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Differences in Weight Changes and the Annual Cycle of Male and Female Arctic Ground Squirrels

IAN G. McLEAN[1] and ALISON J. TOWNS[2]

ABSTRACT. Arctic ground squirrels (*Spermophilus parryii)* were studied for three summers near Haines Junction, Yukon Territory. Population characteristics and the behaviour of individual animals were monitored throughout the study. Ground squirrels entered hibernation in the order adult females, juvenile females, then males. Males emerged from hibernation before females. Males stored food in the autumn when conditions permitted, whereas females did not. Males emerged from hibernation having lost significantly less weight than females over winter. Males lost weight during the mating period, whereas females did not. These data are interpreted in terms of the mating period which for males lasts for approximately three weeks, whereas for females it lasts for less than a day.

RÉSUMÉ. Les Spermophiles arctiques (*Spermophilus parryii*) furent étudiés lors de trois étés près de Haines Junction, au Yukon. Les caractères de la population ainsique les comportements d'individus furent contrôlée durant toute l'étude. Les Spermophiles ont amorcé l'hibernation dans l'ordre suivant: les femelles adultes, les femelles juveniles puis les mâles. Les mâles ont cessé l'hibernation plus tôt que les femelles. Les mâles, contrairement aux femelles, ont entreposé de la nourriture en automne lorsque les conditions les permettaient. Lors de l'hibernation, les mâles ont perdu beaucoup moins de poids que les femelles. Lors de la période d'accouplement une perte du poids s'est faites sentir sur les mâles uniquement. Ces données sont reliées à la période d'accouplement qui s'étend sur environ trois semaines pour les mâles mais moins qu'une seule journée pour les femelles.

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Key words: Ground squirrels, male/female differences, weights, annual cycle

INTRODUCTION

The primary tactic adopted by hibernating mammals for overwinter survival is to deposit large amounts of fat late in the active season, and to utilize this as a metabolic reserve through the hiberating period (Mrosovsky, 1971; Galster and Morrison, 1976). Such fat reserves may be supplemented by stored food substances such as seeds, but no data are available for ground squirrels on the relative importance of these two sources of energy. As much as half of a ground squirrel's energy budget during the hibernating period may be allocated to activity during the inter-torpor (i.e. active) phases (Wang, 1979). Thus stored foods could be an important supplement to stored fat.

As a consequence of the northern and high-elevation environments in which they live, hibernating sciurids tend to be subject to variable, and sometimes extreme, conditions in the spring (Morton and Sherman, 1978). This variability can affect the onset of emergence and breeding (Slade and Balph, 1974; Morton and Gallup, 1975; Michener, 1977, 1979a), and may prevent reproduction by at least some individuals altogether (Morton and Sherman, 1978).

In hibernating ground squirrels (genus *Spermophilus*), females tend to emerge after males (*S. armatus,* Slade and Balph, 1974; *S. beldingi,* Morton and Gallup, 1975; *S. richardsonii,* Michener, 1977; *S. parryii,* Green, 1977; *S. lateralis,* Bronson, 1980), breeding occurs almost immediately after emergence, much of the active season is devoted to the production of independent juveniles, and, although this is difficult to determine, males tend to enter hibernation before females (*S. tridecemlineatus,* McCarley, 1966; *S. franklinii,* Murie, 1973; *S. richardsonii,* Michener, 1977; although see Knopf and Balph, 1977). Autumn immergence may be affected as much by the condition of individual animals as by seasonal events (Michener, 1978, 1979a). Patterns of weight change have been monitored in many studies (e.g. *S. lateralis,* Skyrja and Clark, 1970; *S. parryii,* Green, 1977; *S. richardsonii,* Michener, 1978), but in few have the weights of the same individuals been monitored regularly through the season, or between the seasons. Also, few data exist on food caching by hibernating sciurids, although there are occasional references to its occurrence or absence (Gordon, 1943; Krog, 1954; Mayer and Roche, 1954; Morton *et al.,* 1974; Yahner and Svendson, 1978).

In this paper we show differences in the patterns of food storage, seasonal changes in weight, and dates of entry into and emergence from hibernation, for male and female arctic ground squirrels (*Spermophilus parryii plesius*).

