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Annual Periodicity in a Free-Living Hibernator, the Uinta Ground Squirrel

Fred L. Knopf
Utah State University

ANNUAL PERIODICITY IN A FREE-LIVING HIBERNATOR,

THE UINTA GROUND SQUIRREL

by

Fred L. Knopf

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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Approved:

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Major Professor

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Committee Member

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Committee Member

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Dean of Graduate Studies

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Fred L. Knopf

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ABSTRACT

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the Uinta Ground Squirrel

by

Fred L. Knopf, Master of Science

Utah State University, 1973

Major Professor: Dr. D. F. Balph
Department: Wildlife Science

This study documents the timing of seasonal events and associated changes in body weights of Uinta ground squirrels (Spermophilus armatus) that live at three different altitudes. The investigation provides detailed field data for biologists investigating circannual rhythms and hibernation in the laboratory.

Ground squirrels aroused and subsequently emerged from hibernation in an overlapping sequence: adult males first, followed by adult females, yearling females and yearling males. Within limits some climatic condition(s) delayed emergence and increased the overlap in emergence sequence. The duration of seasonal activities above ground averaged about 90 days for adult and yearling squirrels. Juveniles were active above ground for 60-70 days. Each summer, adult males and adult and yearling females immerged into estivation-hibernation about the same date. Yearling males immerged later and juveniles immerged last.

Adult and yearling squirrels gained body weight rapidly except for brief periods during reproduction. Males began to gain weight after the breeding season. Female weights started to increase immediately after emergence but leveled off during lactation. Juveniles gained weight steadily after emergence from the natal burrow. Mean body weights of squirrels leveled off late in the active season.

Seasonal activities and changes in body weights of Uinta ground squirrels were shifted back 6 weeks in time at higher elevations.

The annual cycle of Uinta ground squirrels appeared to be the result of an interaction between an endogenous timing mechanism and the immediate environmental conditions. Arousal from hibernation occurred about the same date each year and was probably under endogenous control. After arousal, exogenous factors acted to shorten or lengthen subsequent phases in the annual cycle. Later arousal of squirrels at high altitudes indicated that endogenous timing mechanisms of the species are entrained to the environmental conditions encountered at the respective altitudes.

(51 pages)

INTRODUCTION

There is much information on diel activity rhythms. Biologists have documented them in wild animals (Kavanau 1967), livestock (Squires 1971) and laboratory animals (Bruce 1960). Some laboratory studies have sought the timing mechanism of these cycles. Most evidence indicates that they are entrained on light and have an underlying circadian periodicity that is under endogenous control (reviewed by Aschoff 1965 and Sollberger 1965). Since many studies have recorded the environmental setting along with the diel activity of animals in the wild, one can relate the laboratory experiments to the phenomenon as it exists in nature. Some researchers have even speculated as to the ecological significance of the underlying circadian periodicity (Aschoff 1963 and Enright 1970).

Recently interest has developed in annual rhythms, especially those of estivation and hibernation in woodchucks (*Marmota monax*) and ground squirrels (*Spermophilus* spp. Pengelley and Kelly 1966; Davis 1967, 1970; Heller and Poulson 1970; Blake 1972). The studies have been in the laboratory and have sought clues as to what mechanism times these annual rhythms. The results have suggested that seasonal torpor as well as the initiation and cessation of body-weight gains are influenced by several environmental factors, but that they have an underlying annual cycle that is also under endogenous control. However, it has been difficult to assess the ecological relevance of these findings since little is known about the details of annual periodicity of hibernating animals in the wild (Enright 1970). There is a need for more field information on the chronology of important seasonal events and associated environmental conditions. This study provides some of this information for three populations of Uinta ground squirrels (*Spermophilus armatus*).

METHODS

The primary study area was at the Utah State University Forestry Field Station 35 km northeast of Logan, Utah. The station, at an elevation of 1,909 m, included a 0.89 ha central lawn of bluegrass (Poa pratensis) surrounded by an 8.0 ha area of aspen (Populus tremuloides), shrub land, and meadows. An average of 200 adults and yearlings and 400 juvenile ground squirrels resided on the area annually.

Much of the data for this study came from coordinated investigations that began in 1964 on the behavior and ecology of the station squirrel population. Basic to all the research was a capture and observation program. Its purpose was to identify and periodically to locate and record the activity of all squirrels on the study area from their initial appearance from hibernation or the natal burrow until their disappearance from the population.

An attempt was made to capture each squirrel as it emerged from hibernation or the natal burrow and once every 10 days thereafter. Each squirrel was toe-clipped and distinctively marked with fur dye. Upon capture, the identity, location, body weight, and overt reproductive condition of the squirrel were recorded.

Observations of squirrels were made from six 4-m towers distributed in the study area. The identity, location, and activity of squirrels were recorded within prescribed space and time and at irregular intervals throughout the study area. See Balph and Stokes (1963) for details of the study area and Walker (1968) for details of the methods.

Additional data were obtained in 1968 and 1969 by trapping ground squirrels in two other locations. One was a small population bordering agricultural fields at 1,345 m altitude, 14 km southwest of Logan. The other was along a sagebrush (*Artemisia tridentata*)-aspen interface at 2,438 m altitude, 26 km northeast of Logan. These populations approached the lower and upper altitudinal limits of Uinta ground squirrel distribution in Utah. Hereafter, the three populations are referred to as valley (1,345 m), station (1,909 m), and subalpine (2,438 m).

RESULTS

Ground squirrels at the field station were active above ground 4-5 months each year. They began to emerge from hibernation about April 1. Juvenile squirrels appeared about June 1. Adults began to immerge into estivation in late June and all squirrel activity ceased in late August. Squirrels remained under ground until spring. Thus, estivation phased into hibernation as reported for S. mohavensis (Bartholomew and Hudson 1960).

Squirrel reproductive activities at the station commenced shortly after emergence from hibernation (Walker 1968). Adult males and a few yearling males had scrotal testes when they emerged. Adult and yearling females were bred as they emerged from hibernation. Breeding terminated and testes became inguinal, about May 1. Gestation lasted about 26 days and juveniles became independent 24 days after birth.

