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LITTER SIZE AND EMBRYO IMPLANTATION IN NEOTROPICAL RODENTS

Marielle Portugal Lamberti Silva[1], Yuri Luiz Reis Leite[1] and Leonora Pires Costa[1]*

[1] *Universidade Federal do Espírito Santo (UFES), Centro de Ciências Humanas e Naturais, Departamento de Ciências Biológicas, Laboratório de Mastozoologia e Biogeografia, Av. Fernando Ferrari, 514, Campus de Goiabeiras, Vitória, ES, Brazil, CEP: 29075-910.*
E-mails: marielle.portugal@gmail.com, yuri_leite@yahoo.com, leonoracosta@yahoo.com

ABSTRACT

Research on the biology of Neotropical small mammals has increased in recent decades, and many studies have emphasized ecological and population attributes, but information on reproduction is still scarce. Reproduction is one of the most important natural history attributes because it is related to almost every structural, physiological and behavioral adaptation of an individual or a species. Most research on rodent reproduction concentrates in temperate areas and there is an evident lack of data from the Neotropical region. We compared reproductive patterns of sigmodontine and echimyid rodents using necropsy data from 135 specimens collected in the field and belonging to 22 species of sigmodontine and 8 species of echimyid rodents. We estimated embryonic litter size by counting the number of embryos or the number and placement of placental scars in pregnant and parous females. Although smaller in body size, sigmodontines have larger litter sizes (3.6 ± 1.2) than echimyids (2.1 ± 0.7), indicating a tendency toward r and K reproductive strategies, respectively. Embryonic litter size in pregnant females was not statistically different from the number of placental scars, so the latter is a reliable estimate of the former in both sigmodontines and echimyids. Embryo implantation is asymmetric regarding uterine horns in sigmodontines, with predominance in the right horn, but not in echimyids. The data obtained in this study are relevant in understanding the life history of two of the most diverse clades of neotropical mammals.

Keywords: Echimyidae; placental scars; reproduction; Rodentia; Sigmodontinae.

INTRODUCTION

Research on the biology of Neotropical small mammals has increased in recent decades, and many studies have emphasized ecological and population attributes (e.g., Bergallo and Magnusson 1999, Talamoni and Dias 1999), but information on reproduction of small mammals is still scarce (Bronson 1985, Pereira *et al.* 1993). Because of its importance, reproduction is related to almost every structural, physiological and behavioral adaptation of an individual or a species. Therefore, it is considered one of the most important natural history traits. Rodents in general usually reach early sexual maturity, having many litters per year and many newborns per litter (Vaughan *et al.* 2000). These characteristics, associated to the great diversity and abundance of rodents, make them an excellent model for reproductive studies among placental mammals.

Historically, most research on rodent reproduction focused on species from temperate areas (Bronson 1985, Lacher 1992). There are very important contributions based on wild Neotropical rodents raised in captivity (*e.g.*, Roberts *et al.* 1988, Mello 1978, 1986, Mello and Mathias 1987, De Conto and Cerqueira 2007), but most data are scattered in monographic works on local or regional faunas (*e.g.*, Davis 1947, Fonseca *et al.* 1989, Patton *et al.* 2000, Rocha *et al.* 2011), with very few published accounts focusing on reproduction in the field (*e.g.*, Cerqueira *et al.* 1989, Pereira *et al.* 1993, Gentile *et al.* 2000, Cademartori *et al.* 2005, Couto and Talamoni 2005, D'Andrea *et al.* 2007).

Reproductive strategies are usually classified into the conceptual framework of K- and r-selection. K-strategists tend to be larger, long-lived animals that can afford having long, well-spaced, reproductive cycles, in which only a few young are born in an altricial state, and require a long time to mature and become fertile. In contrast, r-strategists tend to be small, short-lived animals that rapidly and repeatedly produce large litters of precocial newborn, which can quickly mature and achieve fertility (Bronson 1989). Rodents typically exhibit small body sizes and short lifespans, which combine with the maximized reproductive output, resulting in r-selected organisms, but there are several exceptions (Merritt 2010).

