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23. TIMING OF REPRODUCTION IN ANTELOPE GROUND SQUIRRELS, *AMMOSPERMOPHILUS LEUCURUS*, NEAR LA PAZ, BAJA CALIFORNIA SUR

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Abstract

Antelope ground squirrels in the Cape Region of Baja California are subject to a complex pattern of environmental seasonality and unpredictability in an ecosystem with diverse plant food resources. The squirrels showed a prolonged season of attempted breeding that was initiated during the dry season, in winter and spring, and extended at least into the beginning of the summer monsoonal rains. Males remained capable of mating for at least four months. Females showed considerable temporal variability (asynchrony) within the population in their attempted production of young. The fact that some elements of the flora reproduce and flourish during the rainy season, others during the dry season, and still others at irregular or continuous intervals suggests that the resource base for breeding by an omnivorous rodent such as *A. leucurus* is likely to be complex, though well served, in this environment.

Key words: *Ammospermophilus*, deserts, environmental predictability, geographic variation, life history, reproduction, Sciuridae

Resumen

Los "Juancitos" (ardillas de tierra, *Ammospermophilus leucurus*) de la región del Cabo en Baja California Sur están sujetos a un patrón complejo e impredecible de estacionalidad ambiental, en un ecosistema con diversos recursos alimenticios de plantas. Los Juancitos mostraron una estación prolongada de crianza, la que inició en la estación seca (invierno y primavera), extendiéndose al menos a principios de las lluvias de verano. Los machos fueron capaces de aparearse por lo menos durante cuatro meses. Dentro de la población las hembras mostraron considerable variabilidad temporal (asincronía), como cuando intentaban producir crías. El hecho de que algunos elementos florísticos se reproduzcan y florezcan en la estación lluviosa, otros durante la sequía e incluso otros que lo hagan en intervalos irregulares o continuosos, sugiere que la base de recursos alimenticios para la reproducción de un roedor omnívoro como *A. leucurus* sea compleja, pero eficaz en este ambiente.

Palabra clave: *Ammospermophilus*, desiertos, predictabilidad ambiental, variación geográfica, historia de vida, reproducción, Sciuridae.

Seasonal breeding by organisms is a reflection of the process of matching life-history traits and accompanying physiological mechanisms to prevailing environmental characteristics. In desert ecosystems, where resources required for reproduction may be both sparse and ephemeral, this matching process involves the use of strategies that promote survival under extreme and unpredictable physical conditions. The increased availability of energy, nutrients, and water for breeding is typically restricted to a particular season. The breeding season may be broadly predictable to a general time of year but remain specifically unpredictable from year to year. Heat, aridity, and the potential of both seasonal and multiyear drought place the scale of desert environmental variability at an extreme among major ecosystems.

The antelope ground squirrel, *Ammospermophilus leucurus*, is the most widely distributed desert-inhabiting sciurid of North America (Hall 1981; Alvarez-Castañeda and Patton 1999). It ranges across the complex of North American deserts (Shreve 1942; Hafner and Riddle 1997, Fig. 1) from the Great Basin Desert in southeastern Oregon, at 43° N, southward through the Mojave and Sonoran Deserts and the Peninsular Desert of Baja California to the Cape Region at 22° N. As an omnivore (Grinnell and Dixon 1919; Bradley 1968), the antelope ground squirrel is suited to maintain itself over the wide range of spatial and temporal variability in food suppy that characterize these North American deserts. The pattern of seasonal breeding by *A. leucurus* is best known near 37° N, at a transition between the northern Mojave and Great Basin Deserts; here the species breeds predictably once a year, at a fixed time. It begins with a short mating period of only about two weeks in late winter, followed by a combined three months of gestation and lactation. It concludes as juveniles venture out onto the surface to become independent of lactation and maternal care at the beginning of summer (Kenagy and Bartholomew 1985). The comparative life history and seasonal breeding tactics of other populations across the enormous latitudinal range of the species have not been studied.

The Cape Region of the Baja California peninsula, in the southern part of the state of Baja California Sur, lies just beyond the southern extreme of the Peninsular Desert of Baja California, which is a southern extension of the Sonoran Desert of northwestern Mexico and southwestern USA (Shreve 1942; Hafner and Riddle 1997). This area lies not only at a climatological interface of desert and subtropical zones, but also at a transition between Cape and Sonoran Desert phytogeographic regions (León de la Luz *et al.* 1996). March represents the beginning of the dry season, with temperatures and solar radiation building to a peak in July. The broad monsoonal rainy season lasts from August to February and typically shows secondary peaks of precipitation centered about September and January (León de la Luz *et al.* 1996).

