

# REPRODUCTIVE BIOLOGY OF A TROPICAL, NON-HIBERNATING GROUND SQUIRREL

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To examine the effects of climate and hibernation on reproductive patterns, I compared tropical and temperate species of ground and tree squirrels. I studied the reproductive biology of a tropical species, the Cape ground squirrel (*Xerus inauris*), by observing marked individuals in the Kalahari-bushveld region in Namibia. Breeding occurred throughout the year, although there was some seasonality. Interestrous intervals were 76.5–146 days, gestation averaged 47.7 days, lactation averaged 52 days, there were one to three litters per year, with litters of one or two young. Subadult males reached reproductive maturity at 8 months, while females had their first estrus at 10 months. Comparisons of these reproductive traits with other species in the family Sciuridae suggest that reproduction in the Cape ground squirrel is influenced by a long active season in an unpredictable habitat. Of the potential factors affecting reproduction in squirrels, I conclude that climate is the most critical, and nutrition, predation, and allometry are less important.

**Key words:** Reproduction, non-hibernating, Cape ground squirrel, *Xerus inauris*, Africa

Studies of ground and tree squirrels have stressed the importance of environmental factors on patterns of reproduction (Dobson and Murie, 1987; Morton and Tung, 1971; Viljoen, 1981; Viljoen and Du Toit, 1985). Availability and predictability of resources is one such factor that greatly influences reproductive characteristics (Armitage, 1981, 1988; Dobson and Murie, 1987; Emmons, 1980; Viljoen, 1981). In many temperate squirrels, reproduction is constrained by limitations on resources imposed by winter. Similarly, reproduction in tropical ground squirrels can be constrained by seasonal (predictable) or unpredictable periods of resource scarcity (Emmons, 1979; Viljoen and Du Toit, 1985).

Most species of Nearctic ground squirrels are obligate hibernators (Dobson and Davis, 1986; Michener, 1983), having only a few months of above-ground activity in which to mate, reproduce, and store fat for the next winter. Breeding occurs shortly after females emerge from hibernation, which al-

lows both females and young-of-the-year to maximize the time to gain weight in preparation for hibernation (Michener, 1985). As a result of this constraint on active time, females are restricted to one litter per year, and their young develop more quickly and grow more rapidly than those of facultative or non-hibernating species (Morton and Tung, 1971). Thus, the restriction in the amount of active time above ground due to hibernation may strongly influence the social and mating systems of many species of ground squirrels (Armitage, 1981; Michener, 1983).

Despite the limits of winter, Nearctic tree squirrels do not hibernate and are active for most of the year (Koprowski, 1991). Unlike ground squirrels, which feed mainly on grasses, tree squirrels survive winter periods of low available energy by feeding off seed caches (Heaney, 1984; Koprowski, 1993). Furthermore, unlike Nearctic ground squirrels, tree squirrels usually have two

breeding seasons per year, spring and summer (Heaney, 1984).

Tropical squirrels, conversely, are not subject to the constraint of severe winters. Reproduction in African tree squirrels is characterized by breeding throughout the year, small litter sizes, and short inter-birth intervals (Emmons, 1979; Viljoen and Du Toit, 1985). Compared with temperate tree squirrels, African tree squirrels have long gestation and short lactation periods (Emmons, 1979; Viljoen and Du Toit, 1985). These reproductive traits are believed to be adaptations to irregular fluctuations in availability of resources, which serve to spread the costs of reproduction over a larger portion of the year (Emmons, 1979; Viljoen and Du Toit, 1985).

Little is known about the life histories and social systems of tropical ground squirrels in the tribe Xerini (O'Shea, 1991). All four species in the genus *Xerus* live in Africa. Although they are closer phylogenetically to the African tree squirrels (Black, 1972; Moore, 1959), they are more similar ecologically to temperate ground squirrels (tribe Marmotini). Like the temperate ground squirrels, xerines are strictly diurnal and semi-fossorial. Unlike most Marmotini, however, they do not hibernate. Few detailed studies of tropical, non-hibernating species have been conducted. Such studies are necessary to provide a basis of comparison with hibernating temperate species to reveal the adaptive mechanisms underlying reproductive patterns in squirrels.

The Cape ground squirrel (*Xerus inauris*) lives in arid regions of Namibia, Botswana, and South Africa (Lynch, 1983; Smithers, 1971). Previous studies describe a highly social ground squirrel that is active throughout the year (Herzig-Straschil, 1978; Smithers, 1971; Waterman, 1995). Although this species is common within its range, little is known about its reproductive ecology (Skinner and Smithers, 1990). Understanding the reproductive ecology of a tropical ground squirrel may reveal what factors, such as climate, ecology, or phy-

logeny, exert the strongest influence on reproduction in ground squirrels.

