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BODY SIZE, BODY COMPOSITION, AND BEHAVIOR OF JUVENILE BELDING GROUND SQUIRRELS

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Abstract.— Juvenile Belding ground squirrels were studied in the Sierra Nevada. Females were more trappable, had smaller home ranges, and tended to enter hibernation earlier than males. The primary sex ratio was 1:1. Individuals first emerged from the natal burrow at three to four weeks of age and a body weight of 35 g. Body weight and linear dimensions increased thereafter until hibernation began. Maximum prehibernatory weight of 200 to 260 g was attained at about 12 weeks of age. Prehibernatory fattening began at about six weeks of age. Maximum lipid stores attained weighed about 80 percent of the lean, dry body compartment. Seasonal changes occurred in weight of white and brown fat depots, adrenal glands, spleen, heart, kidneys, liver, and testes. Annual variations in snowpack and emergence schedule caused the reproductive period, and thus phenology of juveniles, to vary by as much as three weeks. The last animals to immerge were unusually small, being from late litters. Nonetheless, they may have had lipid stores sufficient for surviving hibernation.

In natural history studies of ground squirrels (*Spermophilus* sp.), juvenile members of the population are often ignored or examined only casually. Yet these young, inexperienced animals are logical subjects if one is trying to uncover fundamental adaptations of species to environments, such as high altitude, that are only seasonally accessible. Spermophiles survive in such environments through hibernation, and there is evidence that mechanisms favoring the success of juvenile hibernators, such as an accelerated ontogeny, are particularly important to the species as a whole (Mayer and Roche, 1954; Clark, 1970; Morton and Tung, 1971a).

In this article we present the biology of juvenile Belding ground squirrels, *Spermophilus beldingi beldingi*, from a population residing at high altitude in the Sierra Nevada of central California. Parameters of growth, behavior, prehibernatory fattening, and effects of annual variations in snowpack on the schedule of juveniles are discussed.

Methods

Data were gathered during a five-year period (1969–1973) on *S. b. beldingi* living on the eastern slope of the Sierra at the upper edge of the Mono Basin near Tioga Pass, Mono County, California. In this area there are subalpine meadows at elevations of 2926 to 3048 m (9600 to 10,000 ft) that are occupied by substantial numbers of *S. b. beldingi*.

Squirrels were live-trapped in Tomahawk wire mesh traps baited with peanut butter. Those to be released were toe-clipped for later identification, and those kept for dissection were etherized. Linear measurements were taken with calipers. Body weights were measured to the nearest 0.1 g on a Welch triple-beam pan balance. Fat pads,

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kidneys, heart, spleen, and liver were weighed to the nearest 0.01 g on an Ohaus analytical pan balance. Gonads and adrenals were weighed to the nearest 0.01 mg on a Federal Pacific torsion balance. Carcasses, including dissected portions, were kept frozen for later laboratory analysis of water and lipid content. Water content was determined by drying carcasses to a constant weight in a vacuum oven at 55C. They were then homogenized and extracted for lipid with petroleum ether in a soxhlet apparatus (Morton and Tung 1971b). Data on snow depth at Tioga Pass and predictions of snowmelt runoff from the Mono Basin were taken from Bulletins 120 and 129 of the California Department of Water Resources.

Results and Discussion

Seasonal Schedule of Events and Behavior.— Juvenile *S. b. beldingi* usually appeared above ground in mid-July. During the rest of the summer they gained in body size, deposited fat, and began entering hibernation in September at about three months of age. The last animals disappeared from the surface in the final ten days of September (1970) and the first ten days in October (1969, 1971, 1972, and 1973).

Differences were noted in the behavior of males and females in terms of trappability, size of home range, and onset of hibernation. In 1971 a grid of 64 traps with 20 m spacing was set and centered on a burrow system containing a group of newly born litters. Fifty-five juveniles (30 females, 25 males) born in this burrow system were captured. During the course of the summer, females were captured an average of 9.53 times (range, 1-30), significantly ($P<0.05$) more often than males, 5.32 times (range, 1-21). This difference in number of recaptures may be due to sex-specific differences in home range and dispersal. Thirteen juveniles were always trapped within the outer rows of traps. Six were males trapped an average of 14.2 times, and seven were females trapped an average of 22.3 times. The mean home range of these animals, calculated by the "halfway to the next trap" method (Hayne, 1949), was 6408 m^2 for males and 4434 m^2 for females. The home range of males was significantly larger ($P<0.05$).

