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THE UNIVERSITY OF ALBERTA

ECOLOGICAL AND ENERGETIC ASPECTS OF HIBERNATION OF COLUMBIAN GROUND SQUIRRELS IN RELATION TO PATTERNS OF OVER-WINTER SURVIVAL

BY

Paul J. Young

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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DATE 22 Sept 1988

Elucidation Blues

With a plethora
of words.
The would-be
Explicator
Hides himself
Like a squid
In his own ink.

J. Burns
Biographiti

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ECOLOGICAL AND ENERGETIC ASPECTS OF HIBERNATION OF COLUMBIAN GROUND SQUIRRELS IN RELATION TO PATTERNS OF OVER-WINTER SURVIVAL, submitted by Paul J. Young in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Jan O Murie
Supervisor

Stan Boutin

External Examiner

Date 3 October 1988

ABSTRACT

Columbian ground squirrels (Spermophilus columbianus) from populations at different elevations (LE: 1500 m, HE: 2250 m) in southwestern Alberta did not differ in the amount of fat stored as an energy source for hibernation. Within populations adult males had larger prehibernation fat reserves in proportion to their body size than did adult females and juveniles, which did not differ from each other. Adult males and juveniles depleted a greater proportion of their fat reserves over-winter than did adult females; adults of both sexes emerged from hibernation with a greater proportion (25-48%) of their reserves remaining than did juveniles (10-23%). Yearly variation in fat reserve depletion differed between populations but were similar in direction and magnitude for sex and age classes within populations. Patterns of torpor and euthermia of low elevation squirrels were similar for all sex and age classes except that adult males were euthermic for a longer time immediately before emerging from their hibernacula (7-14 days) than were adult females and juveniles (0.5-1.5 days). The hibernacula of HE squirrels were shallower, larger and better insulated than those of LE squirrels. Within populations adult males used larger, better insulated hibernacula than adult females and juveniles; juveniles at LE tended to use more shallow hibernacula than did adults. HE squirrels experienced colder soil temperatures for the entire hibernating season and spent a greater proportion of the hibernating season at below freezing temperatures (85%) than did LE squirrels (52%) despite deeper and more continuous snow cover at HE. The mean minimum soil temperature was lower at HE (-2°C) than at LE (-1°C) but differences in hibernaculum

insulation resulted in similar thermal environments for squirrels in both populations. Soil temperature is the single most important factor influencing energy expenditure; environmental conditions, arousal patterns, and hibernaculum structure may predispose low elevation populations, adult males, and juveniles to higher rates of mortality than high elevation populations and adult females.

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I. INTRODUCTION

Many ground squirrel species spend as much as 6 to 9 months of each year in hibernation (Davis, 1976). As a consequence every aspect of their life history is centered around and directly influenced by the preparation for hibernation. Because of its central role in the annual cycle, the phenomenon of hibernation and the need to adapt to variable hibernating conditions must be a dominant factor in the evolution of life history patterns of these species, yet little is known about hibernation under natural conditions.

Hibernation is generally considered as a tactic to escape periods of low food availability or harsh environmental conditions when energetic demands for normal activity cannot be met. Metabolic requirements during the hibernating season may be as little as 12-33% of that required for a comparable period of normothermy (Scheck and Fleharty, 1979; Wang, 1979). Aside from the physiological ability to hibernate, an adequate energy supply, a location that provides protection from predators,and conditions that minimize energy expenditures are neccessary to survive hibernation. Usually not all individuals in a population are able to meet these requirements, resulting in some mortality during hibernation. Sheppard and Swanson (1976) considered over-winter mortality to be a major cause of disappearance of juvenile Richardson's ground squirrels (<u>Spermophilus richardsonii</u>). Over-winter mortality also appears to represent a significant portion of the yearly disappearance of Columbian ground squirrels (<u>S. columbianus</u>) (Murie, Boag and Kivett, 1980; Murie and

Harris, 1982; Murie, 1985), arctic ground squirrels (Carl, 1971), and yellow-bellied marmots (Marmota flaviventris; Svendsen, 1974).

Many spermophiline hibernators do not store food for hibernation, but rather rely on body reserves of lipids as a primary source of energy during hibernation (Davis, 1976; South and House, 1967). Their hibernating season consists of cycles of torpor and normothermy, under negative energy balance the entire time. The amount of energy stored as fat, the length of the hibernating season and the rate of energy use determine whether an individual survives or not.

The amount of fat accumulated prior to hibernation depends on a variety of environmental and behavioral conditions and may be regulated by endogenous 'set points' (Mrosovsky, 1976). Weather, by determining the access to and the quality of forage available and the length of the active season, affects the rate at which fat is accumulated and possibly the amount of fat. The timing of spring emergence, breeding, birth and weaning of litters impose some differences on the amount of time individuals have for gaining weight. The length of the hibernating season is strongly influenced by climatic conditions, although endogenous functions also affect the timing of immergence and emergence (Pengelley and Fisher, 1957, 1963).

The rate of fat depletion during hibernation is determined primarily by temperature (South and House, 1967) and the amount of time spent in torpor. Allowing body temperature to drop to near ambient temperature during hibernation results in a 67-88% reduction in total metabolic expenditure over the hibernating season (Scheck and Fleharty, 1979; Wang, 1979). The metabolic cost would be even less without the periodic arousals, demonstrated by all hibernators, which account for 80% of the total energy expended during hibernation (Wang, 1979). The pattern of arousals of most hibernators shows a characteristic decrease in frequency and duration of arousal from immergence to mid-season and then an increase in frequency and duration until hibernation is terminated (e.g. Jameson, 1964; Pengelley and Fisher, 1961; Pivoron, 1976, 1977; French, 1986). The frequency and duration of arousals is temperature dependent in golden-mantled ground squirrels (Twente and Twente, 1965), arctic ground squirrels (S. undulatus; Drescher, 1967), eastern chipmunks (Tamias striatus; Pivorun, 1976, 1977) and Belding's ground squirrels (S. beldingi; French, 1982a), decreasing in frequency and duration as ambient temperature decreases. Sexual maturity and reproductive status modify the general pattern; sexually mature individuals generally emerge earlier than their immature counterparts (French, 1982b) and may spend more time euthermic, particularly at the end of hibernation (Barnes et al., 1986, 1987). The amount of fat reserves and availability of food may also influence arousal patterns. French (1982b) found that heavier individuals were more likely to terminate hibernation in the absence of food than were lighter individuals. Weather conditions, ground cover and insolation determine soil and hibernaculum temperatures. The amount of snow cover, and the insulation it provides, has been suggested to affect survival of yellow-bellied marmots (Marmota flaviventris; Svendsen, 1974) and Columbian ground squirrels (Murie, 1985). But the thermal environment of the hibernaculum may be the most easily altered influence on hibernation; by selecting the location and depth of a hibernaculum or by altering the size and insulation of the hibernaculum, squirrels may be able to hibernate under a favorable temperature regime.

In this study I set out to compare some of the environmental, behavioral and physiological factors affecting over-winter survival of Columbian ground squirrels in south-western Alberta, where they inhabit alpine and sub-alpine meadows from about 1100 meters to 2400 meters above mean sea level (Soper, 1964). Previous studies have examined various aspects of life history and behavior of populations at different elevations. Significant differences in over-winter survival have been noted between age and sex classes as well as between populations at different elevations. In general adults survive better than juveniles, females survive better than males, and all age and sex classes survive better at higher elevation than at low (Boag and Murie, 1981; Murie, 1985; Murie and Boag, 1984; Murie, Boag and Kivett, 1980; Murie and Harris, 1982; Zammuto and Millar, 1985).

Populations at high elevation have a shorter active season (≈10-14 days shorter) and consequently a longer hibernating season (Dobson and Murie, 1987). At high elevations, spring emergence can occur 2-6 weeks later (Murie and Harris, 1982) and immergence occurs about two weeks later than at low elevation. Reproductive output is generally greater at lower elevations (Murie, 1985).

I identified three main factors as being most likely to affect survival; the amount of fat stored in preparation for hibernation, the pattern of torpor and arousals, and the thermal environment of the hibernaculum. The pre-hibernation fat stores are the primary energy source for the hibernating season. Torpor and arousal patterns, and the thermal environment, determine the rate of fat depletion.

I attempted to account for the differences in survival noted by previous investigators by examining the energetics and environmental conditions during the hibernating season. The study can be divided into three interrelated parts. The first compares the primary energetic reserves before and after hibernation of squirrels from different populations at different elevations, and sex and age classes that experience differences in over-winter survival. The objective of this part of the research was to determine if the higher survival rates of some groups can be attributed simply to having larger fat reserves prior to hibernation. The second aspect examined patterns of arousal during hibernation by temperature telemetry. The objective was to establish the general pattern of arousals and compare the patterns between ages, sexes and elevations. The data collected allow determination of the total time spent in torpor and euthermy, making it possible to estimate the rate of fat reserve depletion and the energetic cost of hibernation under different environmental and behavioral conditions.

The third aspect of the study was the thermal environment experienced during hibernation. Squirrels may be able to exercise some control over the temperature of the hibernaculum by selecting the location, depth, size of hibernaculum, and the amount of insulation used. The hibernacula of radio-collared squirrels were examined with respect to their thermal environment and the insulation of the nest.

Information from the three main parts of this study are combined in the summary to produce a simple model of the energy cost of hibernation under different environmental conditions. The predictions of this model and the information on pre- and post-hibernation fat reserves are examined in relation to the survival patterns observed in this and previous studies in an attempt to identify the factors most critical for over-winter survival among Columbian ground squirrel. An understanding of the factors affecting over-winter survival should provide valuable insights into the ecology and evolution of variable life history patterns in these squirrels.

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II. LENGTH OF THE ACTIVE SEASON, POPULATION STRUCTURE, AND SURVIVAL OF TWO POPULATIONS OF COLUMBIAN GROUND SQUIRRELS

Columbian ground squirrels (Spermophilus columbianus) are common in open meadows of the foothills, sub-alpine, and alpine areas of the mountains in southwestern Alberta (Soper, 1964). Because of the wide range of environmental conditions experienced among populations at different elevations the species has been the subject of several studies investigating variable life history patterns (Boag and Murie, 1981; Dobson and Kjelgaard, 1985a,b; Dobson and Murie, 1987; Dobson et al. 1986; Murie, 1985; Murie and Boag, 1984; Murie et al., 1980; Zammuto and Millar, 1985). These studies have found consistent differences in life histories among populations at different elevations. In general, populations at higher elevations have shorter active seasons, lower reproductive success, and greater survival than low elevation populations.

As part of a larger study on factors influencing over-winter survival of Columbian ground squirrels I monitored the population dynamics and seasonal activity of one population at low elevation and one at high elevation in the Sheep River drainage of southwestern Alberta. Here I report on the population structure, length of the active season and survival patterns of these populations.

The low elevation site (LE) was approximately 3 km east of the mouth of Gorge Creek (50°38′N,114°37′W) at an elevation of 1500 m. The site occupied 1.3 ha of the same large meadow (72 ha) studied by Boag and Murie (1981) and was approximately 2 km east of Murie's (1985) Gorge Creek site. The LE study site was level to gently rolling except for 20 to 30 m of the north side that was on a steep south-facing slope. The area was marked off with a 10 by 10 m grid to facilitate recording of capture, burrow, and hibernaculum locations. Vegetation was mostly grasses and forbs, primarily wheatgrass (Agropyron sp.), timothy (Phleum alpinum), and old man's whiskers (Geum triflorum). Large amounts of dandelion (Taraxacum sp.) were present in June of both years and were a major food source for the squirrels. Owing to greater than normal rainfall in 1986 the vegetation was taller (up to 1.5m) than in 1985 (≈0.5 m). The soil is described as shallow, usually 20 cm or less deep, coarse to moderately coarse rapidly drained orthic regesols and rego black chernozems overlaying thick layers of gravel and cobble (Alberta Energy and Natural Resources, 1979). Snowfall and winter temperatures are moderated by periodic warm "chinook" conditions resulting in inconsistent and interrupted snow cover.

Potential mammalian predators observed on the site included coyotes (Canis latrans), badgers (Taxidea taxus), weasels (Mustela spp.); avian predators included red-tailed hawks (Buteo jamaicensis), goshawks (Accipiter gentilis) and golden eagles (Aquila chysaetos).

The high elevation site (HE) occupied 9 ha of a cirque on the west side of Junction Mountain about 12 km south of the mouth of Junction Creek (50°32′N,114°42′W) at an elevation of 2250 m. The site was level to rolling with steep talus slopes and limestone cliffs on the north, east, and south sides. Because of its large size the site was not marked with a grid; instead a series of reference points were marked and mapped. Capture, burrow, and hibernaculum locations were determined by taking the polar co-ordinates from the nearest reference point. Vegetation consisted of dryad mats (Dryas sp.), sedges (Carex spp.), grasses, and patches of dwarf willow (Salix spp.); stunted spruce (Picea sp.), and alpine fir (Abies lasiocarpa). The soil is described as shallow, sandy regosol with large areas of exposed bedrock and rubble (Alberta Energy and Natural Resources, 1979). Snow cover was deep and consistent, usually lasting from September through early June.

Potential predators on the site included coyote, long-tailed weasels (Mustela frenata), black bears (Ursus americanus) and grizzly bears (U. arctos), the latter two identified by scat and tracks only. Avian predators observed were golden eagles and prairie falcons (Falco mexicanus).

Trapping was conducted irregularly on both sites from late-May through August in 1985 and on a bi-weekly basis from late-March to September in 1986 and 1987. Squirrels were live trapped using Tomahawk live traps (16 by 16 by 48 cm) baited with peanut butter. All individuals were ear-tagged with #1 Monel fingerling tags for future identification and dyed with a distinctive mark using hair dye (Clairol #124, blue-black). Weights were taken to the nearest 5 grams with Pesola spring scales and zygomatic width (ZYGW) and lower foreleg length (LFLG) were measured to the nearest 0.1 mm with a modified dial caliper. The breeding status and occurrence of any wounds or injuries were also noted at each capture.

All trapping at LE in 1986 and 1987 was conducted during the first 2-3 hours of activity to reduce errors in weight introduced by varying amounts of stomach contents. Because of the large area at HE trapping was conducted throughout the day, as it was on both sites in 1985. Individuals were classified as juveniles (young of the year) or adults unless their actual age was known or they could be positively identified as yearlings (young of the previous year) based on differences from adults in weight and tooth pigmentation. To determine the pattern of survival a set of 'cut-off' dates were chosen (originally arbitrarily and later confirmed by trapping records of known survivors) as a demarcation between pre-hibernation and over-winter mortality. Individuals caught on or after the cut-off date for their age class were considered to have hibernated on the study areas and those disappearing after the date were assumed to have died during hibernation. The cut-off dates at LE were 15 July for non-juveniles and 21 July for juveniles. At HE the cut-off dates were 28 July for non-juveniles and 14 August for juveniles.

Squirrels in both populations were active, with breeding activity completed when trapping was started in 1985. The emergence schedules for 1986 and 1987 are shown in Fig. II-1. Emergence of LE adult males was 2-3 weeks earlier (median dates 9 April 1986, 4 April 1987) than previously reported by Murie and Harris (1982) for a six year study on a population 2 km away (earliest median date 21 April, mean median date 26 April). Adult females emerged later than adult males (median dates 22 April 1986, 24 April 1987) and slightly earlier than during their study. Juveniles of both sexes emerged at the same time and overlapped greatly with the emergence of adult females. Determination of accurate emergence dates at HE was hampered by spring storms in both years. Ten of 13 adult males were already active on 28 May 1986 as were 3 of 10 females. In 1987 one squirrel was observed active on the site on 5 May at the end of the first trapping session. Two adult males and one adult female were first captured on 10 May 1987 and all squirrels at HE were active by 4 June. Emergence dates were obtained for only nine juveniles at HE over 2 years; all emerged between 24 May and 4 June. The emergence dates at HE in this study were similar to those reported for populations at similar elevations by Dobson and Kjelgaard, (1985a, 9-22 May first emergence date) and Murie and Harris (1982, back-dated from their records of breeding dates).

The date of last capture was used as an index of immergence dates (Table II-1). Squirrels of all age and sex classes in both populations immerged later in 1986 than in 1985. That may have been due to the greater than normal rainfall during July and August 1986 (Alberta Environment, Climate of Alberta 1986, Junction Look-out Records) which appeared to delay fattening. HE squirrels of each sex and age class immerged into hibernation 5-10 days later than their LE counterparts.

Using the median dates of emergence and immergence, and assuming that juveniles emerged from the natal nest at 58 days after the adult females emerged from hibernation (based on dates of emergence, breeding, and gestation from Murie and Harris, 1982) the active season for adults in 1986 was 108 days at LE and 93 days at HE. Juveniles had active seasons of 49 days at LE and 36 days at HE. The estimates for adults are similar to those of Dobson and Murie (1987) for populations at corresponding elevations. The length of the hibernating season in 1986-87 at LE was measured directly by temperature telemetry of hibernating squirrels as 240 -250 days (Ch. IV) giving a corresponding active season of 115-125 days in 1986. From this it would appear that trapping records may underestimate the length of the active season by as much as two [illegible]ks. Trapping from mid-July to late August alternated from LE to HE every 4-5 days; therefore, last capture dates may have been as much as 10 days early for some individuals. Most squirrels also become very inactive and difficult to trap at the end of the season (pers. obs.); one radio-collared adult male was last captured on 12 July but did not become torpid until 31 July (Ch. IV).

The number of squirrels tagged on each study area as well as summer, over-winter, and annual survival rates are presented in Table II-2. The survival of all age and sex classes combined was greater at LE than at HE in both years and was constant between years at LE although there were differences among sex and age classes between years. Juvenile survival increased from 1985-86 to 1986-87 while adult survival declined. The mean annual survival of adults at LE (64%) was similar to that reported by Murie (1985), Murie and Harris (1982), and Dobson and Kjelgaard (1985a); juvenile survival at LE (69%) was higher than reported in these studies. The LE population increased in size at emergence from 62.3/ha in 1986 to 78[illegible]ha in 1987. These densities were higher than those reported by Boag and Murie (1981, 11.6-16.1/ha) and Murie (1985, 12.8/ha) but are similar to those reported by Festa-Bianchet (1985) for a population 3 km to the south of LE at a similar elevation. Festa-Bianchet attributed the high density on his site to better habitat quality and optimal weather conditions. The LE site was situated on part of the large meadow that Boag and Murie (1981) described as having areas of high and low squirrel density. Adults at HE had mean annual survival rates (71%) similar to previous studies (71-76%; Dobson and Kjelgaard, 1985a; Murie, 1985) but juvenile survival was much lower (35% this study, 60% Murie, 1985). The HE population was also larger in 1987 than in 1986 (+50%), due mostly to increased litter sizes in 1986, recruitment of yearlings into the adult age class, and greater juvenile survival. The density of the HE population at emergence was lower in both years (2.3-3.6/ha) than in Murie's (1985) study (11.6-16.1/ha). Some of the differences in densities between this and previous studies may be due to the inclusion of large low density areas in the study areas used for different studies. Although HE squirrels foraged and were captured throughout the entire 9 ha the location of burrow systems was concentrated in a smaller area (approximately 1-2 ha). There was some indication that juvenile mortality was greatest immediately before hibernation, particularly at HE. In 1986, 18 of 22 juveniles at HE were alive on 31 July; by 9 August only 11 were known to be alive on the area and only one of the 7 'missing' juveniles was captured the following year.

All adult females at both sites bred each year. Of 62 juveniles (24 male, 38 female) tagged at LE in 1985, 57 could be assigned to the complete litters of 18 females (mean litter size 3.17, range 2-5). In 1986, 65 juveniles (31 male, 34 female) were tagged at LE; 43 were assigned to the litters of 17 females (mean litter size 2.53). Eight juvenile females from 1985 bred (as yearlings) at LE in 1986. Seven of these successfully reared at least one young. The litter size of yearling females (mean 2.28, range 1-3) did not differ significantly from that of older females (mean 2.70, range 1-4, Wilcoxon 2-sample test, P = 0.310). Yearling females that bred were heavier and had larger fat reserves before and after hibernation than non-breeding females (Ch. III). The low litter size at LE in 1986 compared to 1985 may have been caused by the use of a smoke blower to map burrow systems during gestation and lactation; it was discovered that repeated exposure to the 'non-toxic' smoke could cause lethal lung irritations (App. C). However, other populations in the same geographic area also experienced decreased litter sizes in 1986 (S. Hatfield and D. Wiggett, pers. comm.). At HE 11 juveniles (7 male, 4 female) from six litters were tagged in 1985 for a mean litter size of 1.67 (range 1-2). 22 juveniles were assigned to 9 litters at HE in 1986 (mean 2.44, range 1-4). The litter sizes observed at both populations over the course of this study fell within the range reported by Murie et al. (1980) for populations at similar elevations. Litter sizes were not determined in 1987 and both populations were disrupted to some extent by the excavation of hibernacula from April through June. Only two juveniles were captured at HE in 1987 suggesting an almost complete failure of the cohort.

In summary, the high elevation population in this study was similar to previously studied high elevation populations of Columbian ground squirrels with respect to adult survival, emergence dates and the length of the active season. Juvenile survival recorded over 2 years at HE was lower than reported elsewhere. The low elevation population differed in almost every aspect from previous studies. Survivorship of adults and juveniles was higher, emergence dates were earlier, and a large proportion of the yearling females bred. These changes in population dynamics and life history are in the same direction as reported for populations supplemented with high energy food (Dobson and Kjelgaard, 1985a,b) suggesting that the quality of the habitat may have increased since previous studies (Boag and Murie, 1981; Murie, 1985; Murie and Boag, 1984) or that the LE study area represents an optimal subsample of the larger population. High over-winter survival might also be attributed to mild winter weather during this study. Records of mean monthly temperatures from High River, Alberta (Alberta Environment, Climate of Alberta reports for 1985,1986), which Murie and Harris 1982) used as an index for temperatures at their Gorge Creek site (2 km W of LE), were warmer than the 30 year mean for most months of the winter of 1985-86 and for July to December 1986. Winter snowfall at High River was lower than the 30 year mean in 1985-86 and the first half of 1986-87 as well. Temperature and snowfall records for 1987 were not available at the time this was written. The hibernacula of LE squirrels are well above the soil frost line (Ch. VI), so colder air temperatures than experienced in 1985-87 could potentially increase the energetic demands of hibernation and thereby reduce survival rates.

Table II-1. Median and ranges of last capture dates for Columbian ground squirrels from two populations at different elevations. Last capture dates were used as an index for date of immergence into hibernation.

		Low Elevation			High Elevation		
age/sex	year	n	median	range	n	median	range
Ad. Male	1985	26	22 Jul	16 Jul-06 Aug	11	31 Jul	28 Jul-09 Aug
	1986	24	26 Jul	10 Jul-12 Aug	12	02 Aug	31 Jul-20 Aug
Ad. Female	1985	20	24 Jul	16 Jul-06 Aug	14	30 Jul	28 Jul-09 Aug
	1986	34	08 Aug	20 Jul-25 Aug	13	18 Aug	31 Jul-20 Aug
Juv. Male	1985	13	05 Aug	22 Jul-05 Aug	2	15 Aug	09 Aug-23 Aug
	1986	22	12 Aug	04 Aug-25 Aug	9	18 Aug	31 Jul-22 Aug
Juv. Female	1985	25	04 Aug	21 Jul-06 Aug	2	09 Aug	
	1986	21	11 Aug	01 Aug-25 Aug	4	21 Aug	31 Jul-22 Aug

Table II-2. Population structure and survival rates for 1985-1987 of two populations of Columbian ground squirrels at different elevations in southwestern Alberta, (1500 m, 2250 m).

