REPRODUCTIVE CHARACTERISTICS OF RODENT ASSEMBLAGES IN CULTIVATED REGIONS OF CENTRAL ARGENTINA

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Small mammals were trapped for 2 years at 16 localities on the central-Argentine pampa. Six species (*Akodon azarae, Calomys musculinus, C. laucha, Bolomys obscurus, Oligoryzomys flavescens* and *Mus musculus*) accounted for >95% of captures. The major breeding season, as assessed by pregnancies, was September or October through April or May. Mild weather in late autumn and winter of the second season resulted in a relatively longer breeding season during the 2nd year of the study. Females of all six species comprised significantly <50% of captures throughout the non-breeding season, but >50% of captures during the height of the breeding season. For most species, there was a negative correlation between embryo size and embryos per pregnancy; females with large embryos were poorly represented. *C. musculinus* had the longest breeding season; *C. musculinus* and *Mus* had the highest number of embryos per pregnancy; the two species of *Calomys* and *Oligoryzomys* had the highest percentages of pregnant females during the breeding season. The predominance of animals of smaller mass classes during the winter is thought to represent seasonal weight loss rather than juvenile recruitment.

Key words: Rodentia, reproduction, Argentina

The intensively cultivated areas of the pampa of central Argentina support an assemblage containing six species of rodents that comprise up to 95% of total small-mammal captures (Mills et al., 1991). Five of these are cricetids, *Calomys musculinus, C. laucha, Akodon azarae, Bolomys obscurus,* and *Oligoryzomys flavescens,* and the sixth is the murid, *Mus musculus.* The involvement of rodents as reservoirs for Junin virus, etiologic agent of Argentine hemorrhagic fever, has stimulated much research on the biology and ecology of pampa rodent communities (Mills et al., 1991).

Removal and mark-release trapping studies for these six species have documented two patterns in abundance and habitat use (de Villafañe et al., 1977; Kravetz, 1977; Mills et al., 1991). *Bolomys, Akodon,* and *Oligoryzomys* are captured predominantly in linear or border habitats such as fence-lines, roadsides, and railroad rights-of-way. Their populations peak in late autumn and winter, and a relatively stable population size is maintained throughout the year. *Calomys* and *Mus* make extensive use of cultivated fields, and their populations are subject to extreme annual cycling, peaking in late summer or early autumn with low numbers in winter when crop fields are barren (Mills et al., 1991). These distinct patterns have been explained by different life-history strategies. *Bolomys, Akodon,* and *Oligoryzomys* appear to be behaviorally dominant

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species that prefer stable habitats and are characterized as relatively K-selected species (de Villafañe et al., 1977; Kravetz, 1977). *Calomys* and *Mus* rapidly take advantage of unstable, temporarily suitable, crop habitat available throughout their reproductive period, and are depicted as relatively r-selected (de Villafañe et al., 1977; Kravetz, 1977). Their populations, however, are nearly eliminated each year when the habitat is destroyed by harvest (de Villafañe et al., 1977; Mills et al., 1991).

Reproductive correlates of these fluctuations in rodent numbers have been examined in only a few field studies. Laboratory and limited field research have been conducted on the reproductive biology of *C. musculinus* (Castro-Vazquez et al., 1987; Crespo et al., 1970; de Villafañe, 1981*a*; Hodara et al., 1984; Kravetz, 1978; Polop et al., 1982), *C. laucha* (Barlow, 1969; de Villafañe et al., 1988; Hodara et al., 1989; Kravetz, 1978; Kravetz et al., 1981), *A. azarae* (Crespo, 1966; de Villafañe, 1981*b*; de Villafañe et al., 1977; Pearson, 1967; Zuleta, 1989; Zuleta et al., 1988), and *O. flavescens* (M. J. Piantanida, in litt.) in Argentina. We know of no laboratory or field data for *B. obscurus*. *Mus musculus* has been studied extensively in various parts of the world (e.g., Berry and Jacobson, 1971; Breakey, 1963), but no information on this species in Argentina has been published.

Our purpose is to describe the reproductive characteristics of these six species of pampa rodents. Specifically, we characterize seasonal patterns in reproductive activity, providing average embryo counts, estimates of prenatal or perinatal mortality, patterns of juvenile recruitment, mass-based population structure, and fecundity patterns among different habitats.

MATERIALS AND METHODS

Trapping was conducted 3–4 nights/week during a 24-month period (1 November 1987–31 October 1989) at 22 farm sites in 16 communities in northern Buenos Aires and southern Santa Fe provinces, Argentina (ca. 32°35′–33°55′S, and 60°35′–61°44′W). The maximum north-south distance between sites was ca. 140 km and the maximum east-west distance was ca. 100 km. Sherman live traps (8 by 9 by 23 cm) and Tomahawk live traps (14 by 14 by 40 cm) were baited with rolled oats or bird seed coated with peanut butter. Traplines of 10–20 traps at 5-m intervals were established in fields of crops (primarily corn, wheat, and soybeans) and along fencelines, roadsides, and railroads. Traps were collected the following morning and rodents transported to a field laboratory for processing. Rodents were anesthetized with ketamine hydrochloride or methoxyfluorane, killed by exsanguination, and necropsied. We recorded mass to the nearest 0.1 g, standard external measurements (length of body, tail, right ear, and right hind foot), external reproductive condition (testes abdominal or scrotal, vaginal orifice perforate or not perforate, and nipples dry or lactating), and internal reproductive condition (number of embryos in left and right uterine horns, crown–rump length of embryos, number of resorptions, and length and width of testes). A more complete description of the study area, trap placement, and rodent processing is provided elsewhere (Mills et al., 1991).

