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Reproductive cycle of the Belding ground squirrel (*Spermophilus beldingi beldingi*): seasonal and age differences

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REPRODUCTIVE CYCLE OF THE BELDING GROUND SQUIRREL (*SPERMOPHILUS BELDINGI BELDINGI*): SEASONAL AND AGE DIFFERENCES

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Abstract.— The reproductive cycle in Belding ground squirrels was studied in the Sierra Nevada Mountains at two locations, one at 2,100 m elevation, the other at 3,000 m.

Adults emerged from hibernation completely prepared physiologically for reproduction. Males tended to emerge slightly ahead of females and yearlings tended to emerge later than adults. Yearling females were fertile but produced smaller litters than adults, 4.48 vs. 6.31. Yearling males were infertile. They exhibited a slight seasonal cycle in testicular growth but did not reach sexual maturity. Testicular growth and spermatogenesis were incipient in many adults and in yearlings prior to hibernation.

Hibernation and seasonal breeding are important survival strategems of rodents living at high latitude or high altitude. Typically in these environments there are extreme seasonal oscillations in ambient conditions. Winters tend to be long and cold and summers brief and sharply delimited. Dormancy is employed as a means of bridging the long gap of energy shortage in winter, and breeding is coincident with the clement weather and abundant food of summer. Both responses require advance preparation and accurate timing to be maximally adaptive. The physiology of hibernation is currently a viable, active field of study, whereas seasonal breeding has aroused less interest and its complexities, especially in wild populations, are poorly understood (Chapman 1972).

Herein we report on seasonal changes in reproductive functions of the Belding ground squirrel (*Spermophilus beldingi beldingi*), a hibernator that lives at high altitude in the Sierra Nevada Mountains of California.

Methods

This study extended from 1969 to 1973 and was on *S. b. beldingi* living principally in meadows of Lee Vining Canyon, Mono County, California. A number of squirrels were live-trapped or shot at Big Bend (elevation ca. 2,100 m), but most data are from those living near Tioga Pass (elevation ca. 3,000 m). At both areas we carried on an extensive mark-release program throughout the time squirrels were active above ground. This program enabled us (1) to follow seasonal changes in body weights and dimensions and external appearance in individuals of known age and (2) to collect animals of known age for specimens.

Live-trapping was conducted with Tomahawk wire mesh traps baited with peanut butter. A few specimens were collected with a .22 caliber rifle. Animals trapped for the first time were toe-clipped in a standard pattern never involving more than one toe per foot. All animals were examined externally for appearance of vulva and mammae or of scrotal pigmentation and position of testes.

Freshly excised reproductive organs were fixed in Bouin's solution and transferred to 70 percent ethanol. At the time of transfer they were debrided, blotted, and weighed to the nearest 0.1 mg. Tissues were sectioned at 7 or 10μ and stained with hematoxylin and eosin. Measurements of seminiferous tubules were taken with an ocular micrometer.

Results

Arousal schedule.— The sequence and pace of events in the active season were alike at the two study areas, but the active season at Big Bend usually began at least six weeks in advance of that at Tioga Pass. Snowcover was not comparable at the two sites at the beginning of the season. At Big Bend most burrow sites were clear of snow when emergence occurred. At Tioga Pass emergence tended to begin on knolls that were the first areas to become snow free, but many individuals tunneled out at sites covered by snow up to a depth of 2 m. Similar ef-

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fects of snowpack on emergence of *S. columbianus* were noted by Shaw (1925). There was considerable annual variation in snow conditions and the schedule of *S. b. beldingi* was affected accordingly (see beyond).

Adult males were the first animals seen above ground at a given location, but a few adult females and an occasional yearling could be found within a few days thereafter.

Testes.— At emergence adult males had scrotal testes weighing about 2 to 3 g, the maximum weight seen during the entire active season (Fig. 1). The scrotum was darkly pigmented. Within a month after emergence testicular weight of adults began to decrease noticeably and testes had become inguinal or abdominal in position and scrotal pigmentation was decreasing. Six weeks after emergence testicular weight had decreased to a seasonal minimum that was maintained thereafter at Big Bend until onset of hibernation (Fig. 1, upper). At Tioga Pass, however, considerable increase in testicular weight of adults occurred during the last few weeks of the season (Fig. 1, lower).