LOW ELEVATION

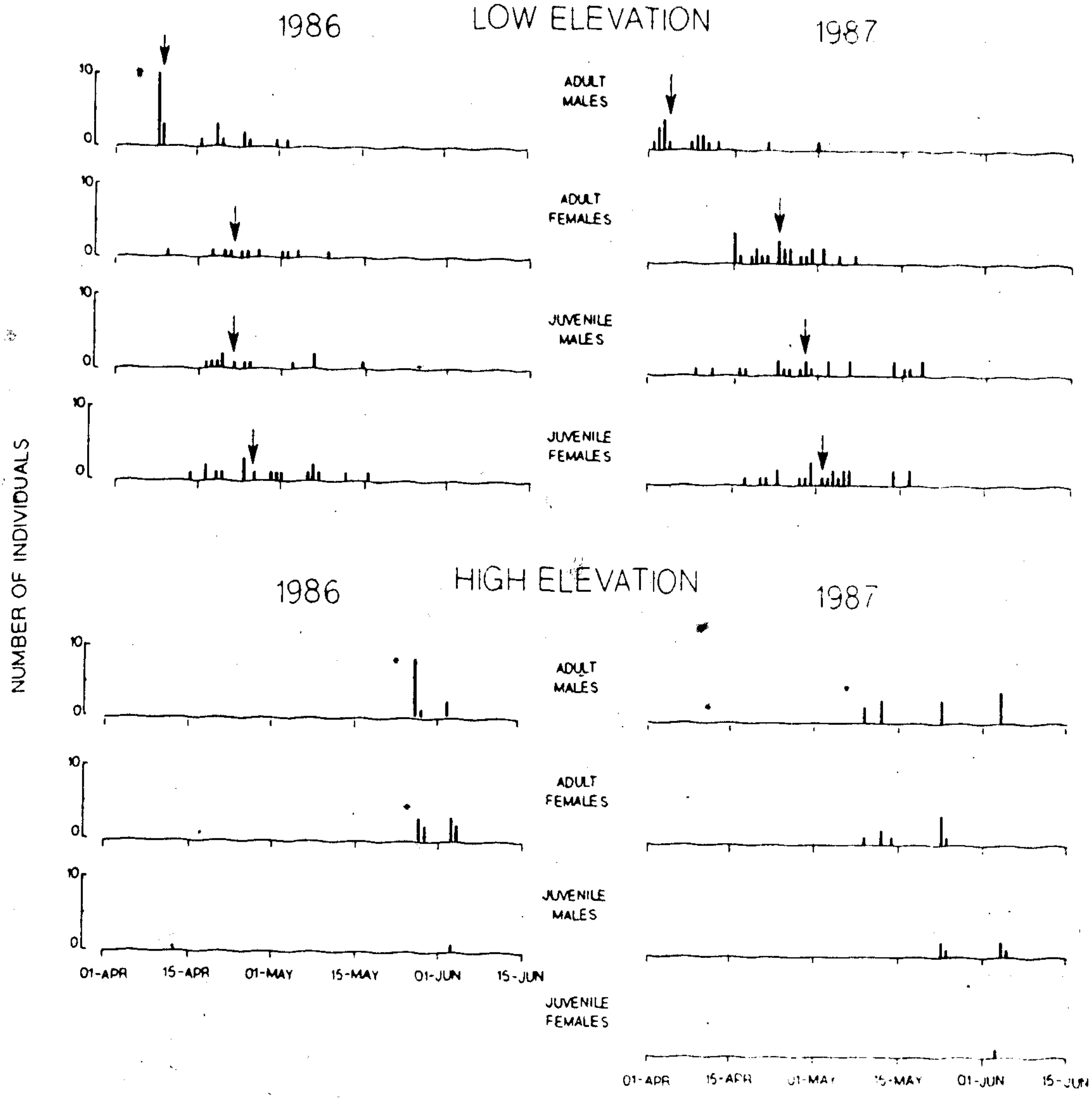
SEX/AGE	TAGGED RESIDENTS 1985	# ON SITE IN FALL 1985	# EMERGING IN SPRING 1986	% SURVIVING			TAGGED RESIDENTS 1986	# ON SITE IN FALL 1986	# EMERGING IN SPRING 1987	% SURVIVING		
				SUMMER	WINTER	ANN.				SUMMER	WINTER	ANN.
AM	17	16	15	94	94	88	17	11	11	65	100	65
AF	18	17	16	94	94	89	21	13	10	62	74	48
YM*	10	10	10	100	100	100	14	13	13	93	100	93
YF*	4	3	3	75	100	75	23	21	16	91	76	70
JM	24	15	14	63	93	58	31	24	22	77	92	71
JF	38	28	23	74	82	61	34	32	30	94	94	88
TOTAL	111	89	81	80	91	73	140	114	102	81	90	73

HIGH ELEVATION

SEX/AGE	TAGGED RESIDENTS 1985	# ON SITE IN FALL 1985	# EMERGING IN SPRING 1986	% SURVIVING			TAGGED RESIDENTS 1986	# ON SITE IN FALL 1986	# EMERGING IN SPRING 1987	% SURVIVING		
				SUMMER	WINTER	ANN.				SUMMER	WINTER	ANN.
AM	8	8	6	100	75	75	12	8	7	67	86	58
AF	10	9	6	90	67	60	12	12	11	100	92	92
YM*	7	3	3	43	100	43	4	4	3	100	75	75
YF*	6	5	4	83	80	67	2	1	1	50	100	50
JM	7	2	1	29	50	14	15	9	7	60	78	47
JF	4	2	1	50	50	25	8	4	3	50	75	38
TOTAL	42	29	21	69	72	50	53	38	32	72	84	60

NOTE: * indicates classification of some individuals based on weight and tooth pigmentation.

Figure II-1. Frequency histograms of emergence dates for Columbian ground squirrels from two populations at different elevations in Alberta. Arrows indicate median dates, '*' indicates when squirrels were known to be active before the start of trapping.



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III. PRE- AND POST-HIBERNATION FAT RESERVES OF COLUMBIAN GROUND SQUIRRELS

A circannual pattern of weight gain and loss is well documented for many species of ground squirrels (Spermophilus) that hibernate (Blake, 1972; Galster and Morrison; 1976; Jameson, 1965; Jameson and Mead, 1964; Morrison,1960; Mrosovsky, 1976; Pengelley and Fisher, 1961). Fat is accumulated during the active season each year and serves as the primary energy reserve for hibernation (Galster and Morrison, 1976; South and House, 1969) and as a supplement to scarce food supplies immediately following emergence (Kenagy and Barnes, 1988; Snyder et al., 1961; Zegers and Williams, 1977). Annual cycles of weight, hibernation and endocrine activity have been shown to be endogenously controlled (see Mrosovsky, 1971 for review) and the amount of fat accumulated for hibernation is apparently regulated to a seasonally adjusted 'set point' (Dark et al., 1986; Mrosovsky, 1976). Weight cycles vary within species; adult males typically put on more weight than do adult females (Blake, 1972; Tomich, 1962) and lose more weight over winter (Morton, 1975; Snyder, et al. 1961; Zegers and Williams, 1977; but see McLean and Towns, 1981). Populations of the same species that experience different climates may also show differences in the amount of post-hibernation fat reserves (Blake, 1972).

The amount of fat accumulated before hibernation and the rate at which it is depleted determines the fasting potential of each individual (Morrison, 1960) and thereby influences survival during hibernation. Differences in over-winter survival between sex and age classes and between populations at different elevations have been documented for several species of ground squirrels and marmots (Bronson, 1979; Boag and Murie, 1981; Murie, 1985; Murie and Boag, 1984; Sheppard and Swanson, 1976; Svendsen, 1974). The cause of this differential mortality is not clear but may be related to the amount of fat accumulated before hibernation (Murie and Boag, 1984) or the quality of the hibernaculum (Murie, 1985; Svendsen, 1974) affecting the rate of energy consumption.

In this study I examined the pre- and post-hibernation fat reserves of Columbian ground squirrels (*Spermophilus columbianus*) from two high elevation and two low elevation populations in southwestern Alberta. The first objective of the study was to determine whether squirrels in high survival categories (adults, females, and high elevation: Boag and Murie, 1981; Murie and Harris, 1982; Murie and Boag, 1984; Murie 1985) had correspondingly greater pre-hibernation fat reserves or lower rates of fat depletion than squirrels in low survival categories (juveniles, males, low elevation). A second objective was to develop a method for accurately estimating the fat reserves of live squirrels. Morton and Tung (1971) found that total body weight was a reasonable though not completely accurate predictor of fat reserves for Belding's ground squirrels (*S. beldingi*). The addition to prediction equations of easily taken morphological measurements increased the accuracy of fat reserve estimates (Gessaman, 1984) by accounting for some of the variation in lean body mass.

METHODS

Squirrels were collected from locations at different elevations before and after two separate hibernating seasons. In 1984-85, collections were made at the Rocking P ranch (RP), elev. 1250 m, 50 km south of Longview, Alberta and at Highwood Pass (HW), elev. 2150 m, approximately 50 km west of Turner Valley, Alberta, 5 km south of the summit of the pass. In 1987-88 squirrels were collected from areas adjacent to the main study areas used during other parts of this study, LE: elev. 1500 m, HE: 2250 m (Ch. II). The timing of collections at RP and HW, relative to the annual cycle, was determined from studies being conducted on squirrel populations within a few kilometers of the collecting sites (D. Hackett and F. S. Dobson, pers. comm.). Squirrels were live-trapped in order to select individuals by sex and age class. Autumn collected individuals were also selected on the basis of weight, preferentially taking above average weight individuals in order to avoid collecting squirrels which may not have survived hibernation (Murie and Boag, 1984). Inclusion of squirrels that would not survive hibernation in the fall sample would bias any comparison with the spring sample of survivors. An attempt was made to collect five individuals of each sex for adult, yearling and juvenile age classes in 1984-85. The yearling age class was later lumped with adults. No juveniles were collected at HE in 1987-88 because very few juveniles were present in the population in 1987. The squirrels were sacrificed by asphixiation in the field and placed in plastic bags and kept frozen until processed for lipid extraction. In the laboratory the total weight (TWT) of all squirrels was measured to the nearest 0.1 g and a series of external morphological measurements (HBL - head and body length, HF - hind foot length, ZYGW - zygomatic width, LFLG - lower foreleg length, LHLG - lower hind leg length), were taken for use in deriving a method for estimating fat reserves on live squirrels. The alimentary tract with contents, from the diaphragm to anus, were removed, stripped of mesenteries and fat which were returned to the carcass, and weighed to the nearest 0.1 g. The heads were also removed at the articulation of the occipital condyles and weighed, leaving the skin and any subcutaneous fat with the carcass. The gut and head free carcass was weighed, refrozen and ground by two or three passes through a commercial meat grinder. Three 15-20 g samples of the homogenized carcass were weighed to the nearest 0.001 g and dried in a convection oven at 45°C to a constant weight to determine water content. The dried samples were finely ground with mortar and pestle and a 3-5 g sub-sample from each was extracted with petroleum ether in a soxhlet apparatus for 4 hr to determine the neutral lipid and lean content. Total carcass fat and carcass lean weight (lean dry weight + water weight) were calculated from the mean of the three samples from each carcass. The carcasses of five radio-collared squirrels that died during the 1986-87 hibernating season were also collected and processed as above to determine their lipid reserves. Comparisons between ages, sexes and locations were done using analysis of co-variance (ANCOVA) on the carcass fat weight with carcass lean weight as the co-variant. ANCOVA removes the confounding effects of body size, reduces the co-efficient of variation within groups and is preferable to using percentages or indices when dealing with allometrically related properties (Packard and Boardman, 1987). A regression equation for estimating fat reserves on live squirrels was chosen by stepwise regression of the external morphological measurements and total weight on fat free weight (carcass lean weight + head and gut weight). The difficulty in obtaining some measurements on live squirrels meant that some of the best predictors of lean body size (head and body length, lower hind-leg length) could not be used for an equation to predict fat reserves of live squirrels. The best regression ($r^2 = 0.95$) using easily taken measurements was:

$$FFWT=(TWT*0.516)+(ZYGW*10.966)+(LFLG*2.944)-311.270 \qquad \text{(Eq. III-1)}$$

where FFWT is fat free (lean) body weight (g), TWT is total body weight (g), ZYGW is the width of the head immediately behind the eyes (mm), and LFLG is the length from the proximal to the distal ends of the ulna and radius with the leg in a flexed position (mm). Fat weight (FWT) was calculated as the difference between the estimated FFWT and TWT. ZYGW and LFLG were measured to the nearest 0.1 mm using a modified dial caliper. TWT was taken to the nearest 5 g using a Pesola spring scale.

Pre-hibernation fat reserve estimates were made for all squirrels captured and released on or after the 'cut-off' dates used for determining over-winter survival (Ch. II). For adults the cut-off dates were 15 July at LE and 28 July at HE. Cut-off dates for juveniles were 28 July (LE) and 14 Aug (HE). Post-hibernation fat estimates were made for all squirrels at their first capture of the season, usually within 2-5 days of emergence. Squirrels with unusually late first captures in the spring were excluded unless there was evidence suggesting recent emergence (e.g. flaky skin). Over-winter energy consumption was estimated from the estimates of fat and lean weight loss of individuals. The energy content of fat was calculated as 39.33 kJ/g (Schmidt-Nielsen, 1983). The amount of protein lost, and presumably catabolized for energy, was estimated from the estimates of lean weight loss on live squirrels assuming that 22% of the fat free wet weight was protein (Galster and Morrison, 1976). The ratio of fat free dry mass to water mass did not differ between pre-hibernating and post-hibernating squirrels used in the fat extractions. The energy content of estimated protein loss was calculated as 17.991 kJ/g (Schmidt-Nielsen, 1983). For calculating rates of energy use, the length of hibernating seasons were considered to be 240 days for adult males at LE and 270 days at HE, 250 days for other squirrels at LE and 280 days at HE (Chs. 2 and 4). All statistical analyses were performed on PC:SAS. Because of the small sample sizes for some groups and the inability [illegible]et assumptions of normality, non-parametric methods were used for most statistical analyses of estimated fat reserves using the F:L ratio as an index. Proportions and percentages were arcsine transformed for analysis (Snedcor and Cochran, 1980).

RESULTS

All comparisons of fat reserves were made using absolute values of fat reserves adjusted for body weight. At RP, LE, and HE, adult males had significantly greater pre-hibernation fat reserves in proportion to body weight than did either adult females or juveniles, the latter two being similar (Table III-1). At HW all age and sex classes had similar pre-hibernation fat reserves. Adult males at HW had smaller pre-hibernation fat reserves than those at RP, LE, or HE. Adult females showed the same pattern, but, the difference is only marginally significant. Juveniles had similar pre-hibernation reserves at all locations.

Adult males at LE had significantly larger post-hibernation reserves than other age and sex classes at LE and adult males at all other locations (Table III-2). All other age and sex classes within and among locations had similar post-hibernation reserves. The relation of pre- to post hibernation F:L ratios are shown in Fig. III-1.

The radio-collared adult female at LE that died during hibernation had fat reserves (F:L = 0.075) similar to those of surviving adult females ($\bar{x}$ = 0.073); the fat reserves of the juvenile female that died were nearly depleted (F:L = 0.004). In contrast, the carcasses of three radio-collared squirrels from HE had fat reserves close to pre-hibernation levels (F:L = 0.200 and 0.175 adult females, F:L = 0.161 juvenile male). The arousal patterns of the HE squirrels were not recorded but the large fat reserves of the carcasses suggest that they died before or early in hibernation.

Within sex and age classes, and within locations the estimated pre-hibernation fat reserves (F:L ratios) of live squirrels did not differ either between years (Wilcoxon 2-sample tests: all $\underline{P} > 0.05$) or between survivors and non-survivors (Wilcoxon: all $\underline{P} > 0.05$). With the data for both years combined (Table III-3), there were no differences in pre-hibernation F:L estimates between locations within sex and age classes (Wilcoxon: all $P > 0.05$). By combining data from years, locations, survivors and non-survivors, sample sizes were large enough to warrant the use of analysis of variance to test for differences in fat reserves among sex and age classes. The results of ANOVA indicate a significant difference among sex and age classes ($F = 22.76$, $P = 0.0001$). Adult males had the largest fat reserves while adult females and juveniles of both sexes had similar amounts (Student-Neuman-Keuls multiple range test).

There were significant year to year differences in the post-hibernation reserves of adult males at LE (Wilcoxon test: $P = 0.0218$) and at HE (Wilcoxon test: $P = 0.0454$) and for juveniles of both sexes at LE (Wilcoxon tests: all $P < 0.01$; Table III-4). Other age and sex classes did not differ between years or had sample sizes too small to be tested. Post-hibernation reserves at LE tended to be greater in 1985-86 than in 1986-87, while the reverse pattern was seen at HE (Fig. III-2). Adults at both locations had larger post-hibernation reserves than did juveniles in both years (Wilcoxon tests: $P < 0.05$).

The proportion of total weight lost over-winter (%TWL) was fairly consistent (25-35%) between sex and age classes, locations, and years, but tended to be higher in 1986-87 at LE and in 1985-86 at HE (Table III-5). Juveniles at LE had greater %TWL than did LE adults in 1986-87 (Kruskal-Wallis test: $X^2 = 11.960$, $P = 0.0075$) and lost a greater proportion of their fat reserves (%FWL) than did adults in both years (K-W: $P < 0.001$, both years). Adult males at HE had higher %TWL and %FWL than did adult males at HE in 1985-86 (Wilcoxon test: $P = 0.0083$ and $P = 0.0017$ respectively). Percent total weight loss and %FWL were similar for adult males in both populations in 1986-87 ($\underline{P} > 0.05$). Adult females in both populations had similar %TWL and %FWL in 1985-86 ($\underline{P} > 0.05$). Adult females at HE had lower %TWL and %FWL than their counterparts at LE in 1986-87 ($\underline{P} < 0.05$). Sample sizes of juveniles at HE were too small to permit statistical analysis, but they appeared to follow the same pattern of weight and fat loss as juveniles at LE. Adult males at HE tended to have greater %FWL than did adult females in both years while the reverse pattern was seen at LE. Estimated percent protein loss (%PL) was generally low, less than 5% pre-hibernation levels (Table III-5).

From the estimates of fat and protein loss it was possible to make rough estimates of total over-winter energy consumption (Table III-6). Adult males had the greatest total consumption, followed by adult females and juveniles of both sexes (Fig. III-3a). Protein contributes only a minor portion of the total over-winter energy budget. The mass specific rate of energy consumption ($J \cdot g \cdot day^{-1}$) was almost uniform among all age and sex classes and between populations (Fig. III-3a). The only significant differences among age and sex classes within or between populations or between years were that adult females at HE had lower rates than those at LE in 1986-87 ($\underline{P} = 0.0287$) and adult males at LE had greater rates of consumption in 1986-87 than in 1985-86 ($\underline{P} = 0.0347$). There is a trend, however, for adult females to have a lower rate of energy consumption than adult males or juveniles. Much of the difference in the proportional rate of energy consumption between adult males and females may be attributed to the greater proportion of the hibernationg season spent in euthermia by adult males.

DISCUSSION

From the results of the lipid extractions it is apparent that, within sex and age classes, Columbian ground squirrels from different populations at different elevations differ little in the proportional amount of pre- and post-hibernation fat reserves (Fig 3.1). This contradicts the findings based on the 1984-85 data alone (Young, 1986) that high elevation squirrels had lower pre-hibernation fat reserves than did low elevation squirrels. The low pre-hibernation reserves of HW squirrels may have been an artifact of collecting squirrels before peak fattening had occurred or collecting too late in the year and consequently missing the heaviest adult squirrels. This is possible because heavier individuals in each sex and age class have been reported to enter hibernation before lighter ones (Michener, 1978, 1979; Morton et al., 1974). The greater pre-hibernation reserves of adult males compared to adult females are reduced to similar levels at emergence indicating that hibernation is more energetically costly for males than for females. Similarly, the pre-hibernation reserves of juveniles are equal to those of adult females but post-hibernation reserves are smaller in juveniles, suggesting a greater energetic cost for them as well. The post-hibernation reserves of adult males at LE were much larger than those of adult males (and other squirrels) from the other locations. This disparity might be due to an apparent change in emergence schedules at LE. Adult males at LE emerged from hibernation in late March to mid-April over the course of this study (1985-87, Chs. 2 and 4), 2-3 weeks earlier than reported for the same area in 1975-79

(Murie and Harris, 1982). By emerging early and feeding, even on scarce food supplies, adult males at LE may have reduced the loss of fat reserves that would have otherwise occurred had they remained in their hibernacula. Adult males are euthermic for 1-2 weeks before emerging (Ch. IV) and weight loss during that time, when soil temperatures are at the lowest (Ch. VI), are no doubt high.

One of the two radio-collared squirrels that died at LE appear to have died of starvation, while the other and those from HE did not. The arousal patterns of the LE squirrels were abnormal and they showed numerous frequent arousals just before they died (Ch. IV). The ultimate cause of their deaths is unknown, but, both had open infected wounds at the time they died (Ch. IV) that may have disrupted their thermoregulation and hibernating patterns. The cause of death for the HE radio-collared squirrels is even more uncertain; some laboratory-held hibernators have been reported to freeze to death when ambient temperatures drop below freezing (Wit and Twente, 1983).

Estimates of fat reserves on live squirrels over two consecutive seasons confirms the findings of the extractions (Fig. III-2). That the estimated reserves (F:L ratios) are similar to those determined from extraction methods (Compare Tables III.1-III.4) validates the use of the estimates for comparing patterns of fat deposition and loss. However, the estimates of fat reserves are subject to error from the regression equation, the variation in the weight of gut contents, and imprecision in weighing and measuring the squirrels. Assuming that the errors are equitable across sex and age classes, and populations, the patterns of fat deposition and loss may be viewed as being accurate whereas the actual values must be considered with caution.

Pre-hibernation fat estimates were higher for adult males than for adult females and juveniles and did not differ between high and low elevation populations. The similarity of pre-hibernation reserves between populations in both years supports the findings in other fasting hibernators that fat reserves are endogenously regulated and that a threshold level is reached before entering hibernation (Dark et al., 1986; Mrosovsky, 1976). Loss of fat reserves varied between years but differences among age and sex classes within populations were consistent. The reversing of the pattern of post-hibernation fat reserves between populations from 1985-86 and 1986-87 (Fig. III-2) coincided with survival patterns, with lower survivorship when post-hibernation fat reserves were low (Ch. II) and suggests that environmental factors may play an important role in determining depletion of fat reserves. Adults emerged with 25-48% of their pre-hibernation fat intact (Table III-5) in contrast to juveniles which had only 10-23% of their pre-hibernation reserves remaining. Columbian ground squirrels in Alberta are not usually reproductively mature until their second year of life (Murie et al. 1980) and adult squirrels emerge from hibernation and initiate breeding behavior before most juveniles emerge. French (1986) suggested that reproductively active members of hibernating species with delayed sexual maturity should emerge as early as possible in the spring to ensure a sufficiently long active season for young of the year to grow and prepare for hibernation; non-reproductive members should continue hibernating until their fat reserves are nearly depleted in order to avoid the scarce food supplies of early emergence. This pattern of 'bet-hedging' appears to occur in the populations in this study. The post-hibernation fat reserves of adult squirrels are important as a supplement to foraging during reproductive activity (Snyder et al. 1961; Zegers and Williams, 1977) and may influence the reproductive development and activity of golden-mantled ground squirrels (*S. lateralis*) but are not used to support gestation or lactation (Kenagy and Barnes, 1988). In 1986, 8 of 21 yearling females at LE bred while only 1 of 18 bred in 1987. Post-hibernation fat reserves of LE juveniles were greater in 1986 than in 1987 (Fig. III-2) and females that bred as yearlings (n=10) differed significantly from those that did not breed (n = 26) in total pre-hibernation weight (x = 412 g, and 330 g respectively, Wilcoxon 2-sample test, *P* =0.0003), post-hibernation total weights ($\bar{x}$ = 298 g and 238 g respectively, *P* = 0.0027), pre-hibernation fat reserves (F:L $\bar{x}$ = 0.53 and 0.48 respectively, *P* = 0.0356), and post-hibernation fat reserves (F:L x = 0.27 and 0.17 respectively, *P* = 0.0225).

Although few statistical differences in energetic costs of hibernation were found within or between populations, clearly adult males and juveniles had higher relative energy consumption than did adult females (Fig. III-3). Adult males are euthermic for a greater proportion of their time in the hibernaculum, particularly at the end of hibernation (Ch. IV). Normal body temperatures are necessary for gonadal recrudescence and spermatogenesis in ground squirrels (Barnes et al. 1987) so the increased time spent euthermic is necessary for the immediate onset of breeding behavior upon emergence (Barnes et al.

1986). Even with higher rates of energy expenditure most adult males emerged with a large proportion of the pre-hibernation fat unused. In contrast, juveniles used most of their fat reserves before emergence and would have been more susceptible than adults to increased energetic demands.

In summary, there were no differences in pre- and post-hibernation fat reserves among populations of Columbian ground squirrels at different locations and elevations. Differences in the proportion of fat reserves depleted over-winter among sex and age classes and populations are consistent with observed patterns of survival (Ch. II) and hibernating patterns (Ch. IV). The estimates of energy consumption based on fat and lean weight loss are not entirely reliable as a result of the inherent errors in the FFWT prediction equation. Recently developed methods for making repeated measures of fat composition on live animals (Walsberg, 1988) should improve the accuracy of quantifying the energetics of hibernation and allow for the determination of relationships between energy reserves, reproductive development and survival.

Table III-1. Summary of pre-hibernation total weight, carcass lean and fat weight and fat to lean ratio (mean±se) of squirrels from four locations in southwestern Alberta. Results of ANCOVA analyses are summarized below.

Location Year	Sex/age	n	Total Weight	Carcass Lean Weight	Carcass Fat Weight	F:L
RP 1984	AM	12	700±14	392±7	173±9	0.304±0.011
	AF	6	569±22	347±14	101±9	0.226±0.019
	J	13	373±7	222±7	64±3	0.225±0.007
HW 1984	AM	5	586±33	353±20	102±17	0.219±0.029
	AF	8	490±24	309±16	64±6	0.171±0.013
	J	6	337±23	199±14	46±7	0.183±0.011
LE 1987	AM	5	793±20	432±6	200±19	0.314±0.022
	AF	5	573±24	338±13	91±13	0.269±0.027
	J	10	355±26	208±19	54±7	0.202±0.012
HE 1987	AM	5	794±18	448±11	173±9	0.278±0.015
	AF	5	592±14	361±6	107±11	0.228±0.018

Within locations:

RP: AM > AF = J F=11.24, P=0.0003
LE: AM > AF = J F= 7.69, P=0.0046
HW: AM = AF = J F= 1.97, P=0.1736
HE: AM > AF F=10.75, P=0.0135

Between locations:

AM: LE = RP = LE > HW F= 4.50, P=0.0132
AF: RP = HE = LE > HW F= 3.31, P=0.0424
J : RP = LE = HW F= 2.66, P=0.0897

Table III-2. Summary of post-hibernation total weight, carcass lean and fat weights, and fat to lean ratio (mean±se) for squirrels from four locations in southwest Alberta. Results of ANCOVA analyses are summarized below.

