REPRODUCTION AND GROWTH IN A PRECOCIAL SMALL MAMMAL, *CAVIA MAGNA*

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Small mammals usually produce large litters of altricial young, resulting in high reproductive rates. In contrast, cavies give birth to few precocial young after a long gestation. The price of this reproductive strategy is a low intrinsic rate of natural increase. We investigated if the patterns of reproduction in a wild population of *Cavia magna* are consistent with the hypotheses that cavies can increase their reproductive output by breeding aseasonally and by maturing extremely early. We collected data on reproduction and growth by capture–recapture during a 26-month field study in a wetland in Uruguay, and from a laboratory population founded with individuals from the same region. Among the Caviinae, *C. magna* is particularly precocial, with individual neonates weighing on average 18% of maternal mass. Reproduction was mostly seasonal, with the main birth season starting at the end of September (austral spring) and extending until May in 1999 and February in 2000, respectively, with only a few females reproducing during the 1st but not the 2nd austral winter. Individual females produced on average 3 litters per year. Some females born in early spring conceived successfully between the age of 30 and 45 days, similar to females in the laboratory. The remainder of the 1st spring cohort and females of subsequent birth cohorts delayed reproduction until the following spring. Body condition and growth rates were highest in the spring, declined through the year, and varied between years, and may be the proximate factors determining whether an adult female or a juvenile initiates breeding. Breeding opportunistically whenever conditions allow might partly compensate for the low reproductive rate of cavies.

Key words: age at maturity, *Cavia magna*, cavies, growth rates, life history, opportunistic breeding, precocial small mammals, reproductive strategy

Why do some mammals produce large numbers of tiny, blind, and naked young, whereas others invest heavily in individual offspring, giving birth to a few, well-developed "miniature adults"? The so-called altricial–precocial dichotomy exists within several taxa, suggesting that the presumably ancestral altricial developmental mode (Case 1978a; Hopson 1972) has been modified toward precociality more than once during mammalian evolution (Derrickson 1992). The potential price mammals have to pay for producing precocial young is a low intrinsic rate of natural increase (Hennemann 1984). The cost of precociality appears to depend on body size, such that differences in potential population growth rates are greatest in small-bodied mammals. This might explain why only few species of small mammals produce precocial young (Hennemann 1984).

But how do small, precocial species cope with this problem? Within the caviomorph suborder, members of the Caviinae,

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neotropical rodents, provide an example that the precocial strategy can be highly successful. After an extraordinarily long gestation period (53–77 days) given their adult body size (150–1,000 g), cavies give birth to usually just 1–3 large young (54–76 g). Neonates are born open-eyed and fully furred, are mobile within hours after birth, and even take solid food within the 1st few days of life (Künkele and Trillmich 1997). Under good conditions, a female *Cavia aperea* might produce 10 young per year, whereas the similar-sized Norway rat (*Rattus norvegicus*), an altricial species, could have more than 100 direct offspring. Despite their low reproductive rate, cavy populations reach high densities (Bilenca et al. 1995; Rood 1972).

So, how can cavies overcome the apparent disadvantages of producing precocial young? For a given level of natural mortality, the annual birth rate and the age at 1st and last reproduction determine how fast a population can grow. The annual birth rate is determined by litter size and the number of litters per year. Assuming that the developmental state of the offspring is a fixed trait, it does not seem possible for cavies to produce much larger litters. Instead, because of differences in the energetics of reproduction between altricial and precocial rodents, cavies might be able to produce more litters per year

than their altricial counterparts. In the domestic guinea pig (*Cavia porcellus*), energy demand is distributed more evenly over the reproductive cycle, and its peak is low relative to that of altricial rodents (Künkele 2000a; Künkele and Trillmich 1997). Additionally, because of a prolonged gestation period, the efficiency of energy conversion into offspring is exceptionally high in guinea pigs (Künkele 2000a). These patterns in reproductive energetics led to the hypothesis that the precocial strategy might be ecologically robust and enable wild cavies to reproduce year-round, even under harsh conditions (Künkele 2000a; Künkele and Trillmich 1997; Neal 1986; Short 1985).

Theoretical models and simulations have shown that age at maturity is an important determinant of population growth, especially in small, short-lived species (Caswell and Hastings 1980; Cole 1954; Lewontin 1965; Oli and Dobson 1999). Although the production of precocial young is coupled with a delayed onset of reproduction in some small mammals (Hennemann 1984), precocial rodents do not mature later than altricial ones (Derrickson 1992). In the laboratory, female *C. aperea* conceive successfully at the age of approximately 1 month when kept with an adult male and at this age they weigh less than one-half of final adult body mass (Trillmich 2000). Thus, an extremely early onset of reproduction might be another feature in the cavies' life history that helps to compensate for their low reproductive rate. Still, to what extent this potential for early maturation is realized under natural conditions is unknown.

Our study species, *Cavia magna*, has only recently been described (Ximénez 1980). Its distribution is limited to the wetlands of northern Uruguay and southern Brazil close to the Atlantic coast (Ximénez 1967, 1980). Here, we present data on basic life-history parameters on this little-known cavy. Specifically, we aimed to determine if the patterns of reproduction in a wild population of *C. magna* are consistent with the hypotheses that cavies can increase their reproductive output by breeding aseasonally and by maturing extremely early. To elucidate potential proximate factors determining the reproductive patterns, we describe temporal changes in body condition of females, and, because growth rates connect age and size at maturity and may affect the optimal timing of maturity, we also document patterns of growth found in our field population.

