ANNUAL CYCLE OF BODY COMPOSITION AND HIBERNATION IN FREE-LIVING ARCTIC GROUND SQUIRRELS

C. Loren Buck and Brian M. Barnes

*Institute of Arctic Biology and Department of Biology and Wildlife,
University of Alaska Fairbanks, Fairbanks, AK 99775*

We monitored a natural population of arctic ground squirrels (*Spermophilus parryii kennicottii*) on the North Slope of Alaska for seasonal changes in body mass and composition and dates of immergence into and emergence from hibernation. Yearlings and adult females were at the lowest body mass of their active season at emergence in spring. Their mean body mass did not increase for 1 month after emergence and peaked in July (adult females) and August (yearlings). Body mass of adult males was near the highest of the active season when they emerged from hibernation and decreased by 21% over the subsequent 10-day mating season. Juveniles gained body mass during their active season, except for significant losses associated with dispersal. During hibernation, females lost >30% of their body mass, but adult males emerged in spring without significant decreases in body mass, fat, or lean. Yearling and nonreproductive males were significantly lower in fat but not lean mass at emergence than immergence, and females were significantly lower in fat and lean mass. Arctic ground squirrels entered hibernation over a >1-month interval beginning in early August; females entered before males, and adults of each sex immerged before juveniles. Reproductive males emerged before females, and fatter females emerged significantly earlier than leaner females. Vaginal estrus was maximal at 3 days post-emergence. Nonreproductive males emerged last from hibernation. Mean ± *SE* days in hibernation was 240.1 ± 12.1 for adult females (69% of the year), 235.8 ± 10.3 for juvenile females, 230.3 ± 4.2 for nonreproductive males, 220.3 ± 12.5 for adult males, and 214.7 ± 6.5 for juvenile males. Timing of immergence into and emergence from hibernation for arctic ground squirrels did not differ significantly from sciurid populations in temperate latitudes.

Key words: *Spermophilus parryii*, ground squirrel, hibernation, arctic, body mass, fat, life history, Alaska

Most ground squirrels (*Spermophilus*) are obligate hibernators with endogenously timed annual cycles of body mass, reproduction, and a dormancy in winter when reserves of energy are conserved through profound reduction of metabolic rate and body temperature (Barnes and Ritter, 1993; Barnes and York, 1990; Kenagy, 1987; Wang, 1979). These reserves, composed primarily of body fat and protein and, in males of several species, caches of food, are obtained during the active season when reproduction and growth of juveniles also must occur. Year-to-year differences in the annual cycle and mortality of ground squirrel populations can depend on when and

whether these reserves are achieved. Timing of autumn immergence into hibernation is delayed until a suitable body mass is reached (*S. beldingi*—Morton et al., 1974), and energy reserves an individual accumulates are correlated positively with overwinter survival (*S. richardsonii*—Michener, 1974, 1978; *S. columbianus*—Murie and Boag, 1984; *S. armatus*—Slade and Balph, 1974). Sufficient time and opportunities to accomplish reproduction, growth, and achieving reserves also may determine altitudinal and latitudinal distributions of hibernating ground squirrels.

The arctic ground squirrel has a Holarctic distribution and is the northern-most hiber-

nator in North America, living in sporadically dense populations that reach the coast of the Arctic Ocean (Hall, 1981). Mayer (1953) and Hock (1960) suggested that, at the northern-most part of their distribution, arctic ground squirrels experience the most severe overwinter environment, the longest hibernation season, and consequently the shortest active season of any hibernator. For populations living in northern Alaska, the growing season of vegetation is usually 6–10 weeks (Chapin and Shaver, 1985), and winter is characterized by extreme sub-zero temperatures ($<-20°C$) for 7–8 months, frozen soils, snow, high winds, and darkness. Unlike most temperate-dwelling ground squirrels, arctic ground squirrels regularly begin their season of activity when environmental conditions are still harsh. This should require strategies for collecting and managing energy reserves, as reflected in annual cycles of body mass, fat, and protein, and schedules of hibernation that differ from populations in less seasonal environments. Further, as has been demonstrated in other species (Barnes, 1996; Michener, 1984; Michener and Locklear, 1990), these patterns should differ with gender and age, reflecting differences in sexual behaviors and requirements for reproductive maturation between females and males.

Three field studies have monitored timing of immergence and emergence and seasonal patterns of body mass change in this species (Hock, 1960; Mayer and Roche, 1954; McLean and Towns, 1981). However, all but the study of Mayer and Roche (1954) were conducted on the sub-arctic subspecies, *S. parryii plesius*. Galster and Morrison (1976) published data on body composition from captive arctic ground squirrels of the northern-most subspecies, *S. p. kennicottii*, at different times in their annual cycle. Information on changes in body fat and lean mass of free-living animals, however, is absent. This information can give insight into nutritional and metabolic requirements of hibernation, especially un-

der harsh environmental conditions. Data also are lacking on changes in body mass and composition of individual animals during winter and changes in body mass in relation to chronologies of immergence and emergence of different age and sex classes. We describe these features of an arctic population of *S. p. kennicottii* and compare them with published values from temperate populations and other species of hibernators.

Materials and Methods

Study area.—Our study was conducted along the shores of Toolik Lake (68°38′N, 149°38′W) at 809 m above mean sea level in the northern foothills of the Brooks Range, Alaska. The site was categorized as cotton grass (*Eriophorum*) tussock and dry tundra, and >98% of the vegetative biomass and productivity was attributable to only 10 species (Shaver et al., 1986). The topography was gently rolling hills underlain by continuous permafrost. Depth of thaw of soil each year was shallow, usually <1 m (Buck, 1998). Predators of ground squirrels on the study site included ravens (*Corvus corax*), ermine (*Mustela erminea*), long-tailed jaegers (*Stercorarius longicaudus*), snowy owls (*Nyctea scandiaca*), short-eared owls (*Asio flammeus*), golden eagles (*Aquila chrysaetos*), northern harriers (*Circus cyaneus*), gyrfalcons (*Falco rusticolus*), wolverines (*Gulo luscus*), red foxes (*Vulpes fulva*), wolves (*Canis lupus*), and grizzly bears (*Ursus horribilis*).

