

# Gestation, maternal behaviour, growth and development in the subterranean caviomorph rodent *Ctenomys mendocinus* (Rodentia, Hystricognathi, Ctenomyidae)

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## Abstract

The first information on the gestation period, maternal behaviour, neonatal development and growth of the subterranean caviomorph rodent *Ctenomys mendocinus* Philippi, 1869, is reported herein. My hypothesis was that, despite its belonging to a typically precocial suborder, the life history traits of *C. mendocinus* would favour its altricial condition. The offspring of *C. mendocinus* were categorized as altricial by using two different classification systems. This condition was also reflected in maternal care. Females built large nests (2000 cm<sup>3</sup>) where, after a long gestation period (95.9 days), they gave birth to litters of blind pups, half-naked, with external ear meatus open and good physical coordination. The mothers suckled the offspring in long bouts (19.9 min), retrieved their pups, and these showed no tactics to reduce the suckling bout. Overall, evidence was consistent with the hypothesis analyzed, although particularities found, e.g. some precocial traits, suggest the existence in *C. mendocinus* of a trade-off between the constraints and advantages related to its subterranean way of life and the phylogenetic inertia typical of caviomorphs.

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## Keywords

Subterranean rodents; *Ctenomys*; reproduction; life history traits; pup ontogeny; maternal behaviour

## Introduction

Mammalian infants can be broadly categorized at birth as either precocial or altricial. Precocial infants (such as fawns and lambs) are typically born as relatively large singletons or twins with a covering of fur and a well-developed nervous system. They can see and hear at birth and they are sufficiently mobile to follow the mother within hours of birth. In contrast, altricial infants (such as kittens and rats) are relatively small at birth and members of a litter that is confined to a nest for the first few days or weeks of life. Altricial infants have closed eyes and ears, little or no fur, and limited mobility at birth (Hill, 1992). Precocial and altricial infants also differ in their thermoregulatory abilities.

Precocial infants can use physiological thermoregulation to maintain a warm internal body temperature even in a cool environment, whereas altricial infants have only a limited ability to defend their internal body temperature by physiological means during the first few days of life, depending on their mother's warmth for heat gain and on a combination of huddling with littermates and the insulation provided by the nest to minimize heat loss in the mother's absence (Blumberg and Sokoloff, 1998). Mothers of precocial species do not build a nest or retrieve their offspring, and they nurse the young in short bouts. Precocial pups exhibit tactics to reduce the suckling bout, e.g. teat order (Kleiman, 1972, 1974).

Martin and Mac Larnon (1985) defined three groups of placental mammals: 1) clearly precocial mammals, in which litter size is less than 1.5 and the eyes are already open at birth; 2) clearly altricial mammals, in which litter size is 3 or more and the eyes do not open until at least 5 days after birth; and 3) intermediate cases, with litter sizes between 1.5 and 3, and eyes opening between birth and 5 days of age. Likewise, Derrickson (1992) ranks eutherian mammals in a scale of altriciality-precocity according to four areas of independence achieved within the first 2 days of birth: thermoregulatory (hair covers the body), sensory processing (eyes open), locomotor (move independent of parent) and nutritional (solid food intake) areas. The sum of the presence or absence of these traits yields five development categories, from 0 to 4, with 0-1 representing different degrees of altriciality, and 2-4 the respective precocity levels.

Several authors (e.g. Kleiman, 1972, 1974; Case, 1978; Pagel and Harvey, 1988; Künkele, 2000; Kraus et al., 2005) stressed that particular life history features like subterranean or cursorial way of life have influenced the evolution of altricial or precocial development. The South American hystricognath rodents, or Caviomorpha, are typically precocial, sharing long gestation periods and small litter size (Weir, 1974). However, there is still large variation in their degree of precocity, for example, regarding the developmental state at birth (Kraus et al., 2005). Thus, the cursorial species *Cavia porcellus*, after 68 days of gestation, produces big and heavy neonates that eat solid food since their first day of life (Weir, 1974). In contrast, the subterranean species *Spalacopus cyanus* (Begall et al., 1999) and *Ctenomys talarum* (Zenuto et al., 2002), after 77 and 90 days of gestation, respectively, produce neonates that eat solid food after 10 days of age.

