Reproduction, development and growth of *Akodon lindberghi* (Hershkovitz, 1990) (Rodentia, Muridae, Sigmodontinae) raised in captivity

De Conto, V.[a] *and Cerqueira, R.*[b]*

[a]Departamento de Genética, Universidade Federal do Rio de Janeiro – UFRJ, CP 68011, CEP 21941-590, Rio de Janeiro, RJ, Brazil

[b]Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro – UFRJ, CP 68020, CEP 21941-590, Rio de Janeiro, RJ, Brazil

*e-mail: rui@biologia.ufrj.br

Received June 6, 2005 – Accepted February 1, 2006 – Distributed November 30, 2007

(With 2 figures)

Abstract

The reproduction, development and growth of *Akodon lindberghi* were studied in captivity. The colony was derived from animals captured in Simão Pereira, Minas Gerais state, which represents a new area of geographical distribution known for this species. Twelve males and twelve females were crossed, producing 144 young in 53 litters. Post-partum oestrus was observed and gestation length was estimated in 23 days. Litter size ranged from 1 to 4 with a mean of 2.72 (SD = 0.97, n = 53) and modal size of 3. Sexual dimorphism was neither present in body mass at birth nor at weaning. There was a significant negative correlation between litter size and mass at birth or weaning. Permanent emergence of adult external appearance occurred at 15 days. Puberty for males and females was 43 and 42 days, respectively, and the first fecundation event for two females was recorded at 47 and 54 days of age. The weight growth was described by fitting a Gompertz model. No significant difference was found in any parameter of growth curves for males and females. Measurements (head-body, tail, hind foot and internal and external ear lengths) obtained for adult individuals also did not reveal the presence of sexual dimorphism.

Keywords: reproductive biology, life history traits, Gompertz growth curve, longevity, morphometrics.

Reprodução, desenvolvimento e crescimento de *Akodon lindberghi* (Hershkovitz) (Rodentia, Muridae, Sigmodontinae) em cativeiro

Resumo

A reprodução, o crescimento e o desenvolvimento de *Akodon lindberghi* foram estudados em cativeiro. A colônia foi derivada de animais capturados em Simão Pereira, Minas Gerais, Brasil, localidade que representa uma nova área de distribuição geográfica conhecida para esta espécie. Doze machos e doze fêmeas foram acasalados, produzindo 144 filhotes em 53 ninhadas. Observou-se estro pós-parto e o período de gestação foi estimado em 23 dias. O tamanho médio da ninhada foi de 2,72 (SD = 0,97, n = 53), com amplitude de 1 a 4 e moda de 3 filhotes. Não houve dimorfismo sexual do peso dos filhotes ao nascimento e ao desmame. O tamanho da ninhada foi negativamente correlacionado com o peso ao nascimento e ao desmame. A emergência da aparência externa adulta (pêlos, dentes e olhos e orelhas abertos) ocorreu aos 15 dias. A puberdade em machos e fêmeas ocorreu aos 43 e 42 dias, respectivamente, e a primeira fecundação para duas fêmeas, aos 47 e 54 dias. O crescimento do peso foi descrito através do modelo de Gompertz. Não houve diferença significativa entre machos e fêmeas em nenhum parâmetro das curvas de crescimento, bem como nas medidas corporais (cabeça-corpo, cauda, pé posterior, e orelhas interna e externa) obtidas para animais adultos.

Palavras-chave: biologia reprodutiva, características bionômicas, curva de crescimento de Gompertz, longevidade, morfometria.

1. Introduction

Basic life history traits such as litter size, gestation length, young size, developmental and growth pattern have been little studied in South American rodents. Due to the difficulty in reporting these traits in the field we may conduct investigations in captivity, chiefly if the study animals are bred from individuals that just came from the field. Moreover, in laboratory experiments, in which representatives of natural populations are raised in the same controlled environment i.e., with environmental variation reduced, we may estimate the genetic basis of life history traits achieved in nature (Aulchenko et al., 2002), and study their ontogenetic trajectories, knowing with certainty the age of the individuals. Therefore, investigations in captivity can be appropriate to elucidate the life-history traits of a species and to allow the accomplishment of studies of geographic variation and interspecific comparisons.