Individuals of the six rodent species were categorized into two classes (subadult and adult) based on total body mass. These mass classes were chosen to correspond, when possible, to maturational stages described for each species. For example, because laboratory-reared *C. musculinus* became sexually mature at ca. 14 g (de Villafañe, 1981*a*), we categorized those ≤14.4 g as subadult, and those ≥14.5 g as adult. Hodara et al. (1989) reported development of *C. laucha* to be similar to that of its congener. Therefore, we assumed the same age-specific maturational pattern and set the division between subadult and adult at 12.0 g (Hodara et al., 1989). Mass classes for *A. azarae* were based on laboratory studies by de Villafañe (1981*b*): adults were those animals ≥14.5 g. As no laboratory data were available for *B. obscurus* and *O. flavescens*, mass classes were assigned according to criteria used for *C. musculinus* and *A. azarae*, and may not be indicative of underlying mass- or age-specific maturational stages. Previous studies of wild populations of *M. musculus* have recognized subadults as those <11 (King, 1950) or <13 g (Brown, 1953). We set the division between subadult and adult for *Mus* at 13.0 g (Brown, 1953).

Three embryo-size classes for *C. musculinus*, *C. laucha*, and *A. azarae* were defined by dividing the total range of crown–rump lengths of embryos at the 33rd and 67th percentiles. Because samples for *M. musculus*, *B. obscurus*, and *O. flavescens* were small, the total range of embryo sizes was not represented. Therefore, based on similar adult body masses, we assumed the true range of embryo sizes for *M. musculus* to equal that of *C. laucha* (≤8 mm, 9–16 mm, ≥17 mm) and that for *B. obscurus* and *O. flavescens* to equal that of *C. musculinus* and *A. azarae* (≤10 mm, 11–20 mm, ≥21 mm). Resorbing embryos were recognized by their darker color, usually smaller size, and abnormal shape (Loeb and Schwab, 1987). Correlations between numbers of resorbing embryos and total embryo counts and female size were tested for each species. For these analyses, pregnant females were divided into three body-length categories at the 33rd and 67th percentile.

Reproductive data were compared among five habitat types. These consisted of each of the primary crops (corn, wheat, and soybeans); the more stable linear borders (fencelines, roadsides, or railroad rights-of-way); and "other," which included the less common crops (e.g., sunflowers and lentils), streamside, and weedy areas around houses or farm buildings. The major habitats were physiognomically uniform at all study sites. We sampled all of the major habitat categories with approximately equal effort at each study site, and the same six common species of rodents were present at all sites. To test for differences among species, we combined data across the 16 study sites. Data were analyzed on an Apple-Macintosh microcomputer, using StatView II (Feldman et al., 1987).

RESULTS

The summer preceding the study (December 1986–February 1987) was hot and dry, with monthly mean maxima 1.5–2.0°C above normal and the absolute maximum for January 1987 (39.9°C) setting a 23-year record (Instituto Nacional de Tecnología Agropecuaria, Pergamino, Argentina). The 12 mm of rainfall in December 1986 contrasts with an 80-year mean of 103 mm, and rainfall for January 1987 was 14% below normal. Late autumn 1987 was unusually cold, with the mean minimum 3°C below normal and 8 days (compared with a 20-year mode of 0 days) of subfreezing temperatures. Rainfall during mid-winter (July) was 2.6 times normal.

Weather conditions were different between 1988 and 1989 (Fig. 1). Mean temperatures, mean minima, and absolute minima for the winter months of May through September 1988 were ≥2°C below the 23-year means. The absolute minimum (−6.9°C) for July was the coldest on record (23 years, Instituto Nacional de Tecnología Agropecuaria, Pergamino, Argentina). The following summer was unusually hot and dry. Mean and mean-maximum temperatures were 1–4°C above the 23-year means during November–February, and rainfall was >35% below normal during November and February. The winter of 1989 was generally warm and there were no subfreezing temperatures in June or August. Temperature patterns during July were normal, but rainfall was 32% below normal. Temperatures in the early spring (September and October) were normal although rainfall in September was 74% below normal.

From 1 November 1987 through 31 October 1989, 3,235 mammals were trapped during 57,048 trap-nights (5.7% trap success). Fifteen species of small mammals were captured including 11 rodents, 3 marsupials and 1 carnivore. The six species of rodents discussed here accounted for 96.3% of all captures and included *C. laucha* (25.6% of total captures), *A. azarae* (24.9%), *C. musculinus* (17.8%), *B. obscurus* (11.0%), *O. flavescens* (9.1%), and *M. musculus* (7.9%). Descriptions of the other species trapped and trap-success rates in each habitat and with different types of traps are reported by Mills et al. (1991).

Although the duration of the major reproductive season, as measured by occurrence of pregnancies, varied from 1988 to 1989, it was typically September or October through May or June for all species (Fig. 2). When data were pooled between years, individuals of *C. laucha* were found pregnant