There are indications that males tended to remain active later in the season than did females. In 1973 juveniles were consistently trapped and released at burrow systems on a section of meadow roughly 300 m x 300 m. Each trapping session was conducted for about four hours with about 40 traps. Traps were checked once per hour. The daily catch increased from late July through August (Fig. 1). During that time, males and females were captured in about equal numbers during each trapping session, and 93 different individuals were handled: 47 males and 46 females. Beyond the first week in September, however, more males than females were captured during every trapping session except the final one, on 5 October. During September 10 individuals were trapped that had not been handled previously; nine were males, and only one was a

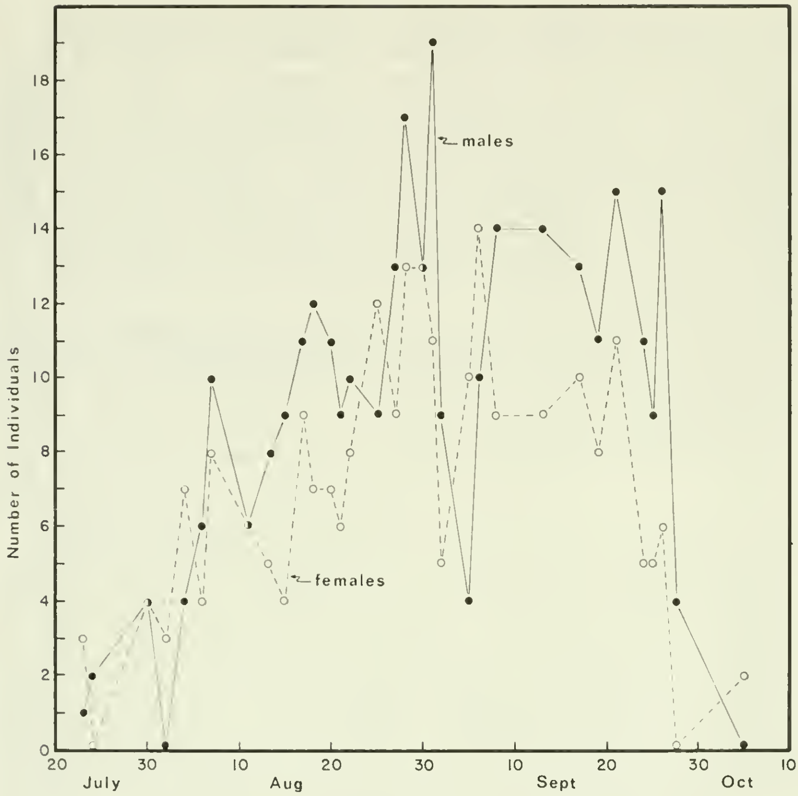


Fig. 1. Number of juvenile *Spermophilus beldingi beldingi* captured per trapping session during the 1973 season.

female. The four males captured on 28 September and the two females captured on 5 October were the last squirrels trapped or observed in the 1973 season, and all six were kept as specimens.

The larger home ranges of males, their lower rate of recapture, and their tendency to enter hibernation later than females are probably all indicators of greater dispersal of males from the natal area. Sex-specific emigration is common among young mammals and has been noted many times in ground squirrels (Quanstrom, 1971; Turner, 1972; Yeaton, 1972). One might predict that the hazards associated with dispersal would lead to greater mortality among juvenile males (Murray, 1967) and that an unbalanced sex ratio in favor of females would exist among those members of the population exceeding one year of age.

These data raise a question concerning the sex ratio in young squirrels. During the five years of this study, juveniles were captured or shot throughout the habitat at Tioga Pass known to harbor

S. b. beldingi. In all, 672 different individuals were handled: 336 males and 336 females. Clearly the sex ratio in juveniles was 1:1.

Seasonal Changes in Body Size.— Growth of young squirrels was evident in terms of their linear dimensions and body weights, as the season progressed. Both body length and hind-foot length increased throughout the summer (Fig. 2). There was considerable variance in foot length, however, and it would seem to be a poor indicator of age. Body length was a more reliable indicator and has been used to show that maximum body size is not achieved in *S. b. beldingi* until the end of the second season of life or beyond (Morton and Tung, 1971a).

In mid-September the oldest, largest juveniles began to enter hibernation, whereas the smallest, most immature individuals tended to remain active. This resulted in a decreased mean body size in late September samples.