Emergence from Hibernation

The timing of emergence from hibernation varied with the sex and age of the squirrels (Figure 1). In 1965, emergence of the station population commenced April 16 and lasted 4 weeks. The sex and age groups emerged rather synchronously that year. In 1966, emergence commenced March 28 and lasted 6 weeks. The peak of adult emergence occurred

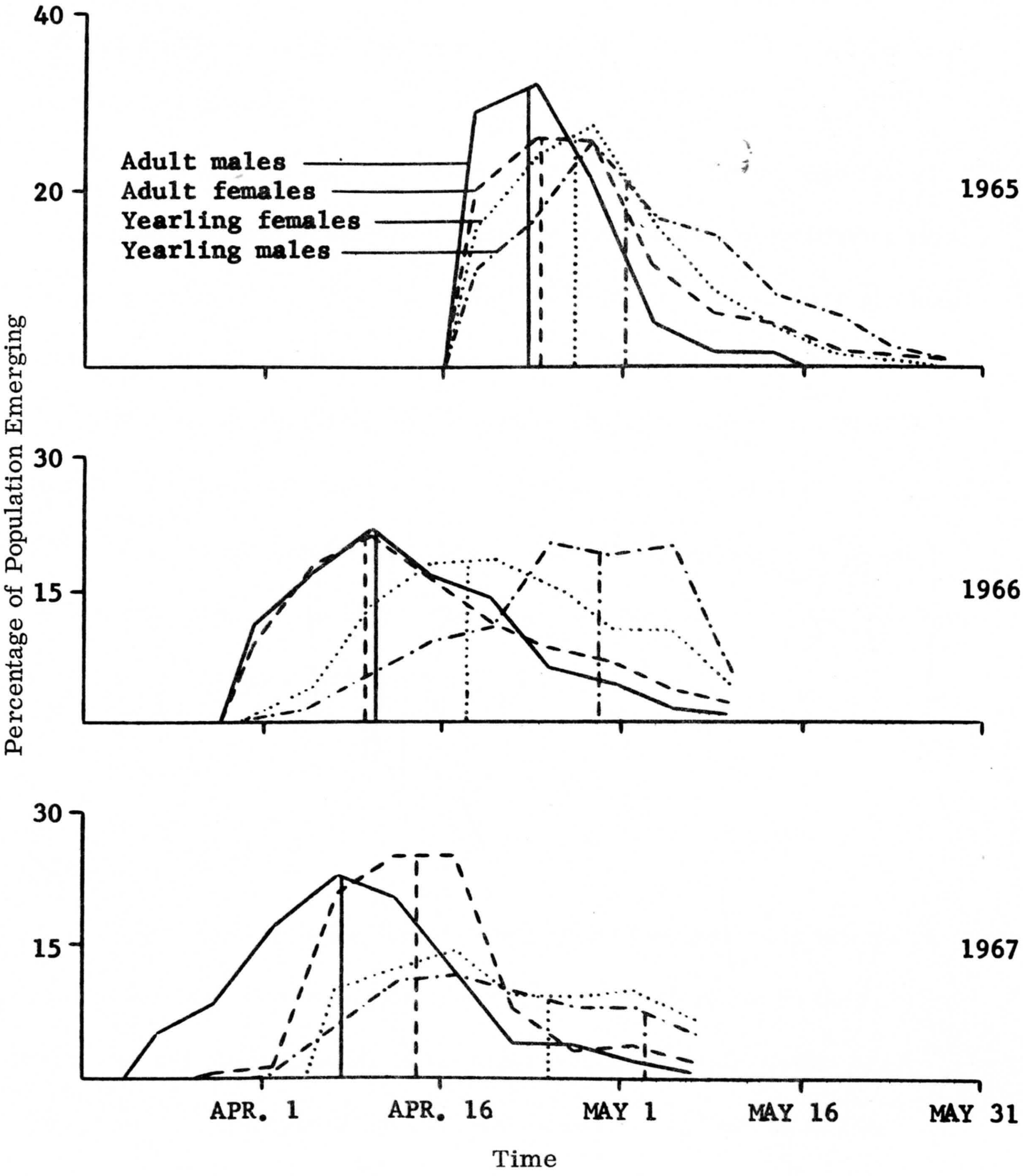


Figure 1. Patterns of emergence from hibernation exhibited by ground squirrels at the field station from 1965-1967 (from Walker 1968). Plotted values represent 3-point running averages. Vertical lines indicate dates by which 50 percent of the members of each sex and age group had emerged.

first, followed by that of yearling females 9 days later and yearling males 20 days later. In 1967, emergence of the population began March 21 and lasted 7 weeks. Emergence was asynchronous in 1967 with adult males emerging first followed sequentially by the adult females, yearling females, and yearling males.

The body weights of ground squirrels at emergence also varied with the sex and age of animals (Table 1). Adult males were heavier than yearling males (1965, $P < .001$; 1966, $P < .001$; 1967, $P < .001$) and adult females were heavier than yearling females (1965, $P < .05$; 1966, $P < .001$; 1967, $P < .05$) in all years. Adult males, which emerged later in 1965 than in other seasons, were lighter that year than in 1966 ($P < .001$) or 1967 ($P < .001$). Adult females were also lighter at emergence in 1965 than in either 1966 ($P < 0.3$) or 1967. The weights of yearling squirrels were not significantly different between years.

Active Season

Duration

The time from the initial observation of a squirrel in the spring until it was last observed in the summer was considered to be the duration of its activity above ground. Since squirrels do not readily enter traps just prior to immergence into estivation-hibernation, only those that lived in view of the observation towers, and thus subjected to both observation and capture procedures, were used for calculations of season lengths.