Based on specimens that had been collected only within a half-hectare plot on the periphery of wet grassland in a park near Brasilia, in the Federal District, Brazil, Hershkovitz (1990) described *Akodon lindberghi*. An expedition led by Drs. Lena Geise and Miguel Angelo Moreira in 1996 to the Municipality of Simão Pereira, Minas Gerais state, collected some specimens that were identified as *A. lindberghi* by morphological comparisons with a voucher specimen (Geise, personal communication). Karyologic analysis of eight of those individuals showed a diploid number of 42 and a fundamental number of 42 (Geise et al., 1996). This diploid number is similar to the one of two specimens of *A. lindberghi* captured in the type locality (Svartman and Almeida, 1994). Up to now, the species is known only from these two localities, which are situated 840 km apart. Except for the original description, the two karyological studies mentioned above and the sequence of the citocrome b gene (Gene Bank accession number AF184057) for this species, nothing else is known of *A. lindberghi*.

In this paper, we investigate reproduction, development and growth and the relationship between reproductive and growth traits in a laboratory-breeding colony of *A. lindberghi* derived from animals collected in the Municipality of Simão Pereira, state of Minas Gerais.

2. Materials and Methods

Wild specimens utilized in this study were captured at Sítio Maglândia, Municipality of Simão Pereira, Minas Gerais state, Brazil (21° 58' S and 43° 19' W) at 500 m altitude using Sherman live traps. The region was formerly covered by semideciduous seasonal forest. The area was altered by crop plantation and cattle breeding, and almost all extant forests of secondary growth were man-reforested (Radambrasil, 1983). Specimens of this study were collected in an area covered by grass, growing on the site of an abandoned trail.

The breeding program was developed at Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, using 5 males and 4 females captured in the field and 7 males and 8 females born in the laboratory from the wild ones. The program started in October 1996 and the last observations were done in December 1999.

Room temperature and relative humidity were kept at 24 ± 2 °C and 70 ± 10% RH, respectively. The light/dark cycle was the natural cycle of Rio de Janeiro City. The diet consisted of fresh fruits and vegetables, commercial equine meals, alfalfa pellets and seeds (corn and sunflower). This diet was made following the method prescribed by Périssé et al. (1989). Water was provided ad libitum. The animals were kept in polypropylene cages (41 by 34 by 18 cm). A 1cm layer of expander vermiculite was used as bedding. Shredded paper was supplied as nest material.

2.1. Reproduction

Wild-caught and captivity-born animals were randomly assigned as pairs but we avoided inbreeding. Some pairs were kept together permanently during the experiment to detect post-partum oestrus. Aggressive behavior was observed between members of some pairs, and between parents and nestling at the moment or just after birth. When this happened the pair was separated.

Cages were checked daily after pregnancy detection, and the day of birth was designated as day zero. Inter-birth interval (i.e. interval between successive litters) was recorded. Gestation length was assumed to be the shorter inter-birth interval between consecutive litters of the same female kept with a male during all the time between subsequent births.

At day of birth, new-borns were weighed, sexed and individually marked by toe clipping. The animals were weaned at 21 days of age. The weaning age was chosen based on previous reports from other Sigmodontinae rodents (Voss et al., 1992; D'Andrea et al., 1996). From the day of weaning, individuals of the same sex were kept together in cages.

Litter size, sex ratio, individual mass at birth and weaning were recorded for each litter born in captivity. The significance of deviation of sex ratio from 1:1 was tested by chi-square test with Yates correction (Zar, 1984). Sexual dimorphism in mass at birth and weaning were tested through one-way analysis of variance. Relationships between mother mass, parity, litter size, mass of young at birth (0 days) and weaning (21 days) were investigated through Spearman's correlation coefficients.