Capture and handling of animals.—Body fat, lean mass, and timing of hibernation were determined for arctic ground squirrels live-trapped in 1993 (22 April–17 May, 13 August–6 September), 1994 (9 April–10 May, 22 August–22 September), and 1995 (9 April–12 May, 6–16 October) using Tomahawk traps baited with carrots. Body-mass changes of the population were collected intermittently from April to September 1987–1995 and were combined. During trapping sessions, 40–80 traps were set in early morning and examined every 1–3 h until traps were closed in late evening. Traps were set at known burrow sites dispersed along 4.0 km within 0.8 km of the north and east shores of Toolik Lake. Burrow sites of arctic ground squirrels were identified easily on small rises on the tundra. Because much of the region was unsuitable for

burrows due to flooding, permafrost, or rocky glacial moraine that makes digging difficult, newly excavated burrows in the Toolik area were rare. In 1987, 53 burrow sites were identified, and only 8 new burrows were discovered over the next 8 years.

Trapped animals were transported to the Toolik Field Station of the University of Alaska Fairbanks, were anesthetized by a 3–5 min exposure to methoxyflurane, and were weighed with a Pesola spring scale to the nearest 1.0 g. Body mass and composition of individual ground squirrels at their last capture in autumn were used to indicate their pre-immergent condition. Body mass and composition at emergence were measured at first capture in spring ≤2 days of each animal's first appearance above ground. Ground squirrels were termed juveniles if trapped during the active season of their birth year and yearlings after their first winter. Animals that hibernated ≥2 seasons were termed adult. Males were scored as reproductive if testes in spring were descended into a pigmented scrotal sac; reproductive males also had a strong musky odor. Nonreproductive males were yearlings that failed to attain reproductive maturity in their first spring. During late April and early May, vaginal lavages were performed on anesthetized females by pipetting 0.2–0.5 ml of saline into the vagina and removing it again with a short-stemmed Pasteur pipette. Contents of lavages were placed between a slide and a coverslip and were examined with a microscope under low power (10×). Percentage of cornified epithelial cells was estimated for a field of ca. 100 epithelial and leucocytic cells.

Newly captured animals were ear-tagged, and their pelage was dyed black in unique patterns for identification in the field. Beginning in autumn 1994, all newly captured animals also were implanted subcutaneously with a passive integrated transponder (Schooley et al., 1993). Animals were released at the site of capture after recovery from anesthesia. Total time in the laboratory ranged from 1–3 h. The Institutional Animal Care and Use Committee at the University of Alaska Fairbanks approved all procedures used in this study.

Beginning in spring 1993, lean mass of animals was estimated by the total-body electrical conductance (TOBEC) method (Walsberg, 1988) with an Emscan Model SA-2 (Springfield, IL). Animals were anesthetized and weighed before being positioned in a restraining tube and inserted into the Emscan unit head first and ventrum up. Measurements of conductance were repeated until three equal values were generated. Care was taken to ensure similar positioning between measures and among animals. Fat mass was calculated as the difference between body mass and estimated lean mass. For predicting lean mass via TOBEC, we generated a species-specific equation for *S. parryii kennicottii*. After measuring for Emscan value, animals (11 females and 6 males weighing 475–1,200 g) used for calibration were euthanized and stored at −20° C. Frozen carcasses were shaved, cut into small pieces, and homogenized with a meat grinder. Three portions (ca. 30 g each) were dried to constant mass in a convection oven at 60°C (12–16 h), and fat was extracted with a Soxlet apparatus with petroleum ether for 12–16 hours (Dobush et al., 1985). The remaining lean tissue was dried to constant mass, percent fat of sub-samples was averaged, and total fat mass was calculated by extrapolating to the total animal. The regression (Zar, 1984) equation to predict lean mass was: lean mass = 185.81 + 0.267 × (Emscan reading), yielding an r^2 = 0.87 for predicting lean mass and r^2 = 0.82 for predicting fat mass ($P < 0.001$).

Chronologies of immergence and emergence.—Dates of immergence were included only for animals that were resident at a burrow site in summer and autumn and were captured again at that same site the following spring. The last day in autumn that the animal was captured was assigned as its immergence date. Some adult females immerged each year before trapping began in August, as indicated by a plugged burrow entrance from which they emerged during the next spring. Dates of immergence for those individuals were listed as <13 August in 1993 and <22 August in 1994. Emergence dates for males were estimated from the first appearance of an exit hole in the snow at known burrow sites and subsequent trapping of an animal at that location. In most instances, detection of an exit hole and capture of the occupant occurred the same day, and all males were trapped ≤2 days of emergence. First emergence of females was estimated similarly. If the emergence hole of a female was not identified, the observation of dandruff on the animal when first captured indicated a recent (24–48 h) end to heterothermy (Barnes and Ritter, 1993). Length of
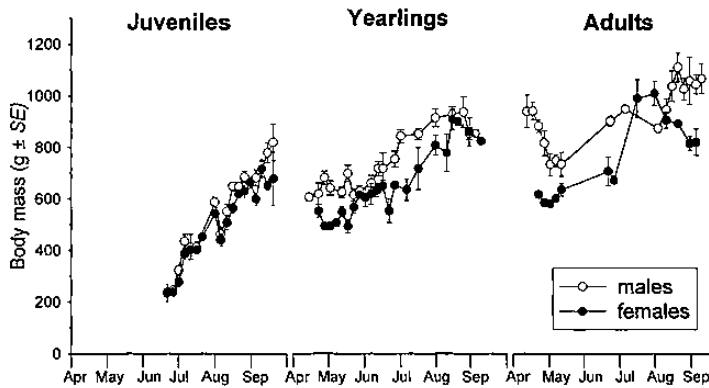
Fig. 1.—Body mass (5-day means ± *SE*) of arctic ground squirrels during their above ground active season, April–October, at Toolik Lake, Alaska. Data from 1987 to 1995 are with sex and age classes separated; sample for juvenile males = 6–40 (median = 16), juvenile females = 2–50 (median = 16), yearling males = 2–17 (median = 6), yearling females = 1–52 (median = 10), adult males = 2–24 (median = 6), and adult females = 3–60 (median = 7).

hibernation was calculated from immergence and emergence dates of individuals overwintering in 1993–1994 and 1994–1995.