Table 1. Emergence body weights of initial 25 ground squirrels of each sex and age group to appear at field station, 1965-1967

	Emergence Body Weights (grams)		
	1965	1966	1967
	Mean ± SD	Mean ± SD	Mean ± SD
Adult males	302 ± 34.5	348 ± 37.8	351 ± 43.4
Adult females	259 ± 31.2	272 ± 32.8	268 ± 29.2
Yearling males	235 ± 37.0	227 ± 26.0	244 ± 37.5
Yearling females	201 ± 19.1	205 ± 18.8	219 ± 20.5

Adult and yearling squirrels at the field station were active above ground an average of 80-103 days a year (Table 2). Males were active longer than females ($P < .01$) by 5-10 days. Adult and yearling males had similar season lengths except in 1967 when the adults were active longer ($P < .05$). Adult and yearling females were active about the same length of time each year. The active season of all sex and age groups were of the same duration in 1965 and 1967 but shorter in 1966 than either 1965 ($P < .001$) or 1967 ($P < .001$).

Juvenile squirrels were active above ground an average of 56-69 days a year. Considering the 24-day post-partum period when they remained in the natal burrow, the juveniles were active about as long as the adults and yearlings. Season lengths of juveniles were shorter in 1966 than in 1965 ($P < .01$), just as they were for the adults and yearlings. In 1967 some juveniles were born relatively late in the season and did not remain above ground a commensurate amount of time. This resulted in a short average season for juveniles in 1967.

Changes in body weights

Those animals that spend a portion of the year in torpor exhibit characteristic fluctuations in body weights. Most gain weight rapidly during the active season--the shorter the season, the more rapid the weight gains. These weight gains reflect the energy reserves necessary to maintain animals in torpor. Under natural conditions, changes in body

Table 2. Number of days that ground squirrels were active above ground at field station, 1965-1967

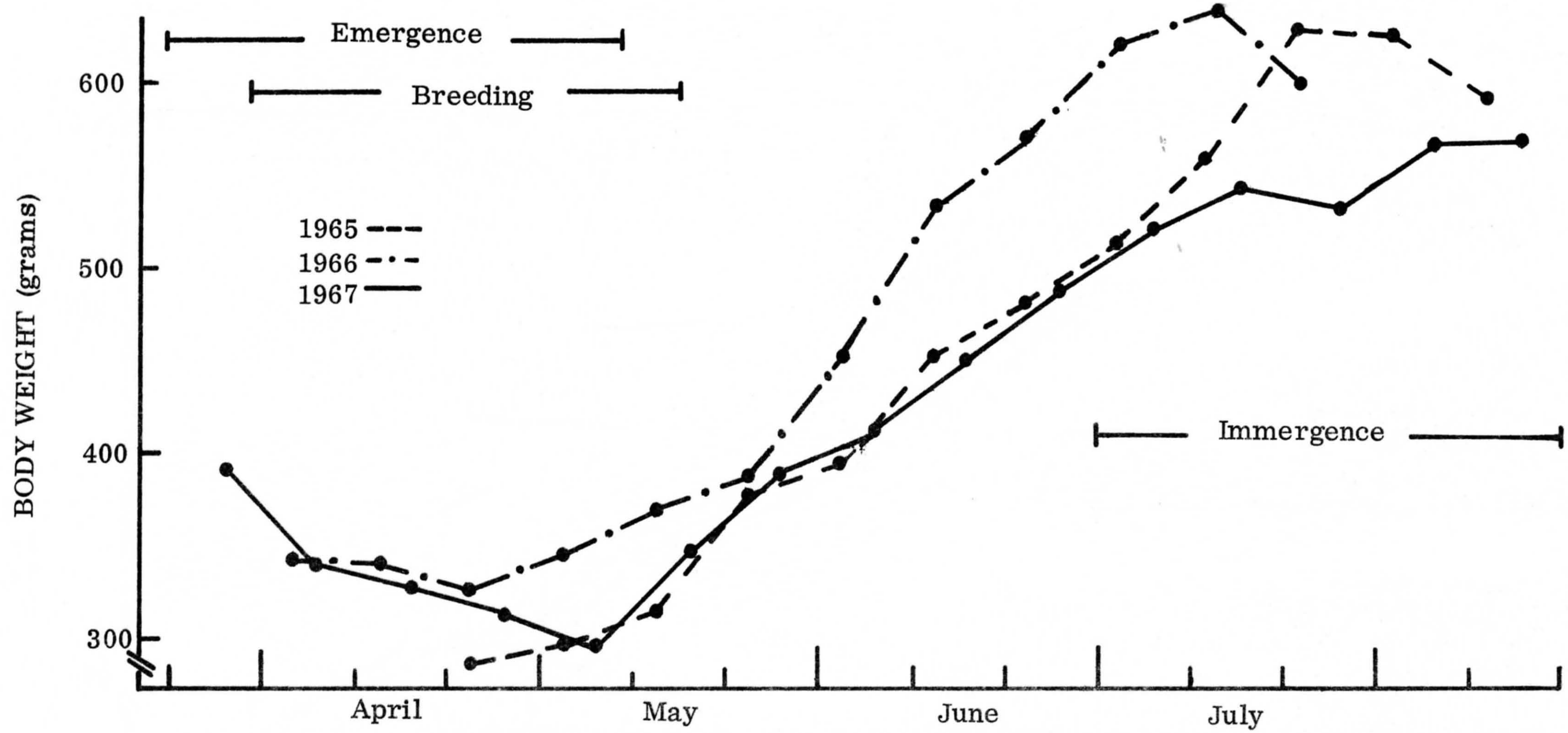
	Season Length (days)					
	1965		1966		1967	
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD
Adult males	8	96.3 ± 17.0	19	90.0 ± 15.2	17	102.9 ± 19.7
Adult females	16	91.3 ± 14.1	25	85.6 ± 14.4	24	89.2 ± 11.6
Yearling males	20	96.5 ± 15.0	28	85.7 ± 16.8	18	94.4 ± 17.4
Yearling females	29	92.1 ± 12.1	31	80.6 ± 12.1	29	87.9 ± 11.9
Juvenile males	47	69.1 ± 10.3	25	64.8 ± 7.3	43	55.8 ± 14.5
Juvenile females	60	67.5 ± 9.8	47	63.6 ± 6.1	56	58.2 ± 36.7

weights may also reflect the state of physiological preparation for hibernation (Hoffman 1964a, b).