In Mendoza, Argentina, *Ctenomys mendocinus*, Philippi 1869 ("tuco-tuco", body mass: 163 g, Rosi et al., 2005), is a solitary subterranean caviomorph that shares wide distribution areas with cursorial caviomorphs known as "cuises": *Microcavia australis* (body mass: 200 g) and *Galea musteloides* (body mass: 400 g) (Rood, 1970, 1972; Weir, 1974; Kleiman, 1974). Cuises, after 53-54 days of gestation, bear 3 precocial pups in the periphery of the shrubs they inhabit (Rood, 1972). After an unknown gestation period, *C. mendocinus* bears litters of 2.9 pups (Rosi et al., 1996a), in deep nest chambers (0.64 m) built inside their galleries (0.30 m) (Rosi et al., 1996b, 2000). The neonatal development of *C. mendocinus* is unknown.

Both cuises and tuco-tucos are herbivores (Rood, 1970; Madoery, 1993; Puig et al., 1999). However, whereas cuises obtain their food by walking on the soil surface, tuco-tucos dig extensive galleries to reach most of their food resources. Among the most conspicuous environmental challenges of subterranean life are high energetic demands

associated with burrowing (e.g. pocket gophers weighing 150 g expend 360–3400 times more energy burrowing 1 m than walking a similar distance on the ground surface; Vleck, 1979), and poor gas exchange in burrows, which creates hypoxic atmospheres (Buffenstein, 2000). These physiological and energetic constraints may cause selection pressures favouring parsimonious energy usage and consequent low metabolic rates in subterranean rodents (Lovegrove, 1986; Buffenstein, 2000). In geomyids, bathyergids, spalacines and ctenomyids, basal metabolic rate (BMR) is lower than that predicted on the basis of body size alone (McNab, 1979; Lovegrove and Wissel, 1988; Busch, 1989; Buffenstein and Yahav, 1991; Bennett et al., 1994, 1996; Marhold and Nagel, 1995). Because BMR is associated with the rate of biosynthesis (Stevens, 1973; Hammel, 1976; Taigen, 1983; Veloso and Bozinovic, 2000), low BMR would impose limits on the deposition of new tissue during gestation (Henneman, 1983, 1984; Hofman, 1983; Martin, 1984a, 1984b; Glazier, 1985a, 1985b). This in turn would impact on the gestation period (making it longer), and on neonatal development (pups being born more altricial).

The precocity of many cursorial caviomorphs has been attributed to the strong predation pressure upon them from a variety of carnivores (Kleiman, 1974; Case, 1978) or to the harsh environmental conditions (Künkele, 2000; Kraus et al., 2005). By contrast, low predation pressure – as that allegedly suffered by subterranean mammals (Nevo, 1979, 1995; Reig et al., 1990) – and the thermally stable environment provided by burrows may be associated with the development of altricial strategies in subterranean caviomorphs (Kleiman, 1974; Case, 1978). All these lines of reasoning lead to the hypothesis that the subterranean way of life of *C. mendocinus* has influenced the evolution of more altricial or less precocial pups than those of its cursorial caviomorph counterparts. Herein, in order to test this hypothesis, I study gestation, maternal behaviour, growth and development in *C. mendocinus*.