Snow cover and depth.—We visually estimated snow cover each day in spring for the Toolik Lake area and recorded it as a percentage of the area with snow ≤1 km of the shore of Toolik Lake. Snow depth was measured on 12 April at the same 18 burrow sites in 1994 and 1995 and was averaged.

Statistical analyses.—Data were reported as mean ± *SE*. To produce a normal distribution, percentages were arcsin-square root transformed before analysis. For comparisons between two groups, we used *t*-tests for independent measures and paired *t*-tests for repeated measures. When assumptions of normality were not met, we used Mann-Whitney rank sum tests (Zar, 1984). For multiple group comparisons of normally distributed data, we used one-way analyses of variance (ANOVA) to test for significant differences among groups and Tukey's tests for pair-wise comparisons. Multiple-group comparisons with non-normally distributed data were analyzed with the Kruskal-Wallis test to examine differences among groups and Dunn's Method for pair-wise comparisons. We used a simple linear regression to examine associations between body mass and composition and emergence date. All differences were considered significant at *P* < 0.05.

RESULTS

Changes in body mass.—Juvenile animals first emerged from their natal burrows in the last week of June. Mean body mass on 24 June (males, 237 ± 8 g; females, 232 ± 32 g) approximately tripled before immergence into hibernation in early to mid-September (males, 820 ± 71 g; females, 678 ± 104 g), yielding mean growth rates of 7 and 5 g/day, respectively (Fig. 1). By September, juvenile females were similar to adult females in body mass, but juvenile males still weighed less than adult males (*F* = 13.71, *d.f.* = 64, *P* < 0.001). Both sexes decreased temporarily in body mass from late July to early August (males, *t* = 2.94, *d.f.* = 38, *P* = 0.006; females, *t* = 3.26, *d.f.* = 53, *P* = 0.002), coinciding with when juveniles began to be trapped away from their natal burrows.

Body mass of yearling males averaged 647 ± 18 g in April and 873 ± 13 g in September, yielding a mean gain of 35.0% over the active season. Body mass of yearling females averaged 506 ± 11 g in April and 855.0 ± 45.8 g for the last week of August and the 1st week of September, a 68% gain during the active season.
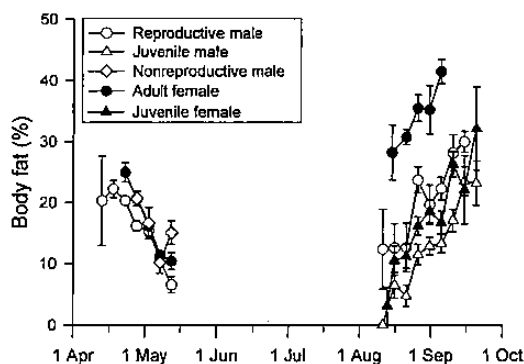
Average body mass of adult males de-

FIG. 2.—Percentage of body fat (mean ± *SE*) of free-living arctic ground squirrels at Toolik Lake, Alaska, 1993–1995. Juveniles were born in May; nonreproductive males are yearlings that did not mature sexually. Data for reproductive male yearlings are combined with adults. Median $n = 13$ for adult males, 14 for juvenile males, 24 for adult females, 18 for juvenile females, and 8 for nonreproductive males.

creased from 941 ± 29 g at emergence in mid-April to 740 ± 23 g in the 1st week of May, a 21% decrease that represented a mean loss of 12 g/day/individual. Gain in body mass was gradual through June and July but rapid in early August. Body mass in adult males peaked at 1026 ± 42 g in mid-August and remained elevated in September until males immerged into hibernation. Average body mass of adult females was lowest at emergence in spring (597 ± 9 g) and peaked at 1010 ± 47 g in late July. The decrease in mean body mass in August–September was likely due to early immergence of the largest females. Peak body masses of adult males and females did not differ ($t = -0.433$, *d.f.* $= 15$, $P = 0.671$), although females achieved maximum mass ca. 1 month prior to males.

Changes in body composition in the active season.—All sex and age classes emerged from hibernation with substantial stores of fat (ca. 20%), which then decreased significantly in spring (Fig. 2). Fat mass of reproductive males decreased from 194 ± 19 g to 48 ± 10 g from mid-April to mid-May ($t = 6.71$, *d.f.* $= 29$, $P <$

0.001), a 68.3% loss, and percent body fat decreased from 22.0% to 7.5% ($t = 6.514$, *d.f.* $= 29$, $P < 0.001$; Fig. 2). Lean mass of reproductive males did not change ($t = 0.392$, *d.f.* $= 29$, $P = 0.39$). Similarly, fat mass in females decreased from 146 ± 11 g to 66 ± 9 g ($t = 5.73$, *d.f.* $= 51$, $P < 0.001$) from late April to mid-May, a 54.8 % loss, and percent body fat decreased from 24.9 ± 1.6 to 10.4 ± 1.3 %. Lean mass in females, however, increased 26.2 % (430 ± 11 to 542 ± 16 g) over the same time period. Fat mass of nonreproductive males decreased from late April to early May ($t = 3.18$, *d.f.* $= 12$, $P = 0.008$), but by mid-May percentage of fat rebounded to levels not different from measures in late April ($t = 2.05$, *d.f.* $= 7$, $P = 0.080$). Lean mass of non-reproductive males did not differ from late April to May ($t = 0.617$, *d.f.* $= 7$, $P = 0.56$).