Adult male squirrels at the station began to gain body weight about May 1, irrespective of when they emerged from hibernation (Figure 2). In 1965, when the first squirrel appeared on April 16, the males began to gain weight shortly after emergence. In 1967, when initial emergence was March 21, the males lost about 25 percent of their emergence weights by early May. This decline resulted in similar average weights of the males in early May of both years. From May until mid July, body weights increased steadily. After mid July, body weights leveled off until the last animal immerged into estivation.

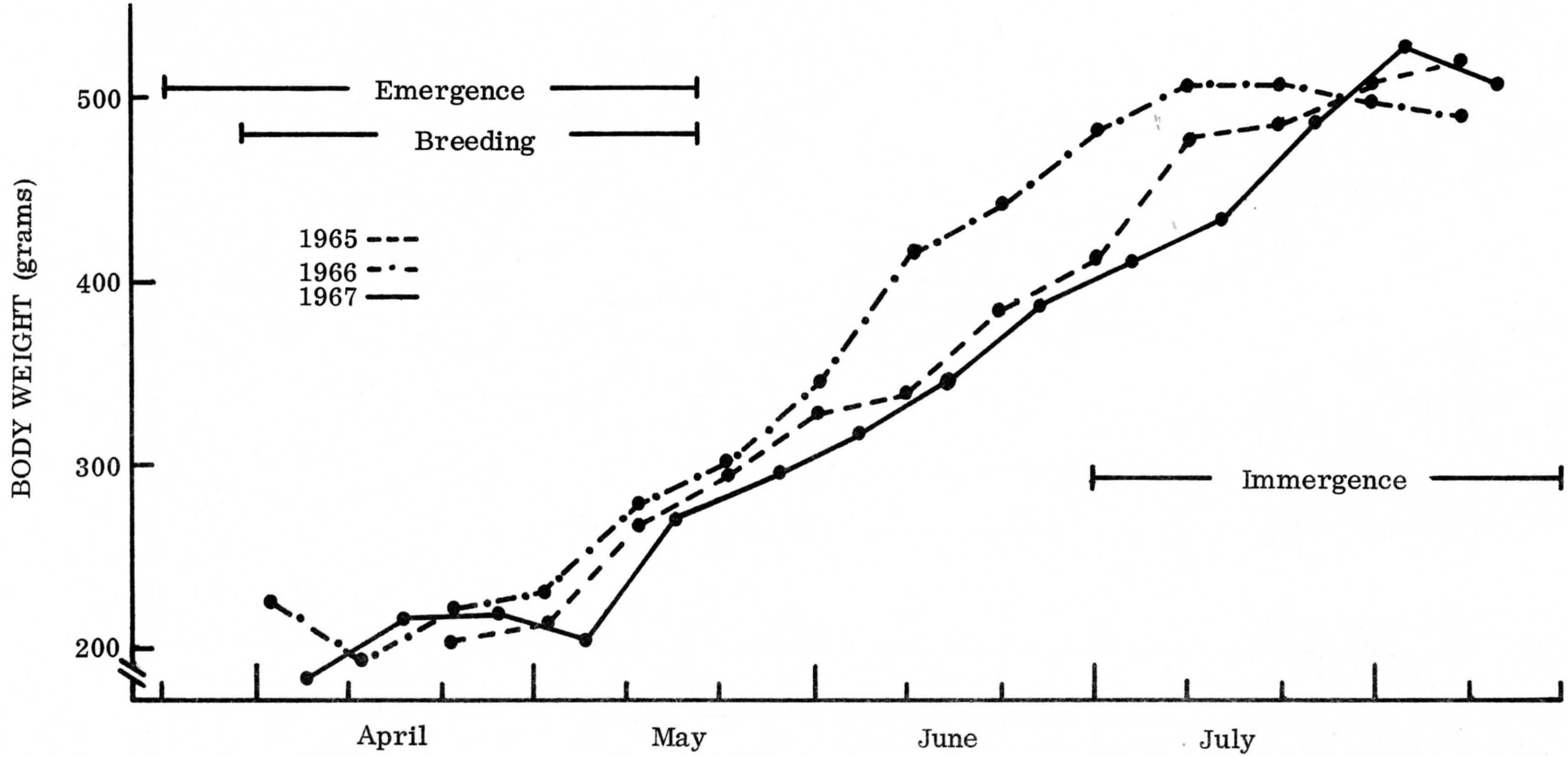
Most yearling males also began to gain weight about May 1, shortly after emergence each year (Figure 3). Like adults, those yearlings that emerged in April failed to gain significant weight immediately. Body weights of the yearlings increased steadily from May to mid July, after which they leveled off.

Adult females gained weight during breeding and gestation each season (Figure 4). Females gained about 50 percent of their annual maximum weight before the young were born. Weights leveled off during parturition and lactation and commenced rising again when the young emerged above ground. Female body weights increased over a 1-month period after the termination of lactation and, as in males, leveled off in mid July.