## Materials and methods

I live-trapped a total of 29 adults (16 females, 13 males) in Cacheuta: 33° 00' S, 69° 10' W (Province of Mendoza, Argentina), during March, for five successive years (1992–1996). I transferred the animals to the Argentine Institute for Arid Zone Research (IADIZA) in Mendoza City. Moreover, I used 12 adult animals (8 females, 4 males) breeding in captivity during the 1992–2000 period. The animals were housed in a basement that received sunlight through a long narrow window above ground level. They were kept separately in plastic containers (50 cm x 40 cm x 70 cm) filled with 3 cm of alluvial soil. A plastic pipe (9 cm in diameter, 2000 cm<sup>3</sup>) was provided as shelter. Room temperature was 19–22 °C. Alfalfa, lettuce, carrots, mixed grasses and stems of shrubs were provided ad libitum. Because *Ctenomys* does not drink water (Camín, 1999; Zenuto et al., 2002) animals were not provided with it. During June–August, I periodically placed males and females together in a neutral arena, according to Camín (1999). On the day of copulation, I weighed and housed the females in individual “dens”: each den consisting of a central box of opaque plastic (60 cm x 40 cm x 33 cm)

with glass ceiling and five lateral tubes of Plexiglas (9 cm in diameter, 2000 cm<sup>3</sup>) attached perpendicularly. I supplied cotton and toilet paper as nest material. I cleaned the dens weekly. At about 80 days of gestation, I checked the pregnant females daily every two hours between 9:00 and 19:30. I studied, altogether, 29 young born in 9 litters to six females, three collected at Cacheuta and three breeding in captivity. I weighed and measured each pup on the day of birth, with 0.01 g and 0.01 mm precision respectively. I calculated relative neonate mass (r.n.m.) as: neonate body mass \*100/mother's body mass on the day of copulation. I weighed the young daily over 60 days; and then weekly until growth ceased. Daily, between 8:00 and 19:00, I performed two observations of 90 min for each litter. At 7 days after birth (d.a.b.) I differentially marked the pups on the back with a correction pencil free from trichloroethylene. I registered the behaviour of mothers and their pups through focal sampling with continuous recording (Martin and Bateson, 1993). Using this schedule, a chronological development of pups and a quantification of interactions between mothers and pups were obtained. I recorded the duration and frequency of suckling bouts, body postures of the mother and pups while feeding, and frequency of retrievals.

I used Martin and Mac Larnon's (1985) and Derrickson's (1992) criteria to establish the degree of neonatal development of *C. mendocinus*.

Following Derrickson's (1992) scheme, I recorded the presence of four traits of neonatal independence since the first day that the pups' bodies were totally covered with hair, opened their eyes, walked and ate solid food. In addition to these two criteria, I considered the state of the ear meatus at birth: open (precocial) or closed (altricial).

I calculated growth parameters using the Gompertz equation (Begall, 1997). I employed such approach after the recommendation of Zullinger et al. (1984), who found the Gompertz model to be most appropriate for describing growth parameters of 331 mammalian species. The equation is

$$M(t) = A * e^{-e^{-k(t-I)}}$$

where  $M(t)$  = body mass (g) at time  $t$  (days),  $A$  = asymptotic value (g),  $K$  = growth constant (days<sup>-1</sup>),  $I$  = age at inflection point (days). I employed the Gompertz model only on those individuals for which the complete data set (from birth to accomplished growth) was available. According to Begall (1997), I fitted the growth curves for each animal separately, and then calculated the means of growth parameters. All analyses were made using the software package STATISTICA 5.0 (1998). I provided mean values ( $\bar{X}$ ) with standard error ( $\pm$ SE) and range (Min-Max values recorded).

This study was carried out at the Ecodes laboratory at IADIZA, CONICET Institute, and it followed all requirements of the Guide for the Care and Use of Laboratory Animals (1996).