MATERIALS AND METHODS

Study site.—The study site was located in the national park Refugio de Fauna Laguna de Castillos, close to the Atlantic coast in the province of Rocha, Uruguay. It consisted of a large caraguatal (about 3.3 ha), a wetland typical of this region. The key species in this habitat is *Eryngium pandanifolium*, a tall spiny shrub. Gambarotta et al. (1999) provide a detailed description of the reserve's fauna. With an average annual precipitation of 1,100 mm, the climate is very humid. In combination with the low elevation (0 m), this leads to partial flooding of the site during the austral winter when evaporation is low. The duration and extent of these inundations exhibit high annual variation. For fieldwork, we established a grid system with wooden stakes at the intersections marking edges of 10 × 10-m squares.

Study population.—Populations of 2 wild cavy species, *C. magna* and *C. aperea*, coinhabited the study site. Cavies used the surrounding short- and adjacent long-grass areas mainly for feeding during twilight periods. However, when disturbed they would run to the caraguatal for shelter. Cavy numbers began to decrease from the austral summer of 1999–2000 onward. By the middle of January 2001, all cavies had disappeared from the study site because of heavy predation by the minor grison (*Galictis cuja*—Kraus and Rödel 2004). Here, we concentrate on *C. magna*, because the data we have on specific reproductive events for *C. aperea* are rather sparse.

Livetrapping.—During the 1st breeding season from November 1998 to April 1999 we conducted monthly sessions of 3 trapping nights with 70 live traps (model 202, 19 × 6 × 6 inches, Tomahawk Live Trap Co., Tomahawk, Wisconsin). Starting in May 1999, the number of traps was changed, with 200 traps distributed over the entire caraguatal. For 2 nights, twice monthly, traps were positioned unbaited on cavy runways and set in the late afternoon 2 h before sunset and again at night 2 h before sunrise. Traps were checked and closed 4–5 h after setting. Trapping was restricted to these hours because cavies were most active during twilight phases, and to minimize stress for the animals caught. Outside the trapping periods, traps were left locked open to habituate the animals to the presence of the traps and to prevent them from changing their preferred runways.

We marked newly caught animals individually with a transponder (model ID 100 Trovan Ltd., Hessle, United Kingdom), injected subdermally between the shoulders, as well as a numbered metal ear tag (6 mm long, 2 mm wide, model 1005-1 National Band and Tag Co., Newport, Kentucky). Individuals were sexed and the reproductive state was determined (females: closed or perforate vaginal membrane, lactating, or visibly pregnant; males: scrotal or nonscrotal testes). Body mass and various other body-size measurements were taken; animals weighing less than 200 g were regarded as juveniles.

Laboratory population.—Twelve *C. magna* (6 females and 6 males) were transferred from Rocha, Uruguay, to Bielefeld, Germany, in March 2001. The laboratory data result from these 12 founder animals and a total of 45 litters including 1st- to 4th-generation descendants. Animals were kept in environmentally controlled rooms on a photoperiod of 14:10 h light : dark at 20–23°C. Laboratory guinea pig chow (Höveler, Langenfeld, Germany), hay, and water were provided ad libitum, supplemented with fresh carrots and beets. One male and 1–3 females were housed in enclosures (1 × 0.8 m or 2 × 0.8 m) with wood shavings for bedding and several huts for shelter. All adult animals were weighed once a week. Pregnant females were checked daily to obtain exact parturition dates and birth mass. Cavies have a postpartum estrus (Rood 1972). Thus, gestation length was estimated as the interbirth interval after postpartum conception. Body mass of young was recorded every day until 3 months of age. The teats of lactating females were checked daily for milk to estimate the lactation period. Data on maturity come from a sample of 11 females, which were placed with adult males at age 20 days (20.5 days ± 1.8 SD). To estimate age and size at maturity, we subtracted the average gestation period of 64 days from age at parturition.

All procedures involving capture, handling, and care in the field as well as in the laboratory followed guidelines of the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp).

Data analysis.—When looking at the temporal distribution of breeding events, time must be treated as a circular variable. We thus used circular statistics to test for seasonality of reproduction in the field population, that is, the temporal pattern of the appearance of new juveniles. The Rayleigh test is a test of a null hypothesis of uniformity against an alternative hypothesis of unimodality (estimated parameters: r = vector length, θ = mean vector of sample, s = angular *SD*—

Batschelet 1981; software Rayleigh & Co. 3.1, Oxalis Softwaresysteme für Wirtschaft und Wissenschaft GMBH, Gütersloh, Germany). Breeding-season length differed between the 2 years of the study; thus, we only used data of the year from August 1999 to July 2000 (data for the following year were very sparse). Because population size changed considerably over this year, we standardized the number of juveniles caught in a given trapping session by the total number of potentially reproductive females (>250-g body mass) known to be alive at this time.

Data on reproduction for the free-living cavies was extracted from the capture–recapture data. Unless stated otherwise, we present only data on females regularly caught to be certain of the reproductive event concerned. For example, for the analysis of successful conception only females that we caught with a perforate vagina and then caught again while pregnant within the 2 following months were counted as "successful estrus." We defined body condition as the relationship between body length and body mass of nonpregnant females. Females that were caught in both years (1999 and 2000) were included in the samples for the year 2000, because population size, and consequently sample size, was very small in winter 2000. Because body length and body mass are not linearly related (power function), we used ln-transformed data to produce a linear relationship between the 2 variables and to achieve normality of the data distributions. Simple linear regressions (model II—Sokal and Rohlf 1995) were performed. Statistical tests for a difference between the coefficients of 2 regression lines were only conducted when the 2 samples concerned consisted of independent data points.