The objective of this paper is to determine which factors influence reproduction in squirrels, using information on the reproductive biology of the Cape ground squirrel. Are the reproductive traits of Cape ground squirrels more closely aligned with those of the closely related African tree squirrels or are they more similar to the more distantly related, but ecologically similar, temperate ground squirrels? If the reproductive traits of Cape ground squirrels are similar to Nearctic ground squirrels, the ecological constraints of semi-fossoriality may have the strongest influence. If their reproductive traits are more similar to African tree squirrels, climate or phylogeny may be a more important factor.

#### MATERIALS AND METHODS

The study was conducted from June 1989 to December 1991 in the Kalahari-bushveld region of Namibia (23°25'S, 18°00'E). Habitat was mostly open veldt with hard-calcareous soil, which allows construction of semipermanent burrows. Dominant species of plants included various grasses, and *Acacia* bushes and trees (Waterman, 1995). Rainfall on the study site averaged  $215.0 \pm 20.7$  mm/year (1980–1991—Windhoek Weather Bureau), with most rain falling December–April. Annual temperatures ranged from  $-5$  to  $42^{\circ}\text{C}$ . Temperatures were lowest during winter (June through August).

Conventional terminology used to describe the spatial dynamics of North American ground squirrels is not suitable for the unique spatial system of the Cape ground squirrel (Waterman, 1995); therefore I have attempted to avoid confusion by using the following terms. A burrow cluster is defined as an aggregation of burrow openings clearly separated from adjacent clusters by areas, larger than the cluster area, that lack burrows (after Herzig-Straschil, 1978). Burrow clusters are composed of a number of burrow systems, which are a series of connecting burrows. A social group, therefore, is defined as a group of animals living together in the same burrow system (after Herzig-Straschil, 1978).

The Cape ground squirrel is a social species that lives in low densities relative to temperate

semifossorial species in North American (Waterman, 1995). Females live together in social groups comprised of one to three adult females and up to nine subadults of either sex. These groups are characterized by female philopatry and male-biased dispersal. Only one female social group usually inhabits a burrow cluster, and burrow clusters usually are separated from each other by a few hundred meters. The area of a burrow cluster averages ca. 700 m<sup>2</sup>. Females in a social group share sleeping burrows and feeding ranges, and social interactions within such groups are highly amicable. Male Cape ground squirrels also form social groups that persist throughout the year (Waterman, 1995). Such male bands can include  $\leq 19$  individuals. Temporary subgroups form among these individuals and the composition and size of these subgroups change daily. Bands of males share a common home range that overlaps with a number of social groups of females (Waterman, 1995).

Individuals were live-trapped in 12 burrow clusters using Tomahawk (15 by 15 by 50 cm) and Havahart (21 by 21 by 90 cm) live traps baited with peanut butter and oats. A total of 161 squirrels was trapped and marked during the study. Individuals were marked with numbered metal tags (National Band and Tag Co., Newport, KY, Monel No. 1), dye marked on the body using hair dye (Lady Clairol Nice N'Easy and Nyanzol), and freeze branded (Quick freeze—Rood and Nellis, 1980). Individuals were weighed, examined for external parasites, and their sex, age, and reproductive condition were recorded. Size of testes in males and the degree of vaginal swelling in females (indicative of the onset of estrus) also were recorded as indications of reproductive condition. Adults and subadults could be distinguished; subadult males were either non-scrotal or partly scrotal (adult males are scrotal year round), and adult females had swollen nipples (nipples remain permanently swollen after first breeding).

Detailed behavioral observations (2,000 h) were made in eight burrow clusters. Squirrels were observed from trees, windpumps, or a vehicle, using 10 by 50 binoculars and a 15–45 by 60 spotting scope. Persistence of adults on the study area was determined by calculating the fraction of individuals sighted (or trapped) in 1 year that were sighted (or trapped) in the next year. I determined intervals between periods of estrus for three groups of females: those that lost

litters before parturition (i.e., females that never lactated); those that lost litters during lactation (i.e., females that lactated, but whose litters never emerged); successful females (i.e., those females whose litters emerged). The dates of estrus that occurred during the months when I was not present (prior to June 1989, in May 1990, and from February to June 1991) were estimated by backdating from emergence of litters, a technique that underestimates the number of estrous periods.

To reduce bias in estimates of reproductive parameters obtained from the literature for other species, I only included data from the center of a species' range. Due to the difficulty in taking accurate body measurements of Cape ground squirrels in the field, I made body measurements from study skins from the State Museum of Namibia, Windhoek. All study skins in the collections were collected from the vicinity of my study area.

