Influence of energy stores on activation of reproductive function in male golden-mantled ground squirrels

Brian M. Barnes
Department of Zoology, University of Washington, Seattle, Washington 98195, USA

Accepted December 18, 1983

Summary. Male golden-mantled ground squirrels were captured in the field in late summer and placed on either unlimited or restricted (80% normal) food rations in the laboratory until each animal began to hibernate. At entrance into hibernation mean body mass was 274.5 g for the unlimited group and 224.5 g for the restricted group. Only six of 21 males subsequently underwent reproductive maturation during winter. Each of these six received the unlimited ration prior to hibernation, and these six included the five heaviest animals in the experiment. In addition to activating their reproductive systems, these heavier squirrels began hibernation later and ended hibernation earlier than the lighter squirrels. Squirrels that remained reproductively quiescent averaged 25.5% body mass as fat in early spring and thus were not severely limited in energy stores during winter.

In another experiment a group of 13 male and female squirrels were housed together in a common outdoor enclosure in order to examine the possible relationship between reproductive condition and social standing of males. Although there appeared to be a social hierarchy among males, each male fattened substantially in fall and became reproductively active during winter.

These results suggest that the level of energy stores accumulated as fat prior to hibernation in fall affects the potential of male ground squirrels to breed in spring. This dependence of reproductive development on energy stores may reflect the high energetic costs associated with breeding in males when they emerge from hibernation in spring when food availability is low.

Introduction

Golden-mantled ground squirrels have a single, brief mating season that begins each year directly after females emerge from hibernation in spring (McKeever 1964; Bronson 1979). A significant proportion of males, however, do not attempt to reproduce each year. Field studies on golden-mantled ground squirrels in the eastern Cascade Mountains of Washington (Kenagy and Barnes, unpublished) and the Sierra Nevada of California (Bronson 1979) have shown that one-quarter to one-third of all males do not undergo testicular development by the time of emergence from hibernation. Such males remain reproductively quiescent throughout spring and do not participate in breeding.

I undertook to investigate whether activation of reproductive function in male golden-mantled ground squirrels is dependent on the amount of energy stored as fat prior to entrance into hibernation. Male golden-mantled ground squirrels, like those of many other species of hibernating ground squirrels, terminate hibernation before females in early spring when snow is still present and before growth of food plants has begun (Davis 1976). Under these conditions males must meet the energetic demands of activity and preparation for the breeding season through the use of fat stored the previous year. Should a male not accumulate sufficient energy stores in fall, it might forego reproductive opportunities and instead continue to hibernate until food becomes abundant.

To determine the relation between pre-hibernatory body mass and spring reproductive status I restricted the food available to captive male golden-mantled ground squirrels in late summer prior
to the hibernation season. I then examined condition of the reproductive system at the end of hibernation in spring by measuring size of the testes and plasma levels of gonadal steroid hormones.

In addition to the influence of energy stores, social interactions may affect the reproductive status of males. Male juvenile Uinta ground squirrels appear to be inhibited from developing reproductively as a result of aggression by dominant individuals (Slade and Balph 1974). Therefore I also examined the influence of social interactions on the development of reproductive function in male golden-mantled ground squirrels.