We have initiated a study of the reproductive seasonality, life history, and population biology of antelope ground squirrels in the desert environment near La Paz, Baja California Sur, within an area centered approximately at 24° 08' North Latitude and 110° 34' West Longitude. The present analysis is based on 36 specimens obtained from April through August 2001. We examine the incidence of reproduction within the population over this period, draw some conclusions about the way in which ground squirrel breeding is adjusted to the pattern of trophic production in the area, and make some comparisons with reproduction elsewhere in the geographic range of *A. leucurus*.

Materials and Methods

The study area is located northwest of La Paz, Baja California Sur, in an area encompassed within 24° 04-12' North Latitude and 110°31-37' West Longitude. The habitat and floral phenology are described by León de la Luz et al. (1996). We obtained precipitation data for the La Paz area directly from the monthly records of the Estación Climatológica La Paz, BCS, of the Comisión Nacional del Agua (CNA); these data included monthly precipation for the 12 months leading up to the final samples in August 2001, as well as monthly values for the entire 21-year period 1980-2000.

We live-trapped animals on the following dates in 2001 using Sherman large folding aluminum traps, with the indicated sample sizes (n): 25-28 April (14), 15-19 May (7), 22 June (4), 12 July (4), and 22-23 August (7). Upon capture, we euthanized animals with an overdose of ether inhalant, then autopsied and prepared them as museum specimens. As a contribution to other ongoing investigations of the biodiversity, systematics, and historical biogeography of the mammals of Baja California, the specimens and associated tissues were deposited in the Mammal Collection of the Centro de Investigaciones Biológicas.

We autopsied males with detailed physical observations and weighing of reproductive organs, including the testes, epididymides, and seminal vesicles. We compared mass of the organs to those of reproductively active males as reported by Kenagy and Bartholomew (1985), using the maximal mean monthly value reported over the course of a three-year study (Kenagy and Bartholomew 1985: Appendix 1, Supplementary Publication Service Document No. 8526 of the Ecological Society of America) for reference as follows: mass of both testes, 2.136 g ; epididymides, 0.832 g; seminal vesicles, 1220 g. Values observed in the present study were averaged and presented as approximate percentage (to the nearest 5%) of the three-year maxima. Though only a few preparations of caudal epididymal smears could be made and examined for presence of spermatozoa, all these corresponded to the same general mass of cauda epididymis for which sperm is reported by Kenagy and Bartholomew (1985).

In females we noted externally the condition of the vulva and the nipples and surrounding hair. Internally we examined the ovaries and uterus visually upon dissection, and the ovaries also, as needed, under stereoscopic microscope to determine the presence of active follicles or corpora lutea. We observed the size and condition of the vagina and uterine horns, as well as the contents or scars in the uterine horns. We examined the ventral body wall for active mammary tissue. We measured uterine swellings and crown-rump length of embryos, and used these data to project parturition dates to the nearest calendar week, as reported by Kenagy and Bartholomew (1985). Using these observations we rated reproductive condition in four sequential categories: 1) Mating, with periovulatory condition recognized by open/active vulva, active follicles on the ovarian surfaces, and enlargement of the vagina and uterus; this category includes post-mating status involving macroscopically unapparent, unimplanted blastocysts 2) Pregnancy, with macroscopically visible embryos. 3) Lactation, with nipples enlarged, possibly (in later stages) with hair worn from around nipples, and active mammary tissue in the abdominal/pectoral wall. 4) Late/post-reproductive, with nipples enlarged and lacking hair around them, and degenerating residual mammary tissue present in the body wall. We designated any female that showed none of the above conditions 1-4 as Reproductively Inactive. Further details of methods are adopted after Kenagy and Bartholomew (1985).

Results

Our five-month sampling period (April through August 2001) began during an eight-month drought (November 2000 through June 2001) during which only 12 mm precipitation were recorded (Table 1). This eight-month total of 12 mm amounted to only 8% of the 12-month total of 153.5 mm recorded from September 2000 through August 2001, the final month of our sampling period. Distributed over eight months, this 12 mm of precipitation must have had nearly no biologically useful effect (Table 1). The climatological context of our five-month sampling period is therefore that we began observing *A. leucurus* in the sixth month of an eight-month drought. The overall context of the 12-month period of September 2000 through August 2001 is that the total precipitation of 154 mm amounts to 84% of the normal annual precipitation, which is 182 mm (SD98) for the 21-year period of 1980 through 2000 (Table 1).

Table 1. Monthly and annual precipitation (mm) patterns at La Paz, BCS representing (a) 21-year averages 1980-2000 and (b) the 12-month period including the present study, from September 2000 through August 2001. Asterisks (*) indicate months of *Ammospermophilus* sampling in 2001; September value begins the previous year.