Where data were normal and homoscedastic, parametric statistics were used (Snedecor and Cochran, 1989; Sokal and Rohlf, 1995; Weisberg, 1985); otherwise, nonparametric statistics were employed (Conover, 1980; Cox and Oakes, 1984). I used a geometric-mean regression (Model II) to regress gestation and lactation against body weight. This model is more appropriate in allometric analysis than a Model I linear regression, because both the (X) and the (Y) axes are measured with error (Ricker, 1973; Sokal and Rohlf, 1995). Unless otherwise indicated, means  $\pm 1$  SE are reported.

## RESULTS

*Reproductive characteristics of Cape ground squirrels.*—Adult males were significantly heavier, by ca. 8%, than females (males,  $\bar{X} = 601.5 \pm 6.1$  g,  $n = 50$ ; females,  $\bar{X} = 550.0 \pm 6.6$  g,  $n = 55$ ; analysis of variance,  $F = 137.0$ ,  $P < 0.001$ ). Although these weights were lower than those reported in Botswana (Smithers, 1971), the relative sexual dimorphism was similar. Length of head and body of adults (based on study skins) did not differ between the sexes (males,  $\bar{X} = 246.1 \pm 1.7$  mm,  $n = 16$ ; females,  $\bar{X} = 247.3 \pm 3.0$  mm,  $n = 20$ ;  $t' = -0.36$ ,  $P = 0.72$ ). These lengths were similar to specimens from South Africa and Botswana (Herzig-Straschil, 1978; Lynch,

1983; Smithers, 1971). Persistence (or re-sighting) of adults in six colonies was not significantly different between years (males—0.80 in 1989–1990,  $n = 15$ , and 0.76 in 1990–1991,  $n = 17$ ,  $\chi^2 = 0.06$ ,  $P = 0.81$ ; females—0.62 in 1989–1990,  $n = 26$ , and 0.78 in 1990–1991,  $n = 23$ ,  $\chi^2 = 1.61$ ,  $P = 0.21$ ) nor between the sexes ( $\chi^2$ ,  $P > 0.05$  for both years).

Breeding occurred in every month of the year, but some seasonality was evident (Fig. 1a). Few litters emerged during winter-spring months (July through October, Fig. 1b). Year-round breeding with lower reproduction in winter also has been observed elsewhere (Herzig-Straschil, 1978; Smithers, 1971; Zumt, 1970). All females had multiple estrous periods in a single year, but in only four cases of 40 were females observed to rear two litters a year, and only one female reared three litters in a single year. In 18 of the 40 cases, females were successful in raising only a single litter to emergence, and in 17 cases, females were unsuccessful in rearing any litters in a year.

Females that were unsuccessful in rearing a litter came into estrus again much sooner than females that reared litters to weaning. Both dates of estrus and losses of litters were known for 23 females. Females that lost their litters during lactation came into estrus, on average, 24 days after loss of litter (range, 15–48 days;  $n = 5$ ), whereas females that successfully weaned their young came into estrus an average of 56 days after emergence of a litter (range, 21–86 days;  $n = 10$ ; Mann-Whitney  $U$  test,  $P = 0.028$ ). The interestrous intervals differed significantly for females that never gave birth (either by failing to conceive or by miscarrying), females that lost litters prior to emergence, and females whose litters emerged (Kruskal-Wallis,  $P = 0.0003$ , Table 1). However, pairwise comparisons (Conover, 1980) indicate that only the interestrous interval of females who successfully raised litters differed (multiple-comparisons test,  $P < 0.05$  for successful litters