2.2. Developmental and growth

The following developmental traits were recorded daily from the day of birth until weaning: presence of dorsal and ventral underfur and fur, external ears and eyes opening and superior and inferior incisor teeth eruption.

The age of appearance of scrotal testes in males and vagina opening in females was recorded in 14 individuals (6 males and 8 females). These traits were used to indicate puberty. The age at which females became sexually mature was determined by introducing an immature female of known age into a cage with a sexually mature male. At the birth of the nestling, the age at sexual maturity was estimated by subtracting the gestation length (see Results) from the age of the female.

All animals born in captivity were weighed weekly since the day of birth until their natural death, to the nearest 0.1 g. Von Bertalanffy and Gompertz equations have been widely used to describe growth. However, the von Bertalanffy model provides a linear adjustment so that growth rate never decreases. Since the Gompertz model allows such decrease, we used this equation instead. This model as well seems to be the one that best fits most mammalian growth curves (D'Andrea et al., 1996; Pillay, 2001; Antinuchi and Luna, 2002; Zullinger et al., 1984). The Gompertz model was fitted to the weekly weights of each specimen from birth until 250 days of life (32 males and 31 females). The parameters obtained for each specimen were the asymptotic mass in grams (A), the constant growth rate (K) and the age at the first inflexion point of the growth curve (I) in the equation:

$$y = Ae^{-e^{-k(t-I)}} \quad (1)$$

The end of growth was determined as the age at which 95% of the asymptotic mass (I 95%A) was attained. The specific growth rate (b) and the maximum rate of growth were calculated from Gompertz derivative (Begall, 1997; Fiorello and German, 1997):

$$\frac{dy}{dt} = Ake^{-K(t-I)}e^{-e^{-K(t-I)}} \quad (2)$$

All parameters were compared between sexes using Kolmogorov-Smirnov non-parametric tests. The mean of each parameter was used to fit the growth curves. Relationships between litter size, mass of young at birth and growth parameters (A, K, I, b) were investigated through Spearman's correlation coefficients.

Morphometric data (maturity mass, head-body, tail, hind foot and internal and external ear lengths) were recorded for adult individuals (above 200 days). Maturity mass was recorded to the nearest 0.1 g and lengths to the nearest 0.1 mm. Sexual dimorphism in maturity mass, body and tail lengths were tested through one-way analyses of variance and through Kolmogorov-Smirnov non-parametric tests for hind foot and internal and external ear lengths.

3. Results

3.1. Reproduction

The colony produced a total of 144 young (74 males and 70 females) in 53 litters. Maximum reproductive output was 14 litters produced by a female over a 16-month period.

Post-partum oestrus was observed, with 89% of effective mating occurring in the first four days after females gave birth. The inter-birth interval varied around 23 to 31 days (n = 28 litters produced by 7 females). The distribution of these intervals is shown in Figure 1. Gestation length, estimated as the smallest inter-birth interval between successive litters, was 23 days (2 pregnancies).

Litter size at birth ranged from 1 to 4 with a mean of 2.72 (SD = 0.97, n = 53) and modal value of 3 (40% of litters). Deviation from the expected sex ratio 1:1 was not significant in 53 litters (74 males: 70 females - $\chi^2 = 0.45$, df = 1, p > 0.05).

The mean body mass at birth was 2.26 g (SD = ± 0.29, n = 39) for males and 2.14 g (SD = ± 0.35, n = 36) for females. The mean body mass at weaning was 9.10 g (SD = ± 1.64, n = 28) for males and 8.60 g (SD = ± 1.35, n = 26) for females. Sexual dimorphism was neither present at birth nor at weaning (F = 2.615, df = 1, p = 0.11 and F = 1.097, df = 1, p = 0.3, respectively). At weaning, mean litter size was 1.62 (SD = 1.40, n = 53). The mortality from birth at weaning was 40.3% and was smaller in litters raised by a female in the male's absence.

