not show significant differences in the stomach chamber size among other opossum species. According to Hildbrand (1995), specialized carnivorous animals tend to have big and elastic stomachs to eat and temporarily store large quantities of meat in each meal. *Philander frenatus* appears to be an omnivorous mammal not well adapted to the function of carnivory but with trends to this (Santore et al. 2004). Tests of laboratory food preferences indicated the same trend for this species (Astúa de Moraes et al. 2003).

Dimensions of digestive tracts of didelphid marsupials may hide phyllogenetic characteristics that mask functional adaptations, becoming difficult to detect them. For example, the neotropical kinkajou *Potos flavus* (Schreber, 1774) (Procyonidae) (Charles-Dominique et al. 1981, Julien-Laferrière 1993) and the African hyena *Proteles cristatus* (Spaarnan, 1783) (Hyenidae) (Anderson et al. 1992) exhibit digestive tracts of carnivores (resembling their ancestral) but today their diets are frugivorous and insectivorous, respectively. Also, the gastrointestinal morphology of Pseudocheiriidae Australian marsupials is conditioned by phylogeny rather than diet or habitat (Crowe & Hume 1997). Phylogeny may have constrained the form of digestive tract of didelphid marsupials, yet differences between species with opposite life strategies suggest that there was space for adaptations in the group. Taxa such as *Caluromys* and *Monodelphis* appear to differ much more in form, differences that are in agreement with their opposite diets.

ACKNOWLEDGMENTS

Thanks to M. Miretzki, T.C.C. Margarido and Tião for administrative and technical assistance, respectively, in the Capão da Imbuia Museum of Natural History (MHNCP), S.A. Morato from COPEL and M.E. Graipel from UFSC for providing me specimens, E.L.A. Monteiro-Filho, H.G. Bergallo and M.V. Vieira for helpful advices on the early drafts of the manuscript, and the “Curso de Pós-Graduação em Zoologia” at the Universidade Federal do Paraná and CAPES/MEC/Brazil for support and grants, respectively. Special thanks to two anonymous referees that contributed to the final version of the manuscript.

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Received in 27.IV.2004; accepted in 11.II.2005.