	(a) 21-year averages 1980-2000	(b) 2000-2001
January	16.85	4.7
February	3.12	0.0
March	2.17	0.2
April	0.71	0.0*
May	0.17	1.5*
June	0.63	0.0*
July	18.33	71.4*
August	48.09	21.4*
September	55.31	29.2
October	6.32	19.5
November	11.24	3.0
December	18.91	2.6
Total	181.85	153.5
SD	98.28	
n	21	

All 10 males captured between April and August were reproductive or post-reproductive adults (Table 2). We captured no juvenile males nor older males that were non-reproductive. The three males in April all had enlarged testes, epididymides (with large tubules of a size typically containing spermatozoa), and seminal vesicles, all indicative of continuing reproductive readiness. Likewise the two males in May also had enlarged reproductive organs, including epididymides that contained spermatozoa. The single male recorded in June had somewhat reduced reproductive organs, but still at least 50% of maximum, and with spermatozoa in the epididymides. The single male observed in July had organs of decreased size and condition similar to that observed in June, indicating some regression and a late-reproductive or perhaps post-reproductive state. The three males observed in August all had reproductive organs of 10% or less of maximal size and were clearly post-reproductive.

Most of the 26 females examined from April to August were in some stage of reproductive activity (Table 3). The large sample of 11 females in April indicates a lack of tight synchrony among the females and demonstrates the full array of all possible reproductive stages (Table 3). Likewise in May and June, despite smaller samples, a wide range of reproductive activities was maintained, and in fact we caught no reproductively inactive individuals (Table 3). This response seems remarkable, considering that the drought continued throughout these first three months of the investigation (cf. Table 1). Finally, in July and August, also with smaller samples than in April, we found an apparent decline in incidence of breeding, with no individuals in early reproductive condition (mating) and only one pregnancy (Table 1). This decline in adult female reproductive output was matched by the collapse of male fertility in August (Table 2). None of the pregnant females showed evidence of concurrent lactation, nor were any lactating females pregnant, which indicates a lack of simultaneous pregnancy and lactation as a mode of multiple reproductive efforts in this population.

Based on seven observed pregancies (cf. Table 3), the mean (SD) litter size during this time was 5.9 (1.5), with a range of 4-8 and mode 5. The individual litter sizes of the pregnant females by month were: April (4, 5), May (5, 5), June (7, 7), August (8).

Using embryonic size to project parturition dates (expressed by month and week), we estimate that the seven pregnant females would have given birth as follows: 2nd week of May, 3rd week of May, 4th week of May (2 females), 2nd week of July, 3rd week of July, and 1st week of September. These patterns are consistent with our general conclusion that females in this population showed a lengthy and protracted period of reproduction.

Table 2. Seasonal mass (g) of male reproductive structures and size in relation to maximum. See Methods and Materials for maximum monthly values.

	Testes		Epididymides		Seminal vesicles		n
	Mean (SD)	Pct. of Max.	Mean (SD)	Pct. of Max.	Mean (SD)	Pct. of Max.	
April	1.40 (0.10)	65	—	—	0.77 (0.06)	65	3
May	1.43 (0.16)	65	0.61 (0.06)	75	1.08 (0.07)	90	2
June	0.99	45	0.46	55	0.68	55	1
July	1.01	45	0.45	55	0.80	65	1
August	0.19 (0.06)	10	0.12 (0.07)	15	0.08 (0.05)	5	3

Table 3. Incidence of reproductive condition in 26 females captured between April and August.

	n	Reproductively active				Inactive	Percent reproductive
		Mating	Pregnant	Lactating	Late/Post-repro		
April	11	4	2	1	1	3	73
May	5	0	2	2	1	0	100
June	3	1	2	0	0	0	100
July	3	0	0	1	2	0	100
August	4	0	1	0	2	1	75

All 10 males captured between April and August were reproductive or post-reproductive adults (Table 2). We captured no juvenile males nor older males that were non-reproductive. The three males in April all had enlarged testes, epididymides (with large tubules of a size typically containing spermatozoa), and seminal vesicles, all indicative of continuing reproductive readiness. Likewise the two males in May also had enlarged reproductive organs, including epididymides that contained spermatozoa. The single male recorded in June had somewhat reduced reproductive organs, but still at least 50% of maximum, and with spermatozoa in the epididymides. The single male observed in July had organs of decreased size and condition similar to that observed in June, indicating some regression and a late-reproductive or perhaps post-reproductive state. The three males observed in August all had reproductive organs of 10% or less of maximal size and were clearly post-reproductive.