## Results

Gestation lasted  $95.9 \pm 0.5$  days (range = 94-97;  $n = 6$ ). The increment in body mass in females at  $90.6 \pm 2.8$  days of gestation was  $67.8 \pm 10.8$  g (range = 21.9-99.8;  $n = 5$ ),

which represents 43.5% of their normal body mass of  $162.8 \pm 20.8$  g (range = 127.3–199.9). Females built one maternal nest ( $\cong 2000$  cm<sup>3</sup>) in one of the five lateral tubes provided,  $4.4 \pm 2.3$  days (range = 1–11) before parturition. Cotton, tall grass and alfalfa were the materials used for nest building. Five litters were born in November, two in October, and two in December. I observed parturition of five litters that were born at 8:00, 10:40, 10:46, 11:35, and 15:30 hours. Prior to parturition, females were restless, patrolling the den, carrying grass to the nest and licking their genitalia. All pups, except one, were born in the nest. Contractions were noticeable as spasms that caused the females' backs to arch. Females tossed and turned and eventually lied on their backs. The pups were born headfirst. After each birth, the mothers bit through the umbilical cord, ate all placentas of the newborns as they were delivered, and subsequently groomed the pups. The entire parturition process took  $269.4 \pm 57$  min (range = 180–360). Six reproducing females produced an average litter size of  $3.2 \pm 0.34$  pups (range = 1–4;  $n = 9$  litters, 29 pups). Mean litter mass was  $50.9 \pm 6.33$  g (range = 20–67.3;  $n = 8$ ). The male/female ratio was 1.2:1. Four pups from two litters died, within one to five d.a.b., killed or abandoned by their mothers.

Except body length, there were no significant differences in body measurements in male versus female neonates (table 1). The r.n.m. of neonates was  $10.0 \pm 0.4$  % (range = 7.4–15.2;  $n = 26$  pups). No statistical relationship between body mass of newborns and litter size was detected (Pearson's correlation,  $r = -0.49$ ,  $n = 8$ ,  $P = 0.21$ ).

At birth neonates struggled to right themselves on four feet. Few minutes later they could walk and attempted to leave the nest but were retrieved by their mother.

**Table 1.**

Morphological measurements in *C. mendocinus* neonates ( $n = 5$  females, 8 litters)

	Males				Females			
	$\bar{X}$	SE	range	n	$\bar{X}$	SE	range	n
Body mass (g) $t = 0.65$ $df = 24$ $P = 0.5$	16.4	0.4	12.5–20.0	14	15.7	1.1	12.0–20.6	12
Body length (mm) $t = 2.23$ $df = 23$ $P = 0.05$	90.6	0.0	64.0–80.0	13	86.5	0.1	73.0–100.0	12
Tail length (mm) $t = 1.0$ $df = 23$ $P = 0.3$	29.6	0.0	23.0–38.3	13	28.4	0.0	23.0–35.6	12
Hindfoot length (mm) $t = 0.2$ $df = 19$ $P = 0.7$	17.0	0.8	13.0–19.0	12	16.7	0.8	14.3–20.9	9

If placed on their backs, pups could right themselves and climb on their mothers' backs. They self-cleaned, and scratched. Some neonates, like adults, used their front paws to catch, manipulate, and nibble at alfalfa fragments. Neonates had eyes closed and ear passages open. The incisors were prominent but, except a singleton, not in mutual contact. While the dorsum was covered with dark grey fur, the venter of neonates was almost naked. They had well-developed vibrissae, tail hairs and the double row of supraungual hairs on the distal phalanges of hindfeet and forefeet, as well as fingers, claws and pads on soles of feet. Tuco-tuco newborns walked at 0.3 d.a.b., started to chew solid food at 3.1 d.a.b., opened their eyes at 6.6 d.a.b., and were totally covered with hair at 7.3 d.a.b. (table 2). According to Derrickson's (1992) scheme, these pups would have attained the development category 1 (altricial) by having only one area, locomotor independence, at 2 d.a.b. Likewise, a litter size of 3.2 pups, and an age of eye-opening of 6.6 d.a.b., would place *C. mendocinus* as totally altricial following Martin and Mac Larnon's (1985) scheme.