Location				Carcass		
Year	Sex/age	n	Total Weight	Lean Weight	Fat Weight	F:L
RP 1985	AM	10	528±12	416±12	35±4	0.077±0.010
	AF	10	456±19	323±13	28±3	0.081±0.007
	J	6	290±11	200±12	6±2	0.030±0.001
HW 1985	AM	11	429±[illegible]	[illegible]±11	24±3	0.069±0.009
	AF	12	370±12	273±10	17±2	0.061±0.006
	J	4	287±33	210±25	11±2	0.048±0.007
LE 1988	AM	5	495±15	345±8	74±11	0.174±0.021
	AF	5	389±14	291±13	23±3	0.073±0.008
	J	10	221±20	153±16	7±2	0.041±0.008
HE 1988	AM	5	494±22	362±9	37±5	0.091±0.012
	AF	5	372±18	273±11	24±5	0.078±0.014

Within locations:

RP: AM = AF = J F= 2.87, P=0.0780
LE: AM > AF = J F=11.67, P=0.0007
HW: AM = AF = J F= 0.88, P=0.4273
HE: AM = AF F= 0.33, P=0.5839

Between locations:

AM: LE > RP = HE = HW F=12.28, P=0.0001
AF: LE = RP = HW = HE F= 1.73, P=0.1838
J : RP = LE = HW F= 1.45, P=0.2647

Table III-3. --Pre-hibernation total weight, lean and fat weight estimates and F:L ratio (mean±se) for squirrels captured and released at low (LE) and high (HE) elevation populations. Samples from two years, 1985 and 1986, are combined. Some adults were present in both years.

Location	Sex/age	n	Total Weight	Lean Weight	Fat Weight	F:L
LE	AM	41	723±16	560±11	163±06	0.287±0.006
	AF	50	555±9	451±6	104±3	0.230±0.005
	JM	35	372±8	308±6	63±3	0.204±0.009
	JF	49	353±8	289±6	65±3	0.224±0.007
HE	AM	25	757±22	580±14	177±9	0.300±0.010
	AF	26	551±14	446±8	109±7	0.242±0.014
	JM	9	373±11	304±9	69±3	0.226±0.010
	JF	5	332±25	265±19	66±7	0.250±0.021

Table III-4. --Post-hibernation total weight, lean and fat weight estimates and fat to lean ratio (F:L) (mean±se) for squirrels captured and released at low (LE) and high (HE) elevation populations.

Location	Sex/age	n	Total Weight	Lean Weight	Fat Weight	F:L
LE 1985-86	AM	21	558±14	483±10	75±4	0.155±0.006
	AF	16	443±15	400±10	43±6	0.104±0.012
	JM	14	279±11	266±8	12±3	0.044±0.008
	JF	21	268±11	249±9	18±3	0.067±0.010
HE 1985-86	AM	9	450±14	411±13	39±4	0.095±0.010
	AF	6	367±18	339±14	29±5	0.083±0.012
	JM	1	285	279	6	0.022
	JF	0	---	---	---	---
LE 1986-87	AM	27	489±14	436±11	75±4	0.119±0.008
	AF	27	392±9	360±6	28±3	0.077±0.007
	JM	14	239±9	238±8	1±1	0.005±0.002
	JF	18	243±7	234±6	8±2	0.033±0.009
HE 1986-87	AM	14	523±14	462±11	60±3	0.130±0.006
	AF	7	472±18	409±12	64±7	0.154±0.014
	JM	3	280±18	263±15	17±3	0.062±0.010
	JF	2	283±58	261±47	22±11	0.079±0.028

Table III-5. --Proportion of total, fat, lean and protein weight loss overwinter (mean±se), estimated from pre- and post-hibernation weights on individual squirrels. For derivation of protein loss see text.

Sex/age	Yr	n	%Total Loss	%Fat Loss	%Lean Loss	%Est. Protein Loss
Low Elevation:						
AM	'86	18	26.4±1.5	56.7±2.6	17.4±1.1	0.9±1.3
	'87	19	31.2±1.8	66.7±3.2	21.2±1.5	5.4±1.8
AF	'86	15	27.0±1.7	64.6±4.2	17.9±1.4	1.4±1.7
	'87	25	28.2±1.2	72.1±3.2	18.3±0.9	2.0±1.1
JM	'86	13	29.2±2.6	83.1±3.1	16.8±2.6	0.2±3.1
	'87	13	34.8±2.0	97.5±1.3	23.3±2.1	7.9±2.6
JF	'86	17	29.8±1.6	79.1±4.3	17.5±1.2	1.0±1.4
	'87	15	31.4±1.7	88.9±3.2	19.8±1.5	3.8±1.8
High Elevation:						
AM	'86	8	36.0±3.1	74.9±4.1	24.9±2.5	9.8±3.0
	'87	9	33.0±3.3	66.4±4.0	22.3±2.6	6.8±3.2
AF	'86	6	26.8±1.3	70.6±4.7	18.4±0.8	2.0±0.9
	'87	7	22.7±1.9	52.4±4.8	14.3±1.1	2.8±1.3
JM	'86	1	26.9	90.5	14.7	2.4
	'87	2	30.2	77.1	20.1	4.1
JF	'86	0	----	----	----	----
	'87	1	35.7	86.7	19.9	3.8

Table III-6. --Estimated total over-winter energy consumption, based on estimated fat and protein loss (mean±se).

Location	Sex/age	Yr	n	Fat Used KJ	Protein KJ	Total J/g·dy^{-1}
Low Elevation	AM	'86	18	3872±254	26±35	21.5±1.3
		'87	19	4270±320	152±44	25.1±1.6
	AF	'86	15	3031±199	29±38	20.3±1.5
		[illegible]	25	2835±149	44±21	21.1±1.1
	JM	'86	13	2417±123	7±49	24.4±1.4
		'87	13	2178±138	110±36	24.9±1.3
	JF	'86	17	2330±130	8±20	25.1±1.6
		'87	15	2113±165	52±23	24.0±1.5
High Elevation	AM	'86	8	4980±652	274±80	25.8±2.4
		'87	9	5213±606	197±83	24.6±2.6
	AF	'86	6	2917±694	36±17	20.9±4.6
		'87	7	2804±330	58±27	15.9±1.9
	JM	'86	1	2242	35	20.2
		'87	2	2045	57	19.7
	JF	'86	0	----	----	----
		'87	1	2832	46	29.4

Figure III-1. Patterns of pre- and post-hibernation fat reserves for four populations of Columbian ground squirrels in southwestern Alberta. Sample sizes shown in parentheses, means and SE given in Tables III-1 and III-2.

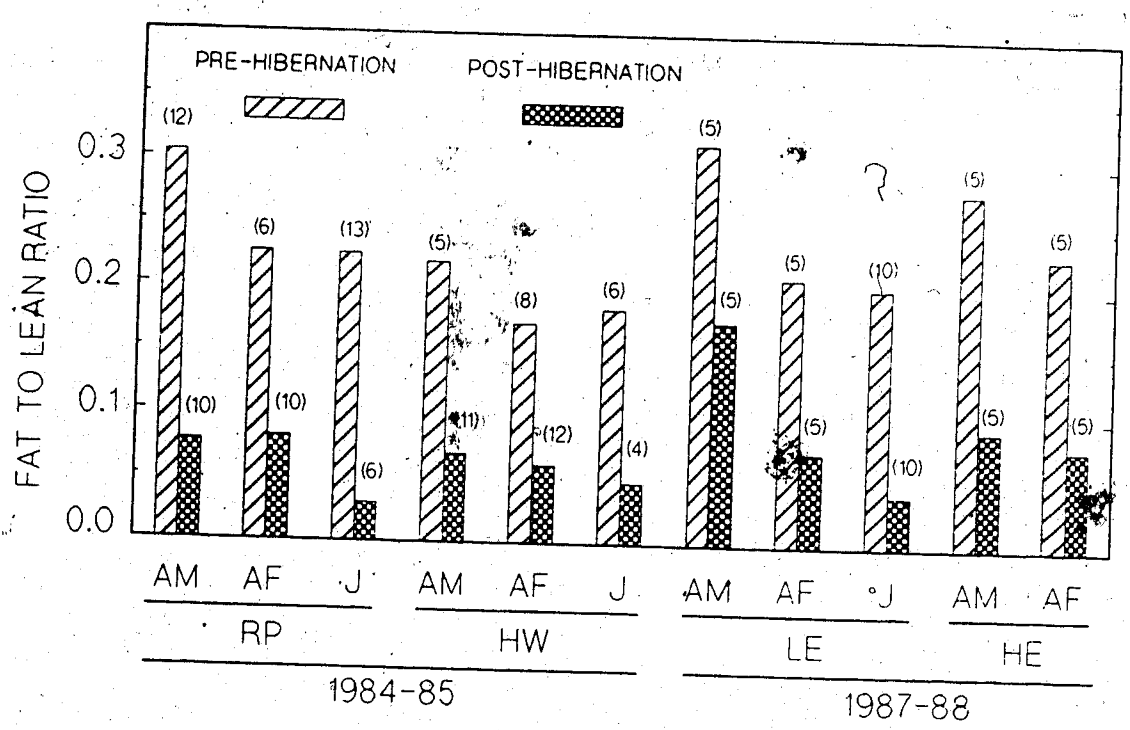


Figure III-2. Patterns of pre- and post-hibernation fat reserve (F:L) estimates for squirrels from high and low elevation populations over two consecutive hibernating seasons.

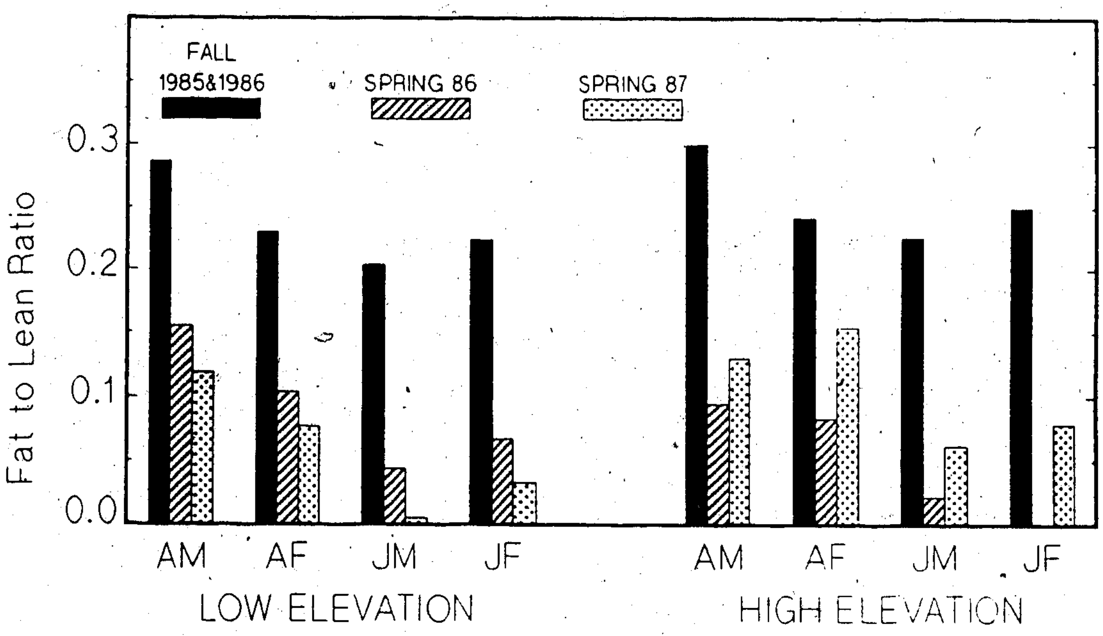
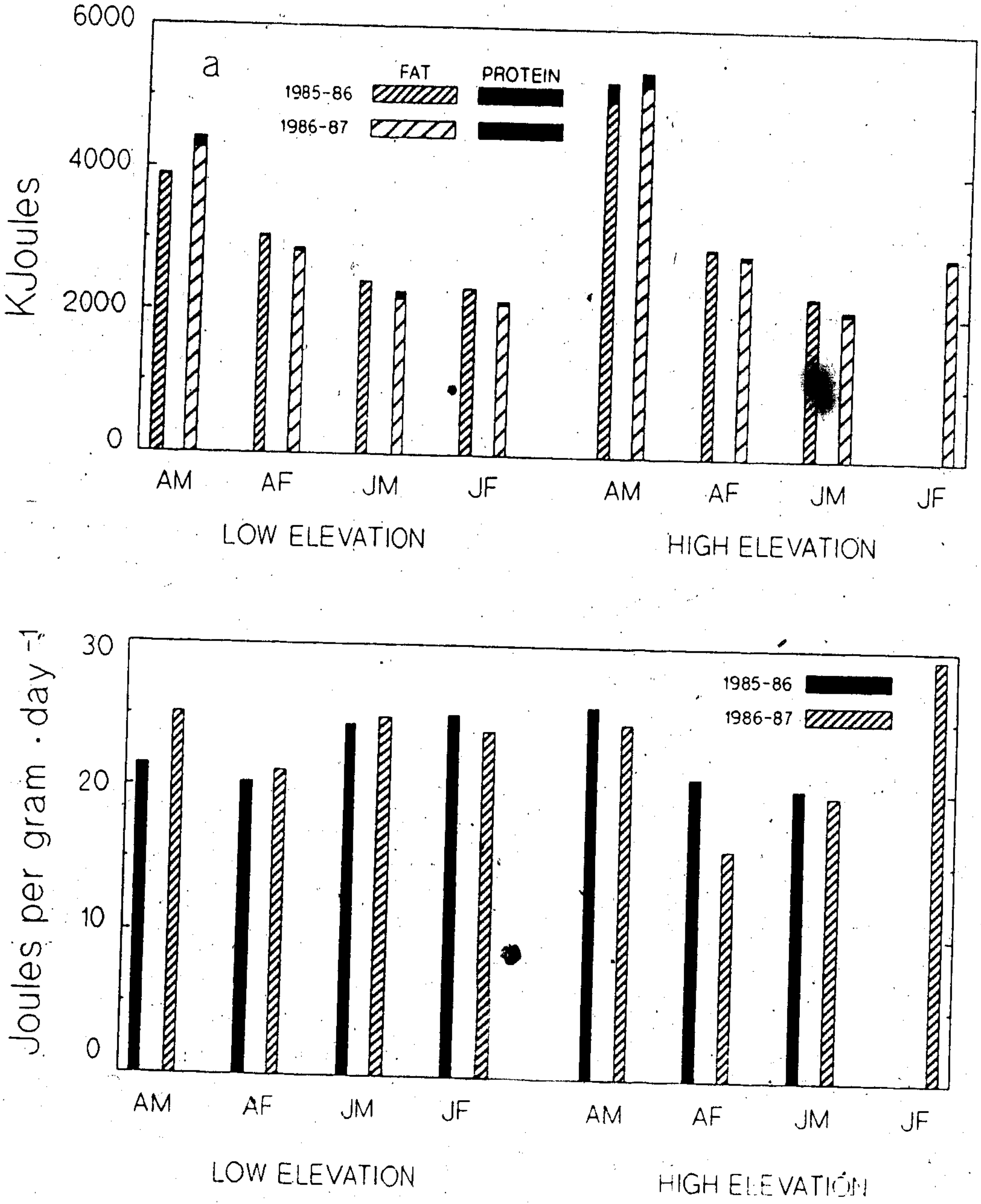


Figure III-3. Estimated energy consumption over-winter for squirrels from high and low elevation populations, a) total energy consumption estimates, b) mass specific rate of energy consumption (J/g·day^{-1}).



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IV. HIBERNATING PATTERNS OF FREE-RANGING COLUMBIAN GROUND SQUIRRELS

Less than 20% of the energy used by an animal in hibernation is used during torpor; the periodic arousals and resulting euthermic episodes account for the remaining 80-90% (Wang, 1979). Despite the high energetic cost of arousals, hibernation results in a 67-88% reduction in energy expenditure over that of a comparable period of euthermia (Scheck and Fleharty, 1979; Wang, 1979). Arousal patterns during hibernation have been studied for many species in the laboratory (Bakko and Nahorniak, 1986; French, 1986; Jameson, 1964; Muchlinsky, 1980; Pivorun, 1976,1977; Twente et al. 1977; Wang, 1973,1979;), all show a similar pattern. Torpor bouts are initially short (1-5 days), increase in length to a mid-season plateau, and decrease in length prior to emergence. Conversely, the duration of euthermic periods decreases as the season progresses and increases when the length of torpor bouts begin decreasing. This general pattern is affected by ambient temperature, colder temperatures causing longer torpor bouts and shorter euthermic periods (French, 1982<u>a</u>; Twente and Twente, 1965,1967), and by the age and sex of the animal (French, 1982<u>b</u>; Pengelley et al., 1979). There are interspecific differences in the duration of torpor bouts as well, larger species generally having longer bouts than smaller ones (Pivorun, 1976<u>b</u>; Twente et al. 1977).

Over-winter mortality has been suggested as an important source of mortality in ground squirrel and marmot populations (Armitage and Downhower, 1974; Barash, 1973; Carl, 1971; Clark, 1970; Murie, 1985;

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Nee, 1969; Sheppard and Swanson, 1976) and differences between age and sex classes in over-winter survival may contribute to the skewed sex and age structures observed (Boag and Murie, 1981; Michener and Michener, 1971,1977); adults generally have higher survival rates than juveniles and females higher rates than males. Higher rates of over-winter loss have been associated with lower pre- hibernation weights (Michener, 1974; Murie and Boag, 1984) and poor snow cover over hibernaculum sites (Barash, 1973; Murie, 1985; Svendsen, 1974) indicating that mortality may be due largely to insufficient energy reserves or to poor hibernaculum conditions that require greater than normal energy expenditures. Because of the high energetic cost of euthermia during hibernation, the frequency and duration of euthermic bouts is an important factor in determining the total energy requirement for surviving hibernation. Differences in torpor and arousal patterns between age and sex classes could be a factor in the differential survival of age and sex classes reported in some studies.

This study was conducted as part of a larger study examining factors affecting over-winter survival of Columbian ground squirrels (S. columbianus). The main focus of this part of the study was to document, with the aid of radio-telemetry, the patterns of torpor and arousal in the field, to determine whether patterns differ between age and sex classes, and to provide additional data for modelling the energetics of hibernation under natural conditions.

METHODS

The study was conducted on the Sheep River Wildlife Reserve, 32 km W of Turner Valley, Alberta, Canada. The study area and population dynamics are discussed elsewhere (Ch. II). For the purposes of this study, individual squirrels were classed as adults or juveniles (young of the year). The adult age class included yearling squirrels as they had already survived one hibernating season and would be reproductively active in most cases the following spring.

Prior to hibernation in 1986, 28 squirrels (7 of each age and sex) were fitted with pre-calibrated temperature sensitive radio collars (model UL81T, Austec Electronics, Edmonton, Alberta; wt. 9-10 g) modified to extend battery life to 10-12 months . The temperature of the collar approximated the body temperature of the squirrel (37-40°C when euthermic) and allowed determination of the hibernating status of the individual (ie. torpid or euthermic) but not the exact body temperature. Squirrels were considered to be euthermic whenever the collar temperature went above 30°C or was 5°C higher than the previous record. Similarly, torpor bouts were considered to start when the collar temperature went below 30°C. The location on a rectangular grid and temperature of each collar on a tagged squirrel were determined using a portable radio receiver (Model LA12-DS, AVM Inst. Co., Dublin, CA) and a hand held stop watch to time the transmitter pulses. The radios were monitored three times daily until the onset of hibernation and from mid-March until emergence, and twice daily during the intervening period. Ten days of telemetry readings were missed over the hibernating season but never more than 36 hrs. at one time. Because of the long time required for a squirrel to return to pre-arousal temperatures after arousal (1.5-2 days) the possibility of missing arousals was considered to be negligible.

The frequency and duration of euthermi[illegible]orpor bouts were determined to the nearest half day and used to compare hibernating patterns. The hibernating season was considered to start when an individual became inactive (remained in the same location for more than three consecutive telemetry readings) and end when the squirrel emerged above ground in the spring. Short (0.5-1.5 days) torpor bouts at the beginning of hibernation followed by an arousal longer than the torpor bout, were not included in the analysis of torpor bout duration.

The radio-collared squirrels were weighed a few days before immergence and within 24 hrs after emergence to obtain estimates of weight loss during hibernation.

Five permanent soil temperature probes, constructed of platic pipe (300 cm by 2 cm dia.) with copper-constantin thermocouples spaced at 20 cm intervals, were located on the study area. Soil temperature profiles, from surface to 200 cm depth, were recorded to the nearest 1°C for each probe on alternate days. The temperatures of the hibernacula were determined from these temperature records and the depth of each hibernaculum, which was determined by excavating them in April and May 1987 (App. A).

Small sample sizes and an inability to meet assumptions of normality meant that all statistical comparisons were done using nonparametric methods unless otherwise stated. Proportions were arcsine transformed for parametric analyses.

RESULTS

Complete records for the entire hibernation season were obtained for 22 squirrels in 1986-87 (6 male and 6 female adults, 5 male and 5 female juveniles). Two of these squirrels (one adult and one juvenile female) died during hibernation. Four radios stopped transmitting before the end of hibernation and two squirrels lost their collars prior to hibernating. No data from the incomplete records were included in the analysis. The radio collars did not appear to affect the radio-collared (RC) squirrelsfor the following reasons: survival of RC individuals ($\underline{n}$= 28, 92.8%) did not differ (X^2=0.2905, $\underline{P} < 0.01$) from that of uncollared (NC) squirrels ($\underline{n}$= 39, 89.7%), and percent weight loss over winter also was not significantly different between groups (34±1% RC vs. 31±1% NC, ANOVA, p=0.09).

Adult males began both to enter and emerge from hibernation before the other age and sex classes. Many squirrels, particularly adult males, were inactive and avoided traps before hibernation; that is reflected in the difference between the median date of last capture and the date of immergence of radio-collared squirrels (Fig. IV-1). Sex and age classes overlapped considerably in the last and first days of capture reflecting the overlap in time of immergence and emergence.

The general pattern of torpor and arousal was similar for all age and sex classes (Fig. IV-2). Torpor bouts less than 1.5 days at the beginning of hibernation were rare; only five squirrels, and no adult males, showed such bouts. Torpor bouts were initially short (2-8.5 days), increased in length during the first 5-7 bouts and generally plateaued at about 28 days in mid-season; most squirrels showed a shortening of the last one or two bouts, but some emerged from hibernation immediately following a long (>25 days) torpor bout (Fig. IV-3).

Euthermic periods were initially 1-2 days long but decreased so that by mid-season squirrels were rarely aroused during two consecutive telemetry readings (ie. <12 hrs). The length of euthermic periods did not increase noticeably near the end of hibernation.

Sex or age classes did not differ significantly in the length of time in the hibernaculum or in the total number of torpor bouts (Table IV-1). Adult males, however, spent more time inactive prior to hibernation, fewer days in hibernation, fewer days in torpor, more time euthermic during hibernation, and more days euthermic before emergence than did other groups. As a consequence, adult males spent a significantly smaller proportion of the hibernation season in torpor than did other squirrels.

Adult males began hibernating when soil temperatures were warmest (Fig. IV-3) and, perhaps as a result, tended to increase the duration of torpor bouts more slowly than did other squirrels. The longest torpor bouts occurred when soil temperatures had dropped below 5°C, resulting in a marked synchrony in the plateau of torpor bout duration among all age and sex classes. Adult males decreased the duration of torpor bouts earlier than other squirrels, but all age and sex classes decreased bout length while soil temperatures were at their lowest level and many squirrels emerged from their hibernacula before soil temperatures started to increase. Torpor bout lengths were strongly correlated with the soil temperature at hibernaculum depth ($r^2 = 76.3$, $P = 0.001$) but the effect of temperature cannot be completely separated from any effect attributable to other factors (ie. endogenous rhythms). No differences were found in the mean soil temperatures experienced by different age or sex classes ($P = 0.73$).

Larger squirrels lost more absolute weight over-winter than did smaller ones; however, this loss expressed as a percentage of immergence weight did not differ between age and sex classes (Table IV-2). Adult males lost significantly more weight per day than other squirrels, and adult females lost significantly more weight per day than juveniles of either sex (Table IV-2).

The juvenile female that died during hibernation was the last squirrel to immerge on the study area. Having first entered torpor on 2 September she exhibited a series of short (<3 days) torpor sessions and arousals until late October (Fig. IV-4) then emerged from the hibernaculum on 27 October and moved to a different burrow. She had lost 38% of her pre-hibernation weight and had several open or partly healed wounds on the head and forelimbs, dying above ground on 4 November. The area around her hibernaculum showed signs of extensive pocket gopher (Thomomys talpoides) activity (fresh earth mounds) during the period of time this squirrel was in hibernation. When excavated in April 1987 the hibernaculum had been destroyed and filled in by pocket gopher activity (App. A), suggesting the gophers may have been a causal agent in the death of this squirrel. The adult female that died showed a similar series of frequent arousals starting in late December and ending in late January after which no further arousals were recorded (Fig. IV-4). This squirrel was found in a typical hibernating posture in the intact hibernaculum when it was excavated in April 1987. She had lost 47% of her pre-hibernation weight and had an unhealed wound on one forepaw, however, in this case, there was no sign of pocket gopher activity near the hibernaculum.

DISCUSSION

The general pattern of hibernation of Columbian ground squirrels in the field was similar to that described for most species under laboratory conditions. The mean duration of those torpor bouts of maximum length for all age and sex classes in this study was considerably longer ($\overline{x}$ = 27.7, range 26-43 days) than that reported for the same species in captivity ($\overline{x}$ = 17.7, range 10-25 days @ 2°C: Twente et al. 1977). This difference cannot be explained by the log linear relationship they found between ambient temperature and bout length. The shorter bout length they reported for captive squirrels may have been due to noisy laboratory conditions as noted by Wang (1978) for _S. richardsonii_.