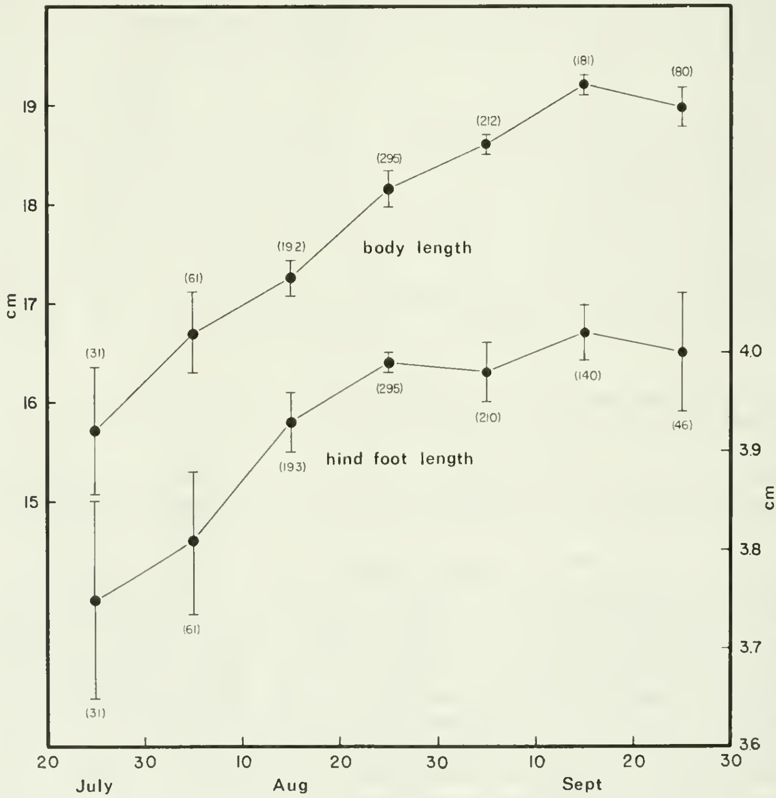
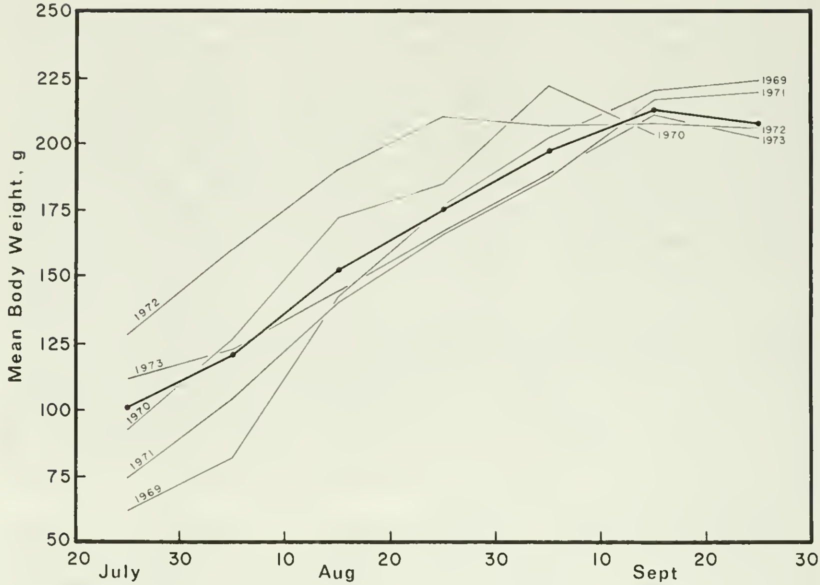


Fig. 2. Seasonal changes in mean body length and hind-foot length in juvenile *Spermophilus beldingi beldingi* at 10-day intervals. Data were pooled from five seasons, 1969-1973. Vertical lines indicate two S.E. Sample size shown in parentheses.

When they first emerged from the natal burrow, juveniles weighed about 35 g. For example, on 15 July 1970, members of one litter of six that were probably venturing out for the first time were observed for 40 minutes, then hand-captured and weighed. They paid no attention to an observer seated one m from them, and they did not go more than 1 m from the burrow entrance. Nevertheless, they sat erect, trilled, nibbled on grass, and when handled everted their anal glands. Coupling this information with that from captives of known age (Morton and Tung, 1971a), we estimate that these juveniles emerged at an age of three to four weeks. Their mean body weight was 36.4 g (range, 33.5-41.2 g), only one-half of what captives weigh at the same age (Morton and Tung, 1971a). Clearly, captives are precocious in comparison to wild juveniles, but the degree of precocity is difficult to determine. Turner (1972) has observed that *S. b. oregonus* juveniles attempt to nurse for the first few days after emerging from the natal burrow. Apparently the same behavior occurs in *S. b. beldingi*. Morhardt (1971) suggests that juvenile *S. b. beldingi* experience maternal care for about the first week following emergence.

Mean body weight increased steadily each season of the study, from about 100 g in late July to about 215 g in mid-September, where it leveled off as the fatter individuals began hibernating and were no longer sampled by us (Fig. 3). Because of the inability of the live traps to retain small juveniles and because of our preoccupation with other projects, no useful sample sizes were obtained until late July each year. As the season progressed thereafter, trapping success increased as the juveniles became larger and more active. During the final portion of September, trapping success decreased as the number of active squirrels decreased. There was considerable variation in mean body weight of the juvenile population from year to year. For example, 15 individuals weighed between 20 and 30 July 1973 were twice as heavy as 10 that were weighed during the same interval in 1969. There was a disparity of as much as three weeks in the dates at which specific mean body weights were reached. Obviously, young squirrels were not born within a certain very limited time year after year. These annual differences in growth schedules indicate that there is considerable variation in the timing of reproduction. Within a given season, variation occurred because females, even on the same meadow, emerged over a span of about a month, with adults tending to emerge ahead of yearlings. Furthermore, small yearling females often did not come into estrous until several weeks after emergence. Their offspring tended to be the ones that were active at the very end of the season.