Echimyidae and Cricetidae rodents are among the most relevant terrestrial small mammal taxa in the Neotropical region, due to their high species diversity and local abundance. The cricetid subfamily Sigmodontinae is the most diverse clade of mammals from the Neotropical region (Weksler 2006), with 380 species (Patton 2015) and the family Echimyidae is the most diverse of the South American hystricognath rodents, with 88 species (Emmons *et al.* 2015). Such diverse groups of animals comprise appropriate models for studying and comparing reproductive strategies and associated life-history traits.

In the present paper, we analyzed and compared the reproductive biology of echimyid and sigmodontine rodents to answer three main questions: 1) is embryonic litter size affected by the adult body size? 2) Is the number of placental scars indicative of embryonic litter size? 3) Is embryo implantation asymmetric regarding uterine horns?

MATERIAL AND METHODS

We compiled field notes on reproduction from specimens of sigmodontine and echimyid rodents collected during field expeditions to several localities across Brazil between 1991 and 2006. Specimens are listed below, and have been deposited in the following collections: Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG). We also used uncatalogued specimens collected by L. P. Costa (initials LC or LPC) and Y. Leite (YL), housed at UFMG, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), or Universidade Federal do Espírito Santo,

Vitória, Brazil (UFES). The field notes are based on necropsies conducted by two of the authors (LPC and YL) during specimen preparation. The reproductive data from pregnant and parous females were the number of embryos in uterus (considered here as embryonic litter size), and the number of right or left placement of placental scars. We used head-and-body length (in millimeters) and body weight (in grams), both taken in the field, as body size estimates.

We present basic descriptive statistics of head-and-body length, body weight, and number of embryos (average ± one standard deviation) for sigmodontines and echimyids. In our sample, specimens of the sigmodontine genus *Nectomys* stand out as having a very large body size, closer to echimyids than to other sigmodontines. In order to verify if body size affects reproduction in spite of phylogenetic constraints, we compared small and large sigmodontines, using 150 mm of head-and-body length as the cutting value. The number of placental scars was compared to embryonic litter size to check whether the former is a reliable proxy of the latter. The average litter size in each uterine horn and the percentage of embryos in the right and left uterine horns were calculated to verify the occurrence of asymmetric implantation. Statistical analyses were performed in R (R Core Team, 2014). We used the Wilcoxon rank sum test (W) to compare differences between litter sizes, Pearson's correlation between litter size and body size, and the t test (t) for left/right implantation, using appropriate degrees of freedom (df) and p-values (p).

Specimens examined

Family Cricetidae, Subfamily Sigmodontinae

Akodon cursor (Winge). (n = 3) —BAHIA: Fazenda Santa Rita, 8 km E Andaraí, 12º48'06"S, 41º15'41"W, 399 m (MVZ 197458); SÃO PAULO: Floresta Nacional de Ipanema, 20 km NW Sorocaba, 23º26'07"S, 47º37'41"W, 701 m (UFMG 2716, 2717).

Akodon montensis Thomas. (n = 11) — MATO GROSSO DO SUL: Fazenda Maringá, 54 km W Dourados, Ponta Porã, 22º16'47"S, 55º18'36"W, 427 m (UFMG 2686, 2700, 2703, 2705, 2707, 2713, MVZ 197459, 197461, 197463; MINAS GERAIS: Parque das Mangabeiras, Belo Horizonte (UFMG/LPC 913); PARANÁ: Parque Nacional do Iguaçu, 25º37'40"S, 54º27'42"W, 230 m (MVZ 197482).

Calomys callosus (Rengger). (n = 2) — MATO GROSSO: Base de Pesquisas do Pantanal - CENAP/IBAMA, 110 km SSW Poconé, 17º07'12"S, 56º56'47"W, 98 m (UFMG 2795, 2796).