METHODS AND STUDY AREA

Arctic ground squirrels were studied at an elevation of 600 m on a 60 ha area called Bear Creek flats located ten km west of Haines Junction, Yukon Territory (61° 47'N; 137° 40'W), and adjacent to Kluane National Park. The study area, described in detail elsewhere (McLean, 1981 and in prep.), consisted of meadows interspersed among areas of willow (predominantly *Salix glauca*) with scattered stands of aspen (*Populus tremuloides*) and spruce (*Picea mariana*).

The area was visited from 28 April through 15 October 1977, 16 April through 26 September 1978, and 2 April through 8 July 1979. The peak of mating was over on our arrival in 1977 and most animals had entered hibernation

[1,2]Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Present address:

[1] Department of Zoology, University of Auckland, Private Bag, Auckland, New Zealand

[2] Department of Psychology, University of Auckland, Private Bag, Auckland, New Zealand

when we left; many males had emerged when we arrived in 1978, but we were present for the emergence of most females; most females but few males had entered hibernation when we left in 1978; we were present for the emergence of all animals in 1979. Most animals active in the area were live-trapped (with National or Tomahawk box traps baited with peanut butter) by 5 May 1977 and 20 April 1978, and we trapped animals as they appeared in 1979. Detailed observations of animals in two areas were undertaken once the mating period was underway and the entire study area was trapped once weekly through the rest of the season.

All animals were tagged with two individually numbered ear tags on first capture. Juveniles were captured as they emerged from natal burrows in the observation areas, and within one or two weeks of emergence in other areas.

RESULTS

Arctic ground squirrels entered hibernation in the order: adult females, juvenile females, males. Adult females began to disappear from the observation areas in late July and the last adult females were trapped on 9 (1977) and 13 (1978) September. Juvenile females began disappearing in late August and the last was captured on 1 October 1977 (18 juvenile females were captured in the last week of trapping, 17 to 24 September 1978). Some adult and juvenile males were still active at the time of the first major snowfall on 14 October 1977. Those that did not enter hibernation at this time did so when temperatures dropped to -20°C on 26 October (B. & G. Jeeves, Mile 1022 Alaska Hwy., Yukon, pers. comm.) The autumn was mild in 1978 and some squirrels remained active into November (Jeenes, pers. comm.). Although males remained active into October, their mean weights peaked during September. A slight decline occurred during October 1977, and mean weights had ceased increasing by late September 1978 (Green, 1977, also found this trend). Thus we consider weights recorded for individual males after mid-September to be a maximum estimate of the weight at entry into hibernation.

In order to determine entry into hibernation quantitatively, we compared the last date of capture of individual animals that were subsequently trapped in a following year. Last-capture dates were combined to give totals for bi-weekly intervals from mid-July onwards (Fig. 1), the earliest time at which animals could be considered to have entered hibernation. This ensured that animals that were lost in the fall due to factors such as predation or disease were not included, although it also excluded any animals for which a valid last-capture date was obtained, but which died during the winter. Data in Figure 1 were compared using contingency table analysis, but because some values (particularly for adult males) were the minimum usually required for such analysis, we also made comparisons using Spearmans rank correlation coefficient (Table 1). Group differences for all data combined were highly significant ($\chi^2 = 146.70$, $p < 0.001$) indicating that differences in the distribution of last-capture dates varied significantly between age and sex classes. Results of pairwise comparisons were similar for both analyses; last-capture dates for adult and juvenile males were similar, and significantly later than for both female classes. Last-capture dates for juvenile females were significantly later than for adult females, yet significantly earlier than for both male classes.