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June	0.99	45	0.46	55	0.68	55	1
July	1.01	45	0.45	55	0.80	65	1
August	0.19 (0.06)	10	0.12 (0.07)	15	0.08 (0.05)	5	3

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May	5	0	2	2	1	0	100
June	3	1	2	0	0	0	100
July	3	0	0	1	2	0	100
August	4	0	1	0	2	1	75

Discussion

The seasonally broad and temporally heterogeneous distribution of reproductive effort by individual antelope ground squirrels in the southern Baja California peninsula (24° N. Lat.) is striking. The breadth of season and lack of synchrony among the females contrasts strongly with the highly synchronous pattern previously observed in California at 37° N. (Kenagy and Bartholomew 1985). How can we account for these differences? First of all, the reproductive effort in Baja California at 24° N, with a smaller average litter size of 5.9 (in contrast to 7.4 at 37° N) represents potentially lower maternal resource allocation, which could make reproduction less risky in Baja California. For example, assuming adult and juvenile masses are not adjusted latitudinally, the mass of a newly born litter at 37° N amounts to 24% of maternal body mass, but only 19% at 24° N (Table 9, Kenagy and Bartholomew 1985). Likewise a weaned litter at 37° N amounts to 292% of maternal mass, whereas it is 232% at 24°. Over the lengthy three months that encompass pregnancy (one month) and lactation (two months), the time of greatest daily energetic burden comes in the latter part of lactation, as it does for all such "income-breeding" small mammals (Kenagy *et al.* 1989; 1990). Female *A. leucurus* should enter into mid and late lactation when the dietary resources that provide energy, nutrients, and water are abundant. Such resources should also be available within the following month when the young must assume independence from their mothers.

Mid-late lactation and weaning of antelope ground squirrels at 37° N occur in late spring, when, on average, herbaceous plant food and associated trophic production are flourishing. This pulse results from the winter rains that drive seasonal production in the Mojave and Great Basin systems (Beatley 1969; Kenagy and Bartholomew 1985). In that system about 60% of annual precipitation falls in December through March, and average annual precipitation is only 137 mm (Kenagy and Bartholomew, 1985-Fig. 12). This total annual precipitation actually amounts to less than that of the La Paz area of Baja California Sur, which averages 182 mm annually (Table 1). The precipitation pattern near La Paz consists of a five-month dry period (February through June) that yields only 4% of the annual precipitation and a seven-month wet season that produces 96% of the rainfall, coming in two secondary peaks centered in September and December (Table 1). The fact that the puzzling lengthy breeding period of *A. leucurus* near La Paz was underway during the dry period suggests a more complex relationship to the flora and perhaps the rest of the food chain than in the Mojave and Great Basin systems.

The flora of the La Paz region, in the southern Baja California peninsula, is complex and diverse in two important ways (León de la Luz *et al.* 1996). First, it shows broadly diversified morphotypes, consisting of trees, shrubs, herbs, succulents, vines, and parasites. Second, the flora employs a variety of reproductive strategies that differ in their seasonal timing; growth and flowering may occur either in the rainy season, in the dry season, or irregularly or continuously throughout the year. Because of their distribution throughout the year, the food resources that could contribute to growth and reproduction of an omnivorous rodent such as *A. leucurus* may allow these animals to breed at various times of the year. In any event, it is clear that the flora of the southern Baja California peninsula does not have the highly seasonal and synchronous structure of the "winter desert" of the Mojave and Great Basin areas far to the north (Beatley 1969). We conclude that the diversity and complexity of the Baja California flora provides a diverse resource base for reproduction by antelope ground squirrels, and that this has allowed for more individually flexible patterns of reproduction by the females. Corresponding to this, male *A. leucurus* must adapt to the females by remaining on standby and in reproductive readiness for mating with receptive females over a broader season as well.

The timing mechanism for the annual cycle of *A. leucurus* has previously been identified as a rigidly endogenous program. This is based on the observation that animals held in captivity under constant conditions are able to maintain a precise annual cycle of reproduction, metabolism, and other functions (Kenagy and Bartholomew 1979; Kenagy 1981). Such an endogenously controlled cycle might not have the same, if any, significance for *A. leucurus* in the southern Baja California peninsula, owing to lack of the strong environmental synchrony of trophic production that characterizes the plant communities of the Mojave and Great Basin Deserts. It will thus be interesting to determine whether such endogenous rhythmicity, as tested in the laboratory, exists in *A. leucurus* from Baja California, and furthermore, what year-to-year consistencies, if any, will be found in the breeding patterns of the natural populations.

We believe that our initial report on breeding patterns of antelope ground squirrels in Baja California Sur raises interesting questions about the phenotypic adjustments of a geographically widespread mammalian species throughout its entire latitudinal range. The ecology of both animal and plant reproduction and thus the trophic resource bases of antelope ground squirrels across their range represent a pattern that is more complex than a simple linear north-south thermal or climatic gradient. The framework of interacting temporal patterns of organisms and their environments should be an important theme in the further comparative investigation of this fascinating system. Populations of *A. leucurus* should be capable of adjusting their physiology and life history to survive and reproduce over the large geographic range. Further cooperative research between colleagues in Mexico and the United States should lead to progress in the understanding of these important questions.

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