All animals increased in fat mass and percent body fat in the weeks prior to immergence into hibernation (Fig. 2). Adult females averaged 41.5 ± 2.0%, juvenile females 32.1 ± 6.8 %, adult males 30.0 ± 1.7 %, and juvenile males 23.2 ± 3.6 % body fat at last capture. Adult ground squirrels had a higher percentage of body fat than juveniles ($t = 8.16$, *d.f.* $=395$, $P <0.001$), and adult females were fatter than all other classes ($H = 75.38$, *d.f.* $= 3$, $P < 0.001$).

Dates of immergence and emergence.— In 1993 and 1994, females immerged before males and adults immerged before juveniles (Fig. 3a). More than 30% of adult females immerged by the 1st day of trapping (13 August), and all had by 11 September. Fewer than 5% of juvenile females immerged prior to the 1st day of trapping, and >90% immerged by the last day of trapping (22 September). Juvenile and adult males began to immerge on 27 August, and 62.6% of juvenile males and 66.5% of adult males immerged by 22 September. No animals were observed above ground after 6 October.
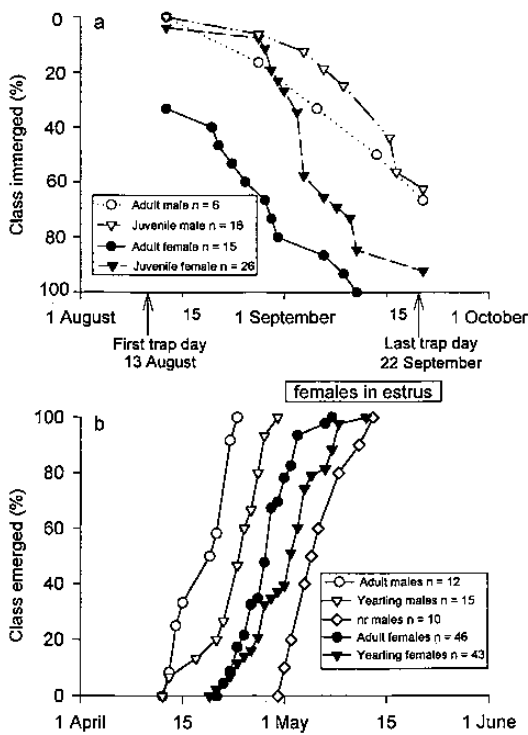
In 1994 and 1995, emergence occurred

FIG. 3.—Hibernation schedule for arctic ground squirrels at Toolik Lake, Alaska; a) immergence (percentage ceasing above ground activity) in 1993 and 1994 and b) emergence (percentage reappeared in 1994 and 1995) of separate age and sex classes. The box labeled "females in estrus" denotes when females with vaginal lavages showing >50% epithelial cells were trapped.

from 12 April to 13 May (Fig. 3b). Reproductive males emerged before females, and yearlings emerged after adults. Nonreproductive males were the last to resume surface activity. Depth of snow on 12 April, the date of emergence of the first male, was 24.4 ± 3.3 cm in 1994 and 36.5 ± 9.5 cm in 1995. Snow cover was still >70% after all animals had emerged. In both years, almost all reproductive males appeared on the surface prior to emergence of the first female. The first nonreproductive male emerged after all other males and 70% of adult females and 35% of yearling females appeared. Among females, date of first

emergence was significantly correlated with body composition but not with body mass. Fatter females emerged earlier than leaner females of the same age class (adult females, $r^2 = 0.229$, $P = 0.001$; yearling females, $r^2 = 0.163$, $P = 0.009$). Emergence dates of males were not significantly correlated with either body mass or composition.

Estimated length of hibernation.—Duration of hibernation for females (237 ± 2.2 days) was longer than for reproductive males (218 ± 3.8 days; $t = 4.21$, $d.f. = 29$, $P < 0.001$) and intermediate for nonreproductive males (230 ± 2.4 days). Duration of hibernation of adult (240 ± 4.3 days) and juvenile females (236 ± 2.5 days) did not differ ($t = 0.91$, $d.f. = 22$, $P = 0.372$).

Body composition in successive autumn and spring.—Mean body masses of ground squirrels at immergence, based on combined data from autumn 1993 and 1994, were 947 ± 37 g for adult males, 733 ± 80 g for juvenile males that were reproductive as yearlings, 765 ± 78 g for juvenile males that were nonreproductive as yearlings, 851 ± 17 g for adult females, and 607 ± 15 g for juvenile females. Body masses of the same individuals at emergence in spring averaged 922 ± 46.8 g for adult males, 644 ± 44 g for yearling reproductive males, 520 ± 35 g for yearling nonreproductive males, 574 ± 17 g for adult females, and 423 ± 14 g for yearling females (Fig. 4a).

Change in body masses of reproductive adult and juvenile males before and after hibernation were not different (adult males, $t = 0.53$, $d.f. = 9$, $P = 0.610$; juvenile males, $t = 2.17$, $d.f. = 4$, $P = 0.095$), averaging 3 and 13.5%, respectively. Change in body masses of nonreproductive males (30%), adult females (33%), and juvenile females (30%) were different before and after hibernation (nonreproductive males, $t = 4.56$, $d.f. = 5$, $P = 0.006$; adult females, $t = 15.57$, $d.f. = 14$, $P < 0.001$; juvenile females, $t = 8.67$, $d.f. = 15$, $P < 0.001$).