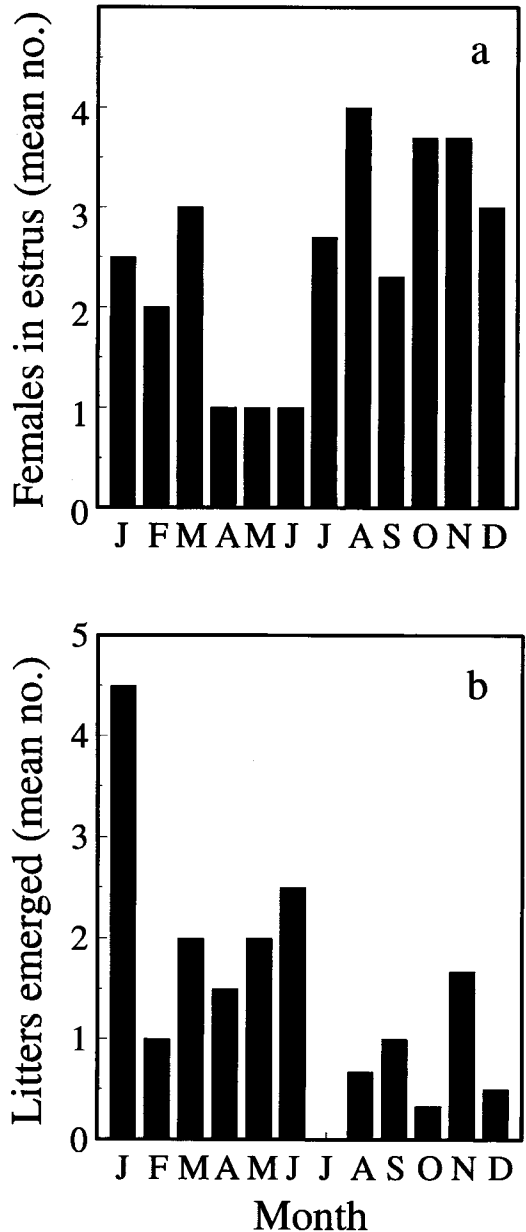


FIG. 1.—Seasonality of reproduction: a, mean number of female Cape ground squirrels in estrus each month; b, mean number of litters that emerged each month. Data were collected over 30 months (June 1989–December 1991).

versus either failures in pregnancy or lactation).

Females usually gave birth in burrows located away from the burrow cluster, but

TABLE 1.—*Interestrous intervals for females that were pregnant but never lactated (presumed loss of litter before parturition), females that lost litters before to their emergence and females whose litters successfully emerged. Parentheses indicate range.*

Period of litter loss	Interestrous interval (days)		n
	median (range)		
Before parturition	76.5 (31–104)		8
Before emergence	90.0 (83–127)		5
Litter emerged	146.0 (114–187)		10

within the feeding range of their social group. Lactating females did not return to sleep with their social group until after weaning or losing their litter. The outcome of breeding attempts was measured in 40 cases in which females were observed for several months, beginning with the onset of estrus. Only 13 litters (32.5%) were produced from these breeding attempts and reared to emergence. Eleven (27.5%) females apparently lost their litters at birth or during lactation, for the females became pregnant and went into isolation prior to parturition, but no litters emerged. In 15 cases (37.5%), females either failed to become pregnant, or they miscarried, for they did not go into isolation. One female disappeared during lactation.

From inspection of their nipples, females appeared to begin lactation at the time they isolated themselves from the group. Using the day of isolation as a likely indication of parturition, gestation was estimated to be  $47.7 \pm 1.7$  days ( $n = 10$ ), which is within the range suggested by Zumpt (1970). Litters emerged  $92.2 \pm 1.2$  days after estrus ( $n = 5$ , median = 92 days, range = 89–96 days). Within the first 7 days after litters emerged, young began eating solid food and nipples of the female became flat. Young appeared to be weaned at this time, and thus lactation was estimated to last ca. 52 days, similar to that found in a captive group (Herzig-Straschil, 1978).

Litter size was either one or two ( $\bar{X} =$

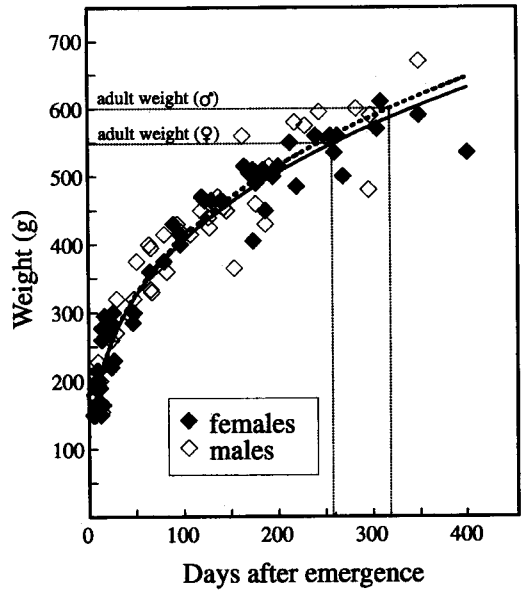


FIG. 2.—Growth of Cape ground squirrels in the first 400 days after emergence: males—dashed line,  $Y = 90.99 X^{0.33}$ ,  $r = 0.95$ ,  $F = 387.5$ ,  $P = 0.0001$ ,  $n = 43$  observations (14 individuals); females—solid line,  $Y = 93.33 X^{0.32}$ ,  $r = 0.93$ ,  $F = 609.2$ ,  $P < 0.0001$ ,  $n = 51$  observations (17 individuals). Adult weights are shown by dotted lines.