There was a significant negative correlation between litter size and mass at birth or weaning (nestlings with a large number of individuals were lighter than nestlings from small litters at birth and weaning). Parity and mother mass was not correlated with any trait (Table 1).

3.2. Development and growth

A. lindberghi neonates were altricial. The timing of developmental events in young and age of puberty are summarized in Table 2. Permanent emergence of adult external appearance occurred at 15 days. Two newly weaned females were mated with adult males to estimate the minimal age of first successful mating. This first fecundation event (sexual maturity) was recorded at 47 and 54 days of age for these two females.

Data on body mass growth were obtained for 32 males and 31 females using weekly weights from birth to 250 days of age. This date was chosen because previous analyses showed that the stabilization of weight starts at 150 days. Table 3 shows the mean, standard deviation and significance of sexual dimorphism for all parameters of growth curves. Figure 2 shows postnatal

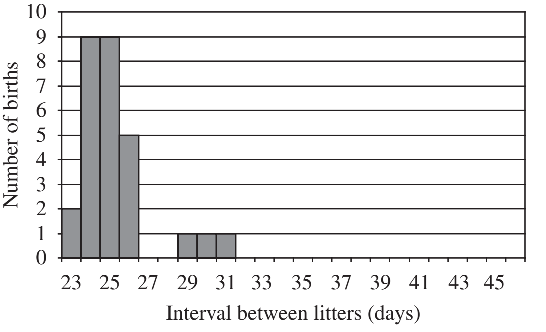

Figure 1. Distribution of interval between 28 successive litters produced by 7 females.

Table 1. Spearman's correlation coefficients between reproductive traits in *Akodon lindberghi*. Boldface indicates a significant positive or negative association.

Trait	Parity	Mother mass	Litter size	Mass at birth	Mass at weaning
Parity	1	-	-	-	-
Mother mass	0.13	1	-	-	-
Litter size	0.06	0.18	1	-	-
Mass at birth	–0.18	–0.003	**-0,43**	1	-
Mass at weaning	0.02	-0.06	**-0,35**	**0,52**	1

growth curves for females and males respectively, calculated from parameters of Gompertz equations. No significant difference was found in any parameter of growth curves for females and males.

Litter size was not correlated with maturity mass, the asymptotic mass A, the growth rate K, the age at the first inflexion point of the growth curve I and the specific growth rate b. Mass at birth was positively correlated with asymptotic mass and maturity mass ($R = 0.36$, $p = 0.003$ and $R = 0.38$, $p = 0.002$, respectively), negatively correlated with the growth rates (K – $R= –0.26$, $p = 0.037$ and b – $R = –0.35$, $p = 0.009$) and was not correlated with I.

Morphometric data (maturity mass, head-body, tail, hind foot and internal and external ear lengths) were obtained for adult individuals above 200 days. No significant difference was found in any measurement for females and males. Table 4 shows this data.

3.3. Longevity

Eight individuals were kept to estimate longevity. The mean longevity was 1311 ± 246 days for males (n = 4) and 1407 ± 320 days for females (n = 4).

Table 2. Range and mode of age (in days) on emergence of developmental events and puberty in *Akodon lindberghi*. For developmental events N = litters and for puberty N = sample size.

Traits	N	Range	Mode
Underful, dorsal	26	0-2	1
Underfur, ventral	20	1-3	2
Inferior incisors	23	4-8	7
Superior incisors	26	5-9	8
Fur, dorsal	24	4-6	4
Fur, ventral	19	5-8	7
Ear opening	23	7-12	8
Eye opening	21	10-15	13
Puberty, males	6	26-61	43
Puberty, females	8	30-56	42

4. Discussion

The gestation length was 23 days for *A. lindberghi*. Gestation length for other Akodontini rodents is very similar (Table 5). It seems that the value found for *A. lindberghi* occurs throughout the Akodontini.