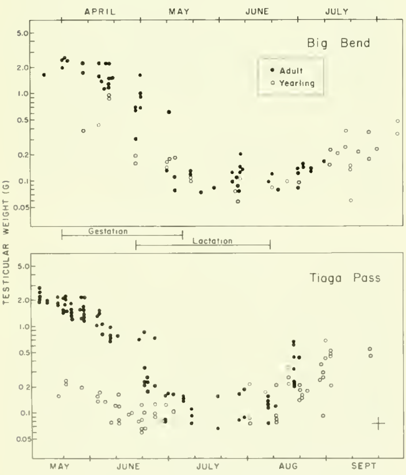

Fig. 1. Paired testes weights of *Spermophilus beldingi beldingi* throughout the active season at two study areas. Note log scale on ordinate. Cross on lower right corner of Tioga Pass data indicates mean testicular weight of juveniles prior to hibernation.

In histological perspective, testes of adults showed intense spermatogenic activity from time of emergence through onset of weight collapse. During this time seminiferous tubules were of large diameter (150 to 250μ) with spermatozoa filling the lumina. As testicular weight decreased spermatogenesis ceased and tubule diameter decreased. During June at Tioga Pass, for example, diameters went from about 150 to 60μ. Beyond June, lumina in seminiferous tubules were absent. Recrudescing testes of adults collected in late August at Tioga Pass had a thickening germinal layer with numerous primary spermatocytes and a few secondary spermatocytes present. Seminiferous tubules had enlarged slightly to a diameter of 80 to 100μ.

Yearling males tended to emerge later than adult males, were of smaller body size (Morton and Parmer, in press), and had considerably smaller abdominal testes (Fig. 1). This was most clearly observed at Tioga Pass where we had a larger pool of marked animals to collect from. Testes of yearlings were about three times heavier at emergence than when they entered hibernation the previous fall as juveniles. A decrease in testicular weight occurred soon after emergence, followed by an increase toward the end of the season.

Two yearlings collected at Big Bend on 18 April 1973 had paired testes weighing 920 and 940 mg. Seminal vesicles of these animals were 37.4 and 34.2 mg, respectively. Although well above resting level, neither set of glands approached those of sexually active adults in weight or cellular maturation.

There was some evidence of a cycle in spermatogenic activity in yearling testes in that a few spermatocytes were produced early in the season. Diameter of seminiferous tubules remained small (below 100μ) throughout the season, and no advanced stage of spermatogenesis was found in any yearling testis. As in adults at Tioga Pass, tubule diameter increased slightly in concert with increased testicular weight, and spermatocyte numbers increased just prior to hibernation.

Seminal vesicles.— Seminal vesicles of adults tended to increase in weight for a few days following emergence, remained at maximum size for a few weeks, then decreased to minimum size for the rest of the season (Fig. 2). These glands were only slightly enlarged in yearlings early in the season and tended to decrease in weight thereafter. As shown in *S. lateralis* by McKeever (1964), seminal vesicle growth is controlled by testicular hormone. The near-maximum size of seminal vesicles in recently emerged *S. b. beldingi* suggests that upon final arousal they have fully secretory testes.

In microscopic appearance the heaviest seminal vesicles of adults had a distended mucosal epithelium and lumina filled with seminal fluid in a colloidal state. As involution occurred the colloid disappeared, the mucosal layer became shrunken and folded, and the lumina nearly disappeared. This appearance was maintained through onset of dormancy. Seminal vesicles of yearlings were without detectable cellular change throughout the active season.

SEXUAL CYCLE OF FEMALES.— Adult females appeared to be sexually receptive almost immediately after emergence as judged by their swollen, open vulvae and enlarged, turgid uteri. Copulation was never observed, but additional evidence that mating occurred soon after emergence is that a few adults were already lactating during the fifth week after the first active females were seen. Gestation period in *S. beldingi* is thought to be 27 to 31 days (Turner 1972).