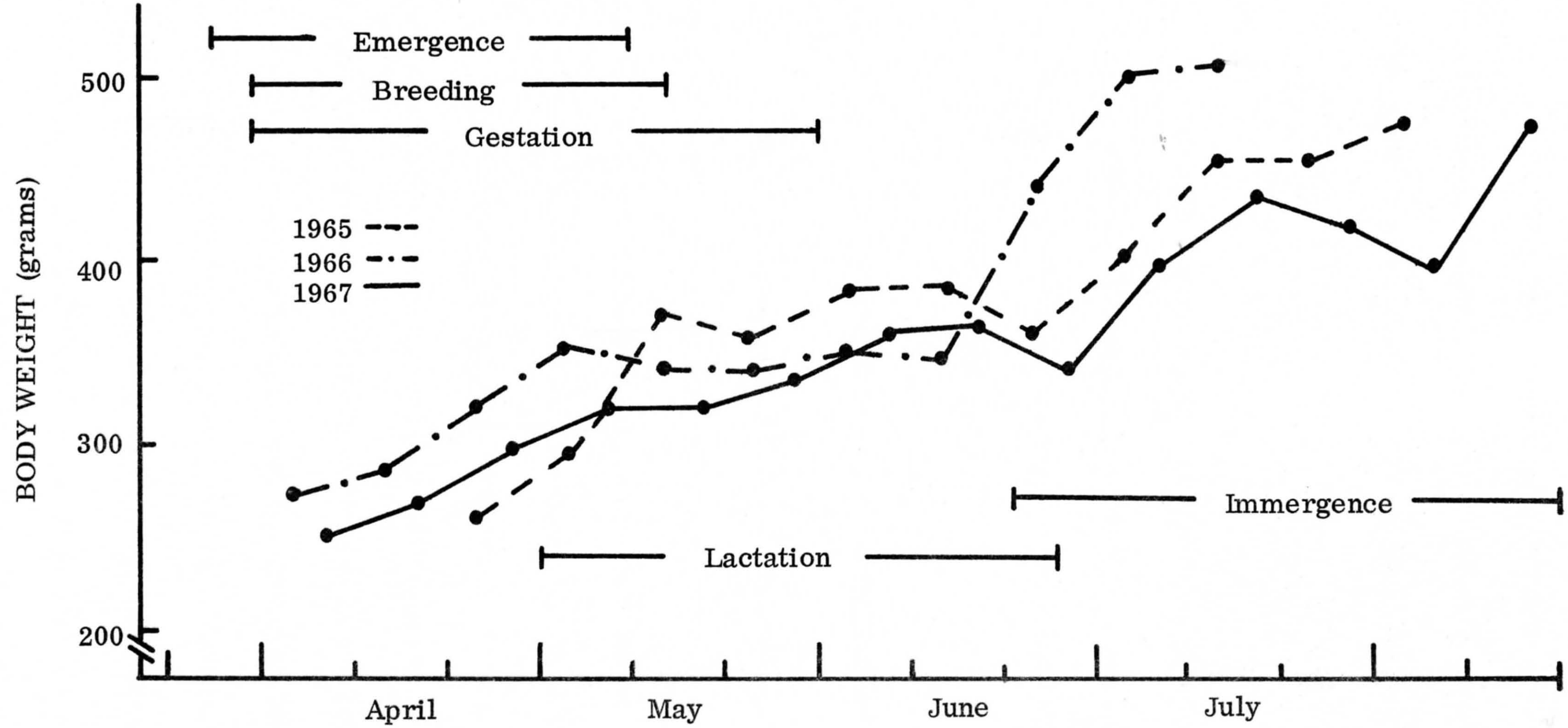
Year																
1965	n	-	-	-	22	25	19	14	16	6	11	10	7	4	3	3
	SE	-	-	-	9.3	7.2	7.1	12.0	14.5	20.8	22.9	25.6	32.5	38.0	39.7	8.3
1966	n	-	18	34	31	29	21	15	8	9	8	13	8	3	-	-
	SE	-	7.8	6.3	3.6	4.3	8.0	10.1	14.3	22.7	32.4	17.1	15.9	59.4	-	-
1967	n	6	16	30	28	24	16	11	11	11	11	13	9	6	4	1
	SE	15.5	18.8	6.7	4.8	8.0	10.6	11.4	18.3	8.2	24.6	24.9	25.1	40.1	29.3	-

Figure 2. Changes in body weights of adult male ground squirrels relative to time of year and important seasonal events from 1965-1967.



1965	n	-	-	-	15	28	30	15	21	5	9	16	17	8	10	4
	SE	-	-	-	9.3	6.9	8.4	11.2	8.5	21.8	17.4	12.5	13.3	20.1	14.6	25.7
1966	n	-	1	14	20	48	35	24	13	18	18	16	24	12	5	7
	SE	-	-	9.3	8.7	5.9	6.5	6.3	11.4	12.2	12.3	13.9	12.8	17.9	25.7	20.4
1967	n	-	2	18	19	22	22	18	11	13	21	20	12	15	9	4
	SE	-	29.0	9.7	8.6	6.3	9.2	8.1	9.4	7.4	6.5	7.6	11.4	13.0	12.4	57.0

Figure 3. Changes in body weights of yearling male ground squirrels relative to time of year and important seasonal events from 1965-1967.



Year																
1965	n	-	-	-	35	34	23	21	26	10	17	16	11	2	2	-
	Se	-	-	-	5.1	5.4	13.2	5.6	6.7	5.6	6.8	13.4	9.5	8.0	43.0	-
1966	n	-	28	43	38	39	29	20	11	20	8	8	3	-	-	-
	SE	-	6.3	5.2	6.6	7.4	5.0	7.5	9.9	10.6	24.7	24.5	45.2	-	-	-
1967	n	-	1	45	39	38	25	21	16	16	18	16	12	3	2	1
	SE	-	-	15.2	6.7	6.6	7.1	6.5	9.3	9.9	13.5	12.9	17.3	37.0	20.0	-

Figure 4. Changes in body weights of adult female ground squirrels relative to time of year and important seasonal events from 1965-1967.