Cerradomys subflavus (Wagner). (n = 1) — MINAS GERAIS: Usina Hidrelétrica Queimado (UFMG/LPC 904).

Cerradomys vivoi Percequillo, Hingst-Zaher, and Bonvicino. (n = 1) —BAHIA: Fazenda Santa Rita, 8 km E Andaraí, 12º48'06"S, 41º15'41"W, 399 m (UFMG 2862).

Delomys dorsalis (Hensel). (n = 1) — MINAS GERAIS: Fazenda do Itaguaré, 16 km SW Passa Quatro, 22º28'S, 45º05'W, 1500 m (UFMG 1873).

Euryoryzomys sp. (n = 4) — MATO GROSSO: Reserva Ecológica Cristalino,

40 km N Alta Floresta, 09º35'49"S, 55º55'49"W, 360 m (MVZ 197523, 197968, 197974, 197969).

Holochilus brasiliensis (Desmarest). (n = 1) — MATO GROSSO: Base de Pesquisas do Pantanal - CENAP/IBAMA, 110 km SSW Poconé, 17º07'12"S, 56º56'47"W, 98 m (MVZ 197486).

Hylaeamys megacephalus (Fischer). (n = 10) — AMAZONAS: Lago Meduini, left bank Rio Negro, 01º46'58"S, 61º23'14"W (INPA/YL 169); Macaco, right bank Rio Jaú, 02º04'30"S, 62º06'21"W, 24 m (INPA/YL 145); MATO GROSSO: Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira, 12º38'29"S, 51º55'56"W, 297 m (UFMG 2920, MVZ 197535, 197536); TOCANTINS: Rio Santa Teresa, 20 km NW Peixe, 11º50'34"S, 48º38'08"W, 205 m (MVZ 197533, 197534, UFMG 2914, 2915, 2917).

Neacomys spinosus (Thomas). (n = 1) — MATO GROSSO: Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira, 12º38'29"S, 51º55'56"W, 297 m (UFMG 2798).

Nectomys squamipes Brants. (n = 4) — BAHIA: Estação Experimental Lemos Maia, Una, 15º17'S, 39º05'W, (UFMG 2993); MINAS GERAIS: Parque Estadual do Rio Doce, 13 km E Marliéria, 19º43'S, 42º39'W, 300 m (UFMG 2992); SÃO PAULO: Floresta Nacional de Ipanema, 20 km NW Sorocaba, 23º26'07"S, 47º37'41"W, 701 m (UFMG 2994, 3010).

Oecomys cleberi Locks. (n = 15) — MATO GROSSO: Fazenda Lagoa Bonita, 36 km N Barra do Garças, 15º34'50"S, 52º22'29"W, 331 m (UFMG 2813, 2814, MVZ 197498); Fazenda São Luís, 30 km N Barra do Garças, 15º38'00"S, 52º21'21"W, 389 m (MVZ 197495, 197496, UFMG 2808, 2811, 2812); Reserva Ecológica Cristalino, 40 km N Alta Floresta, 09º35'49"S, 55º55'49"W, 360 m (UFMG 2816); MATO GROSSO DO SUL: Balança Velha, 55 km W Dourados, Ponta Porã, 22º20'56"S, 55º18'54"W, 518 m (UFMG 2817); Fazenda Maringá, 54 km W Dourados, Ponta Porã, 22º16'47"S, 55º18'36"W, 427 m (UFMG 2820, 2824, 2825, MVZ 197501); MINAS GERAIS: Mata do Edésio, 8 km NW Nova Ponte, 19º07'50"S, 47º44'22"W, 854 m (UFMG 2799).

Oecomys mamorae (Thomas). (n = 1) — MATO GROSSO DO SUL: Rio Miranda, above Passo do Lontra, Corumbá, 19º34'35"S, 57º01'04"W, 100 m (MVZ 197506).