The juvenile squirrels in this study generally weighed less than half that of adult males, yet all groups had similar maximum torpor bout lengths (Table IV-1) and it appears that the relationship between body size and duration of torpor bouts observed among species (Twente et al. 1977) does not apply intraspecifically in Columbian ground squirrels. The decrease in duration of only one or two torpor bouts and the abrupt termination of hibernation observed for most squirrels is in contrast to the gradual decrease of bout length described in laboratory studies

(French, 1986; Wang, 1979) and calls into question whether the shortened bouts can serve as a means for assessing environmental conditions for emergence (Cranford, 1978; Davis, 1977; French, 1977, 1986; Michener, 1977, 1979). In addition, since soil temperatures at hibernaculum depth were at the lowest annual level at the time of emergence of most squirrels, soil temperature can not be a suitable cue for emergence. The soil at ground surface and at -20 cm was colder than at hibernaculum depth during the emergence period of adult males and would also be unsuitable as a cue for emergence (Ch. VI). Michener (1979) suggested that emergence of Columbian ground squirrels was correlated with the increase of the mean daily air temperature and thawing of the soil at shallow depths. However, her soil temperature records were taken from a site more than 50 km away and may not reflect conditions on her study area. The long time spent euthermic before emergence by adult males, despite favorable environmental conditions above ground, suggests that exit shafts are not pre-excavated and the long euthermic pre-emergence period may be used to dig through frozen soil. The shorter pre-emergence euthermic period seen in adult females and juveniles is consistent with this hypothesis; shallow soil temperatures were above freezing when these groups emerged, possibly making the digging of exit shafts easier and hence faster. However, some cue other than soil temperature, must initiate emergence, especially of adult males.

The most pronounced difference in hibernating patterns was seen between adult males and all other sex/age classes. The greater amount of time spent euthermic by adult males undoubtedly results in a greater energetic demand during hibernation; there is a 10-fold difference in metabolic rate between torpor and euthermia (Scheck and Fleharty, 1979). Presumably, any cost of hibernation should be offset by a corresponding benefit. Because much of the increased cost to adult males is incurred during late hibernation when gonadal recrudescence occurs (Christian et al., 1972; Ellis et al., 1983; Morton and Gallup, 1975), the benefit to adult males may be realized in the ability to participate in reproductive behavior shortly after emergence. Adult female Columbian ground squirrels breed within a few days of their emergence (Murie and Harris, 1982) and adult males would maximize their reproductive opportunities by emerging, in breeding condition, earlier than females (Michener, 1983). In golden-mantled ground squirrels (S. lateralis) and Belding's ground squirrels (S. beldingi) normal body temperatures are necessary for successful spermatogenesis (Barnes et al., 1987; Liddle, 1982; Liddle and French, 1982). Barnes et al. (1986) predicted that adult male golden-mantled ground squirrels would require several weeks of euthermia at the end of hibernation in order to emerge, as they do, with scrotal, functional testes. Adult male Columbian ground squirrels generally have fully scrotal testes upon emergence from hibernation and the results of this study support their prediction although the euthermic period from the end of torpor to emergence (Table IV-1) was not as long as they suggested. Another possible benefit from early hibernation is that the risk of mortality during hibernation is less than the risk of predation by staying active in late summer. Adult males could presumably reduce the overall cost of hibernation by immerging later in the year since they normally enter hibernation earlier than other squirrels when food is still available and environmental conditions favorable. Thus, both reproductive capability and avoidance of predation probably play a part in determining the patterns of hibernation among adult males.

The lack of substantial differences in hibernating patterns between adult females and juveniles suggests that the cost of hibernation is similar for these sex and age groups. Such a conclusion, however, may be misleading since the pattern of torpor and arousal is only one factor determining energy requirements. The temperature regime experienced over-winter and the insulative quality of the hibernaculum could also play a major role in the energetics of hibernation because of temperature effects on metabolic rate during both torpor and euthermia. Shaw (1926) found that juvenile Columbian ground squirrels in Washington used hibernacula that were "shallower and less well constructed" than those of adults. Such conditions could result in higher metabolic costs for juvenile than adult squirrels even when hibernation patterns were similar. An analysis of hibernaculum structure is the subject of another part of this study (Ch. VI, App. A).

Both radio-collared squirrels that died during hibernation showed a similar pattern of frequent arousal before death, indicating that the normal pattern of hibernation had been interrupted. Both squirrels had infected wounds on their legs or bodies that may have been the cause of their abnormal arousal patterns. Slade and Balph (1974) reported that some of the Uinta ground squirrels (S. armatus), emerging from hibernation on their study area, "were badly chewed, apparently from small rodents entering the hibernating chamber". Some hibernation mortality of hedgehogs (Erinaceus europaeus) has also been attributed to predation by small rodents (Hoeck, 1987). Even if mice or gophers can't kill a torpid squirrel outright, the injuries they could inflict might be enough to disrupt hibernation and cause the pre-mature depletion of energy reserves. On the other hand, the adult female that died during hibernation was in an area unaffected by pocket gopher activity and her arousals must have been due to other causes. Some of the injuries on extremities may have been due to freezing during torpor; under laboratory conditions, some hibernators do not respond to gradually decreasing ambient temperatures and may freeze to death (Lyman, 1948; Wit and Twente, 1983). The two mortalities observed during this study appear to have been caused by extraneous, random events rather than from behavioral or physiological differences between age or sex classes.

The similarity of hibernating patterns between sex and age classes suggests that, at least within populations where the environmental conditions are similar for all groups, the pattern of arousals cannot account for observed differences in survival between sex and age classes. Other factors, such as hibernaculum insulative quality, energy reserves (fat or food cache), or the stability of the thermal environment may be more important in determining survival.

Table IV-1. Summary of hibernating patterns. Values given are means and (ranges). Asterisks indicate a value that is statistically different from the others (P < .05, Kruskal-Wallis test).

	Adults		Juveniles		*P*
	Males	Females	Males	Females	
n =	6	5	5	4	
Number of Torpor Bouts	13.3 (12-16)	13.0 (11-15)	13.2 (11-14)	14.3 (13-15)	0.476
Days Inactive Prior to Torpor	3.3* (2.5-5.0)	1.8 (1.0-5.0)	1.7 (1.0-2.5)	1.4 (1.0-2.0)	0.007
Days in Hibernation	228.5* (221.5-235.5)	244.7 (233.0-267.0)	242.4 (233.0-251.5)	247.0 (234.0-248.0)	0.008
Days in Torpor	216.8* (211.0-222.5)	236.4 (224.0-259.0)	234.1 (224.5-243.5)	238.9 (234.0-248.0)	0.004
Mean maximum torpor length (days)	27.9 (20.0-43.0)	27.9 (20.5-34.5)	25.3* (20.5-31.5)	28.1 (23.5-32.0)	0.009
Days Euthermic	11.2* (9.0-13.5)	7.9 (6.5-9.0)	8.3 (7.0-9.5)	7.9 (7.0-8.5)	0.009
Days from end of Hibernation to Emergence	8.2* (3.0-12.0)	1.3 (0.5-2.0)	1.4 (0.5-2.5)	0.6 (0.5-1.0)	0.003
Days in the Hibernaculum	240.0 (233.5-249.5)	247.8 (236.0-270.0)	245.5 (235.5-255.0)	247.0 (244.5-248.5)	0.302
% Torpor for Season	90.4* (89.2-91.4)	95.4 (94.9-96.0)	95.9 (95.1-96.1)	95.4 (94.6-95.6)	0.003

Table IV-2. Mean weight loss (and range) of radio-collared squirrels over the hibernating season.

	Adult Males	Adult Females	Juvenile Males	Juvenile Females	P
n =	6	4	6	4	
Immergence Weight (g)	780 705-875	544 510-620	353 330-450	378 345-425	
Emergence Weight (g)	500 465-540	376 330-450	236 215-240	240 215-275	
Weight Loss (g)	285 240-380	188 175-200	117 90-145	138 125-150	
% Weight Loss	36.3 32.1-43.4	34.7 33.3-37.7	32.9 27.3-37.6	36.5 35.3-38.6	0.196
Weight Loss Per Day	1.18 * 1.04-1.52	0.75 * 0.70-0.84	0.48 0.35-0.61	0.55 0.50-0.58	0.001

NOTE: * indicates values that are significantly different from others, Kruskal-Wallis test.

Figure IV-1. Dates of last capture in fall and immergence into hibernation, and first capture in spring and emergence from hibernation. 'X' indicates the last or first capture date of the year for one or more squirrels. Solid circles mark the median date of last or first captures. Solid lines represent the time over which radio-collared squirrels entered torpor or emerged from hibernation. Only records of squirrels known to survive overwinter were used. Trapping in 1986 started on 8 April, some squirrels were known to be active on the study area as early as 30 March (indicated by the open circle).

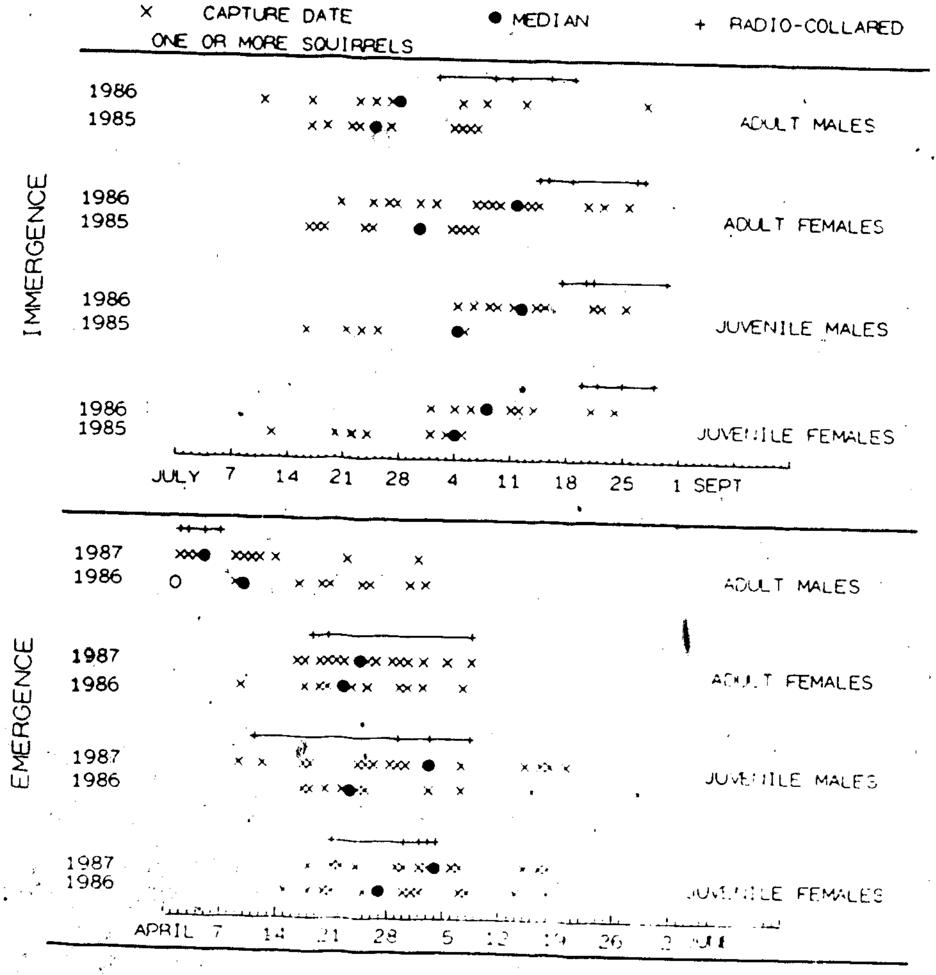


Figure IV-2. Representative hibernating patterns of free-living Columbian ground squirrels, based on temperature recordings from thermosensitve radio-collars. Peaks on the lines represent euthermic episodes, labelled arrows refer to: I - date immerged into hibernaculum; T- date of first torpor, A - last arousal date, E - date emerged from hibernaculum, TD - test drop.

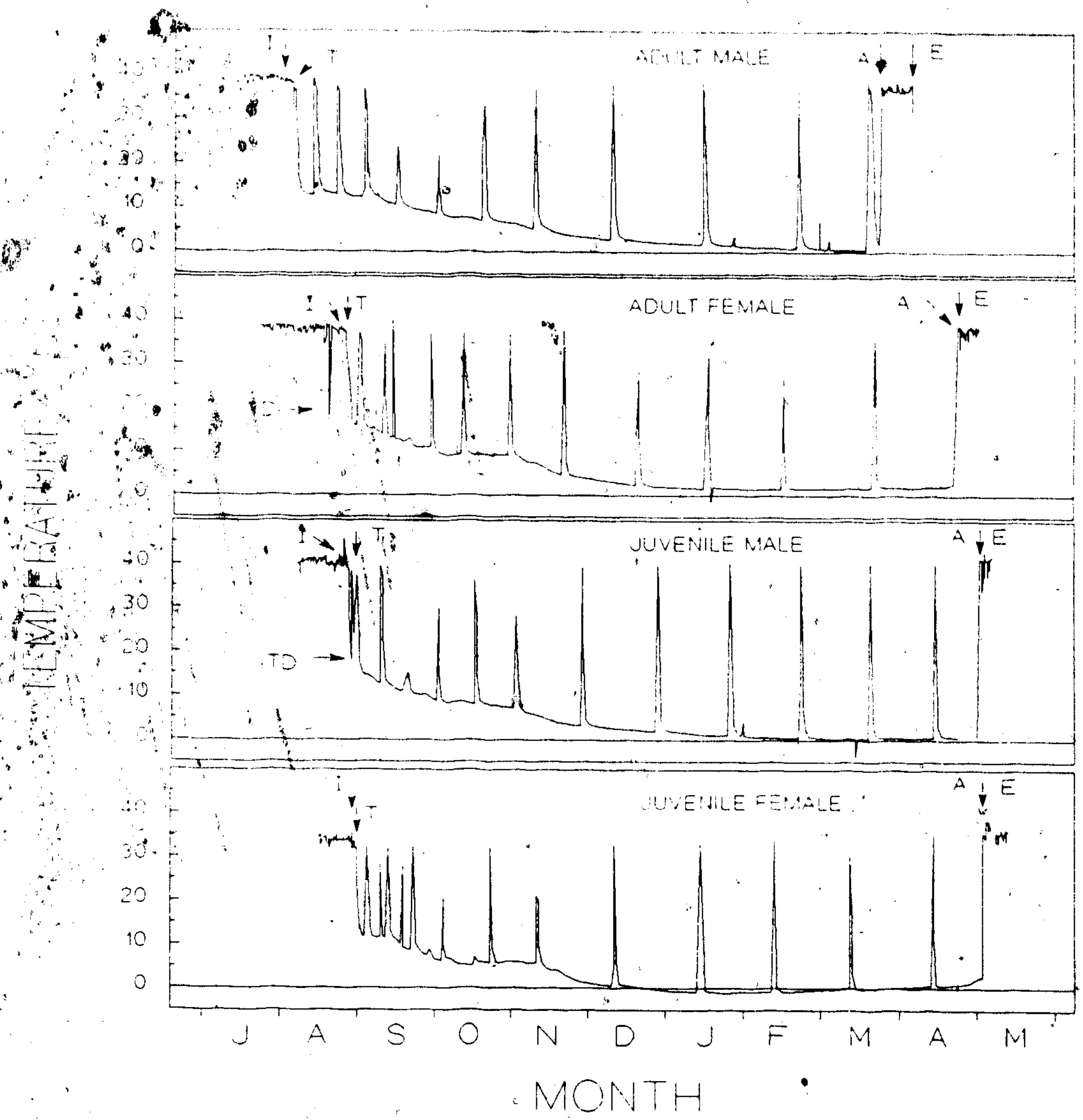


Figure IV-3. Duration of torpor bouts and soil temperature over-winter: Day 0 is 1 July 1986. The length of each bout is plotted at the beginning of the bout. Solid line is the weekly mean soil temperature at 60 cm depth. Different symbols refer to individual squirrels.

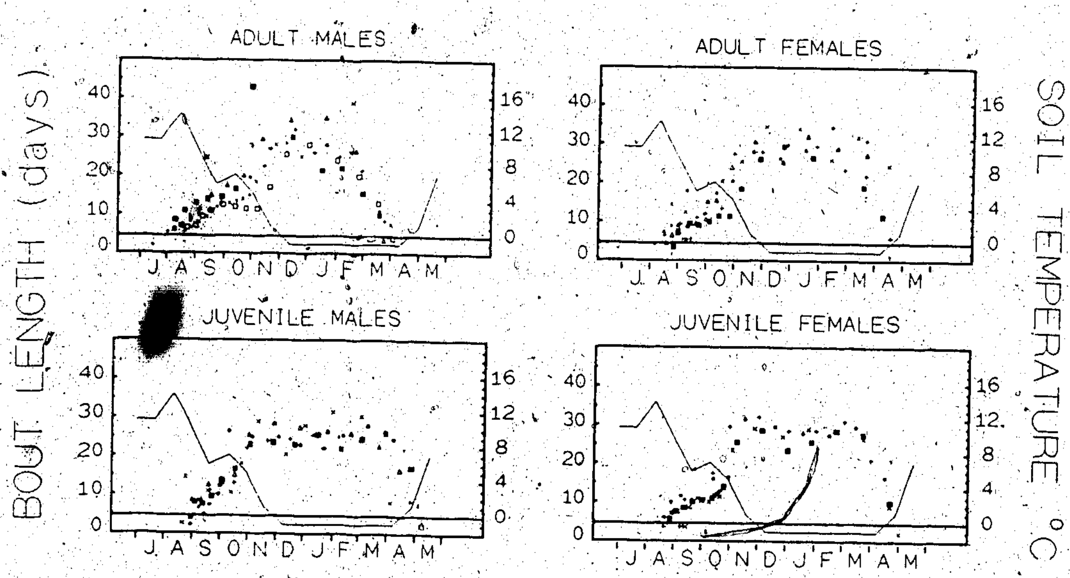
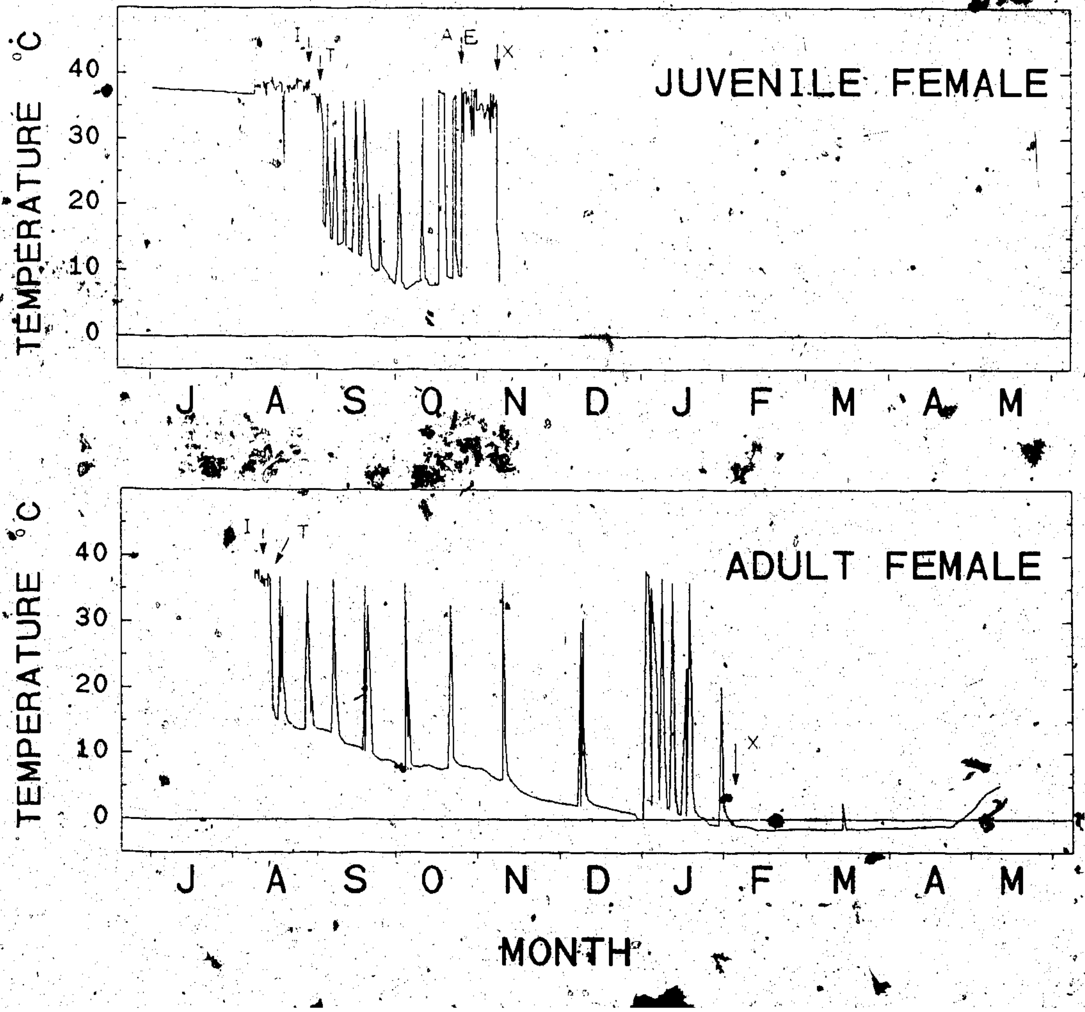


Figure IV-4. Hibernating records based on recordings of temperatures from thermo-sensitive radio-collars of free-living ground squirrels that died during hibernation: A) a juvenile female that died in November after emerging from the hibernaculum in late October 1986 and B) an adult female (bottom) that died in the hibernaculum in February 1987. Labels as in Fig. IV-2 except "X"= presumed date of death.



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V. TEMPERATURE REGIME AND HIBERNATING PATTERNS OF CAPTIVE COLUMBIAN GROUND SQUIRRELS

Several studies of hibernation in ground squirrels (Spermophilus spp.) and chipmunks (Eutamias spp.) have shown that squirrels hibernating at low ambient temperatures (2-5°C) have longer maximum lengths of torpor than those hibernating at warmer temperatures (10-15°C) (French, 1982a; Pivorun, 1976a, 1977; Scott and Fisher, 1972; Twente and Twente, 1965, 1967; Twente et al. 1977). Torpor bouts increase in length at the beginning of hibernation and are characterized by the progressive decrease of the core temperature of the hibernator with successive bouts, to near ambient temperature (Pivorun, 1976a; Twente and Twente, 1967; Wang, 1979). This has been interpreted as a continuation of preparation for hibernation and such bouts were termed "test drops" by Strumwasser (1959). Most laboratory studies have been conducted under constant temperature conditions for the entire hibernating season. Information on the effect of temperature on the length of torpor bouts has been gained from studies on the same or a different group of animals held under different temperatures during one or successive hibernating seasons (French, 1982a; Pengelley and Fisher, 1963; Pivorun, 1976a; Twente, et al, 1977). The effect on torpor bouts of temperature regimes that either simulate or use natural conditions has not been studied adequately. Under natural conditions few species of ground squirrels are likely to experience constant environmental temperatures during the hibernating season. Soil temperatures are warmest at the beginning of hibernation and decline as the season progresses (Wang, 1979), coinciding with the increasing length of torpor bouts.

Populations of Columbian ground squirrels (Spermophilus columbianus) experience different temperature regimes during winter, depending on the elevation and exposure of the site (Ch. VI). To ascertain the effect that a specific temperature regime might have on torpor and arousal patterns at the start of hibernation, torpor patterns were recorded for two groups of squirrels under laboratory conditions that simulated the temperature regimes experienced by high and low elevation populations in the field.

Twenty adult male squirrels were live trapped on the Sheep River Wildlife Sanctuary, 32 km W Turner Valley, Alberta (Ch. II) in June and July of 1987. The squirrels were housed individually in plastic 'shoebox' cages at the Biological Sciences Animal Services facility at the University of Alberta. They were kept under a 12L:12D photoperiod at 23°C and provided with commercial laboratory rat chow and water ad lib, supplemented with lettuce and sunflower seeds. All squirrels were weighed weekly; when all reached a plateau in body weight they were placed in environmental chambers (4 September 1987). Squirrels were assigned randomly to groups of 10 for each of the chambers. Conditions in the chambers were the same (constant darkness and minimal disturbance) apart from the temperature regime. The warm chamber was set initially at 15°C and the cold chamber at 5°C. Temperatures in both chambers were lowered to 0°C over an 80 day period (Fig. V-1). Squirrels were provided with shredded paper, as needed, to construct and maintain nests in their cages. Food and water were provided ad lib and cages were cleaned weekly until an individual began hibernating, after which food and water were removed and the cages no longer became soiled. The hibernating status of each squirrel was determined by daily monitoring of sawdust placed on their back (Lyman, 1948). Sawdust on squirrels that had aroused was disturbed by movement or removed by grooming. Duration of torpor bouts was determined to the nearest day. Some squirrels hibernated irregularly, having short (<3 day) torpor bouts interspersed with euthermic episodes of 3-15 days; these individuals, and squirrels that required [illegible]20 days to enter hibernation were excluded from the analysis. Only the first six torpor bouts were compared as some squirrels were used subsequently in experiments on metabolic rate that required interruption of their hibernating patt[illegible]

Some squirrels in each group began torpor bouts as early as the 2nd day in the chambers. The mean length of time before the 1st day of torpor, the length of the 1st torpor bout, and the length of all bouts after the 3rd bout did not differ significantly between groups (Table V-1). Squirrels in the colder room increased the duration of their torpor bouts abruptly, reaching maximum length in the second bout, in contrast to a more gradual increase in length exhibited by squirrels in the warmer room. This resulted in the latter group of squirrels having one more arousal episode during the first 30 days of hibernation (median 3, range 2-[illegible]) than squirrels in the former group (median 2, range 2-3; Fig. V-1).