Occurrence of new fecundations within a short period after litter birth in *A. lindberghi* shows the existence of post-partum oestrus. Post-partum oestrus was also observed in other South American Sigmodontine rodents such as *Calomys laucha* (Hodara et al., 1989), *Delomys dorsalis* (Cademartori, 2003) *Akodon boliviensis* (Piantanida et al., 1995) *Akodon molinae* (Buzio et al,.

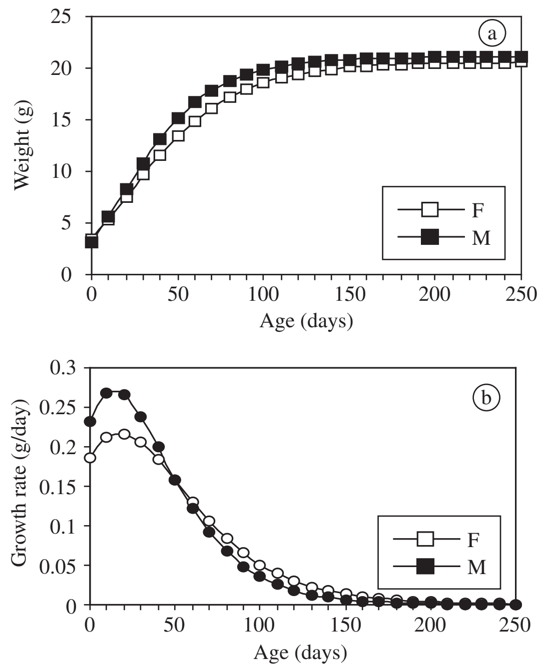

Figure 2. Growth curves of weight for *Akodon lindberghi* fitted from means of individual's parameters of 32 males (M) and 31 females (F), calculated by Gompertz model (a). Variation of body mass growth rates throughout ontogeny, fitted by Gompertz derivative (b).

Table 3. Mean and standard deviation for body mass growth parameters and traits in 32 males and 31 females of *Akodon lindberghi* using Gompertz asymptotic sigmoidal growth model and Gompertz derivative. The last column shows the results of comparative tests for sexual dimorphism.

Weight growth trais	Males	Females	Combined	Test
Asymptotic mass (g) - A	21.06 ± 4.996	20.58 ± 5.706	20.82 ± 5.319	KS = 0.200 p = 0.52
Constant growth rate - K	0.035 ± 0.018	0.029 ± 0.013	0.032 ± 0.016	KS = 0.279 p = 0.16
Age at the inflexion point - I	18.20 ± 8.324	20.42 ± 7.809	19.27 ± 8.091	KS = 0.221 p = 0.39
I 95%A	134.24 ± 79.826	142.50 ± 60.851	138.372 ± 70.494	KS = 0.267 p = 0.20
Specific growth rate - b	1.651 ± 0.540	1.664 ± 0.409	1.675 ± 0.441	KS = 0.253 p = 0.36
Maximum rate of growth	0.180 ± 0.109	0.177 ± 0.082	0.178 ± 0.093	KS = 0.232 p = 0.52

Table 4. Morphometric data of *Akodon lindberghi*. Mean, standard deviation (SD), maximum measure (Max) and minimum measure (Min) are presented for males and males adult animals and for combined sexes. Number in parenthesis are the sample size. The last column shows the results of comparative tests for sexual dimorphism.

Traits	Males		Females		Combined	Test
	Mean ± SD (N)	Max-Min	Mean ± SD (N)	Max-Min	Mean ± SD	
Maturity mass (g)	20.63 ± 4.38 (32)	32.96-12.83	20.44 ± 5.51 (31)	32.20-10.91	20.54 ± 4.92	F = 0.023 p = 0.89
Body lenght (mm)	88.7 ± 5.88 (12)	98-80	88.7 ± 3.66 (16)	95-81	88.73 ± 4.64	F = 0.0005 p = 0.98
Tail lenght (mm)	61.3 ± 4.42 (10)	66-54	56.4 ± 4.51 (10)	65-50	58.88 ± 5.03	F = 3.716 p = 0.07
Hind foot (mm)	18.3 ± 1.86 (16)	22-17	17 ± 1.56 (15)	19-16	18.13 ± 1.23	KS = 0.428 p = 0.11
Internal ear lenght (mm)	13.9 ± 1.42 (14)	16-11	13.4 ± 1.98 (13)	16-11	13.72 ± 1.65	KS = 0.245 p = 0.79
External ear lenght (mm)	12.2 ± 1.67 (14)	15-10	11.7 ± 1.45 (13)	15-10	11.94 ± 1.54	KS = 0.273 p = 0.67

Table 5. Comparison between some reproductive parameters of Akodontini rodents.