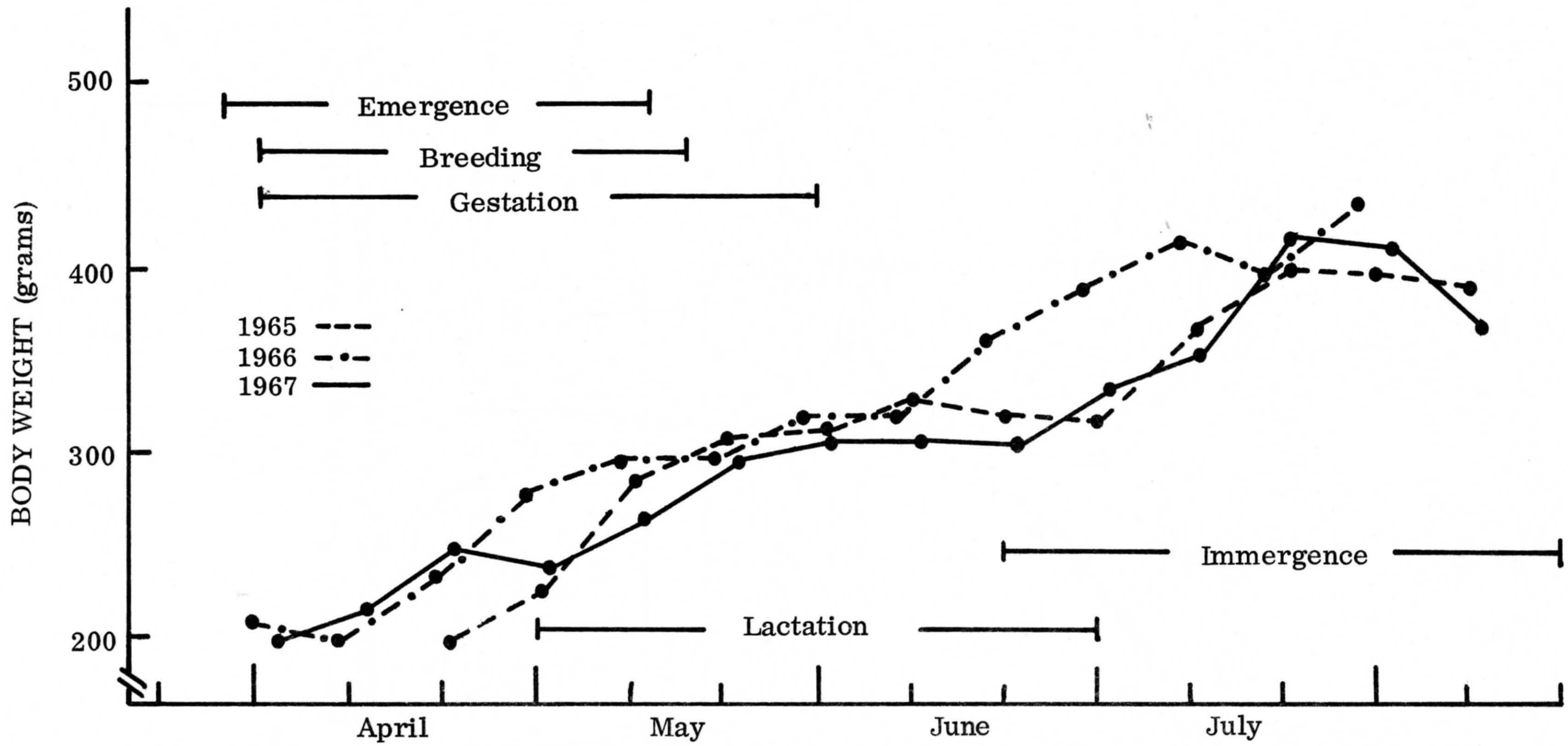
Yearling females also gained approximately 50 percent of their annual maximum weight before parturition each year (Figure 5). Like adults, weights of yearlings leveled off during parturition and lactation, increased after the young became independent, and leveled off again in July.

Juvenile ground squirrels began to gain weight at the rate of 4 g/day immediately after emergence from the natal burrow (Figure 6). Mean weights of both males and females increased rather steadily through June and July and leveled off in August.

Immergence into Estivation-Hibernation

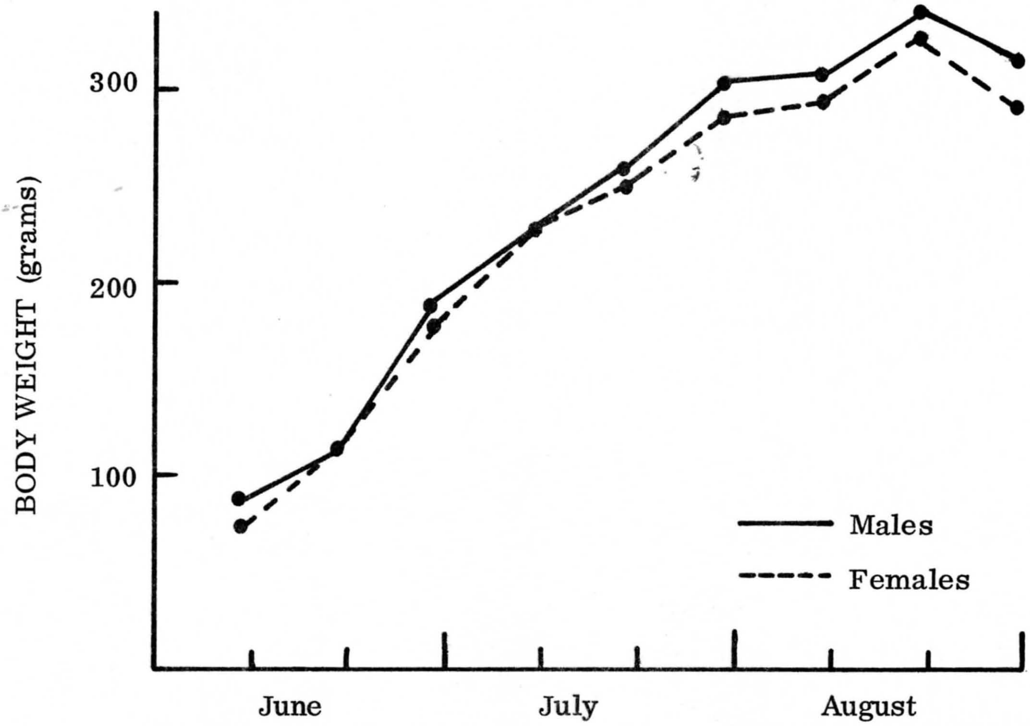
The last sighting or capture of a ground squirrel each season was considered the date that it immerged into estivation-hibernation. As with season length determinations, immergence dates were derived for only those squirrels that lived near the observation towers.