The number of arousals affects the rate of energy expenditure because much of the energy used during hibernation is consumed during euthermic episodes (Pivorun, 1976b; Scheck and Fleharty, 1979; Wang, 1979). With a 10-fold difference between euthermic and torpid metabolic rates (Pivorun, 1976b; Scheck and Fleharty, 1979) the elimination of one arousal could theoretically result in saving enough energy reserves to extend the hibernating season by 10 days of torpor. However, the cost of arousing and maintaining normal body temperature becomes greater as environmental temperature decreases, perhaps offsetting to some degree the potential energy saved by decreasing the number of arousals. Increasing the insulative value of the nest can decrease the effect of environmental temperature on metabolic rate (Casey, 1981) and, together with the decrease in the number of arousals, result in an energetic advantage to squirrels hibernating at colder temperatures. The thermal environment experienced during hibernation under natural conditions is reported in Chapter VI. Determination of energy requirements for the various metabolic states of hibernation is confounded by not knowing how the insulation of the nest material and surrounding soil affects this micro-environment. An analysis of the effect of nest insulation on metabolic rate is necessary before precise estimates of hibernating energy budgets can be derived.

The gradually increasing length of torpor bouts of squirrels in the warmer room is characteristic of the descriptions of hibernating patterns for other hibernating sciurids under laboratory conditions (French, 1982a; Jameson, 1964; Pivorun, 1976a, 1977; Twente et al., 1977; Wang, 1978). The pattern observed for squirrels in the warmer room is similar to that observed for squirrels in the field at low elevation except that the mean maximum torpor bout length was shorter for captive animals (mean 18.3 days) than for animals in the field (mean 28.3 days;

Ch. VI). The maximum length of torpor bouts seen in this laboratory study, although shorter than observed in the field, are similar to those reported for the same species (Twente et al. 1977) and other species (French, 1986; Wang, 1978) in captivity. The shortening of bouts in captivity appears to be an artifact of laboratory conditions and may be related to environmental disturbances such as noisy fans, clicking switches, and the proximity of other squirrels (Wang, 1978).

Assuming that squirrels under natural conditions respond to temperature regimes in the same manner as observed in this experiment, the number of arousals for squirrels at high elevations could be less than the number for squirrels at low elevation because of soil temperature differences (Ch. VI) and the long maximum bout lengths observed in the field (Ch. IV). A decrease in the number of arousals could result in an energetic saving for high elevation squirrels and could partially explain the higher rates of survival observed for populations of hibernating ground squirrels at high elevations compared to low elevations (Bronson, 1979; Dobson and Murie, 1987; Murie, 1985).

It is unclear whether a decrease in the number of arousals occurs in the field. Wang (1973) found arousal patterns of captive and free-ranging Richardson's ground squirrels (S. richardsonii) to be similar, although torpor bouts and hibernating seasons of the captive squirrels were shorter than those in the wild. His captive squirrels were held at 5°C and did not show a reduction in the number of arousals early in hibernation. The length of torpor bouts of Columbian ground squirrels in the field did not reach a plateau until soil temperature fell below

5°C (Ch. IV) which may indicate a critical temperature, above which long torpor bouts are not possible.

It also is not known whether the reduction in number of entry bouts under cold conditions is exhibited by Columbian ground squirrels other than adult males. Differences in torpor patterns occur among sex and age classes of captive Belding's ground squirrels (S. beldingi) but at the end of the hibernating season, not at the beginning (French, 1982b).

Squirrels in this study were all captured from the same low elevation population. Because they were consistently subjected to colder soil temperatures, high elevation populations may have been under selective pressure to have even longer torpor bouts with fewer arousals. Differences in the tendency to hibernate have been observed between wild populations of Turkish hamsters (Mesocricetus brandti; Lyman et al., 1983). 'Super-hibernating' and 'non-hibernating' strains of golden hamsters (Mesocricetus auratus) have been selected artificially in the laboratory in only two generations (Chaffee, 1966), suggesting that hibernating patterns are readily adaptable to local conditions.

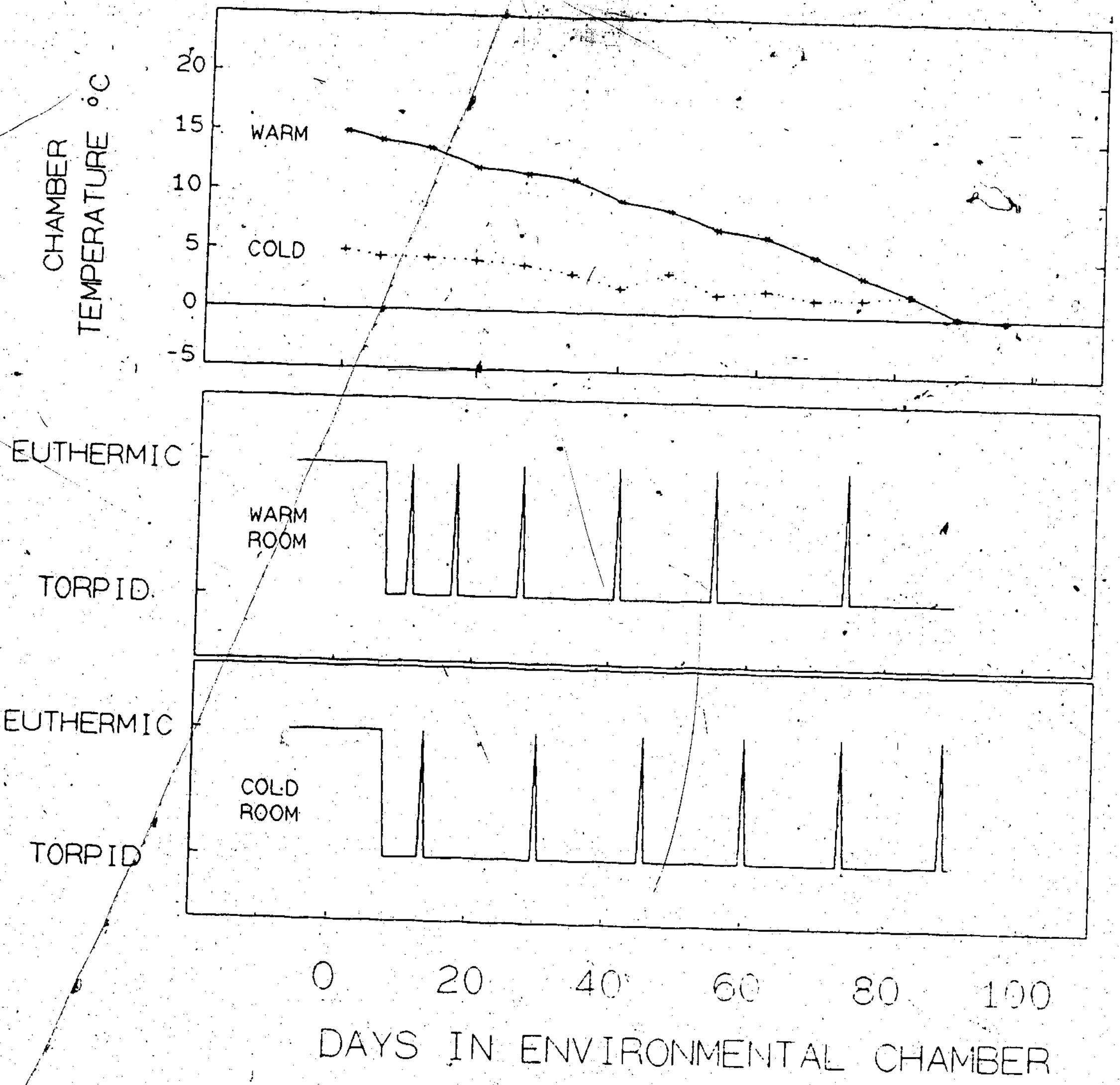
This study suggests that the soil temperature regime experienced by squirrels at high elevations may reduce the number of euthermic episodes early in hibernation. Such a reduction in arousals could reduce the energy expenditure during hibernation and contribute to the greater survivorship of high elevation populations.

Table V-1. Mean (± S.E.) length of time spent in the environmental chambers before hibernation and lenght of torpor bout of squirrels in warm (15-0°C) and cold (5-0°C) conditions.

	Warm Room	Cold Room	P	
n	7	7		
Days in Chamber Before Hibernating	7.3 ± 2.4	7.7 ± 2.4	0.903	
Length of Torpor Bouts (days)				
Bout 1	3.4 ± 0.7	5.6 ± 1.3	0.185	
Bout 2	5.7 ± 1.4	16.1 ± 2.3	0.002	*
Bout 3	7.9 ± 1.8	15.3 ± 1.3	0.006	*
Bout 4	13.3 ± 1.8	14.1 ± 1.5	0.726	
Bout 5	13.4 ± 1.8	13.6 ± 1.5	0.955	
Bout 6	18.3 ± 1.0	13.9 ± 1.6	0.030	*

NOTE: * indicates values thaty are significantly different, ANOVA.

Figure V-1. Environmental chamber temperatures and diagramatic representations of torpor patterns for squirrels under warm and cold conditions, based on mean values from Table V-1.



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VI. COLUMBIAN GROUND SQUIRREL HIBERNACULA: INSULATION QUALITY AND ENERGETIC CONSEQUENCES.

Before hibernation, ground squirrels, marmots and chipmunks plug most or all of the entrances to their burrow system as well as the tunnels leading directly to the hibernating chamber or hibernaculum (Panuska and Wade, 1960; Rausch and Rausch, 1971; Shaw, 1925, 1926). Once sealed into the hibernaculum the occupant is subject to the micro-environmental conditions of that location for the duration of the hibernating season. Poor hibernaculum conditions have been suggested as a cause of overwinter mortality in yellow-bellied marmots (Marmota flaviventris; Svendsen, 1974), Columbian ground squirrels (Spermophilus columbianus; Murie, 1985), arctic ground squirrels (S. undulatus; Carl, 1971) and Richardson's ground squirrels (S. richardsonii; Michener and Michener, 1977). The quality of hibernacula may be correlated with the soil temperature which in turn should be influenced by depth and snow cover that provides insulation over the hibernaculum (Murie, 1985; Svendsen, 1974) or with the size and construction of the chamber and the insulative quality of the nest (Holmes, 1984; Shaw, 1926).

In this paper I describe the quality of hibernacula of Columbian ground squirrels in relation to patterns of over-winter mortality within and between populations at different elevations. Previous studies have shown that over-winter survival within populations of Columbian ground squirrels is greater for females than for males, greater for adults than for juveniles, and greater for high elevation populations than for low elevation populations (Dobson and Kjelgaard, 1985; Murie, 1985; Murie and Boag, 1984). Since hibernation is primarily a means of conserving energy, I assumed that the insulation of the hibernaculum is the major factor determining quality. This study focused on the micro-environment of the hibernaculum, the insulation of the nest and how these might affect the energetic cost of hibernation. The general structure and location of hibernacula are discussed in Appendix A.

METHODS

The study areas, one (LE) at low elevation (1470m) and the other (HE) at high elevation (2250m), were located in the Sheep River drainage approximately 32 km W of Turner Valley, Alberta, Canada and are described in more detail elsewhere (Ch. II). The hibernacula of 28 squirrels at LE and 16 squirrels at HE were located during a radio-telemetric study on the areas in 1986-87 (Ch. IV). Each hibernaculum was marked with an aluminum rod (175 X 0.5 cm) marked at 5cm intervals to record snow depth at each location. Snow depths were recorded daily at LE and bi-weekly at HE during the telemetry study. Soil temperature profiles (from surface to 180-200 cm deep) were obtained from probes constructed of plastic pipe (300 cm by 1.5 cm O.D.) with copper-constantin thermocouples spaced at 20 cm intervals. Five temperature probes placed perpendicular to the ground surface were located at each site. Most radio-collared squirrels were no more than 15 m from a probe at LE and temperature profiles were obtained from areas with similar slopes, exposure and snow cover to all hibernacula at HE. Soil temperatures were recorded on alternate days at LE and bi-weekly at HE.

Soil temperatures for each hibernaculum were taken from the thermocouple nearest the hibernaculum at the appropriate depth determined from later excavations of the sites.

[illegible] emergence of the squirrels and the thawing of the soil in April to June 1987, the hibernacula were exc[illegible]ured and mapped (App. A). The nest material was dried and store[illegible]astic bags [illegible] later analysis. The volume of each hibernaculum was calculated as the volume of a sphere with a radius equal to the mean radius of the height, width, and length of the chamber. To determine insulative values, hibernacula were considered to be completely filled with nest material except for the volume occupied by the squirrel, as that was the situation when squirrels were found dead in excavated hibernacula. Squirrel volume (V_s) was considered to be a sphere equal in volume to the pre-hibernation weight of the squirrel (based on an estimated density of 1g per cm^3) and located in the center of the hibernaculum. The insulative value of the nest material depends on the thermal conductivity and thickness of the insulating material. Since thermal conductivity could not be measured on the intact nests the heat conductivity coefficient (k) of all nests was assumed to be that of straw, 0.05 $W \cdot m^{-1} \cdot {}^{\circ}C^{-1}$, (Weast, 1971) so that the insulative value was determined by the thickness of the material. Total heat loss (q) of an insulated sphere, expressed as milliwatts per degree temperature difference across the insulation ($mWatts \cdot {}^{\circ}C^{-1}$), is dependent on the insulation thickness and surface area of the sphere and is calculated as:

$$q(mW/{}^{\circ}C) = \frac{4\pi k*1000}{(1/r_s)-(1/r_h)} \qquad \text{(Eq. VI-1)}$$

where k - 0.05 (heat conductivity coefficient of straw), r_s - radius of the squirrel in meters, and r_h - radius of the hibernaculum in meters. The calculations used in this study ignore the thermal conductivity and heat capacity of the soil surrounding the hibernaculum and assumed the temperature around the hibernaculum was unaffected by heat flow from the nest.

A subjective analysis of the quality of the nest material was conducted on roughly equal size portions of material from each nest. The samples were grouped in blind trials into categories for age (1- newest to 3 - oldest), texture (1- very coarse to 5 - very fine) and composition (grasses, leaves of forbes or trees, and other). I assumed that old or very coarse nest material would be a less effective insulator than new or fine material. The rankings were then tested for differences between sex and age classes and between populations.

Statistical tests were done on the SAS system using the University of Alberta computer facilities; most comparisons were done using t-tests, analysis of variance or by equivalent non-parametric methods when assumptions of normality could not be met. Juveniles of both sexes were pooled within locations for sex/age groupings, because they are of similar size, used similar sized hibernacula and because only one juvenile female was located at HE.

The total heat loss from the hibernaculum is dependent on the surface area of the chamber and the thickness of the insulation while total heat production is dependent on the size of the squirrel occupying it. Analysis of co-variance, rather than a ratio of heat loss to body weight, was used to remove the confounding effects of body size and metabolic rate (Packard and Boardman, 1987,1988) when comparing q between sex/age classes and populations.

RESULTS

Twenty-six hibernacula at LE and 13 at HE were excavated and provided data on micro-environmental conditions and insulation. The other five hibernacula marked during the telemetry study either could not be located or were destroyed by pocket gopher (<u>Thomomys talpoides</u>) activity before excavation. Three hibernacula contained the remains of squirrels that had died during hibernation and one at HE contained a juvenile squirrel still hibernating on 7 June.

Snow cover at LE was intermittent and never exceeded 30 cm in depth (Fig. VI-1). There were 13 periods of measurable snowfall during the hibernating season. The proportion of the hibernating season that individual hibernacula were covered with 10 cm or more snow averaged 19.6% (range 8.9-37.2%) with a mean maximum snow depth of 21.6cm (range 15-30cm). Snow cover at HE was continuous over most of the study area from 25 September through mid-May. Snow depth was greater than 10cm for 85-90% of the hibernating season at HE. The mean maximum snow depth was 143cm (range 85-220cm). Most adult squirrels at HE emerged in early-May while snow still covered their hibernacula at depths of 20-80cm; most juveniles emerged in mid- to late-May after the snow had disappeared (Fig. VI-1).

At LE adults used deeper hibernacula than did juveniles. Hibernaculum depth at HE did not differ between any age/sex classes. Except for adult females, LE squirrels used deeper hibernacula than did their counterparts at HE (App. A). The soil temperature regimes differed greatly between locations (Fig. VI-2). The mean soil temperature at hibernaculum depth for the start of hibernation was 11.3°C (±1.2°, n=25) at LE and 3.1°C (±0.8°, n=13) at HE (t=20.83, P<0.0001). The minimum temperature experienced over winter was also lower at HE (mean = -3.8°C, ±0.6) than at LE (mean = -2.0°C, ±0.8) (t=7.299, P<0.0001). Soil temperatures of 0°C or lower were earlier (approximately 25 September) at HE than at LE (approximately 15 November), resulting in large differences in the proportion of the hibernating season spent at freezing temperatures (85% HE, 52% LE). The average temperatures during the sub-zero portion of the winter were -1°C and -2°C at LE and HE respectively. There were no differences in temperature regimes between sex and age classes within either location, although adults tended to occupy warmer (deeper) hibernacula. Using radio-collar temperatures as a measure of nest temperature, the mean temperature gradient across the nest insulation was 3°C at LE and 6°C at HE at the start of hibernation. During mid-season the temperature gradient was 3°C at LE and 4°C at HE. Collar temperatures averaged 14°C and 9°C at LE and HE at the start of hibernation but dropped to 2°C at both locations when soil temperatures fell below 0°C.

The dimensions and depths of the hibernacula are described in more detail elsewhere (App. A). In general, larger squirrels used larger hibernacula than did smaller ones and HE squirrels used larger hibernacula than did LE squirrels. Adult males used larger hibernacula in relation to their body size than did other age or sex classes within a population. Within locations there were no significant differences

between sex/age classes in nest material quality, either in estimated age (Kruskall-Wallis Chi square approximation: HE, X^2=1.488, *P*= 0.48; LE, X^2=5.086, *P*=0.08) or texture of the material (X^2= 2.758, *P*=0:252, HE; X^2=5.634, *P*=0.059, LE). Juveniles tended to use nest material that appeared older and finer than that of adults. HE squirrels used nest material that was somewhat older than that of LE squirrels (Wilcoxon test: z=1.372, P= 0.170), but the texture of the material did not differ. The composition of LE nests was uniformly grass. HE squirrels used mostly grass but also included stems of sedges (*Carex* spp.) and willow (*Salix* spp.) leaves and catkins.

Larger hibernacula have thicker walls of nest material and therefore provide more insulation for the occupant. Adult males had significantly lower q values than other sex/age classes both at LE (ANCOVA: F=4.11, *P*=0.019) and at HE (F=5.06, *P*=0.034). Heat loss was also lower for all HE hibernacula compared to LE hibernacula (F= 7.09. *P*= 0.032 adult males; F= 9.13, *P*=0.006 other squirrels; Table VI-1).

To maintain nest temperatures of 2°C (as indicated by collar temperatures) at the average mid-season soil temperature required heat production of 241mW for adult males, 254mW for adult females and 198mW for juveniles at HE. Heat production required at LE was 191mW, 209mW and 169mW for the same respective age/sex classes. Expressed in terms of basal metabolic rate (BMR (mlO_2/hr)=$3.24W_{grams}^{.66}$, Hudson and Deavers, 1973 and mlO_2/hr * 5.58 $\cong$ mW) these values correspond to 15%, 21% and 22% BMR for adult males, adult females and juveniles respectively at HE and 13%, 18% and 19% BMR for the same age/sex classes at LE.

DISCUSSION

Columbian ground squirrels apparently construct hibernaculum nests to match environmental conditions and hibernating patterns. The depth of the hibernaculum may be determined by factors other than soil temperature regime, while colder soil temperatures are partially compensated for by larger, better insulated nests. The results of this study do not support Shaw's (1926) finding that juvenile Columbian ground squirrels use less well constructed hibernaculum nests than do adults. Juvenile squirrels probably do not always construct their own hibernaculum, but may use nest chambers in the natal burrow system or take over abandoned hibernacula (App. A). It might be expected that the insulation in these hibernacula would be lower, due to decay and breakdown of older nest material, than those of adults which are apparently not used from one year to the next (App. A), but the subjective classification of nest quality revealed no discernable differences in nest material quality between sex and age classes or between locations. Heat conductivity coefficients of the nests would be needed to verify this finding.

The primary micro-environmental difference observed between elevations was soil temperature. High elevation squirrels spent the entire hibernating season at lower temperatures than those at LE and a much greater proportion of hibernation at soil temperatures below zero. The greater snow cover at HE compared to LE was not sufficient to prevent freezing and did not result in warmer hibernaculum temperatures as suggested by Murie (1985) but that may have been due to the unusual weather pattern in 1986-87. The winter of 1986-87 was warmer and drier than normal (Alberta Environment records) which may have affected soil temperature patterns. Lower snowfall at HE may have caused soil temperatures to be colder than normal, while warmer air temperatures may have caused warmer than usual soil temperatures at LE. The occurrence of chinook conditions at the LE site prevented snow from accumulating to any appreciable depth, making LE squirrels more susceptible to extremely low air temperatures. Squirrels at both sites appeared to make use of ground cover or natural terrain to hibernate in areas where snow accumulated by drifting. The effect of this on modifying hibernaculum conditions is not known since soil temperatures were not taken from areas where squirrels did not hibernate. Studies manipulating snow cover over hibernacula sites could provide valuable insight into this aspect of the micro-environment of hibernation.

Squirrels were not apparently restricted by soil conditions or obstructions from constructing deeper hibernacula (App. A) and could have experienced warmer soil temperatures had they done so. That was particularly true for HE squirrels where the average hibernaculum depth was only 40cm. The use of shallow hibernacula at HE may be related to the difficulty in digging out through frozen soil in the spring or possibly to improving respiratory gas concentrations in the hibernaculum (App. A). The depth of the hibernaculum could also reflect a preference for hibernating at temperatures near freezing. Torpor and arousal patterns are affected by ambient temperature, colder temperatures resulting in longer torpor sessions and shorter euthermic periods (French, 1982; Twente and Twente, 1965; Twente et al., 1977; Chs. V&IV) which could reduce the total energy expenditure of hibernation.

The use of nests by voles (Microtus longicaudus) and lemmings (Lemmus trimucronatus) has been shown to reduce energetic costs by up to 40% (Beck and Anthony, 1971; Casey, 1981) and to decrease the lower critical temperature of the thermoneutral zone of red squirrels (Tamiasciurus hudsonicus) by as much as 10°C (Pauls, 1981). The use of a well-insulated hibernaculum should reduce the energetic cost of hibernation as well. HE squirrels compensate for the colder soil temperatures experienced by using larger, better insulated hibernacula than squirrels at LE. This pattern of insulation quality could partially explain the higher over-winter survival of HE squirrels previously noted (Murie, 1985; Murie and Boag, 1984); however, when the temperature gradient across the insulation is taken into consideration, LE squirrels are seen to have a slight energetic advantage. That may not be the case, however, during more severe winters when cold air temperatures could cause LE soil temperatures to be lower.

Adult males at both locations had the best insulated hibernacula; however, the hibernating pattern of adult males differs from that of other age or sex classes in that they spend more time euthermic during the hibernating season (Ch. IV) and the increased insulation may be necessary to offset the high energetic cost of euthermia. The pattern of survival observed during this study differed from that reported by Murie and Boag (1984) and Murie (1985) in that LE squirrels had higher rates of survival than during their studies and higher than did HE squirrels. Adult males survived equally as well as adult females (Ch. II). The observed pattern of survival is consistent with the insulative quality and micro-environmental conditions recorded during the study.

Table VI-1. Physical characteristics of hibernacula of Columbian ground squirrels high (HE) and low (LE) elevation sites. AM = adult males, AF = adult females, J = juveniles.

Site	LE			HE		
sex/age group	AM	AF	J	AM	AF	J
n =	7	6	13	3	4	6
Body Weight grams ±se	776 ±24	570 ±26	357 ±10	865 ±22	585 ±23	375 ±9
Depth cm±se	75 ±5.3	63 ±4.0	50 ±3.2	39 ±2.5	56 ±16.9	30 ±13.7
Volume ml±se	9800 ±1019	3840 ±403	2896 ±260	15077 ±567	5744 ±776	6154 ±1688
Insulation cm±se	7.5 ±0.5	4.5 ±0.3	4.5 ±0.4	9.4 ±0.2	5.8 ±0.6	6.5 ±1.0
q mW/°C±se	64 ±2.4	70 ±2.9	57 ±2.2	60 ±1.3	64 ±4.9	49 ±2.7

Figure VI-1. Snow depths for Low elevation (LE) and high elevation (HE) sites. Shaded areas show the range of snow depths for all hibernaculum sites.