Oecomys paricola (Thomas). (n = 4) — MATO GROSSO: Reserva Ecológica Cristalino, 40 km N Alta Floresta, 09º35'49"S, 55º55'49"W, 360 m (UFMG 2839, 2840, 2841, MVZ 197508).

Oecomys roberti (Thomas). (n = 2) — TOCANTINS: Rio Santa Teresa, 20 km NW Peixe, 11º50'34"S, 48º38'08"W, 205 m (UFMG 2848, 2849).

Oecomys sp. (n = 5) — AMAZONAS: Ilha das Onças, left bank Rio Negro, 01º49'57"S, 61º22'49"W (INPA/YL 161); Macaco, right bank Rio Jaú, 02º04'30"S, 62º06'21"W, 24 m (INPA/YL 129, 144, INPA/LC 128, 154).

Oligoryzomys nigripes (Olfers). (n = 5) — MATO GROSSO DO SUL: Fazenda Maringá, 54 km W Dourados, 22º16'47"S, 55º18'36"W, 427 m

(UFMG 2760, 2762, 2763); MINAS GERAIS: Mata do Vasco, 12 km W Nova Ponte, 19º10'15"S, 47º42'29"W, 878 m (UFMG 2747, 2755).

Oligoryzomys sp. (n = 16) — SÃO PAULO: Floresta Nacional de Ipanema, 20 km NW Sorocaba, 23º26'07"S, 47º37'41"W, 701 m (UFMG 2743, 2766, 2767, 2769, 2770, 2775, 2777, 2778, 2781, 2782, 2784, 2785, 2787, MVZ 197519); MINAS GERAIS: Mata do Vasco, 12 km W Nova Ponte, 19º10'15"S, 47º42'29"W, 878 m (MVZ 197515); TOCANTINS: Rio Santa Teresa, 20 km NW Peixe, 11º50'34"S, 48º38'08"W, 205 m (MVZ 198118).

Rhipidomys macrurus (Gervais). (n = 2) — MINAS GERAIS: Mata do Edésio, 8 km NW Nova Ponte, 19º07'50"S, 47º44'22"W, 854 m (UFMG 2943); Ponte do Colatino, left bank Rio Jequitinhonha, Coronel Murta, 16º36'S, 42º12'W, 322 m (UFMG 2934).

Rhipidomys emiliae (J. A. Allen). (n = 10) — MATO GROSSO: Fazenda Noirumbá, 34 km NW Ribeirão Cascalheira, 12º38'29"S, 51º55'56"W, 297 m (UFMG 2955, 2970, 2973, 2974, MVZ 197557, 197558, 197559, 197560, 197562); Fazenda São Luís, 30 km N Barra do Garças, 15º38'00"S, 52º21'21"W, 389 m (UFMG 2946).

Sooretamys angouya (Fischer). (n = 1) — MINAS GERAIS: Passes, 13 km SE Itanhandú, 22º23'S, 44º51'W, 1400 m (UFMG 1880).

Wiedomys pyrrhorhinos (Wied--Neuwied). (n = 1) — MINAS GERAIS: Ponte do Colatino, left bank Rio Jequitinhonha, Coronel Murta, 16º36'S, 42º12'W, 322 m (MVZ 197566).

Family Echimyidae

Isothrix bistriata Wagner. (n = 2)—AMAZONAS: Ilha das Onças, Rio Negro, 01º49'57"S, 61º22'49"W (INPA/YL 162, INPA/LC 169).

Mesomys hispidus (Desmarest). (n = 1) — MATO GROSSO: Left bank Rio Cristalino, 40 km N Alta Floresta, 09º35'49"S, 55º55'42"W 380 m (UFMG 3013).

Phyllomys pattoni Emmons, Leite, Kock, and Costa. (n = 1) — Espírito Santo: Parque Estadual da Fonte Grande, Vitória, 20º21'S, 40º21'W, 264 m (UFES/YL 263).