Species	Litter size	Gestation length (days)	Reference
Akodon dolores	4.6 ± 1.8(1-10)	25.2 ± 2.2	Piantanida (1987)
Akodon cursor	5.6 (2-9)	23	Mello and Mathias (1987)
Akodon azarae	4.10 ± 2.42(1-7)	-	Antinuchi and Luna (2002)
Akodon azarae	-	24.5 ± 0.86	de Villafañe(1981)
Akodon boliviensis	5 ± 1.5(1-6)	25 ± 2	Piantanida et al. (1995)
Akodon molinae	4-5	23	Merani and Lizarralde (1980)
Akodon lindberghi	2.72 ± 0.97(1-4)	23	This study

2001) and *Akodon dolores* (Piantanida, 1987). This process increases reproductive energetic costs, since corporal maintenance, lactation and gestation occur simultaneously. Since Sigmodontine rodents have their reproduction controlled by environmental factors in the wild (Cerqueira and Lara, 1991), this mechanism could provide an opportunity to produce several litters within an optimal period of a given year.

A. lindberghi shows a smaller litter size than other Akodontini rodents (Table 5). Sex ratio at the birth did not differ from expected (1:1) in *A. lindberghi*. Similar sex-ratio also occurred for *A. dolores* (Piantanida, 1987) and *A. molinae* (Merani and Lizarralde, 1980)

The age of first successful mating for females of *A. lindberghi* (47 and 54 days of age) is within the variation of the age of vagina opening (30-56 days of age). This result suggests that vaginal opening is a good indirect external sign of sexual maturation for *A. lindberghi*. Other authors used the same sign for *Akodon cursor* (Mello and Mathias, 1987) and *Akodon olivaceus* (González et al., 1988).

There was no significant sexual dimorphism for the mass at birth, weaning and maturity, nor for the parameters of the Gompertz curve. Absence of sexual dimorphism in the weight was also observed for *A. dolores* for the mass at birth, weaning and maturity and for *A. molinae* after 60 days of age (Merani et al., 1983).

Several factors, mainly of physiological nature, impose tradeoffs between life-history traits (Stearns, 1983; Roff, 1992; Stearns, 1992). These physiological constraints are determined by competition for the limited energy available for reproduction, growth and maintenance (Stearns, 1992). In this study, a negative correlation was observed between litter size and mass at birth or weaning. This fact suggests a division of resources that will be allocated in the gestation and nursing of a larger litter, a trade-off process registered also for other Sigmodontinae rodents, such as *Akodon azarae* (Antinuchi and Luna, 2002) and *Zygodontomys brevicauda* (Voss et al., 1992). However, litter size was not correlated with maturity mass suggesting some compensatory mechanism of mass growth after weaning which reduces the effect of the litter size.

Aggressiveness was observed between members of the pair and between these and the nestling at the birth of the nestling. The mortality of the nestlings was lower in litters raised by a female in the male's absence. This fact suggests that, in natural conditions, only the female nests the young. Aggressiveness between members of the pair and absence of male parental behavior has also been observed in *Akodon azarae* (Suárez, 1996) and *Calomys musculinus* (Laconi and Castro-Vázquez, 1999; Laconi et al., 2000) reared in captivity.