There was also variation in the schedule of reproduction that could be attributed to annual differences in snowpack. Snow depth at the study area was measured every year in February and April, and in May 1969, by the State of California (Fig. 4, upper panel). Snowmelt runoff for the watershed of our study area (Mono Basin) was also forecast by them each month from February through May (Fig. 4, lower). Both of these measurements show that 1969 was



1969	10	12	43	17	39	51	21
1970	10	16	45	50	58	21	0
1971	12	19	41	102	87	78	43
1972	18	20	22	52	26	30	9
1973	15	42	95	131	103	72	67
Total	65	109	246	352	313	252	140

Fig. 3. Seasonal changes in mean body weight of juvenile *Spermophilus beldingi beldingi* at 10-day intervals. Heavy line shows means when data were pooled for all five seasons. Sample sizes are below each class interval.

the heaviest snow year during the study and that 1972 was the lightest. In fact, snowpack in 1969 was the heaviest recorded during the 44 years that the surveys have been taken, and snow was present on the study area for about a month longer than usual. In 1972 runoff was unusually early because of lack of precipitation and hot weather in March. These extremes in snow conditions strongly affected the timing of reproduction. As a result, juveniles reached prehibernatory weights several weeks earlier than usual in 1972, and they were larger early in the season than at comparable dates of other years. It is interesting that, despite their late start, the 1969 juveniles attained prehibernatory weight levels at about the same calendar time as in other years (Fig. 3). The basis for their increased growth rate is not known, but the wet, green phase of the meadow environment persisted much later than usual in 1969. This could have provided a highly favorable nutritional situation for young squirrels.

The data on mean body weights tend to obscure some rather important facets of growth and fattening as it actually occurred in individuals. Our records show that frequently captured, toe-clipped

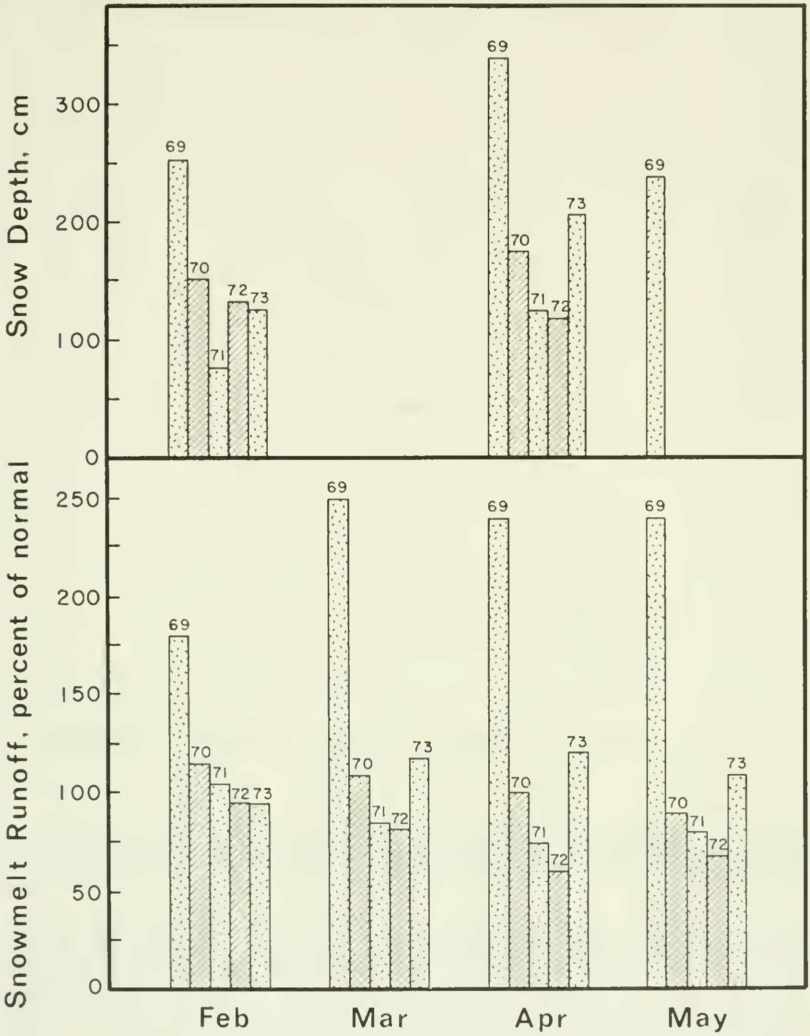


Fig. 4. Snow depth at Tioga Pass (upper) and snowmelt runoff predicted for Mono Basin (lower) from 1969 through 1973.