Proechimys cuvieri Petter. (n = 1) — AMAZONAS: Lago Meduini, left bank Rio Negro, 01º46'58"S, 61º23'14"W (INPA/YL 160).

Proechimys roberti Thomas. (n = 14) — MATO GROSSO: Left bank Rio Cristalino, 40 km N Alta Floresta, 09º35'49"S, 55º55'42"W 380 m (UFMG 3032, 3034); Reserva Ecológica Cristalino, 40 km N Alta Floresta, 09º35'49"S, 55º55'49"W, 360 m (MVZ 197576, 197578, 197579, 197580, 197581, 197582, UFMG 3023, 3026, 3029, 3030, 3031); TOCANTINS: Rio Santa Teresa, 20 km NW Peixe, 11º50'34"S, 48º38'08"W, 205 m (MVZ 197992).

Proechimys sp. (n =12) — AMAZONAS: Lago Meduini, left bank Rio Negro, 01º46'58"S, 61º23'14"W (INPA/LC 167, 179); Macaco, left bank Rio Jaú, 02º05'01"S, 62º07'21"W, 24 m (INPA/LC 126, 150, INPA/YL 114, 115, 125, 128); Right bank Rio Jaú, above mouth, 01º57'54"S, 61º29'14"W (INPA/LC 157, 160, INPA/YL 152); MINAS GERAIS: Usina Hidrelétrica Queimado (UFMG/LPC 900)

Thrichomys apereoides (Lund). (n = 1) — MINAS GERAIS: Parque Estadual do Rio Preto, 15 km S São Gonçalo do Rio Preto, 18º09'S, 43º23'W, 950 m (UFMG 3006).

Trinomys albispinus (I. Geoffroy St.-Hilaire). (n = 2) — Bahia: Fazenda Santa Rita, 8 km E Andaraí, 12º48'06"S, 41º15'41"W, 399 m (UFMG 3042, MVZ 197571).

RESULTS

Embryonic litter size was larger ($W = 1751$, $p < 0.001$) in sigmodontines (3.6 ± 1.2) than in echimyids (2.1 ± 0.7; Table 1). When we compared small- and large-bodied sigmodontines, embryonic litter sizes were not statistically distinct ($W = 121$, $p = 0.2706$): 3.6 ± 1.3, and 4.0 ± 0.6, respectively (Table 1). In addition, we found no correlation between litter size and head and body length ($t = 0.2005$, $df = 71$, $p = 0.8417$). Embryonic litter size in pregnant females was nearly identical to the number of placental scars in parous females in sigmodontines (3.6 ± 1.3 embryos and 3.6 ± 1.2 placental scars, $W = 1039.5$, $p = 0.8933$) and echimyids (2.0 ± 0.9 embryos and 2.1 ± 0.7 placental scars, $W = 80$, $p = 0.8645$; Table 1). Specific litter size data for sigmodontine and echimyid rodents are provided in Appendices 1 and 2.

Embryo implantation in uterine horns was asymmetric in sigmodontines ($t = 2.1046$, $df = 119.996$, $p = 0.03741$): the right horn showed higher mean litter size (2.17 ± 0.98 embryos) than the left horn (1.81 ± 0.92 embryos). In addition, the frequency of implantation was 55% in the right horn, 32% in the left, and 13% occurring equally in both horns (n = 68, Figure 1). In contrast, echimyids showed symmetric implantation showing the same mean litter size (1.22 embryos) in each horn ($t = 0$, $df = 44$, $p = 1$), 41% occurring equally in both horns, 33% in the right horn, and 26% in the left horn (n=27, Figure 1).