During the first week, mothers spent 89% of their time at the nest caring for the young. This care included suckling, retrieving, nest maintenance, carrying of food and, probably, transmission of warmth. Most time, litter members were in mutual contact if alone or in close contact with their mother while eating solid food in the nest. When the pups escaped from the nest the mothers, softly growling, retrieved them by grasping their heads, tails or mid bodies with their incisors. I recorded 647 retrievals ( $n = 6$  litters), 324 during the first week and 172 in the second week after parturition. Suckling bouts lasted  $19.9 \pm 1$  min (range = 13.1–23.5;  $n = 844$ ,  $n = 6$  litters). On several occasions the mothers left the nest with the young attached to the nipples. Out of 477 suckling bouts ( $n = 6$  litters), mothers nursed in the huddle, side-lying, supine and sitting positions in 360, 98, 15 and 4 bouts respectively. The young showed no "teat order", nor did they change between teats during a suckling bout. At  $16.7 \pm 8.0$  d.a.b. (range = 7–33;  $n = 7$  litters) suckling occurred in different parts of the den. At  $23.4 \pm 3.9$  d.a.b. (range = 13–34;  $n = 6$  litters) females rejected pups when they tried to obtain milk. The last retrieval was detected when pups reached  $33.5 \pm 6.8$  days of age (range = 3–58) and a body mass of  $73.5 \pm 17.4$  g (range = 17.6–118.6).

Both sexes reached adult body mass (females:  $167.5 \pm 12.8$  g, range = 100.0–225.0,  $n = 10$ ; males:  $216.0 \pm 13.3$  g, range = 164.0–309.9,  $n = 14$ ) at the same age ( $t$ -test;  $P = 0.78$ ), i.e. at  $130.5 \pm 3.1$  d.a.b. (range = 92–156). Asymptotic values ( $A$ ) and age at the inflection point ( $I$ ) were marginally higher for males than for females ( $t$ -test;  $P = 0.09$  and  $P = 0.06$ ), although growth constants  $K$  did not differ significantly ( $t$ -test;  $P = 0.24$ ) (table 3).

Eight females had their first vaginal opening (Camín, 2004) at  $243 \pm 18.3$  d.a.b. (range = 179–213). At  $257 \pm 12$  d.a.b. (range = 240–274) four males showed copulatory behaviour typical of *C. mendocinus*, described by Camín (1999), with females collected in the wild, two of which achieved pregnancy.

The life span of males and females was  $2.78 \pm 0.63$  years (range = 0.49–9.15;  $n = 15$ ) and  $1.92 \pm 0.58$  years (range = 0.45–2.78;  $n = 9$ ) respectively. There were no significant differences in life span for males versus females ( $t = -0.91$ ,  $df = 22$ ;  $P = 0.37$ ).

**Table 2.**

Morphological and behavioural development in *C. mendocinus* ( $n = 7$  litters, 25 pups). Age and body mass are expressed in days after birth (d.a.b.) and grams (g) respectively

	Age (d.a.b.)			Body mass (g)		
	$\bar{X}$	SE	range	$\bar{X}$	SE	range
Pups wandered out of nest.	0.3	0.3	0-2	16.0	0.5	12.0-20.0
Pups started to eat solid food (alfalfa) carried to nest by mother.	3.1	0.8	0-6	16.8	0.8	13.0-21.0
Play between pups in the form of: locking of incisors, rolling, dragging and gentle bites on neck, tail and sides.	6.4	1.8	2-14	21.5	2.3	16.1-28.4
Open eyes.	6.6	0.6	4-10	20.6	1.2	16.0-26.0
Body furred.	7.3	1.3	3-13	21.2	1.0	14.0-25.0
Incisors in contact.	8.6	0.9	1-14	24.8	2.0	15.2-38.1
Pups gathered food items (stems and roots of grasses, alfalfa, carrots) from food cage and carried them to nest where they ate them.	9.0	3.6	4-16	25.3	3.4	16.1-35.4
Scratching using hindfeet like adults (as described by Camín et al. 1995).	14.1	2.8	9-23	33.7	3.1	30.0-38.7
Short calls ("tuc-tuc") of 1-7 sec detectable 1 m away.	33.3	5.8	20-50	72.8	9.7	51.9-105.7
Pups began to eat shrubs ( <i>Prosopis flexuosa</i> ).	41.0	15.5	30-52	100.5	10.0	70.3-136.3
Young suckled occasionally: weaning.	56.0	3.3	42-63	117.4	13.6	53.7-180.7
Long calls ("tuc-tuc") of 4-100 sec detectable 4-5 m away, like adults (as described by Camín 2004).	69.8	12.7	44-111	136.3	12.7	81.6-179.9
Young attempted flight from den, serious sparring between mother and young. I separated the animals.	80	13.4	42-120	144.6	22.9	84.8-303.6