individuals gained body weight steadily throughout the season (Fig. 5). There often seemed to be a pause, however, in the rate of gain at midseason, followed by another rapid period of gain. The latter may have been caused primarily by prehibernatory fat deposition. Individuals entered hibernation shortly after maximum body weight (200-260 g) was obtained. A practical effect of this was that mean body weights leveled off or even declined as the oldest, fattest juveniles were no longer being trapped.

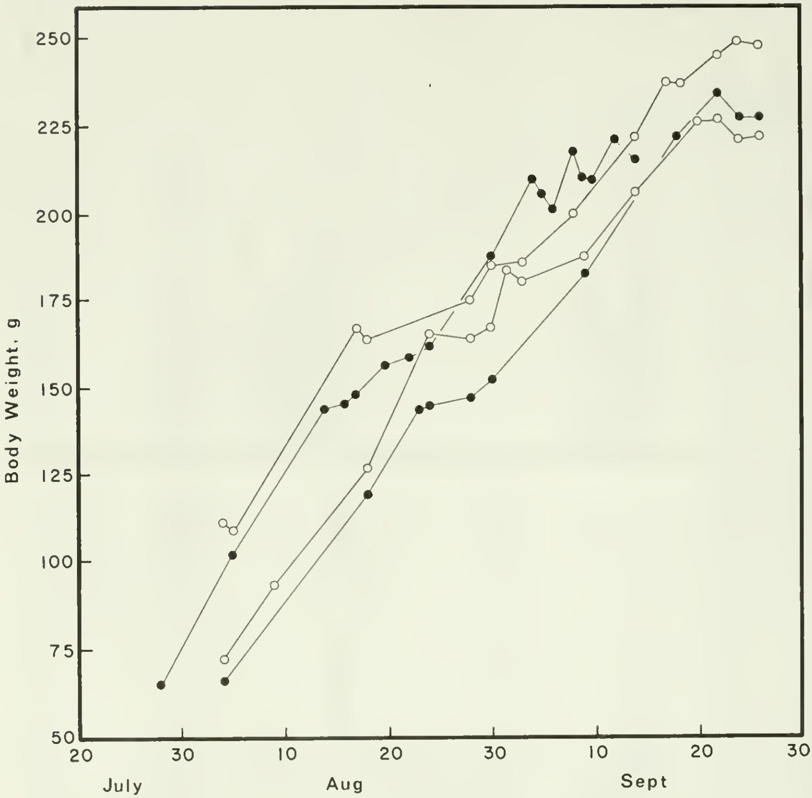


Fig. 5. Seasonal changes in body weight of four frequently recaptured juvenile *Spermophilus beldingi beldingi*. Open symbols represent females, closed symbols males.

To distinguish the prehibernatory fattening response from ordinary growth of nonlipid components, body composition of juveniles was analyzed throughout the season in 1973. These data show that juveniles began depositing significant quantities of lipid in mid-August (Fig. 6) and that the lipid compartment increased in weight for the next month. On the other hand, the lean, dry compartment of body mass increased only through late August then remained constant. Maximum lipid stores in juveniles occurred in mid-September. At that time lipid weighed 80 percent of the lean, dry compartment. In adult *S. b. beldingi*, lipid weighs about 125 percent of the lean, dry compartment at the time of hibernation (Morton, M.S.).

Morton and Tung (1971b) have shown that wet weight of both brown and white fat depots is correlated with total lipid stores in adult *S. b. beldingi*. In juveniles there was a seasonal increase in both absolute and relative mass of these depots (Fig. 7). This was