DISCUSSION

In mammals, larger species tend to produce fewer newborns than smaller ones (Pough *et al.* 2004). We confirmed this expectation found that sigmodontines, although typically smaller than echimyids, have larger litter sizes. Our data suggest that sigmodontines and echimyids show different reproductive strategies in general, the former being r-strategists and the latter being K-strategists. These are, however, two extremes of a continuum, and there is plenty of variation in between. In addition, these two strategies are not based only on body size and litter size: r-selection usually favors rapid rates of reproduction and growth, especially when species occupy unstable habitats, while K-selection favors slow rates of reproduction and growth, typically occurring in species adapted to stable, predictable habitats (Merritt 2010). The sigmodontine and echimyid rodents used in the present study, however, occupy the same general habitats, and several species are often sympatric or syntopic. Ecological factors, such as habitat predictability, are therefore insufficient to explain

Table 1. Descriptive statistics for pregnant and parous females of sigmodontine and echimyid rodents, including sample size (n), mean ± one standard deviation, and range in parenthesis.

Group	Pregnant females				Parous females			
	n	Head-and-body lenght (mm)	Body weight (g)	Litter size	n	Head-and-body lenght (mm)	Body weight (g)	Number of scars
Sigmodontinae	77	120.2 ± 26.9 (74 – 208)	55.1 ± 42.8 (15 – 240)	3.6 ± 1.2 (1 – 7)	29	119.4 ± 18.7 (91 – 171)	45.8 ± 20.2 (19 – 101)	3.6 ± 1.3 (1 – 6)
Small Sigmodontinae (below 150 mm)	71	114.3 ± 17.7 (74 – 149)	44.9 ± 20.1 (15 – 96)	3.6 ± 1,3 (1 – 7)	28	117.5 ± 16.2 (91 – 149)	43.8 ± 17.5 (19 – 82)	3.6 ± 1.3 (1 – 6)
Large Sigmodontinae (above 150 mm)	6	189.7 ± 18.4 (167 – 208)	175.8 ± 60.0 (105 – 240)	4.0 ± 0.6 (3 – 5)	1	171	101	3
Echimyidae	28	204.4 ± 19.4 (159 – 247)	242.8 ± 91.9 (130 – 495)	2.1 ± 0.7 (1 – 3)	6	211.2 ± 18.7 (196 – 246)	226.7 ± 54.7 (167 – 320)	2.0 ± 0.9 (1 – 3)

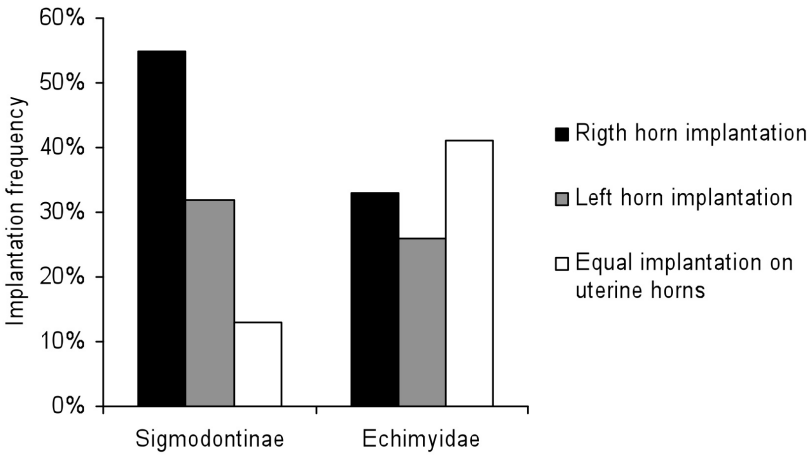

Figure 1. Frequency of embryo implantation in uterine horns of echimyid and sigmodontine rodents.

the occurrence of distinct reproductive strategies in these two rodent groups, and historical factors may play a crucial role in this case. For instance, the sigmodontine water rat *Nectomys* seems to be an r-strategist, despite its larger size. Species of the genus *Nectomys*, although having body size similar to echimyids, have larger litter sizes like other sigmodontines, and this is probably a phylogenetic constraint. Indeed, medium size is the putative primitive condition in Oryzomyini, a clade within sigmodontines composed of a few large-sized species, including *Nectomys, Holochilus,* and *Lundomys* (Weksler 2006).