**Table 3.**  
Growth parameters of *C. mendocinus* estimated according to Gompertz equation

	Females (n = 9)			Males (n = 12)		
	$\bar{X}$	SE	range	$\bar{X}$	SE	range
Asymptotic value (A) (g)	177.5	12.0	105.1-210.3	211.5	14.74	158.0-329.3
t = 1.77						
df = 19						
P = 0.09						
Constant growth rate (K) (days <sup>-1</sup> )	0.03	0.004	0.03-0.03	0.02	0.001	0.01-0.03
t = 1.20						
df = 19						
P = 0.24						
Age at inflection point (I) (days)	30.3	1.1	24.8-45.7	35.3	2.18	29.4-52.7
t = 1.92						
df = 19						
P = 0.06						
Maximum growth rate (K* A* e <sup>-1</sup> ) (g/day)	2.00	0.1	1.27-2.37	2.2	0.1	1.3-3.2
t = 0.95						
df = 19						
P = 0.35						
Determination coefficient (r <sup>2</sup> )	0.9	0.000	0.9-0.9	0.9	0.001	0.9-0.9
t = -1.01						
df = 19						
P = 0.31						



## Discussion

The results of this study, as well as similar results reported for comparisons between other caviomorphs like *Octodon degus* (cursorial, precocial) and *Spalacopus cyanus* (subterranean, altricial) or *Ctenomys talarum* (subterranean, altricial) (table 4), support the idea that life history features could influence the neonatal development of small mammals, including caviomorphs, a typically precocial suborder. In effect, differences between cuises and tuco-tuco neonates were clear (table 4). The newborn pups of *M. australis* resemble miniature adults and exhibit many adult behaviour patterns e.g. rolling, climbing and nibbling at vegetation (Rood, 1972). Instead, the newborn pups of *C. mendocinus* were altricial. After a 40% longer gestation period than cuises, the newborns of *C. mendocinus* were blind and half naked, gained resemblance to miniature adults at 9–14 days of age (table 2), and suckled outside the nest only at 16.7 d.a.b. The maternal and suckling behaviours of *C. mendocinus* were typical of an altricial species, very different from those of cuises and similar to those displayed by other altricial caviomorphs (table 5). In effect, females of *C. mendocinus* delivered in large nests, retrieved their offspring and suckled them in bouts 3–4 times longer than the bouts of cuises. Besides, young tuco-tucos showed no tactics to reduce the suckling bout. When young *M. australis* are about a week old, they probably receive the bulk of their nourishment from solid foods and are capable of living independently (Rood, 1972). In contrast, pups of *C. mendocinus* weaned at 56 d.a.b. and attained independence only 80 d.a.b. (table 2). Between one and two months of age, an adolescent *M. australis* female enters her first estrus and mates with several males (Rood, 1972). Females of *C. mendocinus* came into their first estrus or had their first vaginal opening at 6–8 months of age (Rosi et al., 1992; this study).