Yearlings were in estrous later in the season than adults because they tended to emerge later and because estrous appeared to be delayed in smaller yearlings until additional body growth had occurred.

Seasonal changes in ovarian weight were about two-fold and were similar for the two age groups. For the first six weeks after emergence ovaries weighed 20 to 30 mg. Weight then decreased to 8 to 15 mg for the remainder of the season.

Anovulatory follicles and corpora lutea tended to enlarge during gestation and reached maximum diameters at parturition. These structures shrank in postpartum females. By the end of lactation follicular cavities were much reduced or absent and corpora lutea were becoming indistinct. No ovarian recrudescence was observed in yearlings or adults prior to hibernation, but follicular enlargement

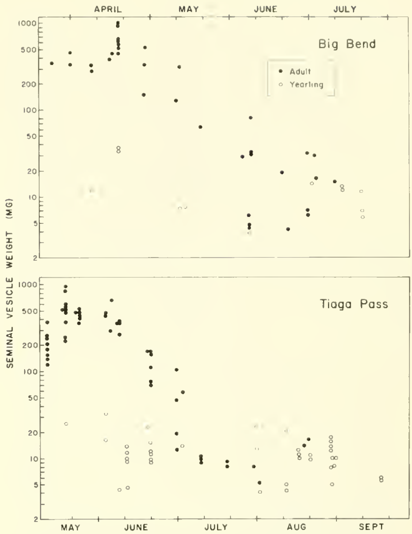

Fig. 2. Paired seminal vesicle weights of *Spermophilus beldingi beldingi* throughout the active season at two study areas. Note log scale on ordinate.

began in juveniles during their last weeks of activity after older animals had already become dormant.

Emergence of females at Tioga Pass occurred over a span of several weeks. As a result parturition dates were spread out and the percentage of females lactating at a given time was almost never 100 percent (Fig. 3). As far as we know, all females reproduced, although some of the smaller yearlings collected in late June at Tioga Pass had unscarred, thin, virgin-like uteri. Note that testicular atrophy was well advanced in adult males at that time (Fig. 1, lower). It is possible that a few yearling females did not bear young. Another possibility is that implantation was delayed in those of small body size. There are indications in other studies that female *Spermophilus* may become impregnated well after testicular collapse has begun in males (Wells 1935; Tomich 1962; McKeever 1966).

If these smaller females do have young, they will be born relatively late in the season (we have observed considerable disparity in size of juveniles at the end of the season; Morton, Maxwell, and

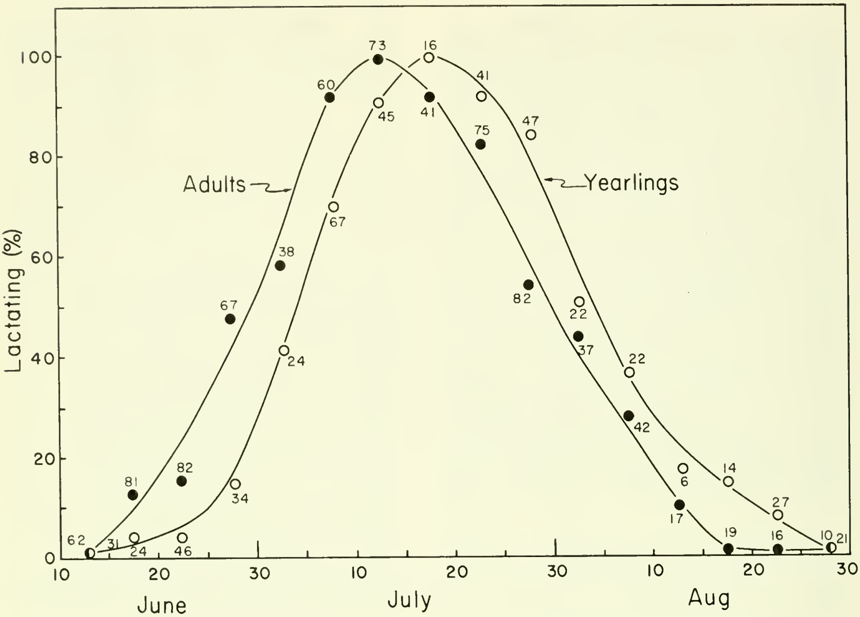

Fig. 3. Mean percentage of female *Spermophilus beldingi beldingi* thought to be lactating at specific 5-day intervals at Tioga Pass. Numerals indicate sample sizes.