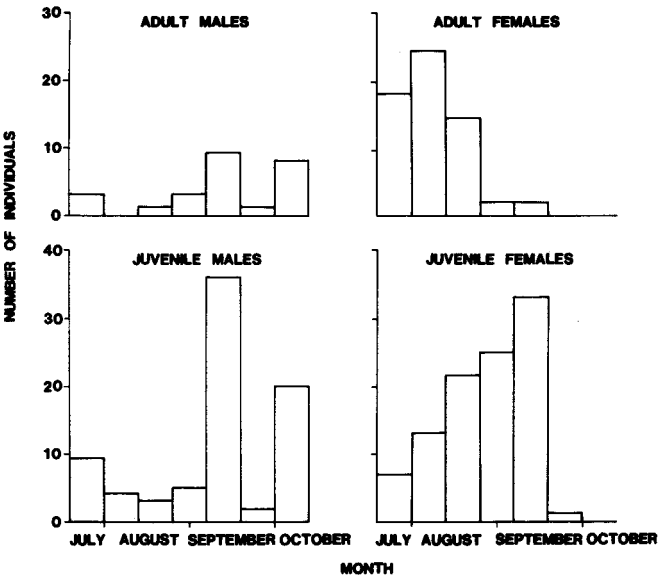

FIG. 1. Last date trapped for individual arctic ground squirrels that were also trapped in a subsequent season. Data for autumn 1977 and autumn 1978 combined. Mid-September peaks for males would probably have shifted to the right if trapping had continued into October in 1978. Data after mid-September for 1977 only.

To further test this result, we compared the week of last capture of juvenile females and the week of last capture for the same individuals in the following year with similar

TABLE 1. Chi-square values and Spearmans rank correlation coefficients for comparison of last date of capture for various age and sex classes of arctic ground squirrels (see Fig. 1)

	Adult females	Juvenile females	Adult males	Juvenile males
Adult females	r_s	51.46⁺	54.46⁺	76.95⁺
Juvenile females	< 0.20		41.30⁺	50.04⁺
Adult males	< 0.20	< 0.20		χ^2 2.92
Juvenile males	< 0.20	0.21	0.88*	

Degrees of freedom for $\chi^2 = 6$ in all cases except comparison of adult females with juvenile females where d.f. = 5.

Overall $\chi^2_{18} = 146.70^+$

⁺ Significantly different $p < 0.001$.

* Significantly correlated $p < 0.05$.

dates obtained for known adults in both years. Nineteen juvenile females were last captured an average of 3.53 ± s.e. 0.80 weeks earlier the following year (i.e. as yearlings entering their second winter of hibernation). Eight older females were last captured an average of 0.25 ± 1.05 weeks earlier. This supports the above indication that adult females enter hibernation earlier than juvenile females. Similar data were not available for males because we did not remain on the study area late enough in 1978.

Males emerged from hibernation earlier than females in both 1978 and 1979. No ground squirrels emerged after 7 May in the observation areas in any year and it is used as an arbitrary cut-off date in the following analysis. On 17 April 1978, seven males and no females were trapped; by 20 April, nineteen males and six females had been trapped. This was not significantly different from an expected ratio of unity ($\chi^2 = 3.63$, $\rho > 0.05$) but was significantly different from the expected ratio of all males to all females (57:73) caught before 7 May ($\chi^2 = 8.74$, $\rho < 0.01$, first captures only used). In 1979, the first male was seen on 7 April, and sixteen males and one female were captured by 17 April. Thirty-eight males and nineteen females were captured by 22 April and this ratio was significantly different from the ratio of males to females (71:106) captured before 7 May ($\chi^2 = 12.22$, $\rho < 0.01$). These data indicate that males emerged earlier than females from hibernation by a factor of one to two weeks.

There was little indication that yearling animals of either sex emerged later than older animals. A few yearling males emerged late and were not sexually active but many of the dominant territorial males were yearlings. The emergence of yearling females was spread over a slightly longer period than that for older females, with some small yearling females not appearing until early May. As a result, first weights of females were taken only for older animals trapped before 30 (1978) and 29 (1979) April, and for yearling animals trapped before 7 (1978) and 6 (1979) May. These dates correspond to the ends of the weekly trapping programs. All females bred during this study.

Adult males and juvenile males lost significantly less weight than adult and juvenile females respectively during the 1977/78 winter (Table 2). All males combined lost significantly less weight than all females ($\rho < 0.05$, all cases, Mann Whitney U tests). Within-sex differences were not significant. These data indicate that males lost less weight than females through the winter.