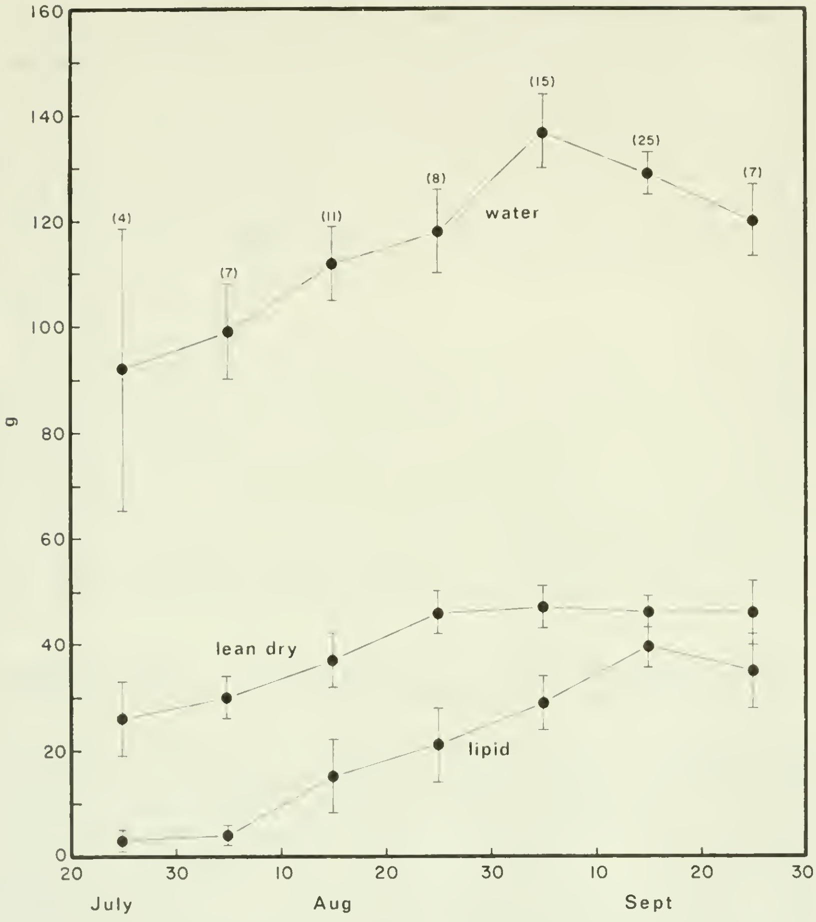


Fig. 6. Seasonal changes in mean weight of body components of juvenile *Spermophilus beldingi beldingi*. Vertical lines indicate two S.E. Sample size shown in parentheses.

expected for white fat because it is the primary form of intracorporeal energy storage in hibernators. Despite their comparatively limited mass, brown fat depots also show marked seasonal changes in size and may also be accurate indicators of general lipogenic activity.

It seems likely that *S. b. beldingi* do not hoard food; thus, all of the energy used during hibernation must come from catabolism of their own body tissues, principally fat. In juveniles it appears that fattening and overall growth were concurrent at first, but that caloric intake was then diverted primarily toward lipid synthesis and storage. This final phase was seen in a slowing of the increase in linear dimensions, in the leveling off of lean, dry body weight, and in the

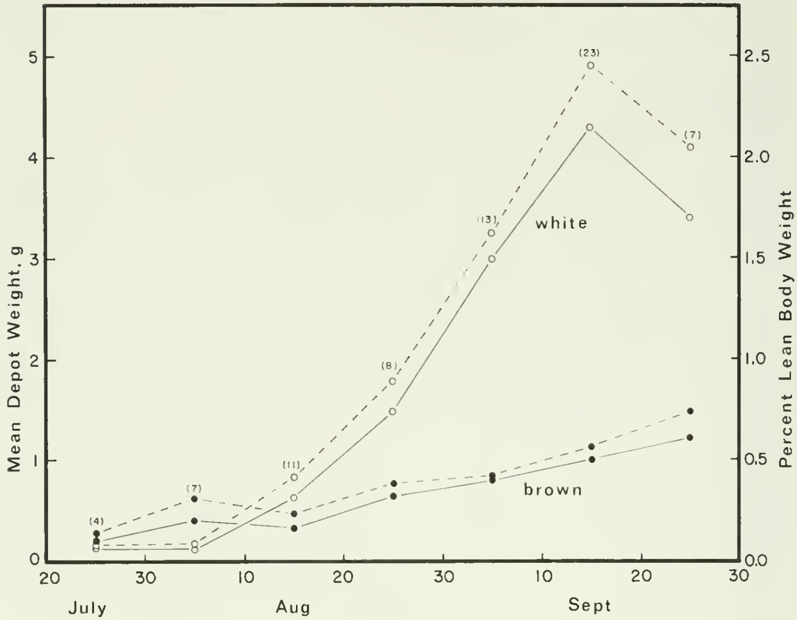


Fig. 7. Seasonal changes in mean absolute and relative weight of fat depots in juvenile *Spermophilus beldingi beldingi*. Sample size shown in parentheses.