Growth rates change with age and thus depend strongly on the time interval over which they are measured. Therefore, we only used data on body mass changes from consecutive trapping sessions. Because the absolute age of wild cavies was unknown, we described growth rates by their dependence on initial body mass. We fitted exponential decay curves rather than logistic ones, because in cavies the initial period of slowly accelerating growth is very short (Künkele 2000b; Raffel et al. 1996), and with our temporal resolution we were unable to detect it. Two-parameter models ($Y = ae^{-bX}$) were used for overall growth rates, because we expected that rates would approach zero with larger body mass. For the data sets split by season (spring, September–November; summer, December–February) we chose the model with an additional intercept parameter ($Y = y_0 + ae^{-bX}$), because we knew that even large animals undergo seasonal changes in body mass (positive in spring, negative in summer). Only data for the reproductive season 1999–2000 were included in the growth data to exclude effects of interannual variability of growth rates. If not stated otherwise, values are given as mean ± SD. All statistical tests conducted are 2-tailed with a significance level of 0.05 and were performed with SPSS 11.0. Curves were fitted with SigmaPlot 2001 (both packages from SPSS Inc., Chicago, Illinois).

RESULTS

Temporal breeding pattern.—Between November 1998 and January 2001, we caught a total of 140 females (1,011 captures) and 168 males (1,146 captures) identified as *C. magna*. Reproduction was seasonal, with most new juveniles caught during the austral spring (October–December; Rayleigh test for August 1999–July 2000: $n = 77$, $r = 0.742$, $\theta = 316°$, $s = 41.2°$, $P < 0.001$; Fig. 1). However, during the 1st year of the study the reproductive season was longer, with a pulse of juveniles as late as May 1999, and single juveniles were caught even during the winter months. In contrast, there was a clear nonreproductive season from May to September 2000. Reproduction was partly
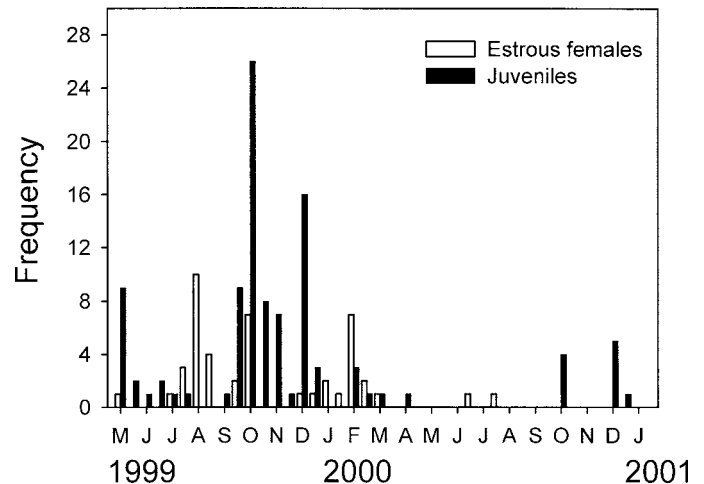

FIG. 1.—Temporal breeding pattern: distribution of estrous female and 1st-caught juvenile (<200 g) *Cavia magna* over the main study period in Uruguay.

synchronized, with 2 months, the length of the gestation period, between the major birth cohorts of October and December, followed by a small peak in February 2000.

No individual female reproduced continuously. The maximum number of litters observed per female per year was 4. Of the 11 adult females we caught over a period of at least 1 year, none could have had more than 4 litters. Of the 6 females we could monitor regularly, 4 produced 3 litters per year and the remaining 2 produced 2 and 4 litters per year, respectively. Of the 16 estrous females caught between July and December, 15 conceived successfully; this was the case for only 5 of 15 estrous females caught between January and June (chi-square test: $\chi^2 = 12.34$, $d.f. = 1$, $P < 0.001$).

At the end of the main reproductive season in May, body condition of young females was similar in the laboratory and field (Fig. 2). With increasing body length, regression lines diverged for laboratory and free-living animals, with laboratory animals being heavier for a given body length (regression equations are given in Fig. 2: 95% confidence intervals of the slopes, b_{lab}: [2.59–3.06], b_{field}: [2.35–2.57], $d.f. = 1$, $P < 0.05$). Body condition of nonpregnant females was slightly better in May 1999, when some females were still reproducing, than in May 2000, when the last juveniles had been caught in April 2000 (Fig. 3). None of the females in May 2000 had body mass above the regression line for those in May 1999. However, neither the difference between the intercepts nor the slopes of the regression lines reached statistical significance. In 1999, body condition was almost identical at the end of the reproductive season in May and the onset of the following breeding season, when most females conceived successfully between the middle of July and August (Fig. 4a). In contrast, body condition of females improved slightly during the nonreproductive season of 2000 (Fig. 4b).