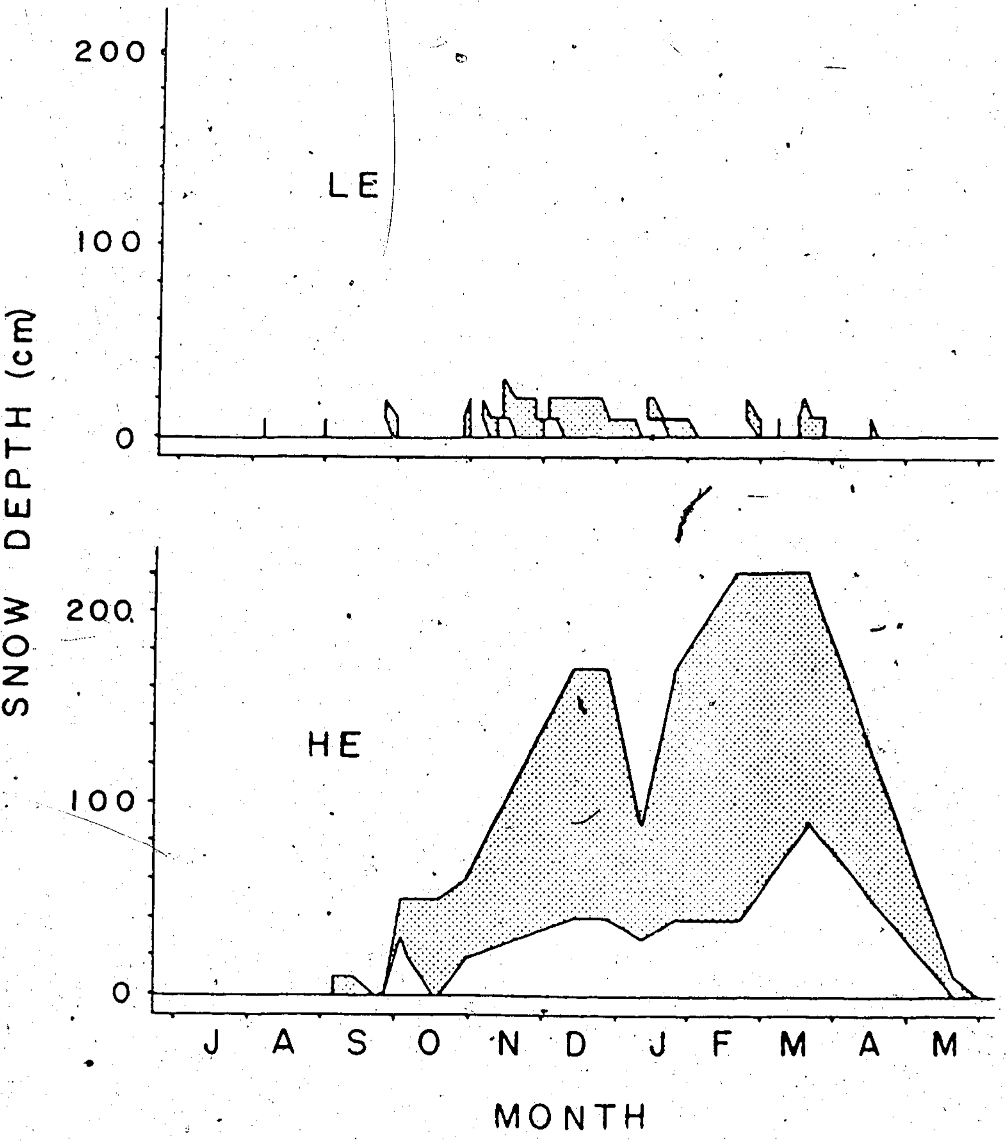
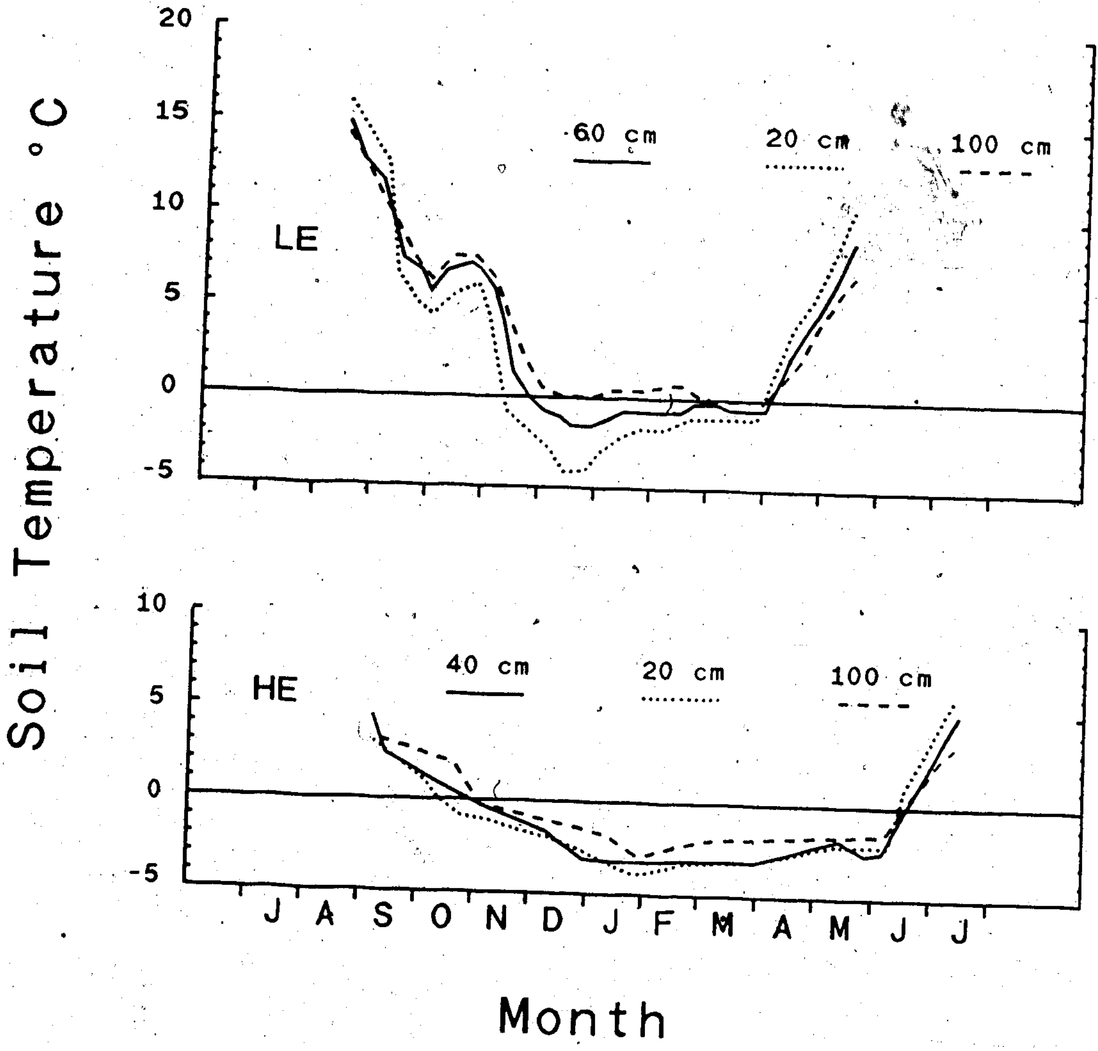


Figure VI-2. Soil temperatures during winter 1986-87 at the average hibernaculum depth (solid line) for low elevation (60cm) and high elevation (40cm), 20 cm depth temperature (dotted line), and 100cm depth (dashed line).



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VII. CONCLUDING DISCUSSION

The main premise of this study has been that over-winter survival of Columbian ground squirrels (Spermophilus columbianus) is determined by the amount of energy they store as fat before hibernation and by the rate at which that energy is used. The results of my study provide evidence that the amount of pre-hibernation reserves may be more critical for juveniles than for adults and that the rate of energy use is affected by size, sex, and age-related hibernating patterns, and can vary significantly among populations and from year to year. In this chapter, I bring together the results of the three main aspects of the study, energy reserves, hibernating patterns, and the thermal environment of the hibernaculum, to evaluate their combined influence on the patterns of over-winter survival within and among populations of Columbian ground squirrels.

From the results of the fat reserve study (Ch. III) come several general conclusions:

1) within sex and age classes there were no differences between populations in pre-hibernation fat reserves,
2) among sex and age classes, adult males had larger pre-hibernation reserves in proportion to their weight than did adult females or juveniles, which did not differ from each other,
3) adult males depleted their reserves to a greater relative extent than did adult females and emerged with proportionally similar reserves,

4) **juveniles depleted their reserves to a greater relative extent than did adults,**

5) there was considerable year to year variation in the relative depletion of fat reserves within populations, the direction of year to year differences being the same for all age and [illegible] classes within the population.

The exceptions to these generalizations were the pre-hibernation reserves determined for adult males at Highwood Pass (HW) in 1984 and the estimated post-hibernation reserves of adult males at the low elevation study area (LE) in 1986. Adult males at HW had significantly smaller pre-hibernation reserves than did adult males from the other three populations sampled. In retrospect, the lower reserves of the HW squirrels were likely the result of collecting those squirrels either before they had reached peak weight or after most of the largest adult males had entered hibernation (Ch. III). However, the pre- and post-hibernation total weights of HW adult males were lower than those of squirrels from the other populations and the possibility that HW squirrels are generally smaller and have smaller pre-hibernation fat reserves can not be completely discounted; Dobson and Kjelgaard (1985) reported that adults from their high elevation reference population (2 km from the HW site) were consistently lighter at emergence than those from their low elevation reference population. The high post-hibernation fat estimates of LE adult males relative to adult females and squirrels from other locations might be accounted for by the earlier than usual emergence dates recorded for the population during this study

(Ch. II). Because adult males are euthermic for a long period before emerging from their hibernaculum much of their fat reserves are used at the end of hibernation. By emerging 2-3 weeks earlier than normal LE males may have avoided some of this late hibernation expense.

The fat reserve study indicated that hibernation is energetically more expensive for adult males and juveniles than for adult females. Mass specific metabolic rate is inversely related to body mass; thus, juveniles would be expected to have higher mass specific metabolism and would require more energy in proportion to their mass than would adults females. The greater proportion of fat reserves depleted by adult males compared to adult females appears to be the result of spending a greater proportion of the hibernating season euthermic (Ch. IV), but adults of both sexes emerge from hibernation with much of their pre-hibernation reserves intact. These results indicate that the pre-hibernation fat reserves of adults are more than adequate to ensure survival over-winter while those of juveniles are marginally adequate. Differences in the amount of pre-hibernation fat reserves used between years are similar for all age and sex classes within populations, suggesting that year to year variation is due to local environmental conditions. Juvenile survival could be expected to be affected more than adult survival by these variations in energy demands owing to their marginal fat reserves.

The rate of fat depletion is dependent on torpor and arousal patterns and the thermal environment of the hibernaculum. The results of the arousal pattern studies (Chs. 4 & 5) may be summarized as follows:

1) all age and sex classes at low elevation had the same number of arousals during the hibernating season,
2) adult males had shorter hibernating seasons and spent a greater proportion of the season euthermic than did adult females or juveniles,
3) the longest periods of torpor occurred when soil temperatures were below 5°C,
4) temperature regimes influenced the length of torpor periods early in hibernation in the laboratory; the colder regime resulted in fewer arousals and longer torpor bouts.

The thermal environment of the hibernacula may be summarized as follows:

1) high elevation squirrels experience colder temperatures for the entire hibernating season and soil temperatures were below freezing for a greater proportion of the season than at low elevation,
2) high elevation squirrels used hibernacula that were better insulated than those of low elevation squirrels,
3) the hibernacula of adult males were more energy efficient with respect to body size (and heat production) than those of adult females and juveniles.

The number and length of euthermic episodes (arousals) during hibernation is a key factor in determining total energy expenditure (Wang, 1978); one euthermic episode can consume approximately the same amount of energy as 10 days of torpor. That the LE squirrels of all age and sex classes showed relative uniformity in the number of arousals and the length of torpor bouts (Ch. IV) suggests that the pattern of arousal is under some endogenous control and/or environmental influence that affects all age and sex classes equally. The amount of time spent euthermic before emerging from the hibernaculum (6-14 days, adult males; ≤1 day, other squirrels: Ch. IV) was the only major difference in hibernating patterns observed at LE. The long period of euthermia may be necessary for gonadal recrudescence and spermatogenesis as has been shown for golden-mantled ground squirrels (S. saturatus; Barnes et al., 1986; Barnes et al., 1987) and ensures that adult males will be reproductively active upon emergence or shortly thereafter.

With the similarity in hibernating patterns among sex and age classes, the thermal environment and insulation of the hibernaculum becomes more important in explaining differences in energy consumption and patterns of survival. Colder soil temperature regimes at higher elevations may increase the duration of torpor bouts early in hibernation (Ch. V); however, the energetic cost of arousing and maintaining euthermic body temperatures increases with decreasing ambient temperatures (Wang, 1978) and may offset some of the energy saved by longer torpor bouts. Hibernators react to decreasing ambient temperatures by decreasing the duration of arousal episodes (French, 1982) and increasing the duration of torpor episodes (Twente et al.

1977). In addition, squirrels that hibernated in colder soil temperatures (i.e. high elevation) or were euthermic for a greater proportion of the hibernating season (i.e. adult males) were found to use larger, better insulated hibernacula (Ch. VI). The combination of shorter arousal episodes and more energy efficient hibernacula may compensate for colder ambient temperatures or increased amount of time spent euthermic.

Because of the interactions between soil temperature, hibernaculum insulation, and arousal patterns it is difficult to ascertain the separate effects these factors have on the energetics of hibernation. In the following section a simple model incorporating these factors is used to address this problem. The model (described in detail in Appendix B) considers only two levels of metabolic rate, torpor and euthermia, and ignores the transitional rates during rewarming and cooling. This bias to the model should result in underestimates of energy consumption as the transitional metabolic rates would be higher than the rates used in the model during transitional periods. The model is designed such that the size of the squirrel, heat loss of the hibernaculum, number of torpor and arousal cycles, and soil temperature regime are all entered as variables and can be changed to simulate different conditions. The first set of conditions were selected to represent the 'typical' squirrel of each age and sex class (adult male, adult female and juvenile; Table VII-1). The values of soil temperature (T_s) and heat loss (q) were increased and decreased separately (T_s±2°C, q±10%) and the torpor/arousal pattern altered by eliminating one day of euthermia during early and late hibernation to test the sensitivity of the estimated total energy expenditure (TEE) to changes in these variables (App. B). From the results of these simulations (Fig. VII-1) it is clear that soil temperature has the greatest influence on TEE. Increasing insulation was less effective in reducing TEE for the adult male simulations than for other squirrels but decreased TEE to about the same extent as eliminating arousals did in most of the simulations. The relatively small reduction in TEE resulting from the elimination of arousals (2-6%) suggests that this may not be as effective for reducing hibernation energy demands as was suggested in other parts of the study (Ch. IV, Ch. V). That is due in part to the relatively small proportion of TEE attributable to euthermia (39-68%; Table VII-1), a proportion lower than expected on the basis of Wang's (1978) findings for Richardson's ground squirrels (80%, S. richardsonii). Part of this disceppancy results from the model's exclusion of higher metabolic rates during the transitions from torpor and euthermia. If the number of arousals is reduced by 1-2 episodes by HE squirrels, as suggested in Chapter 5, the resulting decrease in energy expenditure, though small, could contribute to more energy efficient hibernation and increased survival compared to LE squirrels. However, the extent to which the pattern of arousals is affected by temperature regime is uncertain and no definitive conclusion can be made on the basis of my study.

Soil temperature has the greatest influence on energy use and its effects can be countered by the use of insulation. Soil temperature regimes vary with depth and squirrels in both populations were not restricted from using deeper, and hence warmer hibernacula (Ch. VI, App. A). Insulation can be increased by increasing the size of the hibernaculum and the amount of nest material. The hibernacula of HE squirrels had heat loss values 10% lower (on average) than those at LE but this is just sufficient to offset the effect of 1°C colder minimum soil temperatures. Rather than providing a more energy efficient hibernaculum, the depth and better insulation of HE hibernacula results in hibernating conditions that are almost equivalent to those at LE. Warmer soil temperatures and more insulation would clearly decrease the energy cost of hibernation for squirrels at both locations. Why squirrels at either location did not use deeper or better insulated hibernacula is not clear but may be related to other costs associated with the depth and size of the hibernaculum.

The energy cost of constructing hibernacula presumably increases with depth and size, particularly if the soil removed is taken to the ground surface and not to another part of the burrow. Increasing the insulation (decrease q) of a hibernaculum requires an exponential increase in the volume of the hibernaculum and the amount of nest material. To increase the insulation of the 'typical' LE adult male hibernaculum by 10% requires an increase in volume of 73% (from 8.2 to 14.1 l) and a 90% increase in the amount of nest material gathered (7.4 vs. 13.4 l). Also, the cost of emerging from the hibernaculum in spring must be considered. The soil is still frozen when most squirrels emerge and squirrels at high elevation often emerge through many centimeters of compacted snow (Ch. VI; Murie and Harris, 1982). Digging through frozen soil is energetically expensive (pers. obs.) and could be particularly risky for squirrels with nearly depleted fat reserves (ie. juveniles).

It would be advantageous to use the shallowest hibernaculum possible to reduce the cost of emergence.

The depth, size and insulation of the hibernaculum probably represents a compromise between the cost of spring emergence, the cost of hibernating at sub-zero temperatures, and the risk of having soil temperatures drop below the temperature for which the hibernaculum is insulated. This trade-off can be used to explain the differences in hibernaculum depth and structure between elevations when snow cover is taken into consideration. Squirrels at HE are able to use shallow hibernacula to reduce the cost of emergence by increasing the insulation to offset colder soil temperatures and by virtue of having deep snow cover that provides a relatively stable soil temperature regime during periods of very cold air temperatures. Squirrels at LE do not have consistent snow cover to insulate the soil from changes in air temperature and must use deeper hibernacula to avoid the more variable temperature regime at shallow depths. The tendency of juveniles to use shallower hibernacula than adults (App. A) may make them more susceptible to changes in soil temperature and could explain the lower survivorship of juveniles reported by previous studies (Boag and Murie, 1981; Murie and Boag, 1984). During periods of colder than normal air temperatures all squirrels at LE may be more susceptible to increases in energy expenditure associated with cold soil temperatures than squirrels at HE. Delayed thawing of the soil in late springs may also have a greater impact on survivorship of LE squirrels than those at HE owing to the greater depth of LE hibernacula (App. A). Long term soil temperature data are not available for locations comparable to my study areas and it is impossible to state whether soil temperatures are more variable at low elevations than at high. Intuitively, low elevations should have more variable soil temperatures owing to the inconsistent snow cover caused by chinook weather patterns. It remains unclear why LE squirrels do not use larger, better insulated hibernacula that would provide a greater margin of protection. While studies on non-hibernating species have shown that the use of insulated nests is energetically advantageous for euthermia (Casey, 1981; Pauls, 1981) and insulation should reduce energy expenditure for torpor at below freezing temperatures (Ch. VI), the energetic implications of insulation for torpor at above freezing temperatures is not known. A better insulated hibernacula may increase energy expenditure during torpor at above freezing temperatures by keeping body temperature higher than it would be in a less well insulated hibernaculum.

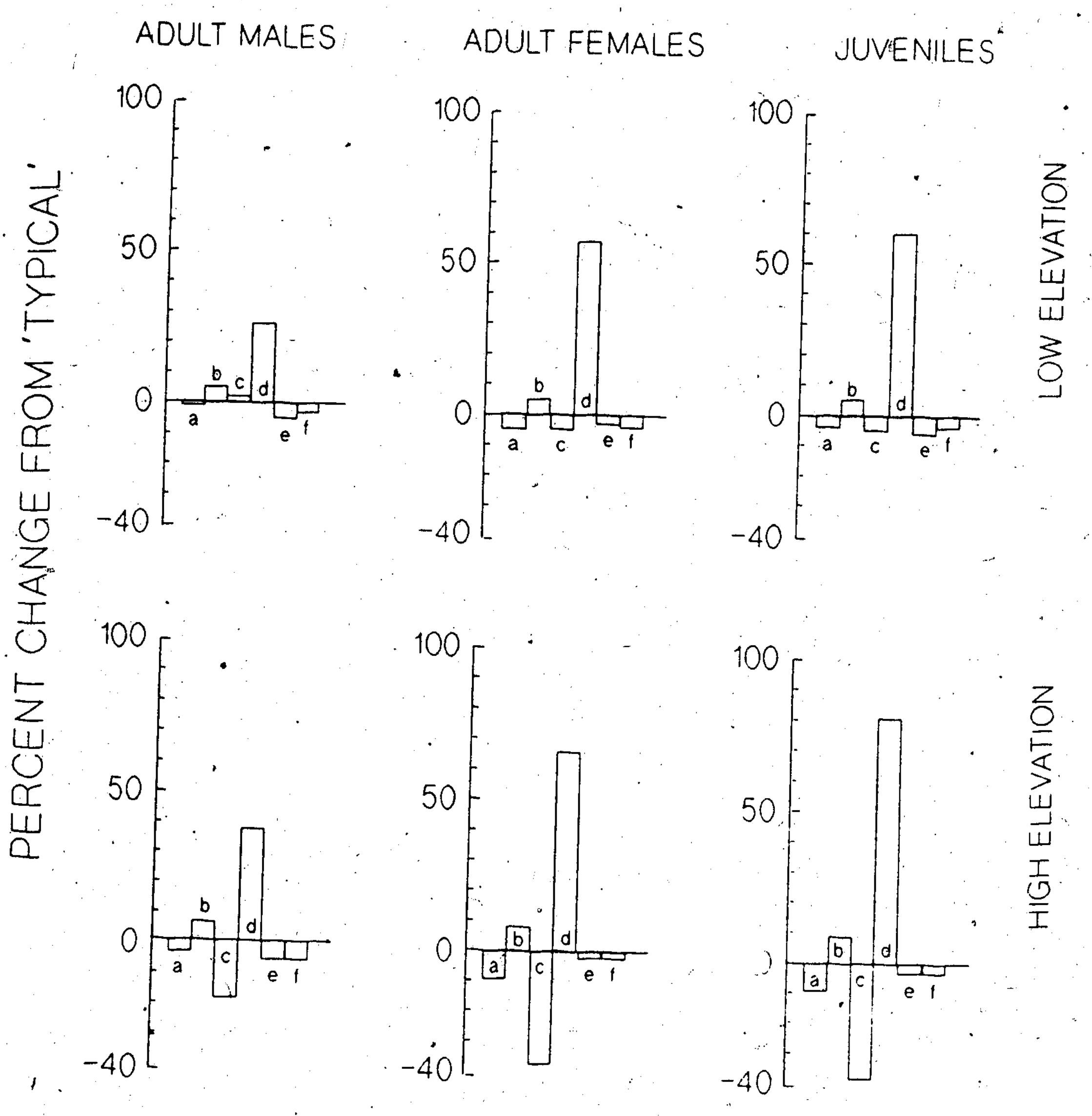
In conclusion, the results of my study indicate that the energetic cost of hibernation for squirrels at HE was equivalent or greater than that for squirrels at LE. Together with the similar pre-hibernation fat reserves this leads to the conclusion that differences in survivorship between elevations are not due to any difference in the amount of energy stored nor in the rate of energy consumption under the conditions I recorded. Juvenile squirrels are more susceptible to increases in energy demands than are adults and are more likely to deplete their already marginal fat reserves. The depth and insulation of hibernacula appear to be adapted to local environmental conditions so as to provide a thermal environment that minimizes energy consumption during hibernation and the cost of emerging from the hibernaculum in the spring. Mortality during hibernation can not be attributed to one cause; some radio-collared squirrels died after depleting their pre-hibernation fat reserves while others had most of their reserves intact. Soil temperature appears to be the major factor affecting the rate of energy consumption and it is likely that the stability of the thermal environment is the primary cause of differences in over-winter survival among populations at different elevations.

Attempting to resolve the mechanisms of long-term life history patterns on the basis of short-term studies is always risky and many more questions have been raised than have been answered by my study. The results of this study lay a foundation for future research that should lead to a better understanding of the phenomenon of hibernation, how it can be adapted to, and how it influences variable life-history patterns. More detailed studies are needed on the thermal environment of hibernators, the energetic implications and constraints of hibernaculum structure, and the effect of temperature regimes on hibernating patterns. Much of this work will require the controlled conditions of the laboratory or artificial environments to measure the relative importance of these various aspects of hibernation in determining over-winter survival of hibernating species.

Table VII-1. Estimated energy consumption during hibernation under simulated 'typical' conditions for squirrels of each sex/age class at each elevation.

	Low Elevation			High Elevation		
	AM	AF	J	AM	AF	J
KJ						
Total	4195	2695	1983	5137	3862	2910
Euthermia	2832	1366	956	3017	1516	1148
Torpor	1363	1329	1027	2120	2346	1762
KJ/Gram	5.59	4.65	5.36	6.85	6.66	7.87
$J/g \cdot day^{-1}$	25.61	19.38	22.33	26.34	25.61	30.26
% of Fat Weight Loss Estimates (Ch. III)	101	90	84	105	133	133

Figure VII-1. Effects of different thermal environments and arousal patterns on simulated energy consumption. Histogram bars show the percent change in total energy expenditure compared to 'typical' conditions for the following parameter changes: a) increase insulation 10%, b) decrease insulation 10%, c) increase soil temperature 2°C, d) decrease soil temperature 2°C, and eliminate one day of euthermia early (e) or late (f) in hibernation.



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APPENDIX A. COLUMBIAN GROUND SQUIRREL HIBERNACULA: STRUCTURE, LOCATION AND AVAILABILITY.

Ground squirrels and marmots spend a large proportion of their lives underground. Svendsen (1976) stated that yellow-bellied marmots (Marmota flaviventris) spend up to 60% of their lives in hibernation and 80% underground. That is no doubt true for most ground squirrels that hibernate for periods of up to 8 or 9 months each year (Davis, 1976). Burrows are an obviously important facet of ground squirrel biology, providing protection from predators, shelter from inclement weather and a relatively stable micro-environment for hibernation. The availability and quality of burrow sites, particularly hibernacula, is thought to restrict the size of some ground squirrel populations (Carl, 1971) and the size and location of some marmot colonies (Svendsen, 1974) as well as being a factor in promoting monogamy in hoary marmots (M. caligata) (Holmes, 1984). Shaw (1925a,1926a) found differences in the location, structure and quality of hibernacula used by different age and sex classes of Columbian ground squirrels (Spermophilus columbianus). Such differences in depth, size and structure of the nest could influence the energetic cost of hibernation and affect the over-winter survival of the squirrels. Studies on Alberta populations of Columbian ground squirrels, which hibernate for about 70% of each year, have pointed out significant differences in over-winter survival between high and low elevation populations and among sex/age classes within populations, which may be related to hibernaculum quality (Murie, 1985; Murie and Boag, 1984).