In 1979, males were trapped as they emerged from hibernation and they gained weight during the period before female emergence (Fig. 2). This gain suggests that the values used in the above analysis for 1977/78 overwinter weight loss by males were underestimates of the actual weight lost (spring weights were of males caught as females were beginning to emerge). However, increasing the above estimated weight loss of 61.4 gms by 31.3 gms (the mean weight gain of twelve males during the two weeks prior to emergence of females in 1979) increases the

TABLE 2. Loss of weight through the winter by individual male and female arctic ground squirrels trapped both in the autumn and in the spring

	1977/78 Oct to 23 Apr	1978/79 17-24 Sept to 15 Apr	
Adult males			
$\bar{X}$ ± s.e. (gm)	61.4 ± 29.87	144.4 ± 24.90	
$\bar{X}$ ± s.e. (% loss)	8.2 ± 4.03	18.3 ± 2.79	
N	7	8	
Juvenile males			
$\bar{X}$ ± s.e. (gm)	114.0 ± 16.73	163.3 ± 32.14	
$\bar{X}$ ± s.e. (% loss)	17.1 ± 2.56	22.0 ± 3.39	
N	10	6	
	1977/78	**1798/79**	**Total**
Adult females			
$\bar{X}$ ± s.e. (gm)	208.9 ± 26.60	205.3 ± 17.55	206.4 ± 14.39
$\bar{X}$ ± s.e. (% loss)	32.7 ± 3.72	31.2 ± 2.50	31.7 ± 2.04
N	9	20	29
Juvenile females			
$\bar{X}$ ± s.e. (gm)	157.4 ± 13.69	134.6 ± 8.02	142.0 ± 7.09
$\bar{X}$ ± s.e. (% loss)	29.2 ± 2.32	25.6 ± 1.47	26.8 ± 1.26
N	17	35	52

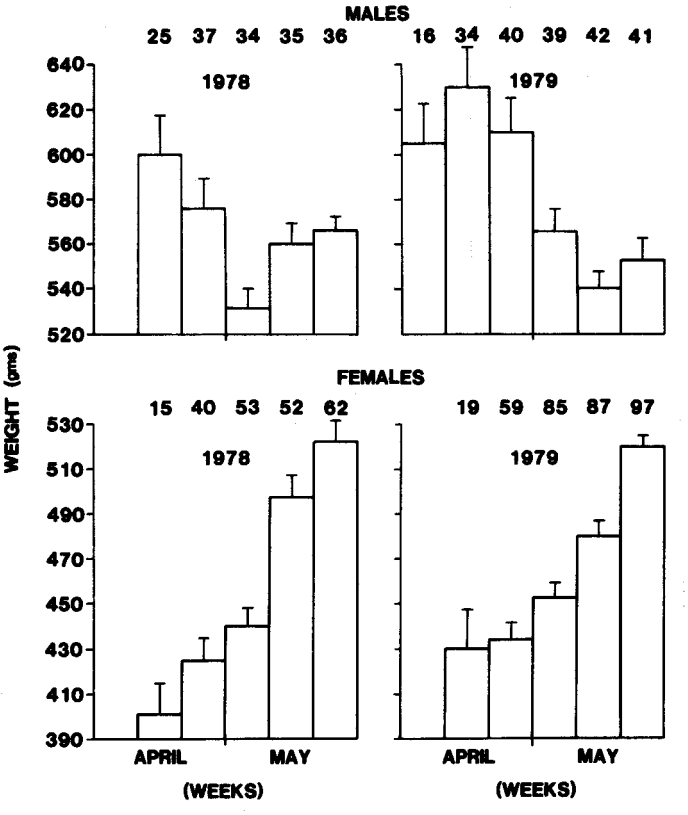

FIG. 2. Weight changes of adult male and female arctic ground squirrels during the springs of 1978 and 1979. Bar gives mean + s.e. Number of animals included in calculation of mean indicated above bar.

percent loss during the 1977/78 winter to 12-13%, still considerably less than the 32.7% recorded for adult females. The gain in weight by adult males in the early spring was followed by a precipitous weight loss during the mating period (Fig. 2). Weights stabilized in mid-May once mating was over. Females gained weight immediately after emerging from hibernation and continued to do so until giving birth during the second 2 weeks of May (Fig. 2). Mean ± s.e. weight loss at parturition of 24 females was 61.3 ± 4.39 gm (maximum of four days between weighings).