Reproduction.—Female cavies produced small litters of 1 or 2 or occasionally 3 young, after a >2-month gestation period (Table 1). All primiparous females that conceived while still growing at a rapid rate gave birth to only 1 offspring. Litter
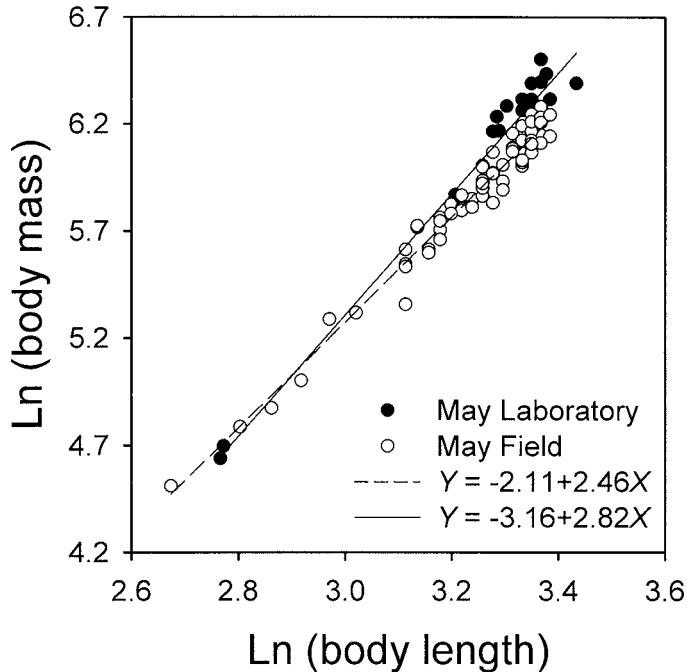
FIG. 2.—Body condition of nonpregnant female *Cavia magna* after the main reproductive season in Uruguay. After ln-transformation of both body mass (g) and body length (cm), linear functions ($Y = a + bX$) were fitted. Compared are animals from the laboratory ($n = 24$, $R^2 = 0.97$, $F = 622$, $d.f. = 1, 22$, $P < 0.001$) and the field in May ($n = 64$, $R^2 = 0.97$, $F = 1,862$, $d.f. = 1, 62$, $P < 0.001$).

FIG. 3.—Body condition of nonpregnant female *Cavia magna* after the main reproductive season, comparing cavies in the field in May 1999 and May 2000 in Uruguay. Linear functions are as in Fig. 2. In May 1999 some females reproduced, whereas in May 2000 no reproductively active female was caught (May 1999: $n = 48$, $R^2 = 0.98$, $F = 2,354$, $d.f. = 1, 46$, $P < 0.001$; May 2000: $n = 16$, $R^2 = 0.96$, $F = 296$, $d.f. = 1, 14$, $P < 0.001$).

mass was ≤40% of maternal body mass. Individual neonates weighed approximately 18% (field) of mother's mass. Birth mass of females and males was similar (females: 79 ± 10 g, males: 78 ± 11 g), but decreased with increasing litter size (litter size 1: 84 ± 11 g; litter size 2: 77 ± 12 g; litter size 3: 72 ± 8 g). Young were highly precocial and fully mobile within 1 h after birth. Lactation lasted 3–4 weeks and perhaps slightly longer in the field. In the laboratory, females conceived at the mean age of 29.5 days when they had attained less than 50% of the adult body mass (Table 1). The age and size at 1st conception observed in the wild population and the laboratory were similar (Table 1). However, in the field, only 6 of 32 young females (18.8%) matured and conceived successfully within the reproductive season of their birth. All these females belonged to the 1st birth cohort of the year. Early-maturing females grew at a similar rate during pregnancy as those that did not reproduce during the breeding season of their birth. Late-maturing females conceived relatively synchronously at the beginning of the following breeding season, that is, when 3–10 months old, at a body size of 319–421 g (362 ± 33 g, $n = 7$).

Growth.—Early growth during the lactation period, as well as subsequent mass gain, was much more rapid for captive than for wild cavies (Table 1). In the field, juvenile females and males began growing at a similar rate, but growth rate decreased more steeply in females, explaining the larger body size of adult males (Fig. 5). Animals continued to increase in body mass for more than 1 year. During the dry summer months in 1999–20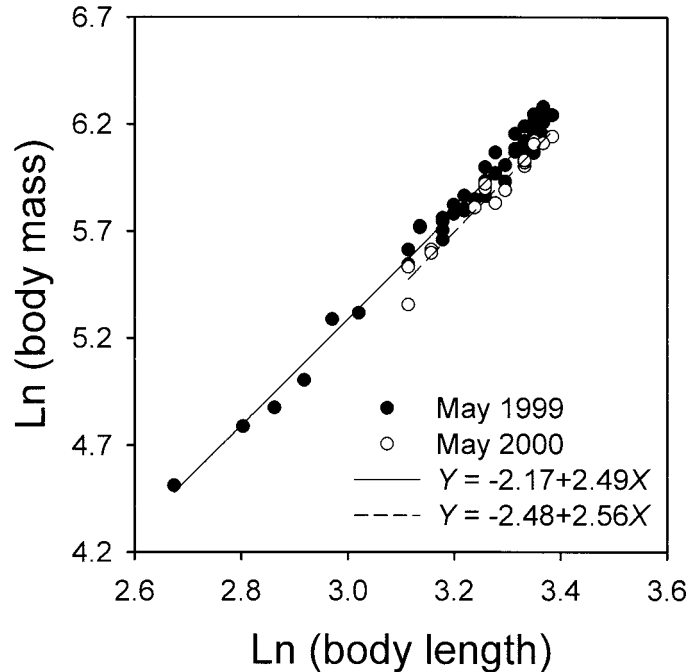00, growth rates were lower than in spring 1999 for all size classes (Fig. 5). Thus, individuals born early in the reproductive season had more time to increase body mass before the onset of winter and grew at a faster rate (Figs. 5 and 6). However, growth rates also seemed to differ among years. Juveniles from the 1st cohort born in 1999–2000 grew at a similar rate as those born late in the reproductive season in 1999–2000 but slower than young born early in 2000–2001 (Fig. 6).

DISCUSSION

We found only partial support for the hypothesis that wild cavies reproduce throughout the year. Female *C. magna* occasionally gave birth in winter. However, at the population level, reproduction was seasonal, and no single female reproduced continuously throughout the year. Evidence concerning the 2nd hypothesis that cavies mature particularly early also was inconclusive. Although in the field some females matured at an early age, comparable to that of captive animals, most young females reproduced successfully only in the breeding season after their birth.