The objectives of this study, part of a larger study of factors influencing overwinter survival of Columbian ground squirrels, were to document the structure of hibernacula used by squirrels of different age and sex classes in two populations, and to gain an insight into what constitutes a 'good' hibernaculum site, how squirrels select hibernaculum sites and whether good hibernacula are a limited resource within populations.

METHODS

The study was conducted at two locations in the Sheep river drainage, approximately 32 and 35 Km west of Turner Valley, Alberta. The low elevation site (LE; elev. 1470m) is located on a large meadow 3km east of the mouth of Gorge Creek. This area was used in a previous study by Murie and Boag (1984) and is close to the site of Murie's (1985) low elevation population. The high elevation site (HE; elev. 2250m) is located in a cirque on the west side of Junction Mt. approximately 12km south of the mouth of Junction Creek. Both areas are described in more detail elsewhere (Ch. II). The hibernacula of 28 squirrels at LE and 16 squirrels at HE were located during a telemetry study on hibernating patterns in 1986-87 (Ch. IV).

Radio-collars were fitted to four adult females and their complete litters at each site to determine the location of the hibernacula of juvenile squirrels relative to those of their siblings and mother. The locations of the 1985-86 hibernacula of four adult squirrels at LE were also known, from telemetry conducted during the first part of that hibernating season, and compared to their 1986-87 locations. The location of each hibernaculum was marked with an aluminum rod (1.75m by

0.5cm) used to measure snow depth and to identify hibernaculum sites for excavation.

Soil temperature profiles perpendicular to ground surface at 20cm intervals at depths down to 200cm were taken at five locations on each study area to examine the temperature regimes at different depths and locations. Micro-envitonmental data is examined in more detail elsewhere (Ch. VI). After snowmelt and the soil had thawed sufficiently to permit digging, the hibernacula were excavated, measured and mapped. Two boards (2.5 by 15 by 300 cm) were placed parallel on either side of the area to be excavated. The boards were elevated, fastened to aluminum stakes, and levelled along their length and across the area they spanned. Measurements of depth, burrow location, and dimensions were taken to the nearest 0.5cm using a long T-square placed across the boards and a plumb line. This provided a level reference plane for determining the slope of the ground surface above the hibernaculum plus accurate positioning of the tunnels, chambers and other physical features on a three dimensional grid. Excavations were usually started at the exit hole at ground surface and followed the exit tunnel to the hibernaculum; measurements were taken every 15 to 20cm and at every turn or branching of the tunnel. Hibernaculum volume was calculated as the volume of a sphere having a radius equal to the mean radius of the width, length and depth of the chamber. Side tunnels were followed as far as the limits of the level-board structure then tested with a smoke blowing apparatus (Vogel et al., 1973) to determine if they were connected to open burrow systems. The depth and dimensions of each hibernaculum were recorded along with notes on the soil texture, ground cover, and location of any large rocks, cobble layers or other obstructions. Nest material from the hibernaculum was collected, dried and stored in plastic bags for analysis of insulation quality (Ch. VI).

Data from Shaw's (1926a) excavations of Columbian ground squirrel hibernacula in Washington State were converted to metric measurements for comparison to the hibernacula excavated in this study. The squirrel weights in Shaw's table, which were recorded at various times during the hibernating season, were adjusted to reflect pre-immergence weights, assuming a 33% weight loss over the entire season, and prorating by the amount of time spent in hibernation since July (Shaw, 1925b).

Statistical analyses were performed on PC:SAS under licence to the University of Alberta Computer Services.

RESULTS

The general structure of the hibernacula (Fig. A.1) was similar to the description of Columbian ground squirrel hibernacula by Shaw (1925a,1926a). The chambers were generally spherical with a short (5 to 15 cm) tunnel leading to the burrow system. This tunnel usually intersected with three others, one leading to the exit hole, one plugged, presumably leading to the main burrow system and one short blind tunnel that typically projected below the level of the hibernaculum and contained large amounts of feces and discarded nest material. The burrow systems were not always plugged close to the hibernaculum; some remained open for 1 to 2 meters and squirrels were occasionally located by telemetry up to 2m from their hibernaculum during arousals. The surface opening of the exit tunnel was small (3 -

6cm diam.) and always opened from within, based on the lack of loose soil around the opening. When the exit tunnels were dug could not be determined, but none were found leading from the hibernacula of squirrels found dead (3) or still hibernating (1). In all but one case the exit hole was the only opening leading from a hibernaculum; the only exception was a pre-existing burrow entrance used by a juvenile squirrel. No food caches or signs of stored food were found in or near any of the hibernacula.

Juvenile squirrels at LE hibernated close to their mothers and siblings. The mean distance between mother and offspring was 10.1m (range 3.2 to 24.6m, n = 9) and between siblings was 7.8m (range 1.1 to 12.4m, n= 9 pairs). At HE three juveniles (2 males, 1 female) were located close to their mothers ($\bar{x}$ 2.7m, range 2.2 to 2.9m) while three others (all males) hibernated at considerable distances from their mother (23.3, 24.6 and 92.2m). Only two pairs of siblings were located at HE, one pair of males was 3.2m apart and also located near their mother. The other pair consisted of a female located close to her mother and a male 94.7m away. Both radio-collared juveniles that died during hibernation (one LE female; one HE male) were more than 20m from their mothers' hibernaculum. The juvenile male at HE found more than 90m from its mother was excavated from the hibernaculum on 7 June still in torpor and there were obvious tooth and claw marks on the still frozen soil plugging the burrow suggesting a failed attempt to exit the hibernaculum. The four adult squirrels, radio-collared in both years, at LE hibernated close to the 1985-86 site in 1986-87 ($\bar{x}$ = 6.8m, range 2.2-10.2), but did not use the same hibernaculum.

The hibernacula at HE were all located under nearly level terrain ($\bar{x}$ slope = 3.8°, range 0-9°) in the bed of the cirque and were beneath shrubby ground cover (Salix spp.) or in shallow depressions which collected snow drifts. No hibernacula were located on the steep sides of the cirque although some summer burrows are located there. Hibernacula at LE were located under more varied terrain ($\bar{x}$ slope = 8.3°, range 0-31°) but only two radio-collared squirrels were located on the steep (27-34°) south facing slope on the north side of the study area. Ground cover other than grass was not available within the study area at LE. The soil at LE hibernaculum locations was fairly coarse and well drained. Soil at HE was finer textured, poorly drained and some hibernaculum sites were subject to flooding during snowmelt or heavy rain. Two hibernacula at HE were located under rocks, though only one of these was large enough to afford protection from the digging of mammalian predators (e.g. bears). Other than the root mats of willow bushes, no other cover or obstacles were encountered above hibernacula.

The depth and size of the hibernacula varied with both the sex and age of the occupant as well as between study areas (Table A.1). The depth of hibernacula at LE differed significantly between all three sex/age classes (ANOVA: F=12.53, P=0.0002, Duncan multiple range test) those of adult males being deepest and juveniles shallowest. There was no difference in depth between sex/age classes at HE (ANOVA: F=1.68, P=0.236), though there was a trend for adults to use deeper hibernacula. With the exception of adult females, squirrels at HE used hibernacula that were shallower than those of LE squirrels.

The volume of a hibernaculum (V_h) was correlated with the size of the occupant (LE: r^2=0.637, P=0.0001; HE: r^2= 0.454, P= 0.012). Since adult squirrels might be expected to use larger hibernacula by virtue of their size alone, the effects of body size on hibernaculum volume were removed by analysis of covariance (Packard and Boardman, 1987, 1988) using body weight as a co-variate to V_h. There were significant differences in V_h between sex and age classes at LE (F=8.38, P=0.002) but not at HE (F=3.10, P=0.095). At LE adult males used larger hibernacula than the other sex/age classes (Duncan multiple range test); the same trend appeared at HE, although somewhat obscured by small sample sizes and the use of large hibernacula, similar in size to those of adult males, by two juveniles. Both of these squirrels were distant from their mothers and siblings. HE squirrels used larger hibernacula than did LE squirrels (F= 8.74, P= 0.021 adult males and F= 11.06, P= 0.003 other squirrels).

Columbian ground squirrels in Washington (WS) (Shaw, 1926a, Table A.1) used hibernacula that were smaller (F=14.30, P=0.0001) than those at LE or HE and deeper than those at HE but not LE (F=19.64, P=0.0001). Interpretation is complicated by the differences in hibernaculum size and depth among sex/age classes within populations. When the effects of body size are removed, the volume of WS hibernacula did not differ significantly between age/sex classes (F=0.31, P=0.734), unlike the situation at LE and HE. The V_h of adult males were significantly different between all three locations (F=12.63, P=0.0003) with HE being largest and WS smallest. Juveniles at HE used larger hibernacula than did those at LE or WS (F=6.06, P=0.009) which did not differ from one another. Adult females showed a pattern similar to juveniles for V_h but differences between locations were not significant (F=4.01, P=0.057).

The pattern of hibernaculum depth between all three locations was less consistent. The depth of the hibernacula of adult females did not differ among the three sites (F=0.19, P=0.829). Those of adult males were shallower at HE than at LE or WS (F=19.64, P=0.0001) which were of similar depth, and juveniles at LE used deeper hibernacula than those at HE and WS (F=4.23, P=0.029) which did not differ. The small sample sizes, particularly at HE and WS for adult females, no doubt contributed to the inconsistent patterns seen in hibernaculum volume and depth.

DISCUSSION

Columbian ground squirrels disperse as yearlings, remaining at the natal nest until after their first winter (Boag and Murie, 1981; Wiggett, 1988) so the proximity of a juvenile's hibernaculum to its mother's is not surprising. The juveniles that hibernated at large distances from their mothers (>20m) raise some interesting questions about the selection and availability of hibernacula. Burrow entrance mapping, using a smoke blower, suggested that hibernacula more than 5m apart were not within the same burrow system, although burrow systems covering more than 20m were recorded (App. C). The HE juveniles more than 20m from their mother were neither within the same burrow system as the mother nor in the natal burrow. The large size of two of these hibernacula suggests that they were not constructed by the juveniles but by adult males. Juveniles hibernating away from mothers and siblings did not survive well during hibernation at either location. The only two juveniles that died and the one that was frozen inside the hibernaculum when it was excavated account for three of the five juveniles found more than 20m from kin. This suggests that there was some advantage to hibernating close to the mother. The number of juveniles at HE hibernating far from their mothers (3 of 6) and in large hibernacula suggests also that good quality hibernacula near either the natal area or mother's hibernaculum may have been a limited resource for this population.

Shaw (1926a) found that some squirrels partially excavated the exit tunnel prior to hibernation. I found no evidence of this behavior in the hibernacula of squirrels that died over-winter. Thirteen-lined ground squirrels (*S. tridecemlineatus*) dig exit tunnels at the end of hibernation (Sheck and Fleharty, 1980) and the squirrels in this study appear to have done so as well. Squirrels at [illegible]nd HE also did not store food as Shaw (1926b) found in some WS hibernacula. Unlike this study, Shaw's study area was in an agricultural area and the availability of seed crops and potatoes, which were the foods cached in the burrows, may have influenced the WS squirrels storing behavior. Squirrels near the LE study area have been observed to cache food (corn) taken from campground refuse (D. Boag, pers. comm.).

Squirrels were not restricted from constructing deeper hibernacula, at either LE or HE, by shallow soil or physical obstructions. Although the depth of the friable soil was not determined, the soil temperature probes were easily inserted to depths much greater than the average hibernaculum depth. At only one location at LE were hibernacula found situated on a layer of cobble stones that might have limited their depth. However, these hibernacula were all near the average depth and tunnels leading down through the rock indicated that deeper hibernacula could have been constructed. The depth of hibernacula is no doubt determined by a number of factors. Deeper hibernacula may provide better protection from predators but exiting the hibernaculum in the spring would require digging out through a thicker layer of frozen soil. Respiratory gas exchange may also be a factor, since gas exchange occurs by diffusion through the soil, and is retarded by cold and wet soil (Withers, 1978). This aspect of the hibernaculum micro-environment may be of particular importance at HE where the soil is cooler and not well drained. Winter soil temperatures are warmer at greater depths and the positioning of hibernacula may reflect a selection of a preferred temperature regime for hibernation. Temperature regimes on exposed south slopes at LE were colder than on the level and hibernacula on the slopes were deeper. If hibernacula are also used as summer nests, the depth may be a function of protection from digging predators and preferred temperatures during the active season rather than during hibernation.

HE squirrels took advantage of ground cover and terrain to hibernate in areas where deep snow accumulates; steep, often snow free slopes were avoided. Some LE hibernacula were located on slight terraces where snow drifted.

A general interpretation of hibernaculum depth and size is complicated by the differences recorded among sex/age classes between locations. If the trends observed are representative of the populations a few general conclusions can be drawn. The size of the hibernaculum is determined partly by the size of the occupant, larger squirrels using larger hibernacula. Adult males and squirrels in colder (soil temperature) locations had larger hibernacula with more insulation, possibly to compensate for time spent euthermic and temperature regimes respectively. The differences in depth between sex/age groups probably reflects trade-offs between protection from predation, optimal hibernating conditions (temperature, gas exchange, etc.), the ease of exiting the hibernaculum in spring, and timing of spring emergence. Squirrels at HE may be minimizing the effort of exiting the hibernaculum. In this study, they always emerged when the soil was still frozen, and compensated for the colder soil temperatures with larger, better insulated hibernacula (Ch. VI). Squirrels at LE and WS showed a pattern of increasing depth of hibernacula with greater body size. That may result more from immergence schedules than a direct relationship to body size. Adult squirrels begin hibernation earlier than juveniles and by using deeper hibernacula would experience cooler temperatures for the early period of hibernation. Arousals from torpor become shorter and less frequent as ambient temperature decreases (French, 1982; Twente et al., 1977), and selecting deeper, cooler soil temperatures could reduce the energy expenditure at the start of hibernation when soil temperatures are warmest.

Table A.1. Comparison of hibernacula size and depth ($\bar{x}$ ± se) between high (HE) and low (LE) elevation in Alberta and a low elevation site in Washington State (WS). AM = adult males, AF = adult females and J = juveniles.

Site	HE			LE			WS[1]		
sex/age	AM	AF	J	AM	AF	J	AM	AF	J
n=	3	4	6	7	6	13	14	3	5
Depth[2] (cm)	39 ±2.5	56 ±16.9	30 ±5.4	75 ±5.3	63 ±4.8	50 ±3.0	- -	- -	- -
Depth[3] (cm)	39 ±2.5	56 ±16.9	32 ±5.7	80 ±5.4	65 ±4.8	51 ±3.3	94 ±3.8	64 ±13.7	33 ±10.9
Volume[4] (ml)	15077 ±567	5744 ±776	6154 ±1688	9800 ±1018	3840 ±403	2896 ±260	7082 ±522	2768 ±770	2113 ±396
Weight[5] (g)	865 ±22	585 ±22	375 ±22	776 ±24	570 ±26	358 ±10	756 ±24	376 ±7	329 ±17

[1] Data from Shaw (1926<u>a</u>) converted to metric measurements; volume calculated as in this study.

[2] Measured perpendicular to ground surface.

[3] Measured as plumbline distance to ground surface, to compare with WS.

[4] Tested statistically by analysis of co-variance, body weight as co-variable.

[5] Shaws's weights adjusted to reflect predicted pre-immergence weights.

Figure A.1. Side and plan view diagrams of excavated hibernacula. Dotted lines - unexcavated tunnels, dashed lines - plugged tunnel opening, stipple - filled tunnel. LE: adult males, a-g; adult females, h-m; juvenile males, n-t; juvenile females, u-z. HE: adult males, aa-ac; adult females, ad-ag; juvenile males; ah-al; juvenile female, am.

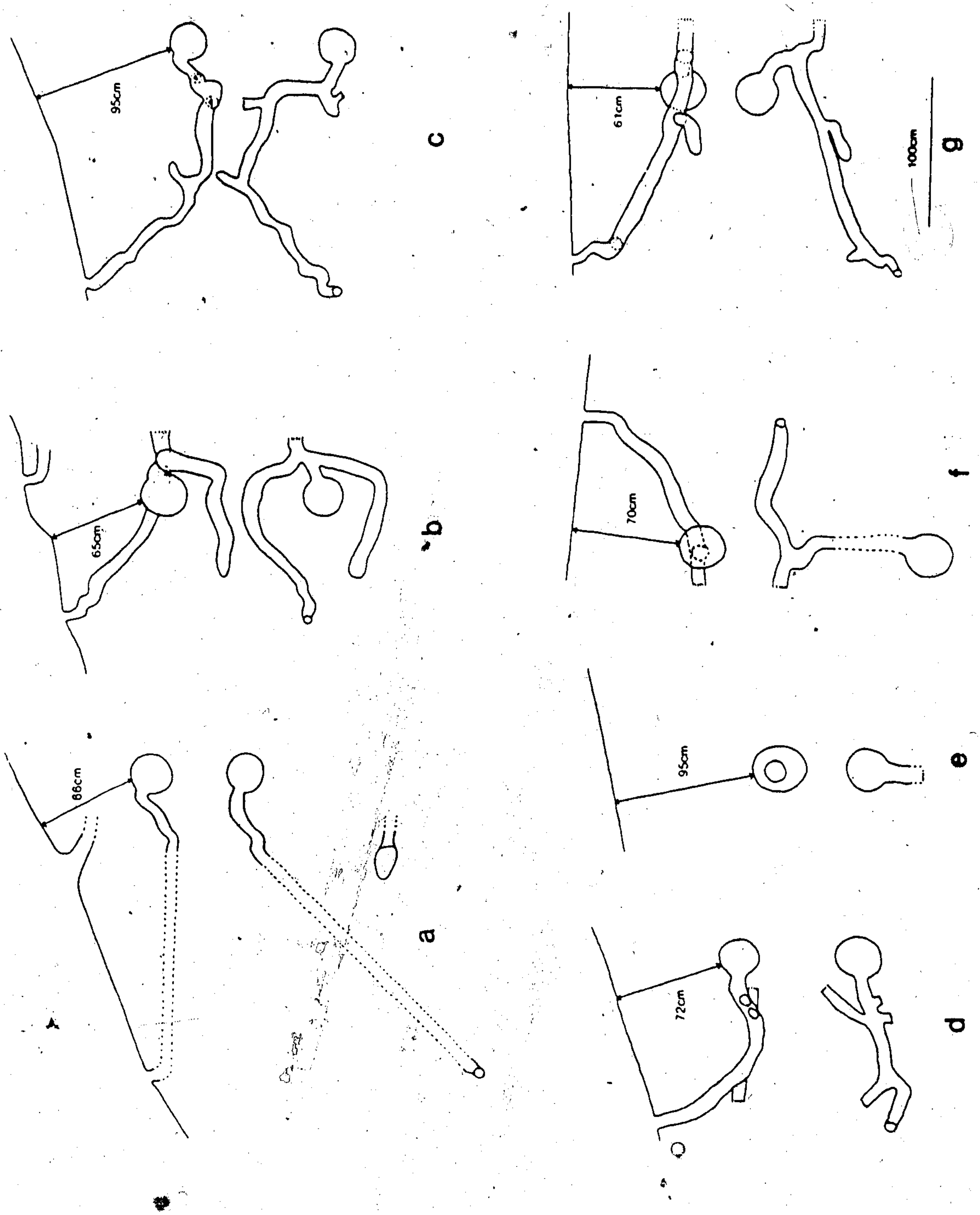


Figure A.1. --continued--

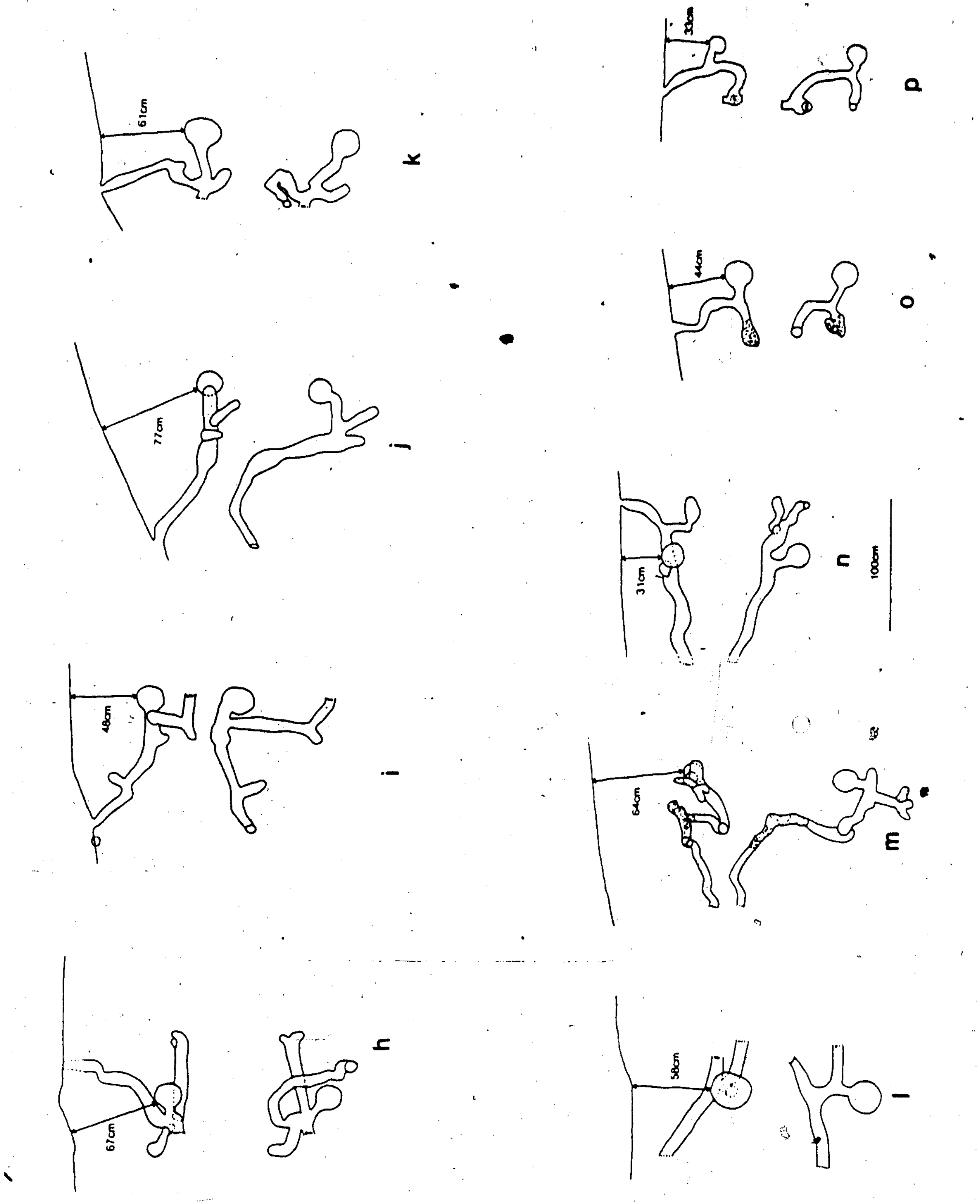
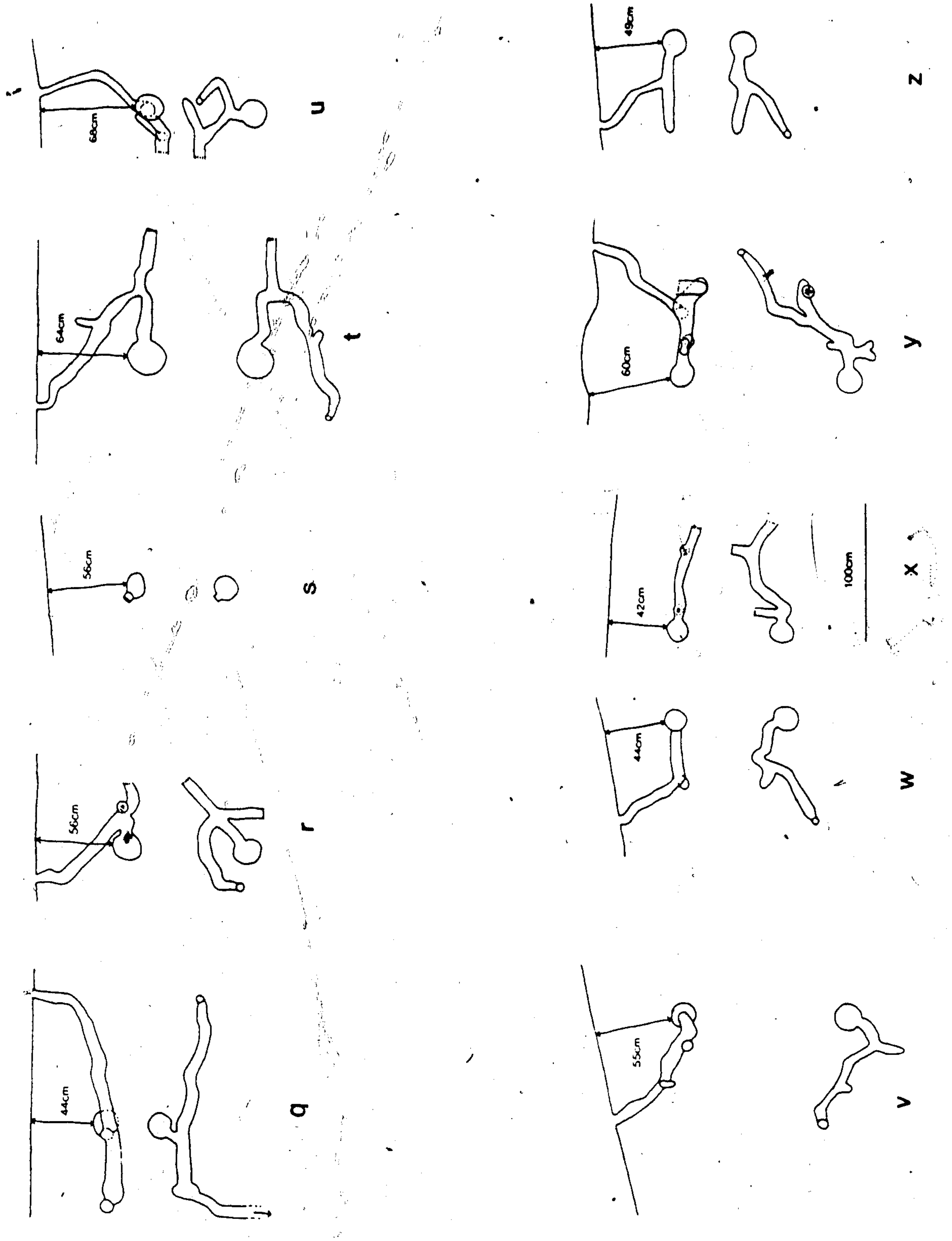