Adult and yearling ground squirrels began to immerge into estivation-hibernation about 80 days after the initial squirrel appeared in the spring. Adult and yearling females and adult males immerged synchronously in 1965 (Table 3). Adult females immerged before the yearling females and adult males in 1966 ($P < .05$) and 1967 ($P < .03$). Yearling males, the last to emerge each spring, were last to immerge each summer excluding juveniles (1965, $P < .05$; 1966, $P < .001$; 1967, $P < .01$). All adults and yearlings immerged earlier in 1966 than in either 1965 ($P < .001$) or 1967 ($P < .001$).



1965	n	-	-	-	36	57	39	40	43	26	34	36	29	14	13	4
	SE	-	-	-	3.8	4.4	9.6	5.9	4.6	4.7	5.1	6.6	10.2	9.7	3.9	15.4
1966	n	-	3	36	36	47	36	34	28	29	26	25	12	5	1	-
	SE	-	10.6	4.4	5.9	7.1	6.1	5.8	6.6	7.2	10.2	9.7	15.4	6.4	-	-
1967	n	-	11	36	39	43	33	22	27	29	29	24	15	10	4	1
	SE	-	5.7	4.0	5.8	5.6	6.8	9.5	5.1	6.7	7.5	9.5	16.2	21.5	19.5	-

Figure 5. Changes in body weights of yearling female ground squirrels relative to time of year and important seasonal events from 1965-1967.



Males	n	143	129	211	191	112	120	77	32	16
	SE	6.6	3.0	6.2	7.4	7.8	7.2	5.4	22.1	7.5
Females	n	143	154	261	230	130	148	109	19	19
	SE	1.1	3.2	6.7	8.6	2.9	3.8	3.9	9.2	9.2

Figure 6. Changes in body weights of juvenile ground squirrels after emergence from the natal burrow in 1965.

Table 3. Mean date that ground squirrels immerged into estivation-hibernation at the field station, 1965-1967

		n	Last Record Day ± SD
Adult Males	1965	8	July 22 ± 14.9
	1966	19	July 3 ± 11.3
	1967	17	July 13 ± 18.4
Adult Females	1965	16	July 19 ± 12.7
	1966	25	June 27 ± 11.0
	1967	24	July 9 ± 13.7
Yearling Males	1965	20	July 28 ± 17.4
	1966	28	July 15 ± 17.4
	1967	22	July 22 ± 17.3
Yearling Females	1965	29	July 21 ± 13.1
	1966	31	July 4 ± 11.5
	1967	31	July 13 ± 14.3
Juvenile Males	1965	56	Aug. 14 ± 8.0
	1966	29	Aug. 2 ± 3.8
	1967	45	July 30 ± 8.7
Juvenile Females	1965	66	Aug. 14 ± 2.7
	1966	50	Aug. 2 ± 3.9
	1967	60	Aug. 1 ± 7.5

Juvenile ground squirrels remained active at the station after most adults and yearlings had immerged (Table 3). Mean juvenile immergence occurred about August 1 in 1966 and in 1967, and 2 weeks later in 1965. Observations of the population terminated 13 August 1966, 15 August 1967, and 31 August 1965. Only a few juvenile squirrels were active on the area after those dates.

At the time of last capture, adult and yearling squirrels had gained 80-120 percent of their spring emergence weights (Table 4). Adults were generally heavier than yearlings. All squirrels tended to be heaviest after the shorter season of 1966. Within a given year, however, squirrels immerging early were lighter relative to those immerging later (Figure 7).

Early immergence at lighter weight did not appear to affect survival of estivation-hibernation. Generally, squirrels still present the subsequent year had similar mean immergence dates to those not returning (Table 5). However, dates of immergence were extremely variable between animals. This variability, plus the possibility that some of the squirrels emigrated rather than immerged, may have introduced a bias into the data.

Table 4. Mean body weights of ground squirrels at immergence into estivation-hibernation, 1965-1967

	Weight (grams)					
	1965		1966		1967	
	n	Mean ± SD	n	Mean ± SD	n	Mean + SD
Adult Males	8	590.2 + 89.9	17	634.9 + 61.0	18	561.6 + 59.3
Adult Females	14	461.8 + 30.7	17	467.3 + 90.2	29	415.3 + 56.6
Yearling Males	23	521.4 + 61.8	39	530.6 + 64.9	28	486.4 + 84.6
Yearling Females	30	414.1 + 41.6	39	407.0 + 53.7	39	372.3 + 67.4
Juvenile Males	27	326.9 + 33.7	30	368.6 + 45.5	40	322.6 + 83.4
Juvenile Females	31	305.9 + 32.9	47	335.3 + 30.1	77	305.4 + 52.7