Reproductive strategy: quality, not quantity.—Newborn *C. magna* belong to the most extreme examples of precocial reproduction. Usually only 1 or 2 young are born after a gestation period of 64 days. Under laboratory conditions the maximum litter size was 3. Consistent with our results, Ximénez (1980) collected 6 pregnant females each carrying only 1 fetus. Derrickson (1992) suggested the use of relative neonatal mass
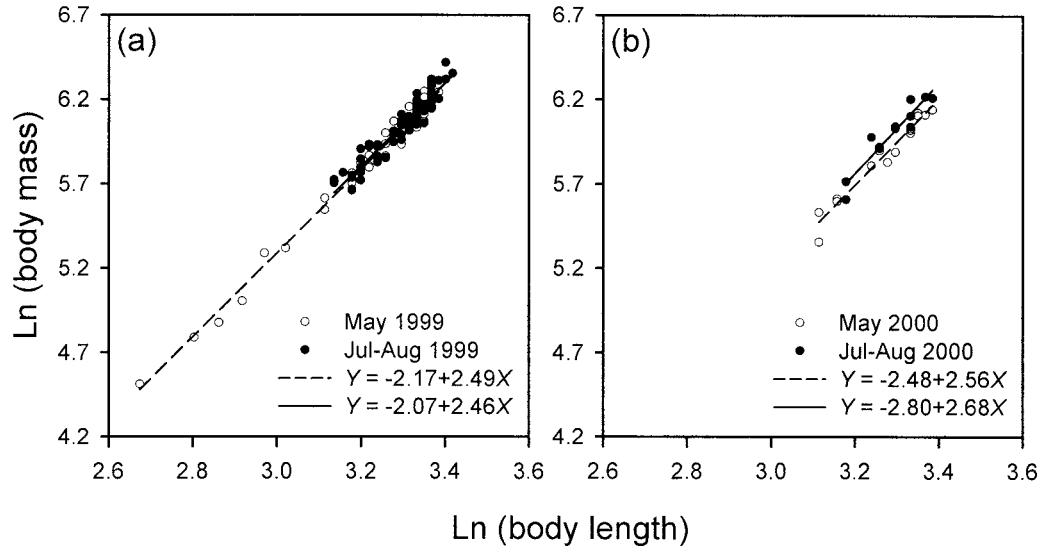
Fɪɢ. 4.—Comparison of body condition of nonpregnant female *Cavia magna* in May (end of the reproductive season) versus July and August (beginning of the next reproductive season) in Uruguay a) for 1999, when some females still reproduced in May, and b) for 2000, when no reproductively active females were caught. Linear functions are as in Fig. 2 (May 1999: see Fig. 3 for statistics; July–August 1999: $n = 68$, $R^2 = 0.90$, $F = 602$, $d.f. = 1, 66$, $P < 0.001$; May 2000: see Fig. 3 for statistics; July–August 2000: $n = 11$, $R^2 = 0.90$, $F = 82$, $d.f. = 1, 66$, $P < 0.001$).

(i.e., neonatal mass as a percentage of maternal mass) as an alternative measure of neonatal development instead of the more common categorical classification (e.g., Case 1978b; Eisenberg 1981). Relative neonatal mass was approximately 18% in free-living females and 14% in captive animals. In comparison, the altricial neonates of eastern gray squirrels (*Sciurus carolinensis*), a similar-sized rodent (568 g—Purvis and Harvey 1995), weigh only 2.7% of their mother's body mass. In the closely related *C. aperea*, relative neonatal mass is on average 12.5%, and females produce up to 6 young in the wild (C. Kraus, in litt.) and for the other genera of the Caviinae

it is approximately 10% (*Galea*: 9.6%—M. Asher, pers. comm.; *Microcavia*: 11.1%—M. Asher, pers. comm.; Rood 1972; *Kerodon*: 8%—Nowak 1999). Newborn degus (*Octodon degus*), a burrowing caviomorph species with much less precocial young, weigh only 5.6% of their mother's body mass (Nowak 1999).

Nonstop reproduction?—In contrast to our laboratory breeding population, which reproduces throughout the year, reproduction in the wild population of *C. magna* was clearly seasonal. However, the length of the reproductive season and the proportion of late-breeding females differed between the 2

Tᴀʙʟᴇ 1.—Basic life-history parameters of *Cavia magna* in captivity and from a field population in Uruguay. For very small samples, single data points are given.

	Laboratory		Field		
	$\bar{X} \pm SD$ (range)	n	$\bar{X} \pm SD$ (range)	n	Notes
Body mass[a] (g)					
Females	569 ± 79	18	426 ± 42	22	Heaviest 10: 552 ± 25
Males	693 ± 64	16	475 ± 32	18	Heaviest 10: 642 ± 31
Litter size	1.67 ± 0.67	45	1, 2	2	
Primiparous mothers	1.25 ± 0.45	16			
Multiparous mothers	1.90 ± 0.67	29			
Offspring body mass (g)	78 ± 11	66	78 ± 13 (66−91)	5	
Gestation (days)	64.3 ± 0.9	13	60, 64	2	
Lactation (days)	25 ± 4	24			Longest 3: >19, >20, >33
Early growth rate[b] (% mass gain/day)	8.12 ± 1.24	33	5.68 ± 0.88	5	
Age at 1st conception (days)	29.5 ± 7.1 (19−48)	11	(~30−321)	12	Earliest 3: ~30, 36, 45
Size at 1st conception (g)	252 ± 33 (220−315)	11	(208−421)	11	Smallest 3: 208, 236, 257