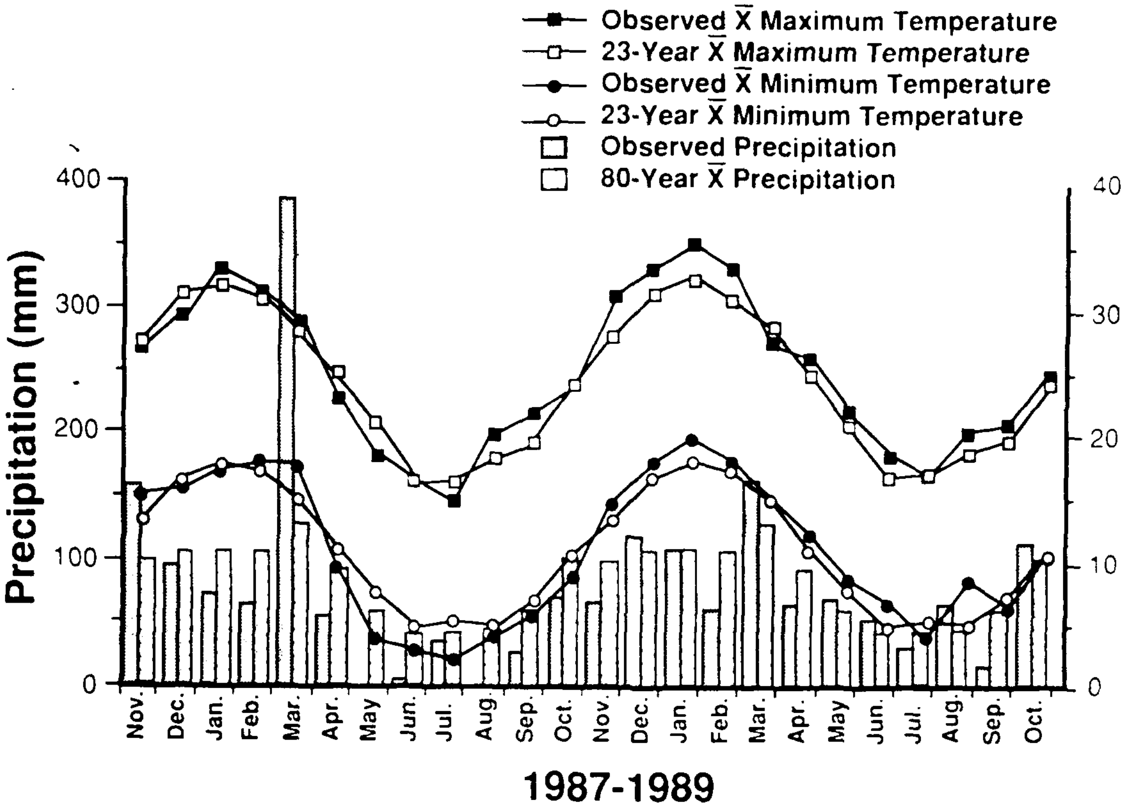

FIG. 1.—Monthly mean minimum and maximum temperatures, and monthly rainfall for Pergamino, Buenos Aires Province, Argentina, 1 November 1987–31 October 1989. Normal values are based on 23-year (for temperatures) and 80-year (for rainfall) means (Instituto Nacional de Tecnologia Agropecuaria, Pergamino, Argentina).

each month. Similarly, *C. musculinus* and *A. azarae* were found pregnant in every month except August, and pregnant *Bolomys* were found in every month except March and September when samples were 0 and 1, respectively. Pregnant *Oligoryzomys* were found in all but the three winter months, and *Mus* were pregnant in every month except June, July, and September (no *Mus* were captured in June or September). Using a criterion of ≥40% of adult females pregnant as an indication of the major breeding period, the season was longest for *C. musculinus* (September through June), intermediate for *A. azarae* and *O. flavescens* (September through May), shorter for *C. laucha* and *M. musculus* (October through May), and shortest for *B. obscurus* (October through February). The seasonal patterns for *Mus*, *Oligoryzomys*, and *Bolomys* were less well defined because of small samples during several months.

Data on testes position in males and presence of perforate vaginal orifices in females closely mirrored pregnancy data for all species (except where samples were small). Percent scrotal and perforate reached 100% by the end of the breeding season and declined dramatically with the onset of winter (Fig. 2).

Calomys musculinus had the highest embryo count (7.5 ± 0.2 *SE*, *n* = 114) combined with the longest breeding season (10 months; ≥40% of females pregnant) and a high percentage of adult females pregnant during the breeding season (65%). At the other extreme, *B. obscurus* had the lowest percentage of adult females pregnant (48%) and the shortest breeding season (6 months), but an intermediate embryo count (6.2 ±