Acknowledgments — We thank several generations of students of the Laboratório de Vertebrados that helped us in collecting and raising the specimens, but we are especially grateful to Janemeri Santos Rebello. As usual Nelio P. Barros and Angela M. Marcondes did their best in the technical and clerical work. An anonymous referee made valuable comments in an earlier version of the manuscript. This research was supported by grants from CNPq (including PIE and PRONEX), PROBIO (Brazilian Ministry of Environment and Global Environment Fund), FUJB and FAPERJ.

References

ANTINUCHI, CD., and LUNA, F., 2002. Assessing the effect of litter size on growth pattern and homeothermy acquisition in the pampas mice *Akodon azarae* (Rodentia, Muridae). *Growth Dev. Aging*, vol. 66, no. 2, p. 63-69.

AULCHENKO, YS., ARARIPE, LO., D'ANDREA, PS., SHISHKIN, AA., CERQUEIRA, R., BORODIN, PM. and AXENOVICH, TI., 2002. Inheritance of litter size at birth in the Brazilian grass mouse (*Akodon cursor*, Sigmodontinae, Rodentia). *Gen. Res*., vol. 80, no. 1, p. 55-62.

BEGALL, S., 1997. The application of the Gompertz model to describe body growth. *Growth Dev. Aging*, vol. 61, no. 2, p. 61-67.

BUZZIO, OL., KONINCKX, A., CARRENO, NB. and CASTRO-VAZQUEZ, A., 2001. Embryo implantation during the short luteal phase of the corn mouse, *Calomys musculinus*, and the apparent lack of a lactational diapause in South American murid rodents. *Reproduction*, vol. 121, vol. 5, p. 815-823.

CADEMARTORI, CV., 2003. Reproductive biology and daily and seasonal abundance patterns of *Delomys dorsalis* (Hensel 1872) – Cricetidae, Sigmodontinae – in an area of mixed forest with conifers, Rio Grande do Sul state, Brazil. *Mastozool. Neotrop./ J. Neotrop. Mammal.*, vol. 10, no. 2, p. 342.

CERQUEIRA, R. and LARA, M., 1991. Rainfall and reproduction of Cricetid rodents in Northeastern Brazil, p. 545-549. In BOBEK, B., PERZANOVSKI, K. and REGELIN, W., (eds.). *Global trends in wildlife management*, vol. 1. Swiat Press, Krakow.

D'ANDREA, PS., HORTA, C., CERQUEIRA, R. and REY, L., 1996. Breeding of the water rat (*Nectomys squamipes*) in the laboratory. *Lab. Anim*., vol. 30, no. 4, p. 369-376.

DE VILLAFAÑE, G., 1981. Reproducción y crecimiento de *Akodon azarae azarae* (Fischer, 1829). *Historia Natural*, vol. 1, no. 28, p. 193-204.

FIORELLO, CV. and GERMAN, RZ., 1997. Heterochrony within species: craniofacial growth in giant, standard, and dwarf rabbits. *Evolution*, vol. 51, no. 1, p. 250-261.

GEISE, L., CERQUEIRA, R. and SEUÁNEZ, HN., 1996. Karyological characterization of a new population of *Akodon lindberghi* (Rodentia, Sigmodontinae) in Minas Gerais State (Brazil). *Caryologia*, vol. 49, no. 1, p. 57-63.

GONZÁLEZ, LA., MURÚA, R., MESERVE, P.L. and JOFRÉ, C., 1988. Consecuencias demográficas de la manipulación experimental en la composición de edades de *Akodon olivaceus* (Rodentia, Cricetidae). *Bol. Soc. Biol. Concepción*, vol. 59, p. 57-67.

HERSHKOVITZ, P., 1990. Mice of the *Akodon boliviensis size class* (Sigmodontinae, Cricetidae) with the description of two new species from Brazil. *Fieldiana: Zool*. (NS), vol. 57, p. 1-35.

HODARA, VL., ESPINOSA, MB., MERANI, MS. and QUINTANS, C., 1989. *Calomys laucha* (Rodentia, Cricetidae): growth and breeding in laboratory conditions. *Lab. Anim*., vol. 23, no. 4, p. 340-344.