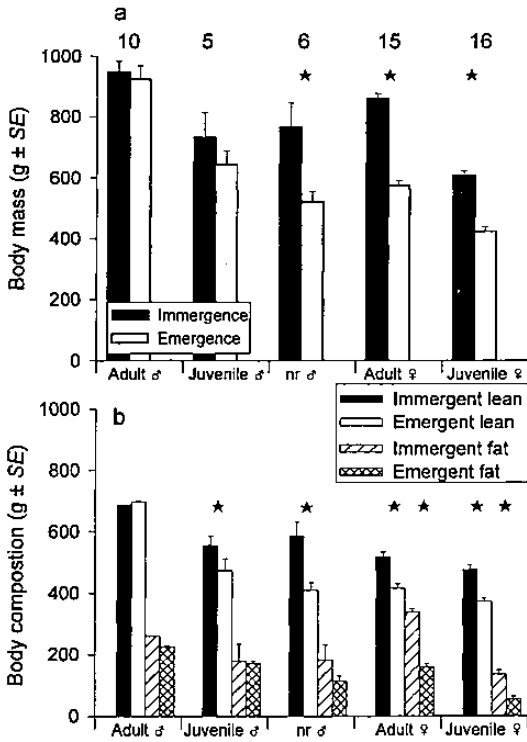Adult males were the only class that emerged from hibernation without a differ-

FIG. 4.—Overwinter change in body condition of arctic ground squirrels at Toolik Lake, Alaska, 1993–1995; a) mean $\pm$ *SE* body mass at immergence and emergence and b) mass of body fat and mass of body lean at immergence and emergence. Values are repeated measures of the same individuals (*n* indicated above bars in top panel) caught before and after hibernation. Immergent versus emergent mass measures that significantly differ within the cohort are designated by (★); nr refers to nonreproductive.
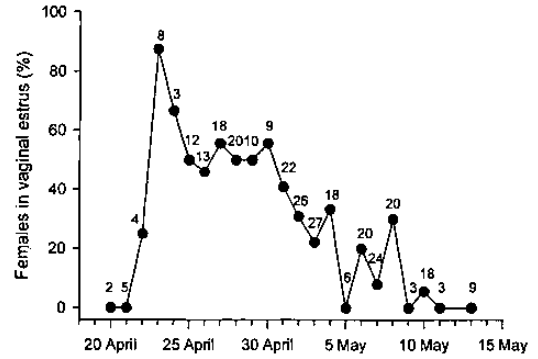
FIG. 5.—Percentage of female arctic ground squirrels with >50% epithelial cells in vaginal lavages. Data are from mating seasons at Toolik Lake, Alaska, 1993–1995; *n* above symbols.

ence in body composition compared with pre-immergent measurements (change in lean mass, $t = 0.31$, *d.f.* = 9, $P = 0.765$; change in fat mass, $t = 1.23$, *d.f.* = 9, $P = 0.250$). Reproductive and nonreproductive juvenile males emerged with less lean mass (reproductive males, $t = 2.94$, *d.f.* = 4, $P = 0.042$; nonreproductive males, $t = 3.8$, *d.f.* = 5, $P = 0.013$) but without a significant reduction in fat mass (reproductive males, $t = 0.13$, *d.f.* = 4, $P = 0.901$; nonreproductive males, $t = 1.80$, *d.f.* = 0.133, $P = 0.133$). Adult and juvenile females lost

lean mass (juvenile females, $t = 4.94$, *d.f* = 15, $P < 0.001$; adult females, $t = 5.44$, *d.f.* = 14, $P < 0.001$) and fat mass (juvenile females, $t = 4.12$, *d.f.* = 15, $P < 0.001$; adult females, $t = 13.26$, *d.f.* = 14, $P < 0.001$) during winter (Fig. 4b).

Vaginal estrus.—At first capture in spring, females had only partial openings to their vaginae and unswollen labia, and vaginal lavages yielded ca. 25% cornified epithelial cells and 75% leucocytes. In the next 3 days, vaginae opened fully, labia became swollen and crenulated, and percentage of epithelial cells increased to >50%, indicative of vaginal estrus. The percentage of females in the population with >50% epithelial cells peaked at 87.5% on 23 April and remained >46% until 1 May (Fig. 5). Individual females with >50% cornified epithelial cells occurred in the population between 22 April and 10 May. Sperm plugs were discovered in females between 28 April and 6 May.

Persistence of resident juveniles.—Of 32 juvenile males and 33 juvenile females caught and marked soon after they first emerged from their natal burrows in July 1993, 25% of males and 73% of females were trapped within the study area 2 months later. Of those, 62.5% of males and 58% of females successfully overwintered

and were caught the next spring. Three of five (60%) of those now yearling males still on the study site in spring were nonreproductive, with undescended testes and no visible scrotum.

DISCUSSION

Our results describe the timing of the annual cycles of hibernation and reproduction and accompanying changes in body mass and composition in a population of arctic ground squirrels living 230 km N of the Arctic Circle. At this latitude, winters are long and climatically severe, and productive seasons conversely short. Compared with more temperate populations and species of sciurid rodents, distinctive features of this arctic population include large body size of individuals, a related ability to store fat, and the inferred importance of stored food to reproductive males. These features may be critical to overwinter survival and reproductive maturation and activity of males in spring. The study population apparently relies on catabolism of lean body mass during hibernation, which may reflect a need for continuous thermogenesis during hibernation in subfreezing burrows.

As in other species of hibernating ground squirrels (Michener, 1984; Michener and Locklear, 1990), pattern and timing of changes in body mass and composition in arctic ground squirrels at Toolik Lake, Alaska, depended on sex and age of individuals. When animals first emerged from hibernation in spring, yearlings and adult females had their lowest body mass of the season, but adult males were near their maximum mass. Adult males then lost body mass from mid-April to early May, while other age and sex classes maintained stable body masses. These differences, together with differences in timing of body mass gain in summer and changes in body composition during winter, may reflect differences among each sex and age class in breeding requirements and strategies, and use of food caches in the hibernacula.