Among the advantages of precocial development are that precocial young are typically quicker than altricial ones to become mature enough to survive the death of their parents, and are more able to evade predators by themselves (Pagel and Harvey, 1988). Among the benefits of altricial development, Case (1978) and Pagel and Harvey (1988) stressed that birth in an immature state might have been favoured in those species that use vigorous pursuit to gather prey, because altriciality could free the pregnant mother early from the encumbrance of retaining young during pursuits. Nest security could also be an influential factor in developing altriciality. Regarding *C. mendocinus*, constraints (low metabolic rates) as well as advantages (low predation pressure in protected nests) linked to subterranean life could have favoured the evolution of altriciality.

Although *C. mendocinus* seems to be a mostly an altricial species, clearly different from its cursorial counterparts, its pups –just like those of other subterranean caviomorphs– are more developed than pups of other non-caviomorph subterranean rodents (table 4). This could denote a trade-off between the constraints and advantages associated with its subterranean way of life, and the phylogenetic inertia typical of caviomorphs.

Altricial and precocial development are not monolithic categories; intergrades exist between the extremes, and a species may be relatively altricial in certain respects and relatively precocial in others (Hill, 1992). For example, the three rodent species studied

Table 4.

Categories of neonatal development (DC) following Derricks's scheme assigned to some caviomorph and non caviomorph rodents with different styles of life. Body mass, age and relative body mass (r.n.m.) of neonates are expressed in grams (g), days after birth (d.a.b.), and percent (%), respectively.

	Adult body mass (g)	Gestation period (days)	Pelage produced (d.a.b.)	Eyes open (d.a.b.)	Movement independent of parents (d.a.b.)	Pups eating solids (d.a.b.)	DC (DC)	Ear meatus at birth	r.n.m. (%)	Source
Surface-dwelling caviomorphs										
<i>Galea musteloides</i>	400	53	0; 2	0; 2	1; 2	1-2; 2	4	Open	10	Rood 1972; Kleiman 1974; Weir 1974
<i>Microcavia australis</i>	200	54	0	0	0	0	4	Open	11	Rood 1970, 1972.
<i>Octodon degus</i>	250	90	–	2-3; 0	0	6-7	2	Open	5.6	Kleiman et al. 1979; Nowak 1999; Reynolds and Wright 1979; Weir 1974.
Subterranean caviomorphs										
<i>Ctenomys mendocinus</i>	163	95.9	7.3	6.6	0.3	3.1	1	Open	10	This study.
<i>Ctenomys talarum</i>	120	95	1-3	7-10	7-10	10	1	Open	8.1	Zenuro et al. 2002.
<i>Spalacopus cyanus</i>	107	77	–	4	0	18	1	–	8.3	Begall et al. 1999.
Other subterranean rodents										
<i>Bathyergus janetta</i>	390	–	4	15	9	13	0	Closed	5	Bennett et al. 1991.
<i>Cryptomys damarensis</i>	100	78-92	6	18	1-2	6	1	Closed	9	Bennett and Jarvis 1988; Jarvis and Bennett 1993.
<i>Georychus capensis</i>	180	44-48	7	9	7	17	0	Closed	4	Bennett and Jarvis 1988; Bennett et al. 1991.

(Continued)

**Table 4.** (Cont.)

Categories of neonatal development (DC) following Derrickson's scheme assigned to some cavimorph and non cavimorph rodents with different styles of life. Body mass, age and relative body mass (r.n.m.) of neonates are expressed in grams (g), days after birth (d.a.b.), and percent (%), respectively.

	Adult body mass (g)	Gestation period (days)	Pelage produced (d.a.b.)	Eyes open (d.a.b.)	Movement independent of parents (d.a.b.)	Pups eating solids (d.a.b.)	Ear meatus at birth (DC)	r.n.m. (%)	Source
<i>Heliophobius argenteocinereus</i>	162	–	0	13-14	–	8-11	1	7.8	Sumbera et al. 2003.
<i>Nannospalax ehrenbergi</i>		28-34	7-8	Closed Eyes	12-14	14-21	0	5	Nevo 1961; Nevo and Shkolnik 1974.
<i>Thomomys talpoides</i>	106	18	9	26	9	17	0	2.8	Andersen 1978.
<i>Tachyoryctes splendens</i>		36-41	2-4	21-28	20	15-21	0	8	Jarvis 1969, 1973; McNab 1966.