Equivalent data for overwinter weight loss for 1978/79 were available for females but not for males, because trapping ended before the males began to enter hibernation. Since accurate emergence weights for males were available in 1979, we obtained a measure of overwinter weight loss by subtracting weights of males trapped before 16 April from weights of the same individuals trapped during the week 18 to 24 September 1978 (the last week of trapping). These values are maximum estimates of loss since weights tended to decrease in October. Mean losses by adult and juvenile males were 18.3% and 22.0% respectively, and by adult and juvenile females were 31.2% and 25.6% respectively (Table 2). Differences between males and females were significant for adults ($p < 0.05$, Mann Whitney U test) but not for juveniles ($p > 0.05$). All males combined lost significantly less weight than all females combined ($p < 0.05$). As with the 1977/78 data, age differences within each sex were not significant.

Arctic ground squirrels spent considerable time collecting various materials (seeds, green and dried leaves, flowers, berries and mushrooms) and carrying them to burrows. Dried grasses were carried in the mouth and were probably used for nests and bedding (c.f. Steiner, 1975); other materials were carried in the cheek pouches. No attempt was made to record the number of animals seen collecting material in cheek pouches; however, it was apparent from our observations that females collected during lactation (late May and June) before they entered natal burrows, presumably to feed litters. Males spent considerable time collecting seeds during July and August and tended to spend only one or two minutes underground when carrying these to a burrow system. Females were only very rarely observed making collections in cheek pouches after June.

Animals with full cheek pouches were often trapped (Table 3). They invariably expelled collected material during handling so that identification of both the sex of the collector and the contents of the pouches was possible. As indicated by observations, most females with full cheek pouches were trapped during June, whereas males with full cheek pouches were trapped rarely before July. Although no attempt was made to quantify the relative proportions of materials collected, female collections consisted primarily of flowers and leaves, whereas male collections were predominantly seeds.

TABLE 3. Number of arctic ground squirrels captured with full cheek pouches and material collected from those animals during 1977 and 1978

	Adult males	Juvenile males	Adult females	Juvenile females	Total	Seeds	Flowers and Leaves	Other	Total
April/May	1	—	—	—	1	—	—	1	1
June	3	—	5	—	8	2*	6	1	9
July	10	—	1	1	12	9	2	3	13
August/ Sept.	4	21	—	1	26	19	8	—	27
TOTAL	18	20	6	2	47+	30	16	5	51+

* Both these were males

\+ Totals different due to some cheek pouch samples containing more than one type of material.

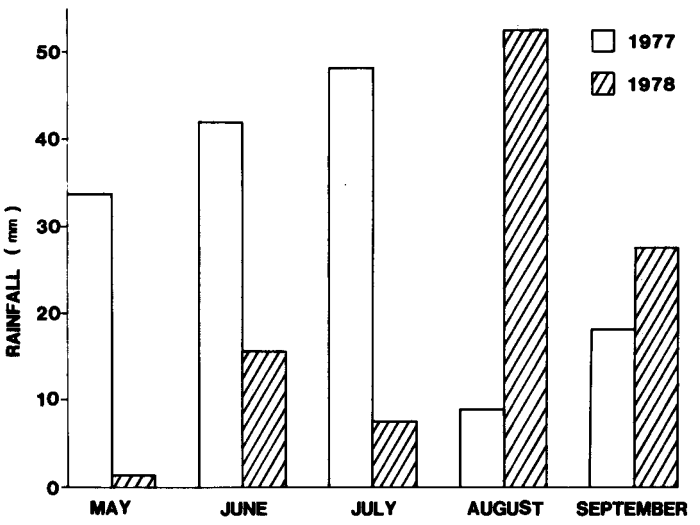

FIG. 3. Rainfall on Bear Creek flats, Yukon Territory, during 1977 and 1978.