mid-season pause in weight gain of individuals. The final relative stage of obesity attained was not as great as that observed in adults; however, the duration of hibernation may be about a month less in juveniles than in adults. A similar relationship was seen in *S. lateralis* (Jameson and Mead, 1964). The last juveniles to enter hibernation were from late litters and were excessively immature. Hock (1960) noticed the same phenomenon in *S. undulatus*. The ability of these immature individuals to survive a prolonged period of dormancy seems questionable, but we have some information suggesting otherwise. Consider, for example, the two females collected on 5 October. They were quite small, weighing only 137.5 and 150.1 g. Nevertheless, they had 19.7 and 30.0 g, respectively, of extractable carcass lipid. This was 61 and 88 percent of the lean, dry weight. In proportion, then, they had fat reserves comparable to those of normal-sized juveniles at the time of immergence. Perhaps the shift from general growth to lipogenesis occurs at an exceptionally small body size in juveniles from very late litters. This could be an important strategy for survival, particularly in populations existing in highly periodic environments. Mrosovsky (1971) has suggested that peak weight of hibernators at immergence is highly variable and will be determined by prevailing environmental conditions. Perhaps some of this variability in weight would seem less critical if the actual fat stores of the animals were known. It is not known how well the smaller juveniles survive hibernation, but we have observed every year that some very lean yearlings were among the first *S. b. beldingi* to emerge at Tioga Pass. This also underscores the difficulty of comparing our data with those of other workers. We have found that three functionally different age groups exist in *S. b. beldingi* at Tioga Pass: adults, yearlings, and juveniles. This can cause considerable confusion and distortion of data, particularly at the beginning and end of the active season, unless animals of known age are being dealt with. For example, in the fall, many of the smallest yearlings were active well into September and, on the basis of body weight, could not be distinguished from the largest juveniles at that time.

Seasonal Changes in Organ Size.— Various easily excised organs are often weighed in wild populations as indicators of growth and environmental adaptation. Our measurements of organs in juveniles are shown in absolute (Fig. 8) and relative terms (Fig. 9). The last sample in September consisted of four animals (all males) that were among the very last juveniles still active. They were smaller in body, kidney, liver, and spleen weight than animals sampled previously in the month and probably were from the last litters born that season. On the other hand, the adrenals of this last group weighed an average of 37 mg and were significantly heavier than those collected from the previous group in mid-September ($P<0.05$).

At one time it seemed that involution and hypofunction of all endocrines might be essential to normal hibernation. However, it eventually became clear that considerable variation existed in the functional status of endocrines, particularly the adrenal glands, at the onset of dormancy (Popovic, 1960). Within the last decade seasonal changes in adrenal size have been determined in several species of juvenile *Spermophilus*. There is considerable variation. For example, adrenal weights decreased seasonally in *S. b. oregonus* (McKeever, 1963), *S. tereticaudus* (Lyman and Chatfield, 1955; Neal, 1965) but increased in *S. beecheyi* (Tomich, 1962) and *S. richardsonii* (Clark, 1970). There are numerous problems associated with interpreting data of this type. Although adrenocortical secretion rate is probably a function of adrenal gland weight (Christian, 1962; Christian and Davis, 1964; Adams and Finn, 1972), there is no real assurance that this is true. The problem is exacerbated in juvenile hibernators in that normal growth and prehibernatory fattening may confuse the relationship between size and secretion rate when either absolute or relative weight changes are considered.

Increased adrenal weight has been most clearly linked to stress caused by increased social interaction (Christian, 1962); however, interplay among a multitude of factors is probably responsible for adrenal hypertrophy in many cases (Sheppard, 1968). In *S. b. beldingi* juveniles active at the very end of the season, for example, stress associated with difficulties in obtaining food and increased threat of predation might affect adrenal function.