$1.64 \pm 0.09$ ,  $n = 28$ ). Distributions of male and female young upon initial emergence did not differ from expected in litters of one (binomial test,  $P = 0.63$ ,  $n = 10$  litters) or litters of two (binomial tests,  $P > 0.15$  in all tests,  $n = 17$  litters). Increases in weight of juveniles (Fig. 2), based on 31 individuals of known age, showed no sex differences over the first 400 days after emergence of litters (analysis of variance,  $F = 0.65$ ,  $P = 0.42$ ). Males reached mean adult weight at 10.2 months after first emergence, whereas females reached mean adult weight at 8.5 months (Fig. 2).

Ages of sexual maturity differed in males and females. Age of first female estrus was  $10.0 \pm 0.7$  months (median = 10, range = 7–13 months,  $n = 10$ ), whereas males became scrotal and participated in breeding at  $8.1 \pm 0.5$  months (median = 9, range = 5–10 months,  $n = 11$ ). These ages of repro-

ductive maturity differed significantly ( $t$ -test,  $t = 2.16$ ,  $P = 0.0439$ ,  $n = 21$ ).

*Reproductive characteristics within the Sciuridae.*—Analyses comparing data from the literature with Cape ground squirrels indicated that length of gestation differed among the four groups included (Nearctic ground and tree squirrels, and African ground and tree squirrels; Kruskal-Wallis,  $W = 18.8$ ,  $P = 0.0003$ ; Table 2). Lengths of gestation in Nearctic ground squirrels were significantly shorter than in all other groups (multiple-comparisons tests,  $P < 0.05$  in all comparisons), and length of gestation in Nearctic tree squirrels differed significantly from that of African tree squirrels (multiple-comparisons tests,  $P < 0.05$ ). No other comparisons were significant (multiple-comparisons tests,  $P > 0.05$  in all tests). Lactation also differed among the four groups (Kruskal-Wallis,  $W = 9.57$ ,  $P = 0.03$ ). However, pairwise comparisons were only significant between the Nearctic ground and tree squirrels (multiple-comparisons test,  $P < 0.05$ ) and between the Nearctic and African ground squirrels (multiple-comparisons test,  $P < 0.05$ ).

These differences in gestation and lactation do not appear to be due to differences in body weight. No allometric relationships between body weight and gestation (Model II regression,  $r = 0.08$ , slope =  $-0.36$ , 95%  $CI = -0.20$  to  $-0.51$ ,  $n = 25$ ) or body weight and lactation ( $r = 0.04$ , slope =  $-0.41$ , 95%  $CI = -0.23$  to  $-0.60$ ,  $n = 23$ ) were evident. However, such an overall regression may be biased by phylogenetic effects (Harvey and Pagel, 1991). Although samples were small, separate regressions of three groups (Nearctic ground and tree squirrels and African tree squirrels) also suggest little effect of body weight on the length of gestation (Nearctic ground squirrels,  $r = 0.26$ , slope =  $0.13$ , 95%  $CI = 0.05$  to  $0.21$ ,  $n = 15$ ; Nearctic tree squirrels,  $r = 0.93$ , slope =  $0.23$ , 95%  $CI = -0.30$  to  $0.48$ ,  $n = 4$ ; African tree squirrels,  $r = 0.31$ , slope =  $0.11$ ,  $CI = -0.20$  to  $0.41$ ,  $n = 4$ ) or lactation (Nearctic ground squirrels,  $r =$

$0.34$ , slope =  $-0.34$ , 95%  $CI = -0.13$  to  $-0.55$ ,  $n = 14$ ; Nearctic tree squirrels,  $r = 0.97$ , slope =  $0.30$ , 95%  $CI = 0.08$  to  $0.52$ ,  $n = 4$ ; African tree squirrels,  $r = 0.29$ , slope =  $-0.21$ ,  $CI = -2.8$  to  $2.4$ ,  $n = 3$ ).

## DISCUSSION

Differences in climatic conditions experienced by tropical and temperate ground squirrels appear to have profound influences on several aspects of their reproductive biology (Heaney, 1984). The breeding season in North American ground squirrels is restricted by climatic constraints on the active season (Armitage, 1981; Michener, 1983). Females emerge from hibernation and usually breed in a period of 1–3 weeks (Dobson, 1984). The brevity of the active season has a large effect on gestation, lactation, and litter size. After females emerge from hibernation, they must breed, gestate, lactate, and then put on weight in order to survive the next winter (Michener, 1983, 1985). By contrast, Cape ground squirrels, which are not constrained by long winters, breed year-round, have small litters, and reach sexual maturity and adult body weight prior to 1 year of age.