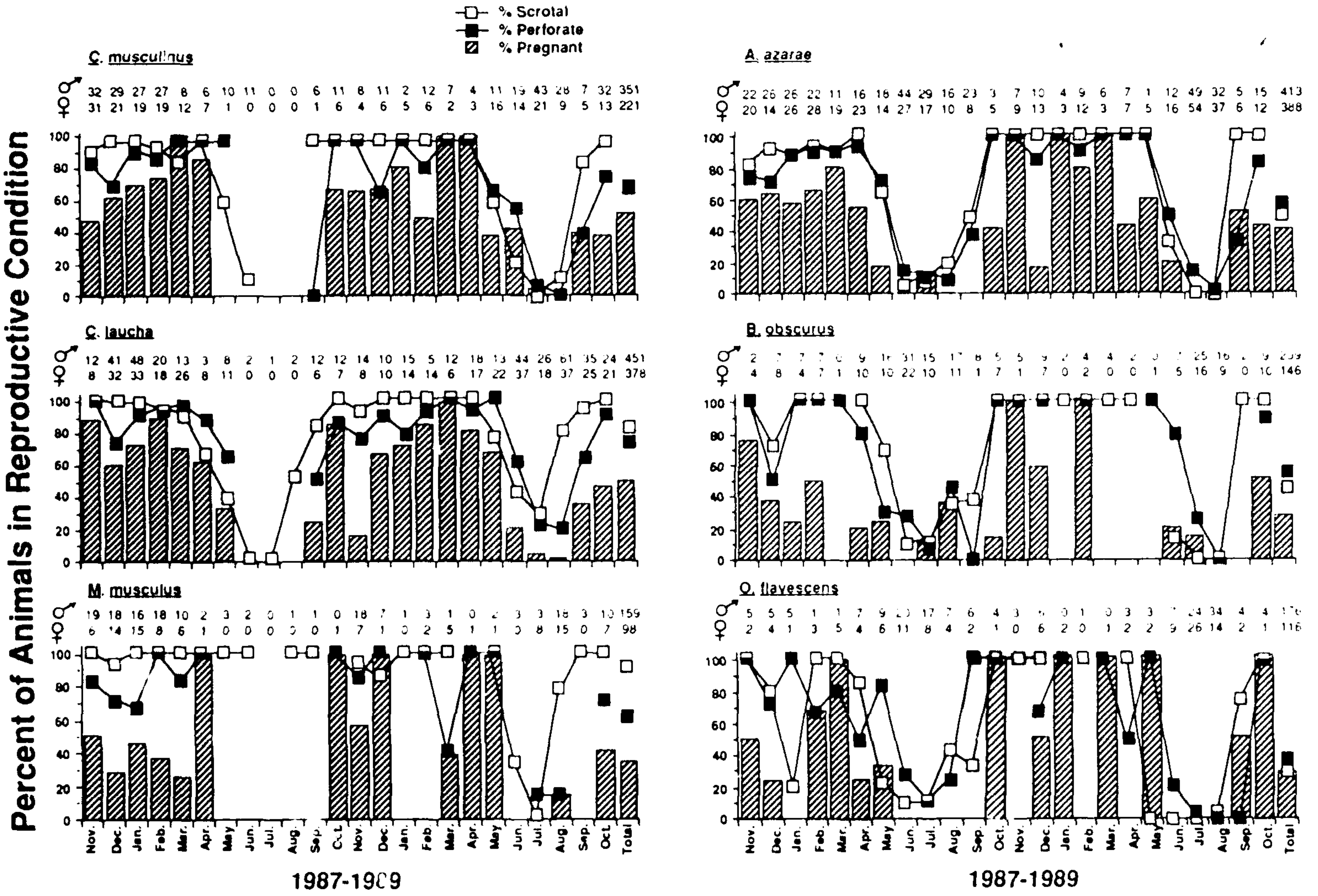

FIG. 2.—Percentage of female rodents pregnant and with perforate vaginal orifice and males with scrotal testes by month, 1 November 1987–31 October 1989. Sample sizes for perforate females and scrotal males are shown above columns. In all cases, sample size for females is greater than that for pregnancy histograms. All age classes of rodents are included, as exclusion of juveniles and young adults did not alter findings.

0.3, $n = 32$). All other species had intermediate patterns of embryo counts, duration of breeding season, and percentage of adult females pregnant: *C. laucha* had 6.2 ± 0.4 embryos ($n = 179$), and 71% of females were pregnant during the 8-month breeding season; *M. musculus* had 6.2 ± 0.3 embryos ($n = 34$), and 44% of females were pregnant during an 8-month season; *A. azarae* had 6.2 ± 0.2 embryos ($n = 119$), and 59% of females were pregnant during a 9-month season; and *O. flavescens* had 5.2 ± 0.3 ($n = 22$) embryos, and 63% of females were pregnant during its 9-month season.

Simple-linear regressions of embryo count (Y) on female length of body (X) showed positive slopes for all six species and were significant for *C. musculinus* ($Y = 0.091X - 0.937$, $r^2 = 10.5\%$, $P = 0.0004$, *d.f.* = 1, 113) and *C. laucha* ($Y = 0.052X + 1.701$, $r^2 = 9.9\%$, $P = 0.0001$, *d.f.* = 1, 178), and marginally significant for *Akodon* ($Y = 0.059X + 0.371$, $r^2 = 2.8\%$, $P = 0.07$, *d.f.* = 1, 118) and *Bolomys* ($Y = 0.059X - 0.428$, $r^2 = 9.5\%$, $P = 0.08$, *d.f.* = 1, 31). Lack of significance of these regressions for *Oligoryzomys* ($P = 0.78$, *d.f.* = 1, 21) and *Mus* ($P = 0.24$, *d.f.* = 1, 33) may be due to small samples.

Regressions of embryo count (Y) on embryo size (X) showed negative slopes for all six species and were significant for *C. musculinus* ($Y = -0.150X + 8.437$, $r^2 = 8.2\%$, $P = 0.002$, *d.f.* = 1, 112), and *A. azarae* ($Y = -0.125X + 7.222$, $r^2 = 9.9\%$, $P = 0.0005$, *d.f.* = 1, 117), and marginally significant for *O. flavescens* ($Y = -0.097X + 6.185$, $r^2 = 17.2\%$, $P = 0.06$, *d.f.* = 1, 20) and *C. laucha* ($Y = -0.043X + 6.541$, $r^2 = 1.9\%$, $P = 0.07$, *d.f.* = 1, 175). These regressions were not significant for *Bolomys* ($P = 0.65$, *d.f.* = 1, 31) or *Mus* ($P = 0.15$, *d.f.* = 1, 32), both of which had small samples.

Larger embryos were poorly represented for all species. The distribution of pregnancies among the three embryo-size classes were: 99 small, 12 medium, and 2 large for *C. musculinus*; 122, 45, and 9 for *C. laucha*; 24, 8, and 1 for *M. musculus*; 84, 30, and 5 for *A. azarae*; 20, 7, and 5 for *B. obscurus*; and 10, 11, and 0 for *O. flavescens*.

Resorbing embryos were rarely observed in *C. musculinus* (four of 113 pregnancies, 3.5%), *C. laucha* (four of 176, 2.3%), and *A. azarae* (four of 119, 3.4%). In contrast, three of 32 (9.4%) pregnant *Bolomys* had evidence of resorptions. None of the 33 *Mus* or 21 *Oligoryzomys* had resorptions. Of the 15 females with resorptions, 2 had one resorbing embryo, 12 had two each, and 1 had five.

All but one of the 15 resorptions were observed in small and medium embryo-size classes (but the largest size class accounted for only 22 (4.5%) of total pregnancies). Resorptions were approximately evenly distributed among female body-length classes (four in small females, five in medium, six in large), and did not suggest a pattern associated with age or size of the animals.

There was a significant variation in embryo counts during the breeding season for *C. musculinus*, *C. laucha*, and *A. azarae* ($P < 0.05$, one-way analysis of variance). These three species showed relatively low embryo counts at the beginning and end of the breeding season with higher numbers of embryos during the summer months (January–March; Fig. 3).