Reproductive males first appeared in

spring with levels of body mass and composition that did not differ significantly from pre-immergence, but females and nonreproductive males decreased substantially in body mass while hibernating. Because low tissue temperatures of hibernation inhibit gonadal development (Barnes et al., 1987), male ground squirrels require a prolonged (1–4 week) interval of high euthermic body temperatures after heterothermy for reproductive maturation (Barnes, 1996; Barnes et al., 1986; Michener, 1992). Their lack of loss of body mass at emergence suggests that male arctic ground squirrels spend this interval of pre-emergence euthermy sequestered within their hibernacula and feeding from caches of food stored the previous autumn. During this time, they are able to fully compensate for body mass lost during the previous 7–8 months of hibernation. Studies of male *S. parryii* in captivity show that males indeed lose body mass during the heterothermic season, decreasing in body mass, on average, by 48% (Galster and Morrison, 1976)—greater than our measurements for females and nonreproductive males. Thus, in the field, reproductively mature adult males undergo an additional sub-cycle in change in body mass, accompanied by changes in appetite, anabolism, and catabolism, gaining 30% during several weeks of pre-emergence euthermy and then promptly losing 21% of body mass during the subsequent mating season. Emergence at high body mass would provide males with endogenous body stores for use during the mating season. This would reduce time needed for foraging when forage opportunities are limited and confer an advantage during competitive male-male interactions in which body size is correlated positively with dominance (McLean and Towns, 1981; Watton and Keenleyside, 1973). These conclusions are similar to those of McLean and Towns (1981) for a southern population of arctic ground squirrels in the Yukon Territory, and those of Michener and Locklear (1990) for juvenile male Richardson's ground squirrels in Al-

berta, and offer a partial explanation for other studies that have demonstrated less loss of body mass in males than females in winter (Kenagy et al., 1989; Mayer and Roche, 1954).

The substantial loss of body mass by adult males during their first 3 weeks after emergence is consistent with depletion of cached food and with increased activity associated with mating. Vaginal lavages showed that this interval corresponds to estrus and mating in females. During this time, males were seldom seen feeding and appeared highly active, searching for females and interacting aggressively with other males. Females, however, remained near their burrow sites and frequently were observed digging around snow-free areas (Buck, 1998). Similar differences between sexes in mating behavior have been observed in other populations of *S. parryii* and other species of ground squirrels (Kenagy et al, 1989; Lacey et al., 1997; McLean and Towns, 1981; Michener and Locklear, 1990).

All age and sex classes of ground squirrels lost fat during spring. Snow cover remained near 100% until late April, and loss of fat was consistent with poor foraging opportunities. Nonreproductive males were the first to replace their body fat, presumably because they did not incur energetic costs of reproduction. Only females increased in lean body mass during spring, which may reflect growth of fetuses.

Juveniles gained body mass from their first appearance above ground in late June until 1 August, after which they lost 16–18% of their body mass. That was when juveniles first began to be trapped away from their natal burrows. Older ground squirrels continued to gain body mass during that period; thus, increased energetic costs, decreased foraging time associated with dispersal behavior, or both, rather than a change in availability of food, appears to have caused the loss in body mass in juveniles. Juvenile males were three times more likely than females to disappear from

the study area in late July and early August, suggesting male-biased dispersal (Holekamp and Sherman, 1989), or a greater risk of mortality in males.

Energetic expenses of lactation appear to delay gain of body mass in female ground squirrels until after the end of June (Kenagy et al., 1989), whereas males began to increase in body mass in early June, coinciding with the beginning of green plant growth (Chapin and Shaver, 1985). Captive male and female arctic ground squirrels begin to gain body mass immediately after ending hibernation and peak in body mass within only 2 months (Boyer et al., 1997). In the field, however, gains in body mass associated with pre-hibernatory fattening began in July in females and were delayed until mid-August and September in males.

Changes in body composition of individuals in winter indicated that lean and fat body mass decreased significantly during hibernation in females. Males presumably metabolized fat and lean mass during hibernation, but restored those before emerging in spring. Our estimates of loss of lean mass and those of Galster and Morrison (1976) for captive arctic ground squirrels suggest that significant amounts of muscle are catabolized during hibernation in this species. Fat is thought to be the major metabolic fuel during hibernation (South and House, 1967), but increased turnover of glucose may be associated with the continuous thermogenesis and elevation of metabolic rate in hibernation that accompanies overwintering in subfreezing soils (Barnes, 1989; Buck, 1998). Protein can serve as a glucose source during prolonged fasts when triacylglyceride turnover and synthesis of glucose from glycerol are low, as during torpor. Galster and Morrison (1976) concluded that replenishment of blood glucose from muscle catabolism occurs during hibernation but is confined to the euthermic phase of arousal intervals.

Because there is essentially no available forage when males first emerge in spring, males that enter hibernation without ade-

quate food stores may be unable to mature reproductively and therefore hibernate longer. Nonreproductive males were the last to emerge in spring and showed changes in body composition during winter more similar to females than reproductive males, which suggests nonreproductive males may have had an inadequate supply of cached food. This proposed dependence of male reproductive maturation on presence of adequate cached food is similar to the relationship between reproductive maturation and pre-hibernation body mass and fat stores in male *S. saturatus* and *S. beldingi* (Barnes, 1984; Forger et al., 1986; Holmes, 1988). In those studies, smaller and leaner males, or males that had adipose tissue surgically removed prior to hibernation, failed or were delayed in their reproductive maturation during the subsequent spring. In our study, however, body mass and percent fat at immergence of yearling males that remained immature did not differ from those that became reproductive, suggesting that both adequate body condition and food stores are required for male ground squirrels to attempt reproduction under arctic conditions.

McLean and Towns (1981) trapped male but very few female arctic ground squirrels with cheek pouches full of seeds in August and September; males emptied their pouches during quick trips to their burrow systems. Carl (1971) reported high levels of interaction and aggression among male *S. parryii* in autumn, which may be associated with behavioral defense of burrows with caches. Caching among several other species of hibernating ground squirrels has been observed to be an activity of males but not females (*S. saturatus*—Kenagy et al., 1989; *S. parryii*—Krogg, 1954; *S. richardsonii*—Michener, 1993; *S. columbianus*—Shaw, 1926). Caching behavior therefore may relate to the requirement for a prolonged interval of euthermy prior to emergence and thus be an additional cost of reproduction for male ground squirrels (Barnes, 1996; Barnes et al., 1986; Michener and Locklear, 1990). Strict dependence

on a cache for reproductive maturation, as hypothesized here for male arctic ground squirrels, likely is limited to environments with minimal foraging opportunities on emergence in spring.