Wade 1974), and if these young survive, a self-perpetuating cycle of late reproduction by small yearling females will have been established.

Litter size.— Our specimens and records of frequently retrapped females indicate that they have one litter per season. This was true even of the earlist females to breed. We obtained measurements of litter size through counts of placental scars and implanted embryos in collected specimens and through litters born in captivity (Table 1). The difference in means between counts of scars and of embryos was not different according to a *t* test (P> 0.05) but some prenatal loss did occur. Ten of the 228 embryos examined (4.4%) were partially reabsorbed. This is similar to the reabsorption rate found in *S. lateralis* (McKeever 1964; Skryja and Clark 1970) and in *S. richardsonii* (Sheppard 1974). The lowest estimate of litter size was obtained from births in captivity. Cannibalism of their young by confined females was noted in a few cases but all cases may not have been detected.

Table 1. Measurements of litter size in *Spermophilus beldingi beldingi*.

	Mean	S.D.	N
Placental scars			
Adults	6.88	1.22	17
Yearlings	5.00	....	2
Implanted embryos			
Adults	6.33	2.01	21
Yearlings	4.75	1.07	20
Young per captive			
Adults	5.71	1.45	17
Yearlings	4.00	1.00	5
Total, all measurements			
Adults	6.31	1.67	55
Yearlings	4.48	1.40	27

When all measurements were summed, mean litter size of adults (6.31) was significantly larger (P< 0.01) than that of yearlings (4.48). This is qüite similar to age differences in litter size observed in *S. armatus* (Slade and Balph 1974).

Discussion

In most published reports there is little indication that yearling *Spermophilus* of either sex are functionally or visually separable from older animals (compare Mayer and Roche 1954; McKeever 1963, 1964; Carl 1971; Zimmerman 1972), although they may constitute a considerable portion of the breeding population. However, yearlings engage in unique behavioral interactions with older animals as they are integrated into the community of reproducers (Michener and Michener 1973) and should be the focus of more study. Even in the larger-bodied sciurids such as *Marmota monax* (Christian, Steinberger, and McKinney 1972) and *Cynomys leucurus* (Bakko and Brown 1967) some males are sexually mature as yearlings.

The lack of reproductive capacity in yearling male but not in female *S. b. beldingi* is an interesting contrast that indicates the operation of sex-specific selection factors. As pointed out by Conaway (1971) the nonpregnant cycle is a rarity and cannot be afforded by most natural populations. The breeding season is delayed slightly in yearling female *S. b. beldingi* by their emergence schedule and the apparent necessity for some to attain greater body size before pregnancy. Nevertheless, all or nearly all do reproduce. In males, however, there is greater total body size to be reached than in females (Morton 1975) and selection seems to have favored the strategy of diverting energy expenditure from reproductive activities toward growth. Indeed from the last half of the yearling season onward males are significantly larger than females (Morton and Parmer, in press). We have additional evidence that delayed sexual development in male *S. b. beldingi* is tied directly to body size. Two males born in captivity and kept under classroom conditions for display became excessively obese in their first autumn, went through bouts of estivation for several months, and possessed scrotal testes soon after resuming normothermia at about nine months of age.

Growth rates of captive *S. b. beldingi* juveniles are comparable to those of other hibernatory *Spermophilus*, but there are indications that growth is much slower in feral animals than in captives even before weaning (Morton and Tung 1971). It may be that it is unusually difficult for *S. b. beldingi* living at high altitude to achieve adult size and reproductive potential simultaneously. We have suggested (Morton and Tung 1971) and now shown clearly (Morton and Parmer, in press) that *S. b. beldingi* do not reach maximum body size until late in their second year of life or beyond. Likewise, Sheppard (1972) found that yearling *S. richardsonii* aged on the bases of eye lens weight, tooth wear, and epiphyseal closure had smaller mean body weights than older animals.