Although climate appears to be an important influence on reproduction, allometric relationships also must be considered. Allometry can have an important influence on reproductive traits in mammals, and a considerable amount of literature is devoted to the allometry of life-history variables (Harvey and Pagel, 1991; Harvey et al., 1989; Stearns, 1992). Certainly, body weight can have a large influence on reproduction in ground squirrels (Armitage, 1981). Armitage (1981) found a correlation between body weight and length of gestation in Nearctic ground squirrels and concluded that gestation was constrained by body weight and only slightly influenced by length of active season. If this trend can be generalized, species with similar weights should exhibit similar reproductive patterns.

However, Cape ground squirrels, whose weight and sexual dimorphism are well

TABLE 2.—Reproductive parameters for Nearctic and African ground squirrels and tree squirrels whose reproductive biology is known.

Species	Weight of female (g)	Gestation (days)	Lactation (days)	Age of emergence (days)	Litter size	Number of estrus cycles/year	Age at maturity* (months)	References
<b>Nearctic ground squirrels</b>								
<b>Obligate hibernators</b>								
<i>Spermophilus lateralis</i>	133	27–31	42		4–9	1	12–24	1
<i>S. beldingi</i>	217	23–25	25–28	25–28	1–10	1	12–24	2
<i>S. richardsonii</i>	223	22–23	30	28–30	3–13	1	12	3
<i>S. armatus</i>	266	23–26	22	22	1–6	1	12	4
<i>S. columbianus</i>	419	24	35–37	30	1–5	1	12–24	5
<i>S. parryii</i>	577	25	28		5–10	1	12	6
<i>Cynomys gunnisoni</i>	644	30	35	28	3–10	1	12	7
<i>C. leucurus</i>	925	30		35–42	3–8	1	12	8
<i>Marmota flaviventris</i>	2,560	30	25	20–30	3–8	1	24	9
<b>Facultative hibernators</b>								
<i>S. variegatus</i>	546	30	56	56	3–8	1–2	12	10
<i>S. beecheyi</i>	574	30	42–56	42–56	1–9	1	9–10	11
<b>Occasional hibernators</b>								
<i>Ammospermophilus leucurus</i>	100	30–35	65	51–58	5–14	1–2	12	12
<i>A. harrisi</i>	113	29	42	35		1–2	10–11	13
<i>A. nelsoni</i>	154	26	37–45	30	6–11			14
<i>C. ludovicianus</i>	864	32–35	35–42		3–4	1	24	15
Median for Nearctic ground squirrels	419	29	37.5					
<b>Nearctic tree squirrels</b>								
<i>Sciurus carolinensis</i>	536	44	70	54–58	1–6	2	9–18	16
<i>Sciurus niger</i>	767	45	70	47	1–6	2	9–12	17
<i>Sciurus aberti</i>	624	40	70	49	2–4	1	10–12	18
<i>Tamiasciurus hudsonicus</i>	188	34	48	37–50	1–8	1–2	12	19
Median for Nearctic tree squirrels	580	42	70					
<b>African tree squirrels</b>								
<i>Aethosciurus poensis</i>	100 <sup>b</sup>	60		18		up to 6	3	20
<i>Funisciurus congicus</i>	112 <sup>b</sup>	56	50	18	3	up to 6		21
<i>Paraxerus cepapi</i>	195	56	35–42	18–22	1–3	up to 6		22
<i>P. pallatus</i>	379	59	48–57	27	1–2	4–6	<12	23
Median for African tree squirrels	153.5	57.5	50					
<b>African ground squirrels</b>								
<i>Xerus erythropus</i>	500–945		45–56	39	2–4	>1	6	24
<i>X. princeps</i>	596 <sup>b</sup>	42–49			1–3	>1		25
<i>X. inauris</i>	550	48	52	45	1–3	3–4	10	26
Median for African ground squirrels	596	46.8	51.25					

\* For females only.

<sup>b</sup> Males and females.