The annual chronology of hibernation of this arctic population of *S. p. kennicottii* is similar to subarctic populations of *S. p. plesius* (Hock, 1960; McLean and Towns, 1981) and is remarkably comparable to more temperate-dwelling species of *Spermophilus* including *S. columbianus* (51°N—Murie and Harris, 1982; Young, 1990), *S. saturatus* (47°N—Kenagy et al., 1989), and *S. lateralis* (40°N—Bronson, 1979; Phillips, 1984). All of these, including our population, emerge from and immerge into hibernation during the same 2–3 weeks within each calendar year (Barnes, 1996). *S. richardsonii* in Alberta, Canada, which emerges and immerges ≥1 month earlier than other species (Michener, 1992), is an exception to this general chronology. Environmental conditions faced by arctic ground squirrels upon emergence, however, are more hostile than for other species, with snow cover and frozen soils lingering well into May. Emergence from hibernation under similar environmental conditions has been associated with high mortality of breeding adults in other species (Morton and Sherman, 1978). Mean duration of hibernation (215–240 days) that we documented is within the range described for *Spermophilus* (Barnes, 1996). However, a requirement for continuous thermogenesis in very cold burrows (Buck, 1998) throughout hibernation should result in the highest absolute cost of hibernation for this compared with nonarctic populations of hibernators. These challenges may be tolerable in *S. parryii* due to its relatively large body size and ability to store fat, which result in physiological efficiencies for thermoregulation and a relatively longer ability to withstand fasts (French, 1986; Morrison, 1960).

In populations of *Spermophilus* for which multiple-year studies are available, timing of spring emergence can vary >3

weeks from year to year (Michener, 1984). Variable timing of emergence is correlated with proximate factors such as snow cover Bronson, 1979; Phillips, 1984), snow depth (Morton and Sherman, 1978; Murie and Harris, 1982), air temperature (Knopf and Balph, 1977; Murie and Harris, 1982), and soil temperature (Iverson and Turner, 1972; Michener, 1978; Wade, 1950). First emergence of *S. p. kenocottii* was consistent in the 2 years of this study, even though air temperature and snow cover varied substantially. The first male emerged from hibernation on 12 April in 1994 and 1995 at Toolik Lake. Mean air temperature on that day was −41.2°C in 1994 and −23.6°C in 1995, and snow thickness differed by 50%. Hock (1960) reported consistent timing of emergence among years with dissimilar environmental conditions for subarctic dwelling arctic ground squirrels (*S. p. plesius*). Relative inflexibility in timing of emergence and breeding may be adaptive in environments like the Arctic with short growing seasons, where animals emerging earlier would find truly intolerable conditions and animals delaying emergence would leave insufficient time for their offspring to grow and fatten in preparation for hibernation.

LITERATURE CITED

BARNES, B. M. 1984. Influence of energy stores on activation of reproductive function in male golden-mantled ground squirrels. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology, 154:421–425.

———. 1989. Freeze avoidance in a mammal: body temperatures below 0°C in an arctic hibernator. Science, 244:1593–1594.

———. 1996. Relationships between hibernation and reproduction in male ground squirrels. Pp. 71–80, *in* Adaptations to the cold (F. Geiser, A. J. Hulbert, and S. C. Nicol, eds.). University of New England Press, Armidale, New South Wales.

BARNES, B. M., AND D. RITTER. 1993. Patterns of body temperature change in hibernating arctic ground squirrels. Pp. 119–130, *in* Life in the cold: ecological, physiological, and molecular mechanisms (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

BARNES, B. M., AND A. YORK. 1990. Effect of winter high temperatures on reproduction and circannual rhythms in hibernating ground squirrels. Journal of Biological Rhythms, 5:119–130.

BARNES, B. M., P. LICHT, AND I. ZUCKER. 1987. Temperature dependence of *in vitro* androgen production in testes from hibernating ground squirrels, *Spermophilus lateralis.* Canadian Journal of Zoology, 65: 3020–3023.

BARNES, B. M., M. KRETZMANN, P. LICHT, AND I. ZUCKER. 1986. The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis.* Canadian Journal of Zoology, 65:3020–3023.

BOYER, B. B., O. A. ORMSETH, L. BUCK, M. NICOLSON, M. A. PELLEYMOUNTER, AND B. M. BARNES. 1997. Leptin prevents post-hibernation body mass gain but does not reduce energy expenditure in arctic ground squirrels. Comparative Biochemistry and Physiology, C. Pharmacology, Toxicology, and Endocrinology. 118:405–413.

BRONSON, M. T. 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). Ecology, 60:272–279.

BUCK, C. L. 1998. Physiological ecology of the arctic ground squirrel: energy metabolism, torpor, and behavioral endocrinology. Ph. D. dissertation, University of Alaska Fairbanks, Fairbanks.

CARL, E. A. 1971. Population control in arctic ground squirrels. Ecology, 52:395–413.

CHAPIN, F. S. III, AND G. R. SHAVER. 1985. Arctic. Pp. 16–32, *in* Physiological ecology of North American plant communities (B. F. Cabot and H. A. Mooney, eds.) Chapin and Hall, Inc., New York.

DOBUSH, G. R., C. D. ANKNEY, AND D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. Canadian Journal of Zoology, 63:1917–1920.

FORGER, N. G., J. DARK, B. M. BARNES, AND I. ZUCKER. 1986. Fat ablation and food restriction influence reproductive development and hibernation in ground squirrels. Biology of Reproduction, 34:831–840.

FRENCH, A. R. 1986. Patterns of thermoregulation during hibernation. Pp. 393–492, *in* Living in the cold: physiological and biochemical adaptations (H. C. Heller, X. J. Musacchia, and L. C. H. Wang, eds.). Elsevier Science Publishing Company, Inc., New York.

GALSTER, W., AND P. MORRISON. 1976. Seasonal changes in body composition of the arctic ground

squirrel, *Citellus undulatus*. Canadian Journal of Zoology, 54:74–78.