LACONI, MR. and CASTRO-VÁZQUEZ, A., 1999. Nest building and parental behaviour in two species of *Calomys* (Muridae, Sigmodontinae): A laboratory study. *Mammalia*, vol. 63, no. 1, p. 11-20.

LACONI, MR., JAHN, GA., and CASTRO-VÁZQUEZ, A., 2000. Influence of different social partners on the survival and growth of pups in two species of *Calomys* (Muridae Sigmodontinae). *Ethol. Ecol. Evol.*, vol. 12, no. 2, p. 187-196.

MELLO, DA. and MATHIAS, CH., 1987. Criação de *Akodon arviculoides* (Rodentia, Cricetidae) em laboratório. *Rev. Bras. Biol*., vol. 47, no. 3, p. 419-423.

MERANI, MS. and LIZARRALDE, MS., 1980. *Akodon molinae* (Rodentia Cricetidae), a new laboratory animal: breeding, management and reproductive performance. *Lab. Anim*., vol. 14, no. 2, p. 129-131.

MERANI, MS., VERCELLINI, O., ACUNA, AM., HORGAN, C. and ROLDAN, ER., 1983. Growth and reproduction of two species of *Akodon* and their hybrids. *J. Exp. Zool*., vol. 228, no. 3, p. 527-535.

PÉRISSÉ, M., FONSECA, CRSD. and CERQUEIRA, R., 1989. Diet determination for small laboratory-housed wild mammals. *Can. J. Zool.*, vol. 67, p. 775-778.

PIANTANIDA, MJ., 1987.- Distintos aspectos de la reproducción en la naturaleza y en cautiverio del roedor cricetido *Akodon dolores* (Thomas, 1916). *PHYSIS*, Secc. C, vol. 45, no. 109, p. 47-58.

PIANTANIDA, MJ., PETTOVELLO, A. and BORDARRAMPE, P., 1995. Reproduccion y crecimiento en cautiverio de *Akodon boliviensis* y *Akodon alterus* (Rodentia, Cricetidae). *PHYSIS*, Secc. C, vol. 50, no. 118-119, p. 55-61.

PILLAY, N., 2001. Reproduction and postnatal developmental in the bush Karoo rat *Otomys unisulcatus* (Muridae, Otomyinae). *J. Zool., Lond*. vol. 254, p. 515-520.

RADAMBRASIL, 1983. *Levantamento dos recursos naturais: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra*. Folhas SF.23/24 - Rio de Janeiro/ Vitória. Ministério das Minas e Energia. Rio de Janeiro, vol. 32, 780p. 6 mapas.

ROFF, DA., 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York, 535p.

STEARNS, SC., 1983. A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution*, vol. 37, no. 3, p. 601-617.

-, 1992. *The evolution of life histories*. Oxford University Press, Oxford, 249p.

SUÁREZ, OV., 1996. Estrategias reproductivas y cuidado parental en *Akodon azarae* (Rodentia, Muridae). Tesis doctoral, Faculdade de Ciências Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires. 215p.

SVARTMAN, M. and ALMEIDA, JC., 1994. The karyotype of *Akodon lindberghi* Hershkovitz, 1990 (Cricetidae, Rodentia). *Rev. Bras. Genet*., vol. 17, no. 2, p. 225-227.

VOSS, RS., HEIDEMAN, PD., MAYER, VL. and DONNELY., TM., 1992. Husbandry, reproduction and postnatal development of the neotropical muroid rodent *Zygodontomys brevicauda*. *Lab. Anim*., vol. 26, no. 1, p. 38-46.

ZAR, JH., 1984. *Biostatistical Analysis*. 2nd edition. New Jersey, Prentice Hall, 718p.

ZULLINGER, EM., RICKLEFS, RE., REDFORD, KH. and MACE, GM., 1984. Fitting sigmoidal equations to mammalian growth curves. *J. Mammal*., vol. 65, no. 4, p. 607-636.