<sup>c</sup> References are: 1) Bronson (1979), McKeever (1965), Phillips (1981, 1984); 2) Morton and Parmer (1975), Sherman and Morton (1984), Trombulak (1991); 3) Davis and Murie (1985), Michener (1977, 1980, 1985); 4) Balph (1984), Slade and Balph (1974); 5) McLean (1978), Murie and Harris (1982); 6) Kiell and Millar (1980), Mayer and Roche (1954), McLean (1983), McLean and Towns (1981); 7) Fitzgerald and Lechleitner (1974), Longhurst (1944), Rayor (1985, 1988); 8) Bakko and Brown (1967), Hoogland (1979), Tileston and Lechleitner (1966); 9) Armitage (1965, 1981), Armitage and Downhower (1974), Armitage et al. (1976), Johns and Armitage (1979); 10) Baker (1956), Johnson (1981), Ortega (1990); 11) Dobson and Davis (1986), Evans and Holdenreid (1943), Tomich (1962); 12) Belk and Smith (1991), Hall (1946), Kenagy and Bartholomew (1985), Smith and Jorgensen (1975); 13) Neal (1965a, 1965b, 1965c); 14) Hawbecker (1958, 1975); 15) Garrett et al. (1982) Hoogland (1979, 1992), Hoogland et al. (1989), Tileston and Lechleitner (1966); 16) Barkalov and Soots (1975), Brown and Yeager (1945), Hayssen et al. (1993), Horwich (1972), Koprowski (1991), Pasitschniak-Arts and Bendell (1990), Shorten (1954), Thompson (1978); 17) Allen (1942), Brown and Yeager (1945), Hayssen et al. (1993); 18) Farentinos (1972a, 1972b), Keith (1965); 19) Ferron (1977), Ferron and Prescott (1977), Lair (1985), Layne (1954), Price and Boutin (1993), Rusch and Reeder (1978); 20) Emmons (1979); 21) Viljoen (1981), Viljoen and Du Toit (1985); 22) Viljoen (1977), Viljoen and DuToit (1985), Skinner and Smithers (1990); 23) Viljoen and Du Toit (1985); 24) Kingdon (1974), O'Shea (1991); 25) Herzig-Straschil and Herzig (1989); 26) Herzig-Straschil (1978), Zumpt (1970), this study.

within the range of most Nearctic ground squirrels, have a much longer gestation than any North American ground squirrel, regardless of size. The mountain ground squirrel, *Xerus princeps*, has been estimated to have a similar gestation period (42–49 days, Table 2). Nearctic tree squirrels, which also fall within the same size range, but are not constrained by hibernation, have gestation periods similar to the Cape ground squirrel. Although Armitage (1981) included more species in his analysis of the Marmotini, he excluded the genus *Ammospermophilus* (which is not an obligate hibernator), and the correlation he found between gestation and body weight was not strong. Dobson and Murie (1987) also did not find such a correlation in an intraspecific analysis of *Spermophilus columbianus*. Therefore, body size does not appear to account for differences in observed patterns of gestation.

Furthermore, African tree squirrels (whose smaller size would suggest shorter gestation) have even longer gestation periods than any other group. Corresponding to this increased length of gestation, the young of African tree squirrels characteristically are born in a more precocial state than are most European or North American tree squirrels (Emmons, 1979) and certainly appear to be more precocial than Cape ground squirrels (see Herzig-Straschil, 1978, for a description of their development). Such a precocial state in newborn African tree squirrels may be responsible for the shorter time young spend in the nest.

Length of lactation in ground squirrels does not appear to be related to allometry, but instead it appears to be influenced by ecological factors. Armitage (1981) found no correlation between body weight and length of lactation in the North American ground squirrels, but he did find lactation to be highly correlated with the length of the active season. Development during lactation is much more rapid in hibernating species of ground squirrels than in non-hibernating species (Morton and Tung, 1971).

Furthermore, North American species that are facultative and non-obligate hibernators have longer lactation periods than obligate hibernators, as do other groups that do not hibernate; African ground and tree squirrels, and especially, Nearctic tree squirrels (Table 2). In African ground squirrels, length of gestation and lactation are equivalent, while all other groups have longer periods of lactation than gestation. The extremely long gestation and relatively shorter (compared to the Nearctic tree squirrels) lactation in the African tree squirrels, has been suggested to be an adaptation to unpredictable availability of food (Emmons, 1979; Viljoen and Du Toit, 1985). Nutrition is an important factor affecting reproduction in both tropical and temperate tree squirrels, where females tend to breed during times when food is at a maximum (Viljoen, 1981). Nearctic desert ground squirrels also show peaks in breeding during times of high rainfall and rapid growth of plants (Hawbecker, 1975; Ortega, 1990). Emmons (1979) suggests the long gestation and shorter lactation periods of African tree squirrels enable them to reduce lactation costs through times of food scarcity. Additionally, the time spent in the nest is shortest in the African tree squirrels. Females actually evict young squirrels from their groups at times of food scarcity (Viljoen and Du Toit, 1985).