[a] Body mass of approximately 1-year-old animals; age of heaviest 10 is unknown.
[b] Laboratory, growth at ages 1–15 days; field, growth of animals weighing <100 g at 1st capture and recaptured about 15 days later.
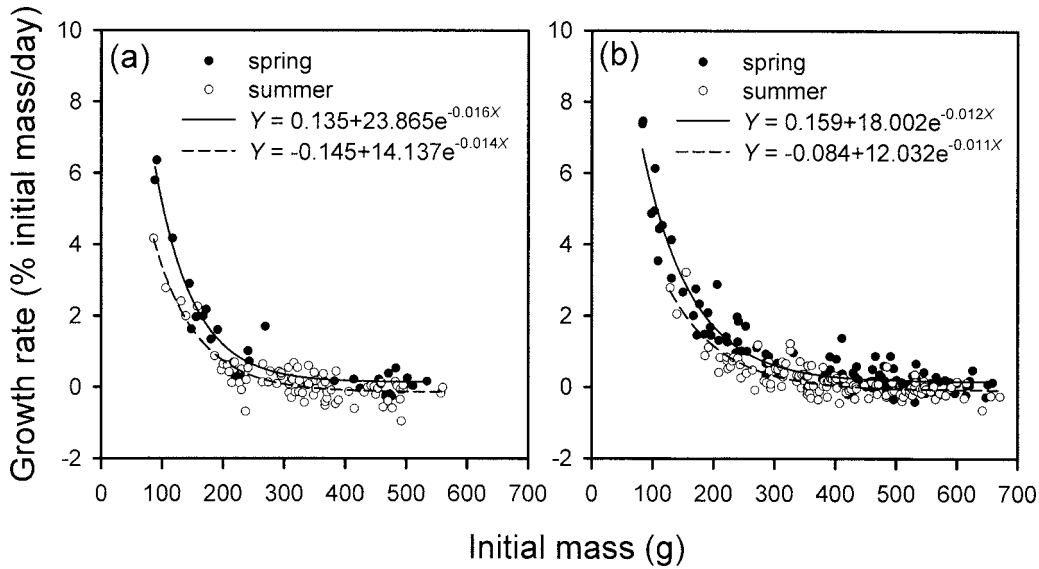
FIG. 5.—Growth in body mass of *Cavia magna* in the field in Uruguay. Exponential decay functions with 3 parameters ($Y = Y_0 + ae^{-bX}$) were fitted to describe seasonal growth rates in 1999–2000 a) for nonreproducing females in spring ($n = 29$, $R^2 = 0.94$) and summer ($n = 82$, $R^2 = 0.82$) and for b) males in spring ($n = 110$, $R^2 = 0.93$) and summer ($n = 127$, $R^2 = 0.70$).

years of the study. The main breeding season extended until May in the 1st year, but only until February in the 2nd year. Thus, during the 1st year many females suspended reproductive activity for only 2 months, because the 1st young of the following reproductive season were conceived in late July 1999. The same temporal breeding pattern was evident in the sympatric population of *C. aperea* (C. Kraus, in litt.), suggesting that environmental factors were responsible. For the province of Buenos Aires, Argentina, Rood (1972) reported minor seasonality with reproductive activity throughout the year for the same species and another caviomorph, the cui (*Galea musteloides*), but a restricted birth season of 9 months

with a breeding pause from May to June for the desert cavy (*Microcavia australis*).

Photoperiod alone cannot explain the interannual and site variability of breeding-season length. Neither a seasonal change in photoperiod nor low temperatures inhibited reproductive activity in female *C. aperea* kept under ad libitum food conditions (Trillmich 2000). Millar (1981) suggests that food resources are the most likely factor in determining breeding patterns in small mammals. Female *C. aperea* in good physical condition usually conceive successfully during postpartum estrus (Trillmich 2000). At the end of the reproductive season in May, body condition of adult female *C. magna* in the field
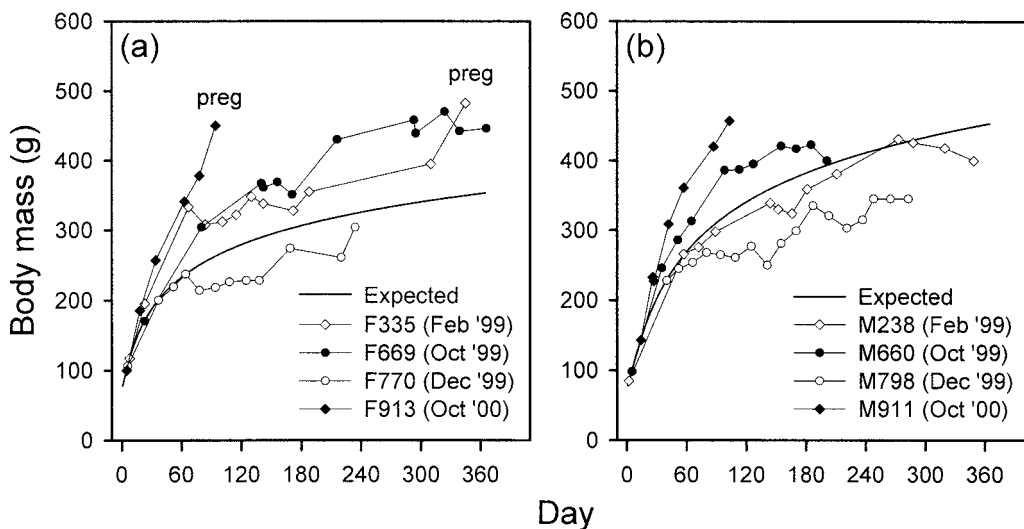