HALL, E. R. 1981. The mammals of North America: Second ed. John Wiley & Sons, New York, 1:1–600 + 90.

HOCK, R. J. 1960. Seasonal variations in physiologic functions of arctic ground squirrels and black bears. Pp. 155–171, *in* Mammalian hibernation (C. P. Lyman and A. R. Dawe, eds.). Bulletin of the Museum of Comparative Zoology, 124.

HOLEKAMP, K. E., AND P. W. SHERMAN. 1989. Why male ground squirrels disperse. American Scientist, 77:232–239.

HOLMES, W. G. 1988. Body fat influences sexual maturation in captive male Belding's ground squirrels. Canadian Journal of Zoology, 66:1620–1625.

IVERSON, S. L., AND B. N. TURNER. 1972. Natural history of a Manitoba population of Franklin's ground squirrel. The Canadian Field-Naturalist, 86:145–149.

KENAGY, G. J. 1987. Interrelation of endogenous annual rhythms of reproduction and hibernation in the golden-mantled ground squirrel. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology, 135:333–339.

KENAGY, G. J., S. M. SHARBAUGH, AND K. A. NAGY. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia, 78:269–282.

KNOPF, F. L., AND D. F. BALPH. 1977. Annual periodicity of Uinta ground squirrels. The Southwestern Naturalist, 22:213–224.

KROGG, J. 1954. Storing food items in the winter nest of the Alaskan ground squirrel, *Citellus undulatus*. Journal of Mammalogy, 55:586.

LACEY, E. A., WIECZORECK, J. R., AND P. K. TUCKER. 1997. Male mating behaviour and patterns of sperm precedence in Arctic ground squirrels. Animal Behaviour, 53:767–779.

MAYER, W. V. 1953. Some aspects of the ecology of the Barrow ground squirrel, *Citellus parryii barrowensis*. Pp. 48–55, *in* Current biological research in the Alaskan Arctic. Stanford University Publications, Stanford, California.

MAYER, W. V., AND E. T. ROCHE. 1954. Developmental patterns in the Barrow ground squirrel, *Spermophilus undulatus barrowensis*. Growth, 10:53–69.

McLEAN, I. G., AND A. J. TOWNS. 1981. Difference in weight changes and the annual cycles of male and female Arctic ground squirrels. Arctic, 34:249–254.

MICHENER, G. R. 1974. Annual cycle of activity and weight changes in Richardson's ground squirrel, *Spermophilus richardsonii*. The Canadian Field-Naturalist, 88:409–413.

———. 1978. Effect of age and parity on weight gain and entry into hibernation in Richardson's ground squirrels. Canadian Journal of Zoology, 56:2573–2577.

———. 1984. Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality. Pp. 81–107, *in* The biology of ground dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.

———. 1992. Sexual differences in over-winter torpor pattern of Richardson's ground squirrels in natural hibernacula. Oecologia, 89:397–406.

———. 1993. Sexual differences in hibernaculum contents of Richardson's ground squirrels: males store food. Pp. 109–118, *in* Life in the cold: ecological, physiological, and molecular mechanisms (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

MICHENER, G. R., AND L. LOCKLEAR. 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology, 71:855–868.

MORRISON, P. M. 1960. Some interrelations between weight and hibernation function. Pp. 75–91, *in* Mammalian hibernation. (C. P. Lyman and A. R. Dawe, eds.) Bulletin of the Museum of Comparative Zoology, 124.

MORTON, M. L., AND P. W. SHERMAN. 1978. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Canadian Journal of Zoology, 56:2578–2590.

MORTON, M. L., C. S. MAXWELL, AND C. E. WADE. 1974. Body size, body composition, and behavior of juvenile Belding ground squirrels. The Great Basin Naturalist, 34:121–134.

MURIE, J. O., AND D. A. BOAG. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. Journal of Mammalogy, 64:688–690.

MURIE, J. O., AND M. A. HARRIS. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). Journal of Mammalogy, 63:431–439.

PHILLIPS, J. A. 1984. Environmental influences on reproduction in the golden-mantled ground squirrel. Pp. 108–124, *in* The biology of ground dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.

SCHOOLEY, R. L., B. VAN HORNE, AND K. P. BURNHAM. 1993. Passive integrated transponders for marking free-ranging Townsend's ground squirrels. Journal of Mammalogy, 74:480–484.

SHAVER, G. R., F. CHAPIN III, AND B. L. GARTNER. 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaska tussock tundra. The Journal of Ecology, 74:257–278.

SHAW, W. T. 1926. Age of the animal and slope of the ground surface, factors modifying the structure of hibernating dens of ground squirrels. Journal of Mammalogy, 7:81–96.

SLADE, N. A., AND D. F. BALPH. 1974. Population ecology of Uinta ground squirrels. Ecology, 55:989–1003.

SOUTH, F. E., AND W. A. HOUSE. 1967. Energy metabolism in hibernation. Pp. 305–324, *in* Mammalian hibernation III (K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schonbaum, and F. E. South, eds.). Oliver and Boyd, Edinburgh, United Kingdom.

WADE, O. 1950. Soil temperatures, weather conditions, and emergence of ground squirrels from hibernation. Journal of Mammalogy, 31:151–161.

WALSBERG, G. E. 1988. Evaluation of a nondestructive

method for determining fat stores in small birds and mammals. Physiological Zoology, 61:153–159.

WANG, L. C. H. 1979. Time patterns and metabolic rates of natural torpor in Richardson's ground squirrel. Canadian Journal of Zoology, 57:149–155.

WATTON, D. G., AND M. H. A. KEENLYSIDE. 1973. Social behavior of the arctic ground squirrel, *Spermophilus undulatus*. Behaviour, 15:77–99.

YOUNG, P. J. 1990. Hibernating patterns of free-ranging Columbian ground squirrels. Oecologia, 83:504–511.

ZAR, J. H. 1984. Biostatistical analysis. second ed. Prentice-Hall, Inc. Englewood Cliffs, New Jersey.