Spleen size increased throughout the season. The same trend was

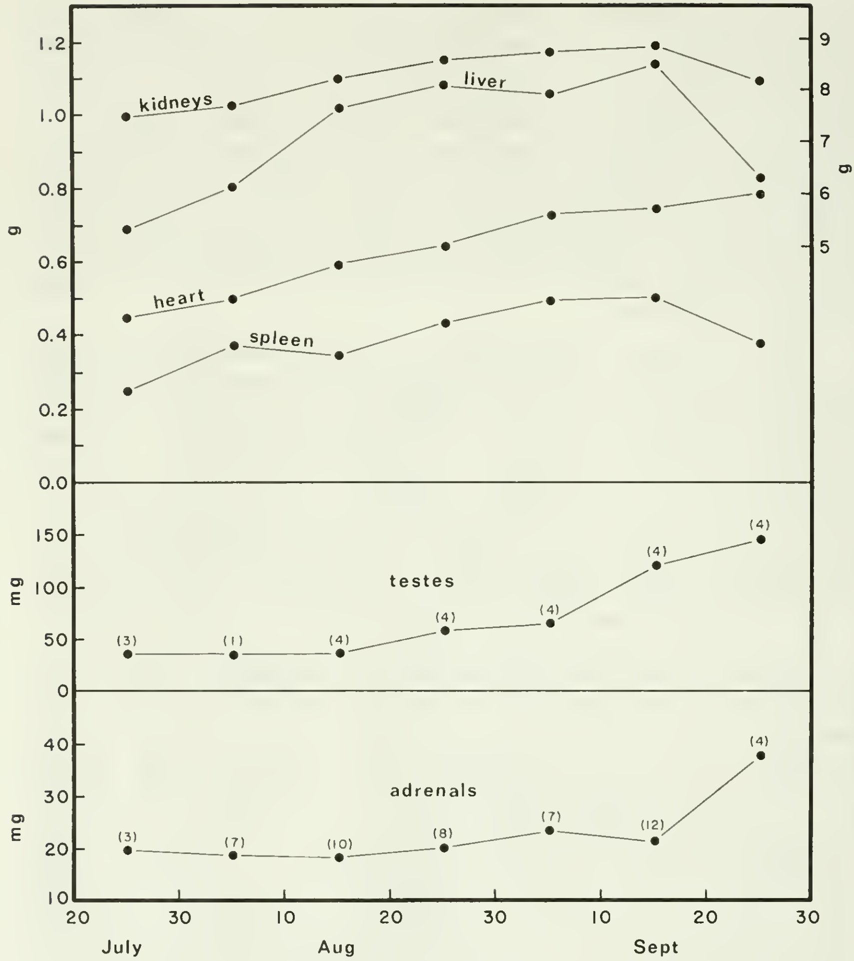


Fig. 8. Seasonal changes in mean organ weights of juvenile *Spermophilus beldingi beldingi*. Sample size shown for adrenals applies to other organs except testes.

observed in *S. b. oregonus* (McKeever, 1963), but, despite their similar body sizes, the spleens of juvenile *S. b. oregonus* were approximately twice as heavy as those of *S. b. beldingi*. The functional significance of this dramatic difference awaits investigation.

Kidneys enlarged slightly, in absolute terms, as the season progressed. Relative weight decreased, however. Heart weight increased in both absolute and relative terms. It is tempting to relate the size of these organs, particularly the heart, at the end of the season to their probable functional roles during torpor. The heart has a major role in the circulatory adjustments made during the

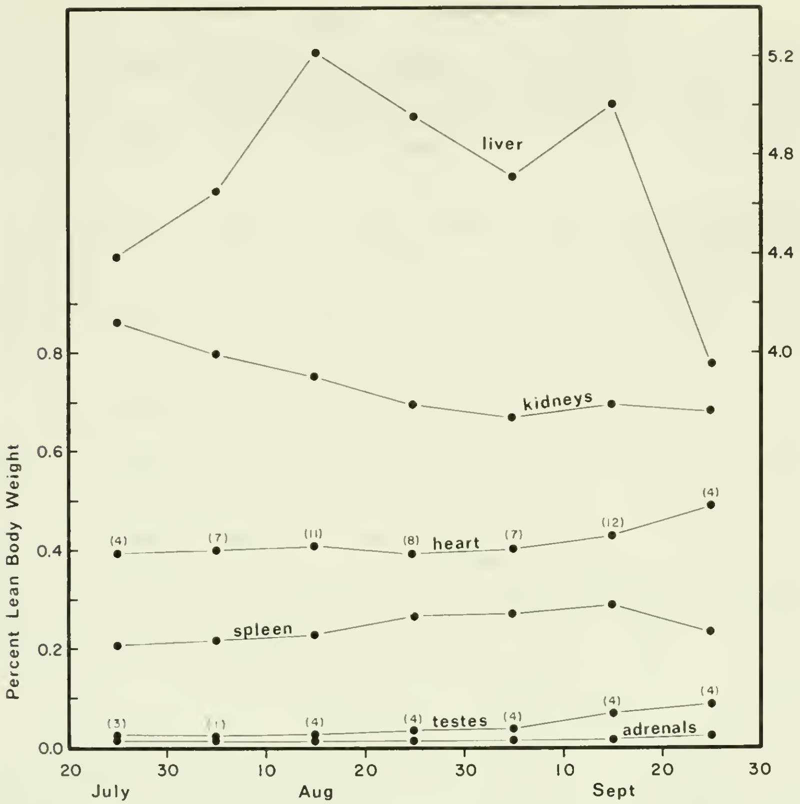


Fig. 9. Seasonal changes in organ size as a percentage of lean body weight in *Spermophilus beldingi beldingi*. Sample size shown for heart applies to other organs except testes.

arousals that occur regularly throughout the hibernation period. It may also be a source of heat that supplements the heat production of brown fat during arousals (Burlington et al., 1972). A small increase in heart weight was detected even during hibernation in the hedgehog, *Erinaceus europaeus* (Johansson and Senturia, 1972). Pretorpor and intratorpor hypertrophy of cardiac muscle could facilitate cardiac efficiency during arousals.

Livers reached maximum size early in the season then decreased significantly between our last two samples in September ($P<0.05$). This final decrease is difficult to understand but may be related to the unusual immaturity of animals active at the very end of the season.

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