The habitual lack of a reproductive cycle among certain male members of a population could not be tolerated unless a mating system were employed that assured impregnation of all receptive females. A priori one might expect reproductively active males in such a system to be polygamous. The details of the mating system of *S. b. beldingi* should be elucidated shortly by behavioral studies in progress at Tioga Pass by Paul Sherman of the University of Michigan.

The social system of a ground squirrel population has recently been implicated in sexual development of yearling males. Slade and Balph (1974) found that yearling male *S. armatus* seldom had scrotal testes and rarely, if ever, bred. After the population was artificially reduced, however, many yearling males were sexually active. Slade and Balph associate this precocity with low harassment as juveniles, early arousal from hibernation, and decreased encounters with aggressive squirrels following emergence. They did not report on body size in these animals.

It is possible but improbable that we have been studying a ground squirrel population with unique growth patterns and mating system. It is important to recognize that accurate aging in many studies has not been possible due to their brevity or to lack of history on recognizable individuals. For example, in his study of *S. b. oregonus* conducted in Lassen County, California, at 1,370 to 1,730 m elevation, McKeever (1963) refers only to adults and juveniles. Body weights shown for adult *S. b. oregonus* are 5 to 10 percent lower throughout the season than those of *S. b. beldingi* (Morton 1975), but juvenile *S. b. oregonus* are at least

20 percent heavier than *S. b. beldingi* (Morton, Maxwell, and Wade 1974) before entering hibernation. Mean maximum testicular weight occurs in both subspecies at the beginning of the active season, but it is about three times greater in *S. b. beldingi* than in *S. b. oregonus*. This seems anomalous to us and, coupled with body weight data and McKeever's observation that only 70 percent of adult male *S. b. oregonus* were sexually active, suggests that at least some yearling *S. b. oregonus* could be distinguished from older animals on the bases of body size or reproductive capacity if ages were known.

Finally, it should be recognized that unusual ecological conditions exist at high altitude. Many factors, both terrestrial and extraterrestrial in origin, could function as inhibitors of growth and development in young animals.

Seasonal breeding.— Growth of the reproductive tract during the whole hibernation period is well known among *Spermophilus*. Remarkably, gonadal recrudescence, at least of testes, begins even prior to dormancy in several species with short active seasons such as *S. undulatus* (Mitchell 1959; Hock 1960), *S. b. oregonus* (McKeever 1963), *S. lateralis* (McKeever 1964), *S. richardsonii* (Clark 1970), and *S. b. beldingi* (present study). McKeever (1963) noted that *S. b. oregonus* emerged with testes of maximum size. Usually the final stages of spermatogenesis in hibernatory *Spermophilus* are not reached until ten days or more after emergence even in species at high latitude (Hock 1960). The total readiness of *S. b. beldingi* to reproduce at time of emergence is undoubtedly a response to conditions imposed by the short summers of high altitude.

Seasonal breeding is highly adaptive in that young are born at a time favorable for their survival. At high altitude this favorable season is compressed temporally and has rather sharply drawn boundaries. To cope successfully with these circumstances the cycle of sexual maturation in *S. b. beldingi* is completed during dormancy. A corollary is that reproductive preparation must have a precise phase relationship to average snowmelt patterns and related environmental effects. There is sensitivity, however, on the part of newly emerged animals to ambient conditions. At Tioga Pass considerable annual variation in snowpack, schedule of snowmelt, and emergence of vegetation were documented (Morton, Maxwell, and Wade 1974; Morton, in press). The schedule of *S. b. beldingi* was affected accordingly. In 1969, for example, snowpack was about 240 percent above normal, whereas in 1972 it was 35 percent below normal. As judged by subsequent emergence times of juveniles and their growth curves, reproduction occurred about three weeks later in 1969 than in 1972 (Morton, Maxwell, and Wade 1974). Reproduction is not delayed inordinately, however, even in heavy snow years, because about 25 percent of prehibernatory fat reserves still remain at emergence, providing a buffer to food requirements during the first weeks of activity (Morton 1975).

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