Materials and methods

Food restriction

Male Spermophilus saturatus were captured in the eastern Cascades, Chelan County, Washington during the last week of August 1981. S. saturatus, found in Washington and British Columbia, is closely related and possibly conspecific to the more familiar golden-mantled ground squirrel S. lateralis which is common to the mountains of much of western North America (Hall 1981). Without dissection it is difficult to distinguish juvenile from older animals at this time of year (Kenagy and Barnes, unpublished); but, based on the late date in the season, it is likely that all of the animals captured for this experiment were juveniles. Squirrels were separated into two groups of equal distribution according to body mass and housed separately in metal cages with burlap cloth for bedding. One group (n=10) received Purina Rodent Laboratory Chow ad libitum, the other (n=15) received limited amounts of lab chow every three days because it represents the difference between the mean spring food and non-reproductive squirrels under natural conditions (Bronson 1979). Both groups were exposed to changes in daylength that approximated natural daylengths at the area of capture (47°N. Lat.) and to an ambient temperature of 20 °C which was lowered weekly by two or three degrees until 4 °C was reached on 1 November 1981. Each animal was examined daily for torpor, and sawdust was placed on hibernating squirrels to indicate by its subsequent presence or absence whether an arousal had occurred between observations. Food was removed from each animal’s cage on the second consecutive day of torpor. In spring food was replaced on the third day of continuous activity or on 5 May, whichever came first. Animals were weighed twice per week until 1 November and thereafter every three weeks. Blood samples (0.8 ml) were taken by cardiac puncture at three week intervals between 1400 and 1600 hrs PST after exposure to ether. In all cases blood samples were obtained within two min after each animal was picked up.

Four hibernating males died on 24 March 1982 during a mechanical failure that led to a temporary excursion of ambient temperature below 0 °C. The carcass of each was dried and extracted with chloroform in a Soxhlet apparatus for an analysis of total body fat.

On 18 May each male was removed from the cold, anesthetized with ether, and, upon laparotomy, the length and width of one testis was measured from which mass of both testes was estimated (Kenagy 1979). At the same time the scrotal skin was scored as being either pigmented or nonpigmented.

Radioimmunoassays. Concentration of testosterone was measured in plasma by RIA using procedures similar to those of Wingfield and Farner (1975). 100–200 µl of plasma were equilibrated with approximately 2000 cpm of 3H-testosterone and extracted with 10 volumes of dichloromethane. Extracts were dried, redissolved in 10% ethyl acetate in isoctane and transferred to columns of Celite:ethylene glycol:propylene glycol (6:1.5:1.5, w:v:v) with Celite:water (3:1, w:v) “glycol traps”. Testosterone was eluted with 20% ethyl acetate in isoctane after elution of dihydrotestosterone with 10% ethyl acetate in isoctane. The dried extracts were then assayed for testosterone in duplicate and individual values corrected for recovery. Minimum detectable levels of hormone for an average plasma volume ranged from 40–50 pg/ml. The hormone values compared were measured within one assay.

Social behavior. Nine males and four females were housed together on the roof of Kincaid Hall in Seattle in an outdoor enclosure (2 x 3 x 2.5 m) with wire screen sides and a translucent roof. Four males and four females were captured in May 1981 and placed in the enclosure; the remaining 5 males were captured and put into the enclosure in August 1981. Each squirrel was toe clipped and distinctively marked by black hair dye. Lab chow and water were provided ad libitum. Nine wooden nest boxes with burlap were provided, and a series of runways allowed squirrels to move throughout the height of the cage. From September to December, 35 half-hour observation sessions were conducted from a blind on separate days. At the beginning of each session 50–100 g of sunflower seeds (a highly preferred food) were scattered over the floor of the enclosure. The order in which individuals emerged from nest boxes to feed and the identity of squirrels involved in agonistic behaviors (chases and fights) were recorded. Each month animals were weighed and the reproductive condition of males was determined by the externally apparent size of the testes and the presence or absence of black pigment in the scrotal skin.

Results

Body mass and reproduction

At the end of the hibernation season only six of the 21 squirrels housed individually had become reproductively active, and all of these were from the group with unrestricted food. Mean testis size, plasma testosterone levels, and scrotal skin pigmentation in these six males (Table 1) were similar to those in reproductively active males at a similar date in the field (Kenagy and Barnes, unpublished; Barnes 1983) or in the laboratory (Licht et al. 1982; Barnes 1983). Testes in the other squirrels remained undeveloped, plasma testosterone at low levels, and scrotal skin unpigmented (Table 1).

Mean body mass of the six males that became reproductively mature measured either at the seasonal maximum in early fall or on the first day of hibernation was significantly greater than that of the non-reproductive males at the same times (Fig. 1; Table 1). At the time of capture mean body masses of the subsequently reproductive and non-reproductive groups were not significantly differ-