The proportion of females captured over the 2-year period was significantly lower than the expected 0.5 for all species except *Akodon* (Table 1). The proportion of female *Akodon* was significantly lower than 0.5 only during the first season (November 1987–October 1988). Most species showed an undercapture of females throughout the nonbreeding season and into the early breeding season (June–December). There was a contrasting trend toward overcapture of females during the height of the breeding season (March–April). This pattern held except for *Bolomys*, which showed an overcapture of females in September and October (Table 1).

There were no differences in mean embryo counts among the five habitat categories (soybeans, wheat, corn, linear, other)

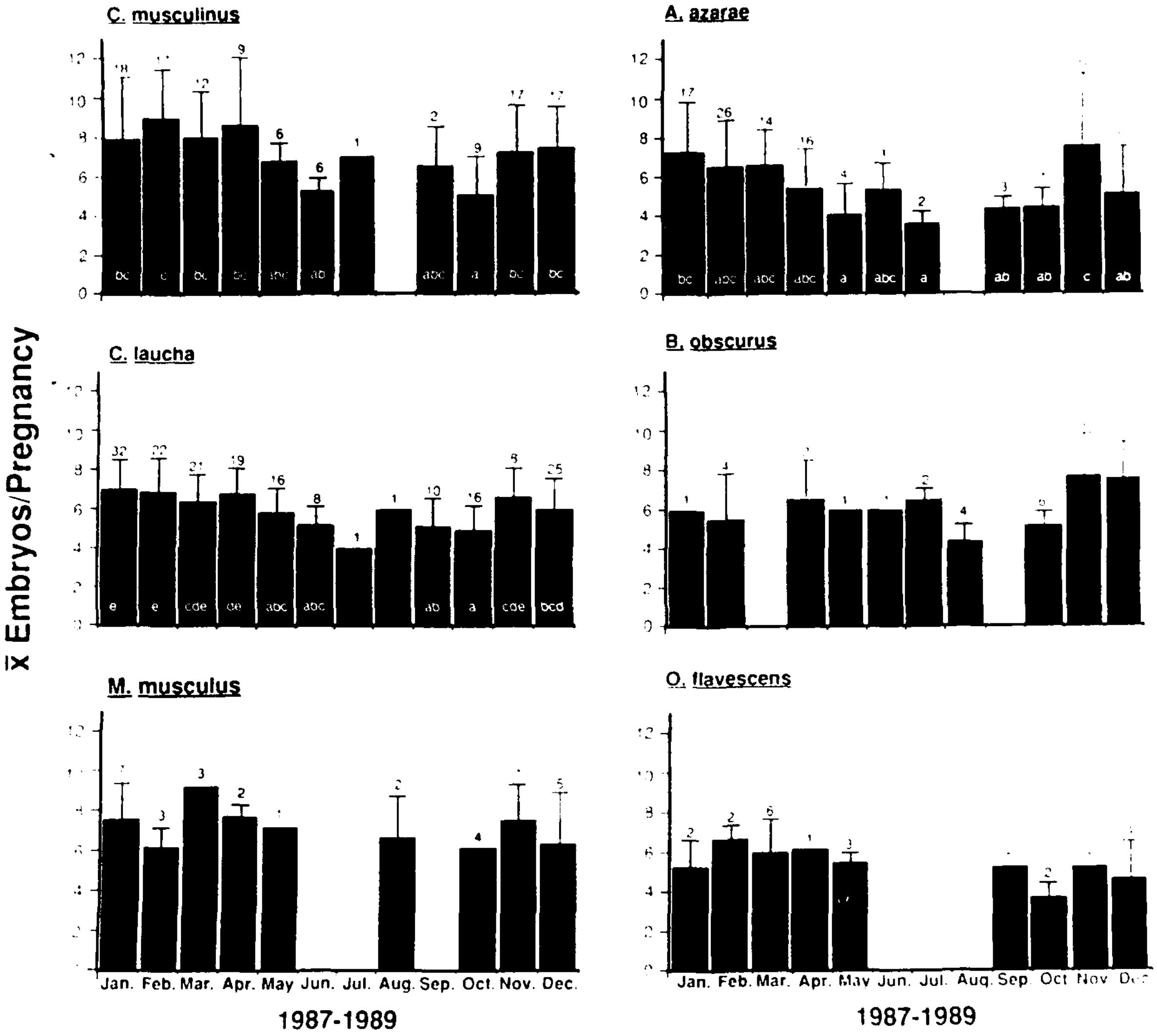

FIG. 3.—Mean embryos per pregnancy (±*SD*) pooled by month over 2 years for six species of rodents captured in central Argentina, 1 November 1987–31 October 1989. Sample sizes are indicated above *SD* bars; different letters within histograms indicate statistically significant differences (one-way analysis of variance, $P < 0.05$; followed by Fisher's least-significant-difference multiple-range test).

for any of the six species ($P > 0.10$, one-way analysis of variance). However, length of the reproductive season varied with habitat. Reproduction in cultivated habitats ended in May with harvest and plowing of fields, while in linear habitats, pregnancies extended into July for *Calomys*, *Akodon*, and *Bolomys*, and into August for *Mus*. A significantly higher proportion of female *Akodon* were pregnant in cultivated habitats (75.6%) than in linear habitats (51.7%, $\chi^2 = 6.63$, $P = 0.01$). There were no differences among habitats for the other species.