Two factors affected the collection of these data:

1. Because females were entering hibernation during August and September, the number captured decreased through this period. However, females were more abundant in the population than males (McLean, unpubl.) so that it was not until August that the number of females captured weekly fell below those of males. We compared the number of captures of males to captures of females (1252:1042) during July, August, and September of 1977 and 1978 with the equivalent ratio of animals captured with full cheek pouches (34:3). These were significantly different ($\chi^2 = 20.07$, $p < 0.01$) indicating that the greater number of males than females captured with full cheek pouches in the later part of the season was not an artifact of capture frequency.
2. Almost no rain fell on the study area from snow melt until early August in 1978 (Fig. 3). As a result most of the vegetation in the meadows had turned brown by mid-July, and the seed crop, which in 1977 had been extensively harvested by males, failed almost completely. Very few animals were

seen making cheek pouch collections, and only one was trapped with full cheek pouches after June 1978.

These data suggest that, conditions permitting, males spent more time than females making collections of foods suitable for storage. The short time spent underground by males who emptied their cheek pouches further suggests that collected material was stored.

DISCUSSION

Immediately after emergence in the spring, female arctic ground squirrels are mated by one, or perhaps several, males (McLean, in prep.; see also Sherman, 1981), after which they gain sustenance both for themselves and for the developing litter. Males attempt to copulate with females as well as to prevent other males from gaining access to those females (Carl, 1971; McLean, in prep.). Female arctic ground squirrels probably mate on their first day of estrus, and are in estrus for one or two days at most (Unpubl. data; see also Murie and McLean, 1980). However, the mating period, which is of primary interest to males, lasts for up to three weeks. Once mating is over, females may have a higher energy drain than males (Galster and Morrison, 1976), particularly if males do not behave paternally, as in *S. richardsonii* (Michener, 1979b) and *S. beldingi* (Sherman, 1980), but not in *S. parryii* (McLean, 1979, and in prep.). The possibility that males and females may follow different tactics in coping with these different behavioural and physiological factors has rarely been addressed.

Greater overwinter weight loss by female arctic ground squirrels may be attributed to two factors: 1) their longer time (one to two months) in hibernation, and 2) their lack of food stores. That males actually use food stores during the winter was suggested by the greater overwinter weight loss recorded for 1978/79, when food stores were not available, than for 1977/78 when they were. Unfortunately, the data are not strictly comparable. By entering hibernation early, females presumably avoid above-ground predators (Slade and Balph, 1974) and may avoid a period when the vegetation is of poor quality (Bliss, 1962; Scotter, 1972). Males, by remaining active, may maintain their pre-hibernation fat reserves until later in the season and also amass greater food stores. Males may also enhance their access to females in the spring by territorial behaviour in the fall (Carl, 1971; Green, 1977).

Suitable physiological data for comparison with the present study are difficult to obtain. Loss of weight by males in the spring has been reported in various species (e.g. *S. richardsonii*, Zegers and Williams, 1977; *S. armatus*, Knopf and Balph, 1977); however, in some of these species females also lost weight. Differential weight loss between the sexes over winter and in the spring has been reported for arctic ground squirrels (Mayer and Roche, 1954; Green, 1977) yet males have been found to lose less fat than females before the end of June (Kiell and Miller, 1980). A weight loss during the "reproductive period" was reported by Galster and Morrison (1976) for female arctic ground squirrels, but their samples were small and weights were of laboratory animals.

In addition to the above factors, male arctic ground squirrels are involved in large numbers of interactions, sustain considerable wounding, and show different activity budgets than females during the mating period (Carl, 1971; Green, 1977; McLean, in prep.). Vegetation is of poor quality in the spring in northern ecosystems (Billings and Mooney, 1968) and high-energy food stores (seeds) and metabolic reserves could presumably allow males to devote more time to sexual activity during this critical period (Green, 1977). Heavier animals could be more dominant in interactions over estrus females (Watton and Keenleyside, 1973), and food stores left over from the winter may serve to attract females into a male's area (we consider this latter hypothesis unlikely). The data presented here show intersexual differences in the tactics adopted by males and females. Although some differences appear to be unique to arctic ground squirrels, detailed analysis of the patterns shown by individuals in other species may show similar trends.

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