FIG. 6.—Examples of individual body mass growth for a) female (preg = pregnant) and b) male *Cavia magna* from different birth cohorts in Uruguay compared to the expected growth based on exponential decay functions with 2 parameters ($Y = ae^{-bX}$), which were fitted to describe average growth rates for a) nonreproducing females ($n = 231$, $Y = 36.0295e^{-0.0186X}$, $R^2 = 0.80$) and b) males ($n = 361$, $Y = 19.0028e^{-0.0127X}$, $R^2 = 0.81$). Growth of other animals from these cohorts followed the same pattern.

was worse than in the laboratory, and for females in the field, it was better in 1999 than in 2000. In 2000, body condition of females improved from May until the onset of the following breeding season. Cavy densities were extremely high from May 1999 until the long and dry summer of 2000. Food availability seemed poor thereafter, based on subjective assessment of the muddy, short-grazed grass fringe around the caraguatal and the lack of fresh green grass among the stands of long grass a bit further away.

Rüweler (2001) showed that female *C. aperea* are less likely to reproduce when kept under mild food restriction. These findings suggest a threshold condition for successful reproduction by females. This could partly explain the similar birth mass and body condition of laboratory and free-living juveniles. As Pontier et al. (1993) pointed out, if females only reproduce when in good physical condition, prenatal and instantaneous growth rates can always be maximized. However, a minimum body condition per se might not be a sufficient condition to trigger reproduction. Body condition of females did not differ between the last month of the reproductive season (May) and the 1st month of the following one (July–August) in 1999, but the proportion of breeding females differed greatly. If foraging requires much time, females might not be sufficiently able to increase food intake and therefore refrain from reproduction. Alternatively, a decline in an otherwise good body condition over the austral winter months might also inhibit reproduction. The role of small differences and changes in body condition in determining whether or not a female reproduces can only be clarified with experiments.

Single females reproduced successfully in the wild even during midwinter, and the proportion of females reproducing during winter varied between years. Most females reproduced successfully 3 times per year. Assuming an average litter size of 1.7, fecundity in our population was approximately 5.1 young per year. In the laboratory, female wild cavies produce a maximum of 5 litters per year (F. Trillmich, in litt.), yielding a potential annual fecundity of 8.5 offspring. Thus, the difference between realized and potential annual fecundity was small (approximately 60% of the potential fecundity realized in the field), compared to an altricial small mammal (*Peromyscus nudipes*: 30%—Heidemann and Bronson 1993). Given the lack of comparative data, we can only speculate that precocial small mammals might show a higher ratio of realized to potential reproductive rate than do altricial ones. Based on the fecundity allometry equation for rodents given in Allainé et al. (1987), *C. magna* should produce 6.7 young per year, which compares favorably with our estimated annual fecundity of 5.1.

Growing up—to mature or not to mature?—Female *C. magna* have the potential to mature and conceive successfully at approximately 1 month of age, a time when they have reached only about 50% of their final adult mass. Based on the allometric relationship between body mass and age at 1st reproduction (given by Charnov [2001]), the expected age at 1st reproduction for an animal the size of *C. magna* would be 7.5 months or, conversely, they should weigh only about 80 g if 1st reproduction is possible at 1 month after birth. The minimum age at conception of 19 days was similar to that of much smaller microtine

rodents. For instance, the earliest age of reproduction in the 60-g Townsend's vole (*Microtus townsendii*) was 17 days (Lambin and Yoccoz 2001). Precocious reproduction, that is, reproduction before final adult mass is reached, is quite common in small mammals, such as microtines (e.g., Lambin and Yoccoz 2001; Prévot-Julliard et al. 1999; Tkadlec and Zejda 1995), caviomorphs (e.g., Rood 1972), and lagomorphs (e.g., Swihart 1984). A strong positive relationship between adult mortality and age at 1st reproduction exists among mammals, suggesting that the high levels of extrinsic mortality (e.g., through predation) ultimately selected for the early onset of reproduction (e.g., Harvey and Zammuto 1985; Sutherland et al. 1986).

However, not all young female *C. magna* in our study population reproduced precociously. Most of them delayed breeding until the onset of the reproductive season after their birth. Only females born early in the reproductive season matured early. The phenomenon of a cohort-dependent maturation probability has been frequently documented for small mammals (cavies—Rood 1972; microtines—e.g., Negus and Berger 1988). The conditions experienced during early development can have profound long-term fitness effects (Lindström 1999). Animals of later birth cohorts suffered several disadvantages. They grew more slowly, matured later, and their survivorship to independence was low compared to that of spring-born young (Kraus et al. 2005). If growth rates are necessarily reduced, and juvenile survival decreases concurrently, females should delay maturity. This might increase offspring survival by balancing an increase in extrinsic mortality with a decrease in intrinsic mortality (Stearns and Koella 1986). Late-born animals seem to be making the best of a bad situation.

Young *C. magna* of a given cohort grew faster in the breeding seasons of 1998–1999 and 2000–2001 than in 1999–2000. Thus, the proportion of early-maturing females might vary among years, as in other small mammals (Ergon et al. 2001; Lima et al. 2001; Norrdahl and Korpimäki 2002). Circumstantial evidence suggests that young of the year from later births were among the females breeding in May 1999. As in the case of winter breeding, seasonal and interannual variations in food quantity or quality might be responsible for this pattern. Nutrition affects growth as well as maturity (Andreassen and Ims 1990), and the availability of specific plant compounds (Negus and Berger 1988) or dietary protein (McAdam and Millar 1999) have been shown to limit maturation ability in several small mammal species.