Another factor that may influence the length of gestation and lactation is vulnerability of offspring to predators. African tree squirrels emerge from the nest much earlier than do North American tree squirrels, which may reduce the chances of predation (Emmons, 1979). African tree squirrels emerge from the nest nearly 3 weeks before weaning. In contrast, young ground squirrels, including Cape ground squirrels, are weaned within the first week after emergence from the nest (Table 2). There was little evidence that juvenile Cape ground squirrels in burrows were particularly susceptible to predation. Although Cape ground squirrels lost 27.5% of litters during



lactation, only in two cases were these losses known to be caused by predation (one nest was preyed upon by a Cape cobra, *Naja nivea*, and another individual was consumed by a monitor lizard, *Varanus exanthematicus*). These ground predators were not active during winter; it is unlikely that the low recruitment in winter was caused by predation. Therefore, predation may be an important influence on reproduction in some species, but not in others. However, Viljoen and Du Toit (1985) noted low predation in *Paraxerus cepapi*, an African tree squirrel, and they suggested that limited food resources were a more important influence on length of nestling period and lactation than predation.

Litter sizes tend to decrease with latitude in the North American tree squirrels (Lord, 1960), and in tree squirrels worldwide (Viljoen and Du Toit, 1985). Although this trend was not evident in North American ground squirrels (Lord, 1960), expanding this analysis to include the tropical ground squirrels in the genus *Xerus* may reveal a similar relationship between litter size and latitude. Certainly, squirrels in the genus *Xerus* have small litters compared to the North American ground squirrels (Table 2). Litter sizes of the Cape ground squirrel, usually restricted to one or two, only reach as high as three in areas of higher rainfall (Herzig-Straschil, 1978). Although these small litters may be due to phylogenetic constraints with the closely related African tree squirrels, the evidence for ecological pressure is strong. Among tree squirrels, all 30 tropical species, including Central American and Asian species, had average litter sizes of 1.0–2.8, much smaller than litter sizes of two to four for temperate tree squirrels (Viljoen and Du Toit, 1985). Thus, a similar effect in ground squirrels is more likely due to ecological pressures than to phylogenetic relationships.

The longer breeding seasons of mammals inhabiting southern latitudes may favor the production of several small litters during the season, which may explain the latitu-

dinal trend toward smaller litters (Spencer and Steinhoff, 1968). In an unpredictable environment, where the likelihood of reproductive failure is relatively high, it may be advantageous to spread the risk over several litters. The Cape ground squirrel and the African tree squirrels are able to breed more than once a year (Table 2). Females could be spreading the cost of reproduction over several small litters instead of producing a single large one (Spencer and Steinhoff, 1968; Viljoen and Du Toit, 1985). The Kalahari region where Cape ground squirrels live is prone to unpredictable rains and often to drought (Main, 1987; Thomas and Shaw, 1991), and does not provide the luxury of a predictable food supply in spring. Female Cape ground squirrels either failed to conceive or miscarried in 37.5% of documented estrous periods, and an additional number of litters were lost during lactation. Thus, females may minimize the cost of reproduction by resorption of the litter or desertion during lactation.

Such losses due to nutritional stress have been documented in other species. Only 30–40% of nutritionally stressed, female, European red squirrels, *Sciurus vulgaris*, successfully gave birth (Wauters and Dhondt, 1989). North American ground squirrels also may be subject to high reproductive failure (e.g., *Marmota marmota*—Arnold, 1990; *Spermophilus armatus*—Slade and Balph, 1974; *S. beecheyi*—Tomich, 1962). These losses are much more costly in temperate species because they must wait an entire year for another opportunity to reproduce. However, these costly losses may be ameliorated by timing reproduction to coincide with the predictable, abundant resources in spring. Cape ground squirrels, conversely, apparently have adopted a different reproductive strategy. Resources are not as predictable as in temperate regions, so the expected payoff per litter is much lower. However, they can resume breeding within a few weeks after losing a litter, so they maximize reproductive output by pro-

ducing several small litters throughout the year.

The opportunity to breed throughout the year also can affect the age at first reproduction. This reproductive trait is extremely important, and can have strong effects on the demography of a population or species (Stearns, 1992). The early maturity (prior to 1 year of age) observed in Cape ground squirrels also occurs in other squirrels that are not obligate hibernators (Table 2). In species that hibernate, maturity often is delayed beyond the first year. Large size of body, delayed maturity and reproduction, and restricted breeding seasons are traits associated with the most social species of North American ground squirrels (Armitage, 1981; Michener, 1983; Ortega, 1990). Armitage (1981) suggested that delayed maturity, due to restricted growing seasons, may be an important factor in the evolution of sociality in ground squirrels. However, the fact that the Cape ground squirrel is a highly social species living in matrilineal kin clusters (Herzig-Straschil, 1978; Waterman, 1995), despite its early age at maturity, does not support this hypothesis.

In summary, although Cape ground squirrels are semi-fossorial like the North American ground squirrels, the ability to breed throughout the year has a strong influence on their reproductive biology. Early reproductive maturity, small litter sizes, and long periods of gestation and lactation appear to facilitate reproductive success during a long active season in an unpredictable environment.

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