The proportion of small animals (subadults) in the population was highest during the winter (June–August) for all species. The percentages of winter captures that were subadults for each species were: *C. musculinus*, 77.2% ($n = 145$); *C. laucha*, 50.4% ($n = 228$); *M. musculus*, 58.4% ($n = 4$); *A. azarae*, 31.3% ($n = 314$); *B. obscurus*, 53.9% ($n = 165$); *O. flavescens*, 44.1% ($n = 143$). Based on comparisons with reproductive data (Fig. 2), these findings probably reflect loss of mass in many adult individuals, rather than a period of maximum-juvenile re-

TABLE 1.—*Proportion of female to total captures and total sample size by month, for six rodent species captured in northern Buenos Aires and southern Santa Fe provinces, Argentina, from 1 November 1987 through 31 October 1989. Values ≥0.5 are underlined. Significance of Chi-square with Yates' correction as given.*

Month	*C. musculinus*		*C. laucha*		*M. musculus*		*A. azarae*		*B. obscurus*		*O. flavescens*	
	Proportion	*n*	Proportion	*n*	Proportion	*n*	Proportion	*n*	Proportion	*n*	Proportion	*n*
September	0.316	19	0.397	78	0.000	4	0.333*	42	0.909*	11	0.286	14
October	0.306**	62	0.438	64	0.444	18	0.486	35	0.548	31	0.200	10
November	0.456	79	0.381	42	0.260**	56	0.500	58	0.417	12	0.200	10
December	0.406	67	0.452	93	0.375	40	0.422	64	0.484	31	0.476	21
January	0.463	54	0.427	110	0.469	32	0.492	59	0.308	13	0.375	8
February	0.391*	64	0.561	57	0.323	31	0.563	71	0.450	20	0.600	5
March	0.483	29	0.561	57	0.500	22	0.564	39	0.200	5	0.857	7
April	0.500	20	0.544	46	0.500	4	0.566	53	0.476	21	0.375	16
May	0.447	38	0.611	54	0.167	6	0.500	38	0.407	27	0.400	20
June	0.318*	44	0.446	83	0.000	5	0.434	99	0.415	65	0.426	47
July	0.328**	64	0.400	45	0.727	11	0.476	149	0.394	66	0.453	75
August	0.243**	37	0.370*	100	0.441	34	0.495	97	0.377	53	0.317*	60
Total	0.386***	577	0.456*	829	0.381***	257	0.484	804	0.411***	355	0.399***	293

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

cruitment. The proportion of large animals (adults) in the population was greatest during the summer (December–February) for *C. musculinus* (76.7%, $n = 184$) and *C. laucha* (81.5%, $n = 254$); and in the spring (September–November) for *M. musculus* (66.7%, $n = 72$), *A. azarae* (88.2%, $n = 135$), *B. obscurus* (77.8%, $n = 54$) and *O. flavescens* (79.4%, $n = 34$).

Discussion

All six species of pampa rodents showed strong evidence of seasonal breeding. These patterns of major unimodal breeding periods, with some low level of reproduction in all months, are similar to North American temperate rodents of this latitude (Bronson, 1989). The annual variation in the duration of breeding activity (Fig. 2) can partly be explained by differences in weather patterns between years. Hot, dry summers and cold, wet winters have been described as the conditions most unfavorable for populations of pampa rodents (Crespo, 1944, 1966; de Villafañe and Bonaventura, 1987; Mills et al., 1991). Hot, dry summers could decrease reproductive effort by diminishing food supply and habitat quality. Cold, wet winters, which increase mortality of small mammals due to exposure, would leave a smaller and possibly weakened population base to begin reproduction the following spring. The year preceding our study had both an unusually hot and dry summer and an early, cold winter, which may have severely curtailed reproductive efforts in the 1987–1988 season. Later, the early, cold winter and continued, unusually cold spring of 1988 may have resulted in an early termination of the breeding season, poor survival through the winter, and a delayed 1988–1989 reproductive season. In contrast, the longer breeding season observed for *Calomys* and *Akodon* in 1989, and early breeding the following spring, may reflect the relatively mild weather patterns in late autumn, winter, and spring during that year (Fig. 1). Similar results have been obtained for small mammals occupying mid-temperate latitudinal zones of the United States. For example, prairie voles (*Microtus ochrogaster*) and white-footed mice (*Peromyscus leucopus*) show distinct periods of breeding activity in Kansas (Rose and Gaines, 1978; Svendsen, 1964), but also will breed through the winter when temperatures and food availability permit.

Observed average embryo counts for five of the six species agree closely with those from other field studies (Barlow, 1969; Berry and Jacobson, 1971; Crespo, 1966; Crespo et al., 1970; de Villafañe et al., 1977; Kravetz et al., 1981). However, our value of 6.2 embryos per pregnancy for *Bolomys* is appreciably higher than the only other published study for that species ($\bar{X} = 4$, $n = 3$—Barlow, 1969). Our value of 5.2 embryos per pregnancy for *Oligoryzomys* closely agrees with the average of 5.1 of Barlow (1969) rather than with the average embryo count of 3.6 reported by Dalby (1975).

Underrepresentation of embryos in large size classes may be a general phenomenon when sampling rodents with short gestation periods. This has been noted for *Peromyscus maniculatus*, *Thomomys bottae* (Loeb and Schwab, 1987), and *Microtus pennsylvanicus* (Beer et al., 1957). This phenomenon may reflect a sampling bias due to the increased growth rate of embryos at the end of gestation, resulting in a shorter period of time, and correspondingly less chance of being captured, in the large size class, or decreased feeding and movement of females shortly before parturition. Regardless of its cause, this undercapture of females with large embryos, combined with the negative correlation between embryo size and embryo count, would result in the overestimation of litter sizes when average embryo counts are used as a predictor (Loeb and Schwab, 1987). In fact, average embryo counts from our study were much higher than average litter sizes from laboratory studies for the same species: *C. musculinus* had 5.4 young per litter (de Villafañe, 1981*a*); *C. laucha* had 5.3 (Hodara et al., 1989); *M. musculus* had 6.0 (Brown, 1953);

A. azarae had 3.5 (de Villafañe, 1981*b*) and 4.6 (Dalby, 1975); *O. flavescens* had 3.4 (M. J. Piantanida, in litt.); no data are available for *B. obscurus*. This suggests a high rate of intrauterine or perinatal mortality that is not accounted for by observation of resorptions. Averaging embryo counts from the two larger embryo-size classes should more accurately predict the average litter size at birth. For *C. musculinus* and *A. azarae*, these averages (5.6 and 4.9, respectively) are close to average litter sizes from laboratory studies (de Villafañe, 1981*a*; Dalby, 1975). For *C. laucha, M. musculus*, and *O. flavescens*, these averages (5.8, 6.6, and 4.6, respectively) are still higher than observed average litter sizes for laboratory studies (Brown, 1953; Hodara et al., 1989; M. J. Piantanida, in litt.).