Figure A.1. --continued--



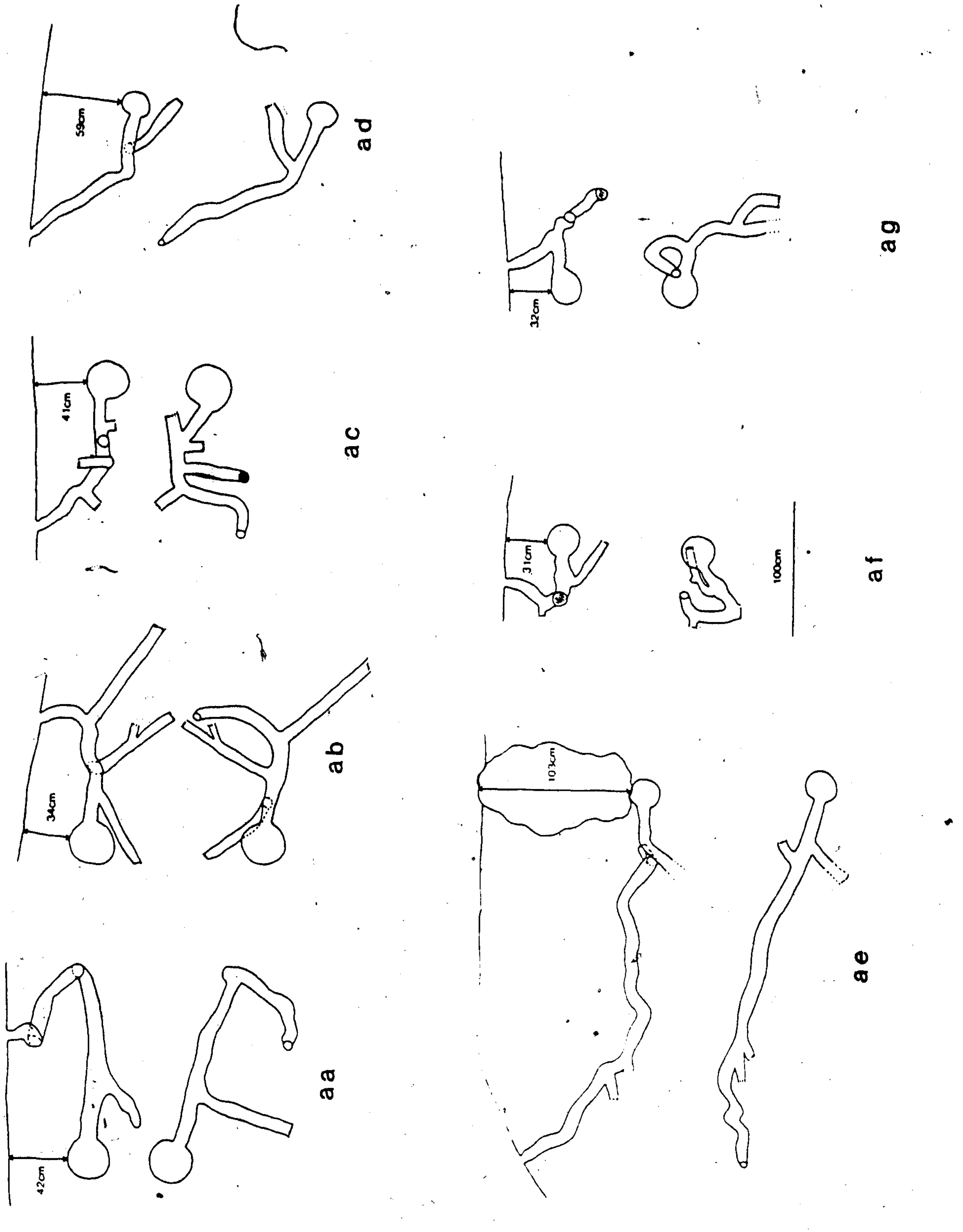
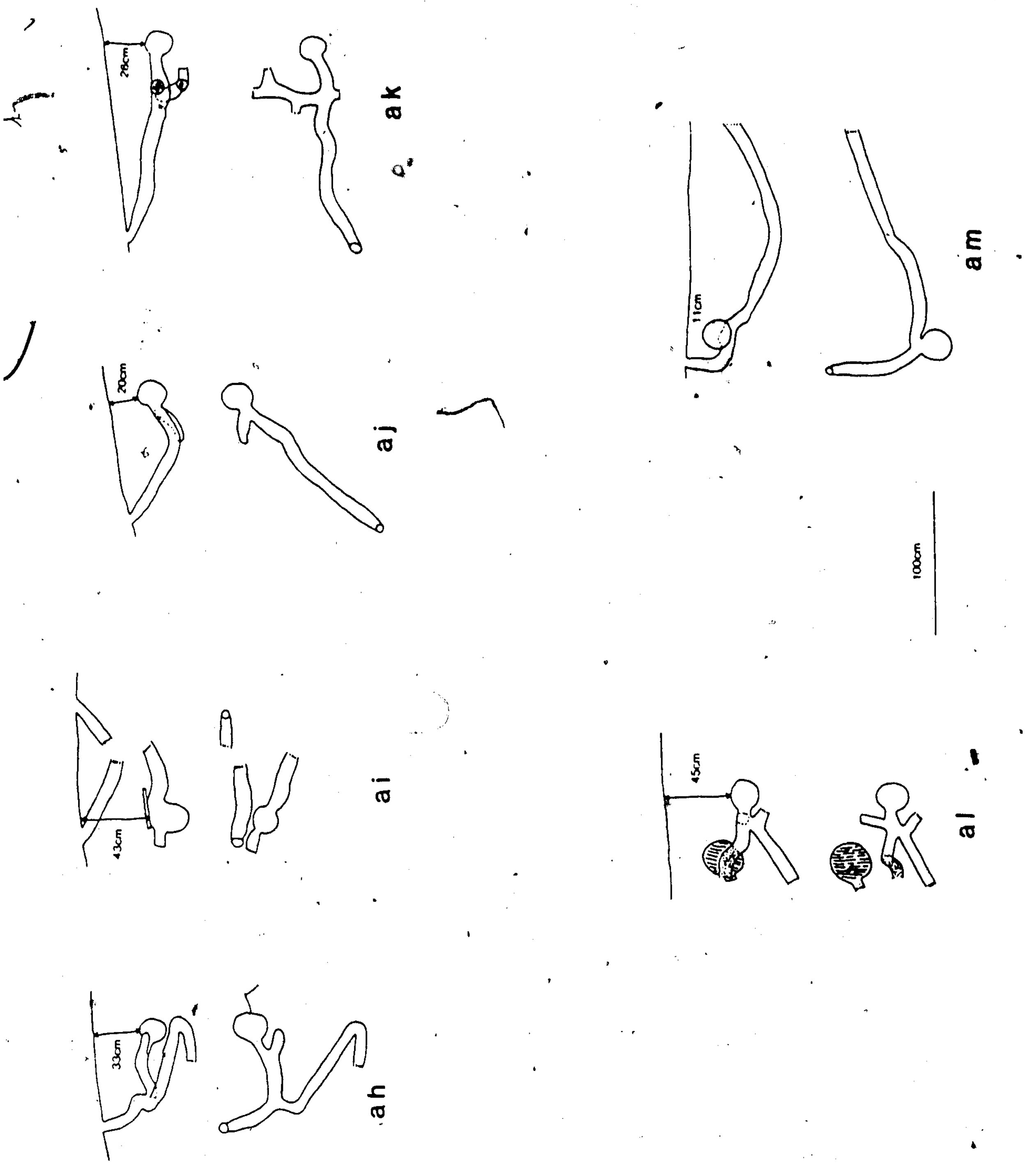


Figure A.1 --continued--

Figure A.1. --continued--



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APPENDIX B. ENERGETIC MODEL OF HIBERNATION

The model referred to in Chapter VII and listed below, calculates energy consumption on the basis of individual torpor and arousal cycles. Ambient temperature was held constant within each cycle but followed the lae seasonal soil temperature regimes reported in Chapter 6. Metabolic rates were based on Hudson and Deavers' (1973) equation for resting metabolic rate (RMR) from 8 species of ground squirrels (<u>Spermophilus</u> spp.):

$$\mathrm{RMR}(\mathrm{mlO_2/hr}) = 3.24 * \mathrm{Wt}_g^{.66}$$

Torpor metabolic rate (TMR) was calculated from RMR assuming $Q_{10} = 2.5$, which is typical of biological rates and is appropriate for TMR of ground squirrels (Snapp and Heller, 1981). Body temture during torpor (T_b) was assumed to be 2°C above ambient (T_s), but below 2°C T_s never fall below 2°C (Wang, 1973). RMR and TMR were considered to be the minimal rate of energy expenditure during the appropriate portion of any torpor and arousal cycle unless additional energy was required to maintain the inside temperature of the hibernaculum (T_h) at 21°C during euthermia and 0°C during torpor. 21°C was chosen as the minimum T_h for euthermia because it is within the thermoneutral zone of the Richardson's ground squirrel (<u>Spermophilus richardsonii</u>; Abbotts and Wang, 1980). 0°C was chosen as the minimum T_h for torpor because many hibernators allow their deep body temperature to drop to within 1-2°C of the ambient temperatures above zero during torpor (Wang, 1979; Twente and Twente, 1965) and radio-collar temperatures recorded during the telemetry study (Ch. IV) suggest that minimum T_h during torpor may fall as low as 0°C. The energy required to maintain T_h at the appropriate minimal temperature was calculated from the rate of heat loss (q, Ch. VI) and the temperature gradient across the insulation. Metabolic rates are expressed in watts (W) or milliwatts (mW), where $\mathrm{mlO_2/hr} * 0.0558 = \mathrm{W}$. Energy consumption is given in joules (J, J/sec=W) or kilojoules (KJ). In the simulations, torpor bout duration is based on the data collected in the field at LE. Simulations were run for the 'typical' squirrel of each sex and age class having the average number of torpor and arousal cycles, of average duration for each cycle at average soil temperatures for the time of year (Table B.1). Separate simulations were run to test the effect on energy expenditure of increasing and decreasing heat loss by 10%, increasing and decreasing the soil temperature by 2°C for all torpor and arousal cycles, and eliminating one euthermic period during early or late hibernation. Soil temperature regimes were determined from the records taken during the telemetry study in 1986-87 (Ch. IV).

The simulation for the 'typical' LE adult male resulted in estimates of total energy expenditure (TEE) equivalent (101%) to the mean energy expenditure for both winters as estimated from fat weight loss (Ch. III). The simulation of an HE adult male with the same torpor and arousal pattern as at LE resulted in en estimate of TEE 105% of the value determined from fat weight loss. Simulations for the 'typical" adult female and juvenile gave energy consumption estimates less than those from fat weight loss (90% and 84% respectively) at LE but higher than the values from fat weight loss (133% both age/sex classes) at HE. These results indicate that the model is a reasonably accurate reflection of the energetics of hibernation considering the assumptions of the model and the time scale on which torpor and arousal patterns were measured (±0.5 days). The interpretation of the simulation results is based on the direction and magnitude of changes in energy expenditure so the discrepancies in TEE estimates should not alter the interpretation. The detailed metabolic rates and hibernating patterns were not available to make the model a more accurate reflection of hibernation energetics so the model is intended only as a means of determining which of the three factors examined in this study (soil temperature, insulation and arousal pattern) has the greatest effect on energy expenditure during hibernation.

The computer program, written in BASIC, for modelling energy consumption of Columbian ground squirrels during hibernation, is as follows:

```
10  INPUT "SQUIRREL SEX"; SEX$
20  INPUT "SQUIRREL AGE"; AGE$
```

```
30  INPUT "SQUIRREL WEIGHT"; WEIGHT  'weight in grams
40  INPUT "      SIMULATION"; SIM$
50  INPUT "HIBERNACULUM HEAT CONDUCTIVITY"; QNEST   'watts/degree
60  INPUT "Number of torpor and arousal   cycles"; N
70  DIM TSOIL(N), TBODY(N), DUROUSAL(N), DURTORP(N)
80  DIM TNZDIFF(N), TNZWATTS(N), EUDIFF(N), TMR(N)
90  DIM TMRWATTS(N),EUWATTS(N), NESTDIFF(N),  NESTWATTS(N)
100 DIM TORPDIFF(N), TORPWATTS(N), KJTORP(N), KJEUTH(N)
110 FOR B= 1 TO N
120   PRINT
130   PRINT "                         BOUT NUMBER ";B
140   INPUT "AMBIENT TEMPERATURE"; TSOIL(B)
150   INPUT "AROUSAL DURATION"; DUROUSAL(B)
160   INPUT "TORPOR DURATION"; DURTORP(B)
170 NEXT B
180 LPRINT "SQUIRREL SEX ";SEX$
190 LPRINT "SQUIRREL AGE ";AGE$
200 LPRINT "SQUIRREL WEIGHT";WEIGHT
210 LPRINT "SIMULATION   ";SIM$
220 FOR C = 1 TO N
230   LPRINT "                         BOUT NUMBER ";C
240   LPRINT "AMBIENT TEMPERATURE ";TSOIL(C), "DAYS AROUSED ";
                DUROUSAL(C), "DAYS TORPID ";DURTORP(C)
260   RMR = ((WEIGHT^.66) * 3.24)
270   IF TSOIL(C) > 2 THEN TBODY(C) = TSOIL(C) + 2  ELSE TBODY(C) = 2
280   TMR(C) = RMR * (2.5^((TBODY(C)-38)/10))
290   RMRWATTS = RMR * .00558
300   TMRWATTS(C) = TMR(C) * .00558
310   TNZDIFF(C) = 21 - TSOIL(C)
320   IF TNZDIFF(C) < 0 THEN TNZDIFF(C) = 0
330   TNZWATTS(C) = TNZDIFF(C) * QNEST
340   EUDIFF(C) = TNZWATTS(C) - RMRWATTS
350   IF EUDIFF(C) < 0 THEN EUDIFF(C) = 0
360   EUWATTS(C) = RMRWATTS + EUDIFF(C)
370   NESTDIFF(C) = 0 - TSOIL(C)
380   IF NESTDIFF(C) < 0 THEN NESTDIFF(C)=0
390   NESTWATTS(C) = NESTDIFF(C) * QNEST
400   TORPDIFF(C) = NESTWATTS(C) - TMRWATTS(C)
410   IF TORPDIFF(C) < 0 THEN TORPDIFF(C) = 0
420   TORPWATTS(C) = TMRWATTS(C) + TORPDIFF(C)
430   KJTORP(C)=((DURTORP(C)*86400!) * TORPWATTS(C))/1000
440   KJEUTH(C)=((DUROUSAL(C)*86400!) * EUWATTS(C))/1000
460   LPRINT "METABOLIC RATE IN EUTHERMIA  ";
470   LPRINT USING "##.####";EUWATTS(C);
480   LPRINT " WATTS"
500   LPRINT "METABOLIC RATE IN TORPOR ";
510   LPRINT USING "#.####";TORPWATTS(C);
520   LPRINT " WATTS"
550   LPRINT "ENERGY USED DURING AROUSAL ";
560   LPRINT USING "#####.##"; KJEUTH(C);
570   LPRINT "  kJOULES"
590   LPRINT "ENERGY USED DURING TORPOR";
```

```
600   LPRINT USING "#####.##";KJTORP(C);
610   LPRINT " kJOULES"
650 NEXT C
660 FOR D=1 TO N
670   KJEUTOTAL = KJEUTOTAL + KJEUTH(D)
680   KJTORTOTAL = KJTORTOTAL + KJTORP(D)
690 NEXT D
700 KJTOTAL = KJEUTOTAL + KJTORTOTAL
710 KJPERGRAM = KJTOTAL/WEIGHT
720 LPRINT "TOTAL ENERGY FOR HIBERNATION";
730 LPRINT USING "##########.##"; KJTOTAL;
740 LPRINT " kJOULES"
760 LPRINT "TORPOR ENERGY EXPENDITURE ";
770 LPRINT USING "########.##";KJTORTOTAL;
780 LPRINT " kJOULES"
790 LPRINT "EUTHERMIC ENERGY EXPENDITURE ";
800 LPRINT USING "########.##";KJEUTOTAL;
810 LPRINT " kJOULES"
830 LPRINT "MASS SPECIFIC ENERGY CONSUMPTION";
840 LPRINT USING "######.##";KJPERGRAM;
850 LPRINT "KJ/G"
860 LPRINT CHR$(12)
```

In the LE simulations euthermia accounted for 68% of TEE for the adult male, 50% for the adult female and 48% for the juvenile. The proportion of TEE accounted for by euthermia in the HE simulations was 59%, 39% and 39% for the adult male, adult female and juvenile, respectively. Almost half of the euthermic energy expenditure of adult males is used during the long euthermic period (10-11 days in the model) from the end of torpor to emergence (38%TEE at LE, 26% at HE). In the LE simulations RMR provides sufficient heat to maintain T_h at 21°C at soil temperatures (T_s) of -2°C for the adult male, 4° for the adult female, and 5° for the juvenile. The minimum TMR (T_b=2°C) was sufficient to maintain T_h at 0°C or above until T_s fell to -1°C for all age/sex classes. In the HE simulations the euthermic metabolic rate increased above RMR when T_s was ≤-3°C for the adult male, 2°C for the adult female and 3°C for the juvenile. TMR increased above the minimum when T_s was ≤-2°C for the adult male, and -1°C for both the adult female and juvenile. Additional insulation is beneficial only at soil temperatures that require increased heat production to prevent freezing during torpor or to maintain T_h within the thermoneutral zone during arousals. HE squirrels experience these temperatures for a greater proportion of the hibernating season and would be expected to benefit more from increased insulation than would LE squirrels. For this same reason, lower soil temperatures have a larger impact on energy expenditure of HE squirrels than on LE squirrels. Increasing soil temperatures by 2°C actually increases the energy expenditure of LE squirrels during early hibernation by increasing the energy expenditure in torpor when soil temperature is greater than 2°C.

Table B.1. List of the hibernating conditions and parameters used to simulate energy expenditure of "typical" hibernators.

Low Elevation Adult Male, 750 g
Hibernaculum heat loss = 0.064 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	13	11	9	7	5	5	4	1	0	0	-1	-1	-1	
Days in Torpor	5	7	9	11	13	15	17	22	26	28	28	28	8	217
Days Euthermic	4	1	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	11	22

Low Elevation Adult Female, 580 g
Hibernaculum heat loss = 0.070 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	12	10	7	6	5	4	3	0	0	-1	-1	-1	0	
Days in Torpor	5	7	9	11	13	17	20	28	28	28	28	28	15	237
Days Euthermic	3	1.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	12

Low Elevation Juvenile, 370 g
Hibernaculum heat loss = 0.057 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	12	10	7	6	5	4	3	0	0	-1	-1	-1	0	
Days in Torpor	5	7	9	11	13	17	20	28	28	28	28	28	15	237
Days Euthermic	3	1.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	12

Table B.1. --continued--

High Elevation Adult Male, 750 g
Hibernaculum heat loss = 0.057 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	5	3	2	1	0	-1	-2	-2	-2	-2	-2	-2	-2	
Days in Torpor	5	7	9	11	13	15	17	26	32	32	32	26	10	235
Days Euthermic	4	1	1	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	2	11	25

High Elevation Adult Female, 580 g
Hibernaculum heat loss = 0.064 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	4	3	1	0	-1	-2	-2	-2	-2	-2	-2	-2	-1	
Days in Torpor	5	7	9	11	13	19	25	28	28	28	28	28	18	247
Days Euthermic	3	1.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	1.5	13

High Elevation Juvenile, 370 g
Hibernaculum heat loss = 0.049 W/°C

Bout #	1	2	3	4	5	6	7	8	9	10	11	12	13	Days Total
T_{soil}	4	3	1	0	-1	-2	-2	-2	-2	-2	-2	-2	-1	
Days in Torpor	5	7	9	11	13	19	25	28	28	28	28	28	18	247
Days Euthermic	3	1.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1.5	1.5	13

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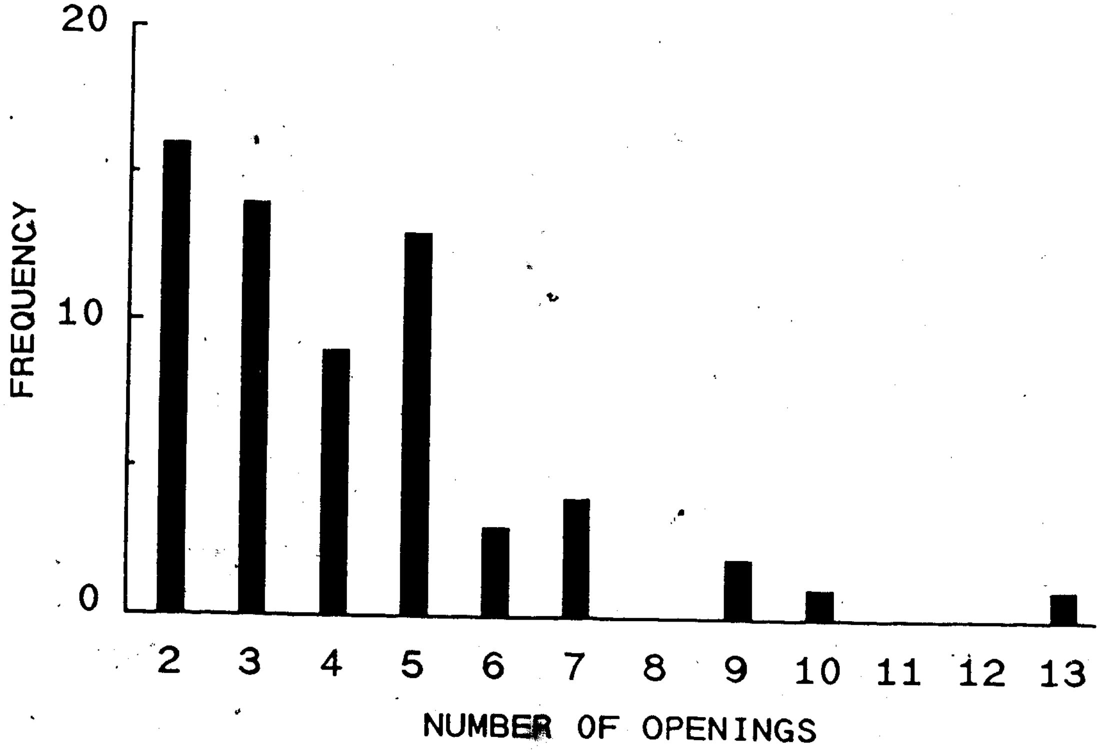
APPENDIX C. INTERCONNECTION OF BURROW OPENINGS

In 1985 an attempt was made to locate all burrow entrances on the LE study area and map the location and interconnection of entrances as a means of determining the size of burrow systems. Over the summer 523 entrances were located on the 1.3 ha study area. The position of each entrance was measured to the nearest 5 cm using a 10 X 10 m grid and marked with a numbered aluminum tree tag (Canadian Forestry Supplies) anchored with a nail. The interconnections of entrances were determined by blowing "non-toxic" smoke (zinc oxide, 30-second white signal smoke candles, Ben Meadows Forestry Supplies) into each entrance with a portable smoke blower patterned after Vogel et al. (1973), and observing which entrances the smoke exited from. Only 346 of the 523 entrances were tested before the supply of smoke candles was exhausted; 73 of these were not connected to any other entrance at the time of testing and are referred to as "single opening" burrows. 273 entrances were connected to one or more other entrances to make up 58 "multiple opening" burrows. Multiple opening burrows had as many as 13 entrances but most had 2-5 entrances (median 3; Fig. C.1). The mean distance between connected entrances was 4.26 m (range 0.11-35.40); only 7 burrows had entrances more than 10 m apart and only one had any entrances more than 20 m apart. It became apparent during 1985 that the stucture of the burrows was very dynamic and the pattern of interconnections changed often. In 1986 10 burrow system were selected to be mapped with smoke repeatedly over the summer. They were first mapped on 27 April and bi-weekly until 13 July. In mid-July two squirrels were found dead at the mouth of one of these burrows. Subsequent laboratory tests at the Alberta Provincial Animal Health Laboratory concluded the squirrels had died of "acute toxic lung injury". As the smoke was implicated in causing these mortalities the burrow mapping was discontinued at that time.

The results of the 1985 mapping suggest that the burrow systems of Columbian ground squirrels are not very large. If the mean distance between burrow entrances is used as an index of the size of the systems it seems reasonable to conclude that burrow entrances more than 5 m apart are not likely to be part of the same burrow system. The dynamic nature of the burrow systems suggests that many of the single opening systems may be connected to other entrances at certain times and that the pattern of the number of entrances per burrow system as represented in Figure C.1 may vary throughout the summer. The results of the repeated mappings are not presented here.

Figure C.1. Frequency distribution of the number of entrances to Columbian ground squirrel burrow systems with multiple openings.



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