Synthesis.—*Cavia magna* shares several reproductive characteristics with "typical" small mammals. Females have the potential to mature very early, in fact, relative to their body size, much faster than microtine rodents. They produce more than 1 litter per year and show high phenotypic plasticity for these reproductive traits. On the other hand, newborn *C. magna* belong to the most precocial among small mammalian offspring, and females invest much time in litters of few young. Which factors might have selected for this unusual reproductive strategy? High levels of adult mortality favor an early onset of reproduction (e.g., Schaffer 1974), and cavies are indeed a popular prey of many predators (Jaksíc 1986; Kraus and Rödel 2004; Kraus et al. 2005; Rood 1972). In addition to seasonal variability, environ-

mental conditions fluctuate randomly. Because of their small size, this might yield unpredictable variation in the demographic environment as well. This variability of the environment may select for phenotypic plasticity (e.g., de Jong 1995). Thus, the typical rodent traits of cavies are in accordance with theoretical predictions. An early start of reproduction and breeding opportunistically whenever conditions are favorable compensate at least partially for the low reproductive rate.

More difficult to explain are the factors that could have selected for precociality in cavies. All caviomorph rodents produce precocial young; thus, phylogenetic inertia is likely to constrain a shift to altriciality. However, there is still large variation in the degree of precociality within this suborder, for example, regarding relative neonatal mass, developmental state at birth (fur, eye opening, early locomotion, and start of solid food consumption—Case 1978b; Derrickson 1992). Case (1978b) was the 1st to comment on the convergence of some caviomorph rodents toward ungulates and pointed to their similar ecological habits. He suggested grass feeding and rearing their young on open ground in the face of high predation risk as causally related to precociality. Indeed, cavy species that protect their young through the use of burrows (*Galea* and *Microcavia*) have larger litters of smaller young than do species of *Cavia* (Rood 1972).

Neal (1986) hypothesized that precocial species are adapted to constant and predictable food resources of poor quality. We speculate that, on the contrary, nonconstant and unpredictable food availability might have selected for the extreme precociality of *Cavia*. Several reports of localized migration of *C. aperea* exist, for example, after an overexploitation of their crop-field habitats (Bilenca et al. 1995; Galante and Cassini 1994; Rood 1972). This high level of mobility would be impossible with altricial young. In other words, grass becomes a more constant and predictable food resource as a result of high mobility of adult and young *Cavia*. In the present study, a large influx of *C. magna* arrived at the study site after a severe storm that flooded parts of the area (Kraus et al. 2003). The semiaquatic *C. magna* has to face the additional unpredictable hazard of periodical and sudden inundations. Ximénez (1980) observed them to cross waters more than 250 m wide. Precocial but small young that are left hidden in dense vegetation by the mother would have low chances of survival under such circumstances because of risks including drowning, hypothermia, and getting lost. This could explain why the young of *C. magna* are even more precocial than those of *C. aperea*. Opportunistic breeding and high juvenile survival (Kraus et al. 2005) resulting from the advanced developmental state of the young might be the cavies' answer to the high reproductive rate of altricial rodents.

RESUMEN

En general los pequeños mamíferos tienen camadas numerosas de juveniles altriciales, resultando así altas tasas reproductivas. Contrariamente, los cávidos paren pocos juveniles precoces luego de un largo período de gestación. El costo de esta estrategia reproductiva es una baja tasa de crecimiento poblacional. En el presente trabajo se investiga si los patrones reproductivos en una población silvestre de *Cavia magna* son consistentes con la hipótesis de que cávidos pueden incrementar su resultado reproductivo multiplicándose estacionalmente, alcanzando la madurez sexual muy tempranamente. Los datos de reproducción y crecimiento de la población estudiada fueron colectados mediante el método de captura–recaptura durante un estudio de campo de 26 meses en un ambiente de bañado en Uruguay, trabajando además comparativamente con una población de laboratorio creada con individuos de la misma región. *C. magna* parece ser uno de los ejemplos extremos de reproducción precoz en los Caviinae, ya que individuos neonatos pesan promedialmente el 18% de la masa corporal de su madre. En el área de estudio la reproducción observada fue estacional, comenzando la época principal de nacimientos a fines de setiembre (primavera austral), extendiéndose respectivamente hasta fines de mayo en 1999 y hasta febrero de 2000. Sin embargo, algunas hembras se reprodujeron en el área durante el primer invierno de nuestro estudio, pero no durante el segundo. Individualmente, se observaron hembras que tuvieron 3 camadas por año (máximo observado 4). Algunas hembras nacidas en la primavera temprana fueron fecundadas exitosamente entre los 30 y 45 días de edad, al igual que las hembras de laboratorio (media: 33 días, mínimo: 19 días). El resto de la cohorte de la primera primavera y las hembras de las cohortes subsiguientes demoraron su reproducción hasta la siguiente época reproductiva. La condición física y la tasa de crecimiento fueron máximas en la primavera, declinando a lo largo del año y variando dentro de los dos años del estudio. Estos factores pueden ser determinantes del momento en que una hembra adulta o juvenil intente reproducirse. Es probable que la variación estacional e interanual de los recursos alimentarios sea responsable del patrón reproductivo observado. En conclusión, una reproducción oportunista, cuando las condiciones son favorables podría compensar parcialmente la baja tasa reproductiva de los cávidos.

ACKNOWLEDGMENTS

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