Our observations of higher embryo counts for larger *Calomys* and *Akodon* are only partly supported by data from laboratory colonies. A strong correlation between litter size and age was seen for *A. azarae* (de Villafañe, 1981*b*), but similar studies showed no relationship between litter size and age or mass of the mother for *C. musculinus* (de Villafañe, 1981*a*).

Females of all six species of pampa rodents represented <50% of captures, except during the breeding season. Increased trappability of female rodents during the breeding season may be a consequence of greatly increased energy requirements during pregnancy or lactation (Millar, 1989), which places females at increased risk (Dalby, 1975).

Specifically, our findings of a general undercapture of females of *A. azarae* during the non-breeding season and overcapture during the height of the breeding season corroborate findings by Dalby (1975). They contrast sharply, however, with those of Crespo (1966) who found the undercapture of female *A. azarae* most pronounced during the breeding season (28.5% females in January). Dalby (1975) hypothesized that the results of Crespo (1966) may be due to the use of snap traps instead of live traps. Our study contrasts with that of Dalby (1975) in that we found a trend toward overcapture of females of *O. flavescens* during the height of the breeding season, while Dalby found an undercapture of female *O. flavescens* throughout the year. No published data exist for the other species examined in this study, which all exhibited patterns similar to *Akodon*.

Any analysis of the age structure of a population based solely on body mass is necessarily confounded by interactions with climate and resource availability. Our data indicated the highest proportion of individuals of lower mass for all species during the winter, after most reproduction has ceased. It is likely that these data actually reflect loss of body mass due to seasonal effects, rather than peak juvenile recruitment. The finding of maximum numbers of animals of higher mass in the spring or summer is likely to be a more accurate reflection of the population structure based on corroborating evidence from the reproductive profiles of individuals and our previous studies of population fluctuations (Mills et al., 1991).

Environmental variability is a major factor in the evolution of life histories in mammals (Boyce, 1988). The seasonal environmental fluctuations that lead to population declines in *Calomys* and *Mus* (harvest and onset of cold weather) are predictable, occur after the breeding season, and primarily affect adult survivorship. Under these conditions, models of life-history strategies predict that relatively higher fecundity (many young and a larger reproductive effort) would distinguish the group inhabiting relatively unstable cultivated fields (Boyce, 1988; Stearns, 1976). Our data place *C. musculinus* at one extreme of the fecundity gradient, with the highest embryo counts, longest breeding season, and a high percentage of pregnant females. *Bolomys* was at the other extreme, with low values for most characteristics, but between these extremes was a gradient of values for the other four species (e.g., *Oligoryzomys* had a low average embryo count, but a long breeding season and intermediate percentage of females pregnant). Interspecific behavioral interactions, rather than purely physiological adaptations, may strongly influence the habitat associations that characterize this group of rodents (Kravetz, 1977), and must be considered in conjunction with reproductive profiles.

RESUMEN

Durante un período de 2 años se capturaron mamíferos pequeños a 16 localidades de la pampa Argentina. El 96.3% de las capturas incluyeron las siguientes seis especies de roedores: *Akodon azarae, Calomys musculinus, C. laucha, Bolomys obscurus, Oligoryzomys flavescens* y *Mus musculus.* La estación reproductiva generalmente incluyó el período comprendido entre septiembre u octubre hasta abril o mayo, pero el tiempo templado durante el otoño e invierno del segundo año ocasionó una prolongación del segundo período reproductivo. Las hembras constituyeron >50% de los animales capturados durante la estación reproductiva, mientras que durante la estación no reproductiva, su captura fue significativamente <50% para las seis especies. Se observó una correlación negativa entre la longitud de los embriones y el número de embriones por preñez. Hubo baja representación de hembras con embriones grandes en los muestreos. *C. musculinus* tuvo el período reproductivo más largo; *C. musculinus* y *Mus* tuvieron el mayor número de embriones por preñez. Las especies con los porcentajes más altos de hembras gestantes durante el período reproductivo fueron *Calomys* y *Oligoryzomys.* Aunque hubo un predominio de animales pequeños durante el invierno, es probable que este hallazgo no indique el reclutamiento de animales jóvenes durante este período, sino que refleje la pérdida de masa en animales adultos frente a una época desfavorable.

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LITERATURE CITED

Barlow, J. C. 1969. Observations on the biology of rodents in Uruguay. Life Sciences Contributions, Royal Ontario Museum, Toronto, 75:1–59.

Beer, J. R., C. F. MacLeod, and L. D. Frenzel. 1957. Prenatal survival and loss in some cricetid rodents. Journal of Mammalogy, 38:392–402.

Berry, R. J., and M. E. Jacobson. 1971. Life and death in an island population of the house mouse. Experimental Gerontology, 6:187–197.

Boyce, M. S. 1988. Evolution of life histories: theory and patterns from mammals. Pp. 3-30, *in* Evolution of life histories of mammals (M. S. Boyce, ed.). Yale University Press, New Haven, 373 pp.

Breakey, D. R. 1963. The breeding season and age structure of feral house mouse populations near San Francisco Bay, California. Journal of Mammalogy, 44:153–167.

Bronson, F. H. 1989. Mammalian reproductive biology. The University of Chicago Press, Chicago, 323 pp.

Brown, R. Z. 1953. Social behavior, reproduction, and population changes in the house mouse (*Mus musculus* L.). Ecological Monographs, 23:217–240.