Counting placental scars, the previous site of attachment of the fetus on the uterine wall (Feldhamer *et al.* 2007), in rodents is very useful when studying the reproductive history of individuals (Lidicker 1973). We found the number of placental scars to be indicative of litter size in both sigmodontine and echimyid rodents. Therefore, litter size can be inferred from parous females by counting the number of placental scars, but estimating litter size by counting placental scars may not be entirely accurate because resorption of embryos can occur, and placental scars may persist at the site of resorption and may be indistinguishable from a placental scar of a term embryo (Rolan and Gier 1967). Staining improves the detection of placental scars and increases the reliability of this method by reducing the observer effect (Fournier-Chambrillon *et al.* 2010). Despite this caution, the present study shows that counting placental scars is a good method for inferring the size of the last litter. This method is especially useful for obtaining reproductive data when fieldwork takes place after females have given birth.

Asymmetric implantation occurred in sigmodontines, with predominance in the right uterine horn. Pereira *et al.* (1993) observed the same tendency in

three species of sigmodontine rodents in the Brazilian Atlantic Forest, suggesting larger success of fertilization in the right ovary. Studies with hamsters, rats, and mice showed that the right uterine horn contains more sperm after mating than the left, and therefore it is a more propitious place for fertilization than the left horn (O and Chow 1987, Clark *et al.* 1994). Furthermore, the right uterine horn has more implantation sites and sustains more alive embryos than does the left (Buchanan 1974, Wiebold and Becker 1987). In the Mongolian gerbil (*Meriones unguiculatus)* more implantations of male eggs occur on the right horn than in the left, and possibly, ova sheds in the right ovary are more likely to be fertilized by Y-bearing spermatozoa (Clark *et al.* 1994). In the present study, the sex of fetuses in each uterine horn was not obtained, but all evidence indicates the importance of these data in studies of the natural history of rodents.

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Appendix 1. Litter size for each species of sigmodontine rodent analyzed in the present study.

Species	Mean litter size (± s.d.)	n	range	mode
Akodon cursor	4.7 ± 2.1	3	2–7	5
Akodon montensis	3.9 ± 1.2	11	2–6	3 and 4
Calomys callosus	5	2	–	–
Cerradomys subflavus	3	1	–	–
Cerradomys vivoi	3	1	–	–
Delomys dorsalis	4	1	–	–
Euryoryzomys sp.	3.0 ± 0.8	4	2–4	3
Holochilus brasiliensis	3	1	–	–
Hylaeamys megacephalus	3.6 ± 0.8	10	2–5	4
Neacomys spinosus	4	1	–	–
Nectomys squamipes	4.0 ± 0.7	4	3–5	4
Oecomys cleberi	2.9 ± 0.8	15	1–5	3
Oecomys mammorae	2	1	–	–
Oecomys paricola	2.5 ± 0.6	4	2–3	–
Oecomys roberti	3.5 ± 0.7	2	3–4	–
Oligoryzomys fornesi	2	1	–	–
Oligoryzomys nigripes	4.0 ± 0.6	5	3–5	4
Rhipidomys macrurus	3.5 ± 0.7	2	3–4	–
Rhipidomys emiliae	2.6 ± 1.2	10	1–5	3
Sooretamys angouya	4	1	–	–
Wiedomys pyrrhorhinos	5	1	–	–

Appendix 2. Litter size for each species of echimyid rodent analyzed in the present study.

Species	Mean litter size (± s.d.)	n	range	mode
Isothrix bistriata	1	2	–	–
Mesomys hispidus	1	1	–	–
Phyllomys pattoni	1	1	–	–
Proechimys cuvieri	3	1	–	–
Proechimys roberti	2.1 ± 0.7	14	1–3	2
Thrichomys apereoides	2	1	–	–
Trinomys albispinus	2.5 ± 0.7	2	2–3	–