**Table 5.**  
Patterns of maternal behaviour in some precocial and altricial caviomorphs

	Nursing site	Retrieval behaviour	Suckling bout (min)	Suckling posture	Nursing Tactic	Source
Precocial species						
<i>Galea musteloides</i>	Exposed area	No	5	Sitting, lying	Rapid alternation of teats	Rood 1972; Kleiman 1974; Camín 2004
<i>Microcavia australis</i>	Exposed area	No	6	Sitting, lying	Rapid alternation of teats	Rood 1970, 1972; Kleiman 1974
Altricial species						
<i>Ctenomys mendocinus</i>	Subterranean nest	Yes	19.9	Huddling	Pups attached to the nipples	This study
<i>Ctenomys talarum</i>	Subterranean nest	Yes	–	Huddling	–	Zenuto et al. 2002
<i>Spalacopus cyanus</i>	Subterranean nest	Yes	–	Lying, huddling	–	Begall et al. 1999

by Dempster and Perrin (1989) would all be classified into category 1 of Derrickson's scale. However, *Petromyscus* attains some physical and behavioural developmental stages before *Gerbillus* and could be described as less altricial than the *Gerbillus* species. Likewise, *C. talarum* and *C. mendocinus* are both altricial animals classified into category 1 of Derrickson's scale. However, the pups of *C. talarum* start moving independently and start eating solid food much later than *C. mendocinus* pups (table 4). Moreover, *C. talarum* produces larger litters (4.09 according to Malizia and Busch, 1991; 4.52 according to Malizia and Busch, 1997) of smaller young than does *C. mendocinus* (Rosi et al., 1992; this study: table 4). Derrickson's scheme has obvious merits, as it contributes to organize the inherent natural variability observed in growth processes, but suffers from its categorical nature and needs to be taken with caution.

Kraus et al. (2005) assign higher precocity to *Cavia magna* than to other cavies because it inhabits harsh environments. Given the large geographic range and habitat types occupied by the genus *Ctenomys*, intra-genus variation in neonatal development might reflect differences in local climate or habitat productivity. Under this line of reasoning, *C. mendocinus*, which inhabits arid regions of lower productivity than *C. talarum* (Malizia and Busch, 1991, 1997; Rosi et al., 1992), would have developed higher precocity.

Studies of some tuco-tucos have revealed that these animals are frequently preyed upon by an array of vertebrates (Vasallo et al., 1994; Massoia et al., 1987). The putative lower predation pressure exerted on subterranean caviomorph pups compared to their cursorial counterparts has been suggested as a factor linked to the development of altricial strategies (Kleiman, 1974). Despite the plausibility of such hypothesis, no quantitative studies of predation on *C. mendocinus* have been conducted thus far and, therefore, the role of predation in the population ecology of tuco-tucos is still uncertain.

Promotion of altriciality in small mammals has been given other explanations, such as small body size (adult size of 10 g or less; Hopson, 1973; Case, 1978) or short gestation time (Derrickson, 1992). The relatively big adult size (163 g) and long gestation period (95.6 days) of *C. mendocinus* do not seem *per se* to be conditioning factors of altriciality.

The study of life-history traits is central to evolutionary biology (Futuyma, 1986; Hare and Murie, 1992). With subterranean as well as non-subterranean forms, the group of caviomorphs is unique. The ctenomyids, by far the most species-rich group of extant subterranean rodents (Lacey et al., 2000), share wide distribution areas with cursorial caviomorphs. Further studies on life history of other tuco-tucos and their cursorial counterparts may reveal which other reproductive and developmental parameters are constrained by phylogeny and ecology.

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