Castro-Vasquez, A., N. B. Carreno, R. A. Cutrera, A. R. Martinez, and A. Konincky. 1987. The corn mouse (*Calomys musculinus*) as an experimental model for reproductive studies. Pp. 274–282, *in* Laboratory animals in the quest for health and knowledge (H. A. Rothschild, A. Rosenkranz, and A. Moura Duarte, eds.). International Council for Laboratory Animal Science, Sao Paulo, Brazil, 331 pp.

Crespo, J. A. 1944. Relaciones entre estados climáticos y la ecología de algunos roedores de campo (Cricetidae). Revista Argentina de Zoogeografía, 4: 137–144.

———. 1966. Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Provincia de Buenos Aires. Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Ecología (Buenos Aires), 1:79–144.

Crespo, J. A., M. S. Sabattini, M. J. Piantanida, and G. de Villafañe. 1970. Estudios ecológicos sobre roedores silvestres. Observaciones sobre densidad, reproducción y estructura de comunidades de roedores silvestres en el sur de la Provincia de Córdoba. Ministerio de Bienestar Social, Secretaria de Estado de Salud Pública, Buenos Aires, Argentina, 45 pp.

Dalby, P. L. 1975. Biology of pampa rodents (Balcarce area, Argentina). Publications of the Museum, Michigan State University, Biological Series, 5:149–272.

de Villafañe, G. 1981*a*. Reproducción y crecimiento de *Calomys musculinus murillus* (Thomas, 1916). Historia Natural (Mendoza, Argentina), 1: 237–256.

———. 1981*b*. Reproducción y crecimiento de *Akodon azarae azarae* (Fischer, 1829). Historia Natural (Mendoza, Argentina), 1:193–204.

de Villafañe, G., and S. M. Bonaventura. 1987. Ecological studies in crop fields of the endemic area of Argentine hemorrhagic fever. Mammalia, 51:233–248.

de Villafañe, G., S. M. Bonaventura, M. I. Bellocq, and R. E. Percich. 1988. Habitat selection, social structure, density and predation in populations of cricetine rodents in the Pampa region of Argentina and the effects of agricultural practices on them. Mammalia, 52:339–359.

de Villafañe, G., et al 1977. Dinámica de las comunidades de roedores en agroecosistemas pampásicos. Medicina (Buenos Aires), 37(supplement 3): 128–140.

Feldman, D. S., J. Gagnon, R. Hofmann, and J. Simpson. 1987. StatView II. Version 1.03 manual. Abacus Concepts, Inc., Berkeley, California, 278 pp. (on disk).

Hodara, V. L., M. B. Espinosa, M. S. Merani, and C. O. Quitans. 1989. *Calomys laucha* (Rodentia, Cricetinae): growth and breeding in laboratory conditions. Laboratory Animals, 23:340–344.

Hodara, V. L., A. E. Kajon, C. Quintans, L. Montoro, and M. S. Merani. 1984. Parámetros métricos y reproductivos de *Calomys musculinus* (Thomas, 1913) y *Calomys callidus* (Thomas, 1916) (Rodentia, Cricetidae). Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Zoologia (Buenos Aires), 13:453–459.

King, O. M. 1950. An ecological study of the Norway rat and the house mouse in a city block in Lawrence, Kansas. Transactions of the Kansas Academy of Science, 53:500–528.

Kravetz, F. O. 1977. Ecología y control de reservorios. Ciencia e Investigación (Argentina), 33:235–242.

———. 1978. Ecología de la comunidad de roedores involucrados en la fiebre hemorrágica Argentina. Ph.D. dissert., Facultad de Ciencias Exactas, Universidad de Buenos Aires, Buenos Aires, Argentina, 193 pp.

Kravetz, F. O., M. C. Manjon, M. E. Busch, R. E. Percich, P. Marconi, and M. P. Torres. 1981. Ecología de *Calomys laucha* (Rodentia, Cricetidae) en el departamento de Río Cuarto (Córdoba). I. Dinámica de población. Ecología (Argentina), 6:15–22.

Loeb, S. C., and R. G. Schwab. 1987. Estimation of litter size in small mammals: bias due to chronology of resorption. Journal of Mammalogy, 68:671–675.

Millar, J. S. 1989. Reproduction and behavior. Pp. 169–232, *in* Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr. and J. N. Layne, eds.). Texas Tech University Press, Lubbock, 366 pp.

Mills, J. N., B. A. Ellis, K. T. McKee, J. I. Maiztegui, and J. E. Childs. 1991. Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. Journal of Mammalogy, 72:470–479.

Pearson, O. P. 1967. La estructura por edades y la dinámica reproductiva en una población de ratones del campo, *Akodon azarae*. Physis (Buenos Aires), 27:53–58.

Polop, J. J., C. N. Gardenal, and M. S. Sabattini. 1982. Comunidades de roedores de cultivos de sorgo en la Provincia de Córdoba y su posible vinculación con la fiebre hemorrágica Argentina. Ecosur (Argentina), 9:107–116.

Rose, R. K., and M. S. Gaines. 1978. The reproductive cycle of *Microtus ochrogaster* in eastern Kansas. Ecological Monographs, 48:21–42.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology, 51:3–47.

Svendsen, G. 1964. Comparative reproduction and development in two species of mice in the genus *Peromyscus*. Transactions of the Kansas Academy of Science, 67:527–538.

Zuleta, G. A. 1989. Estrategias de historia de vida en el ratón del pastizal pampeano, *Akodon azarae*. Ph.D. dissert., University of Buenos Aires, Buenos Aires, Argentina, 161 pp.

Zuleta, G. A., F. O. Kravetz, M. Busch, and R. E. Percich. 1988. Dinámica poblacional del ratón pastizal pampeano (*Akodon azarae*) en ecosistemas agrarios de Argentina. Revista Chilena de Historia Natural, 61:231–244.

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