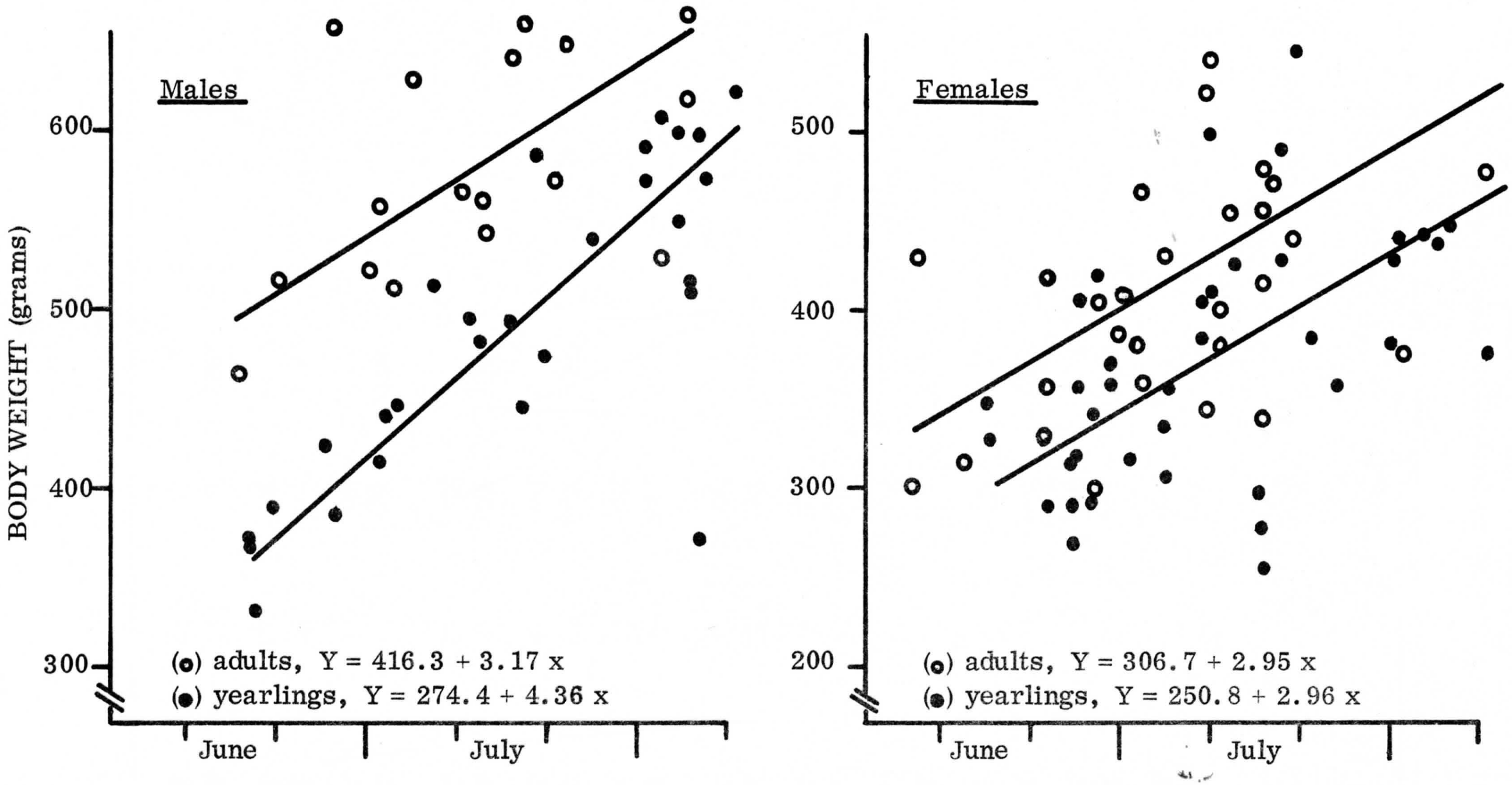


Figure 7. Body weights of adult and yearling ground squirrels at immergence into estivation-hiberation in 1967.

Table 5. Comparison of immergence dates of adult and yearling ground squirrels that reappeared or did not reappear the next year, 1965-1967

	Year	Appeared Next Year	n	Last Record Day ± SD
	1965	Yes	5	July 22 ± 13.2
		No	3	July 21 ± 21.3
Adult Males	1966	Yes	8	July 6 ± 11.3
		No	11	July 1 ± 11.4
	1967	Yes	10	July 20 ± 14.9
		No	7	July 4 ± 20.0
	1965	Yes	8	July 14 ± 14.1
		No	8	July 24 ± 9.2
Adult Females	1966	Yes	14	June 30 ± 12.7
		No	11	June 24 ± 7.0
	1967	Yes	12	July 6 ± 17.0
		No	12	July 11 ± 9.0
	1965	Yes	14	July 16 ± 12.4
		No	15	July 23 ± 12.5
Yearling Males	1966	Yes	13	July 1 ± 11.2
		No	18	July 7 ± 11.3
	1967	Yes	19	July 10 ± 12.6
		No	12	July 17 ± 17.3
	1965	Yes	13	July 27 ± 8.6
		No	7	July 25 ± 21.2
Yearling Females	1966	Yes	16	July 6 ± 25.6
		No	18	July 20 ± 13.7
	1967	Yes	11	July 22 ± 16.4
		No	11	July 22 ± 19.2

Annual Cycle at Different Altitudes

The valley and subalpine populations were trapped in 1968 and early 1969. My objectives in 1968 were to compare the chronology of population activities at the three altitudes, and to toe-clip adult/yearling and juvenile animals at the valley and subalpine areas. Squirrels so identified were used in 1969 to describe the emergence sequence and weights of the sex and age groups that year.

Seasonal activities in 1968

In 1968 I captured 22 adults and yearlings and 55 juveniles at the valley population, and 123 adults and yearlings with 89 juveniles at the subalpine population. I was unable to distinguish adult from yearling squirrels in 1968.

The valley study area was free of snow by late February in 1968. The first squirrel appeared March 18 and all squirrels had emerged by April 20.

Observations of the subalpine area commenced April 1 in 1968 and initial emergence occurred April 30. The area had 2-3 m of snow when the first squirrels emerged. Squirrels that emerged early congregated on objects that protruded above the snow. Animals continued to emerge through mid June.

The time of squirrel emergence at the field station was intermediate to the other populations. The first squirrel appeared March 26 when the snow depth was about 1 m. New animals emerged through mid May.

Squirrels at all three populations began reproductive activities soon after they emerged. Juveniles first appeared above ground 56, 60, and 56 days after initial spring emergence of the adults in the valley, field station, and subalpine populations respectively.

The adult and yearling squirrels were active above ground for similar durations at the lower and upper elevations in 1968 while the intermediate population was active 25 percent longer (Figure 8). The juveniles also appeared to be above ground longer at the field station. The last squirrel was recorded on July 19 in the valley, August 23 at the field station, and September 7 at the subalpine area. A few squirrels may have remained active longer at the field station.

In 1968, body weights of adult/yearling squirrels were comparable at all three populations. However, the pattern of seasonal weight gains was shifted back in time with increasing altitude (Figure 9). This temporal shift coincided with a later growing season at high elevations. The longer active season at the field station did not result in heavier body weights. In 1968 as in 1965-1967, the weights of squirrels at the station tended to level off the last 30-50 days that the squirrels were active above ground.

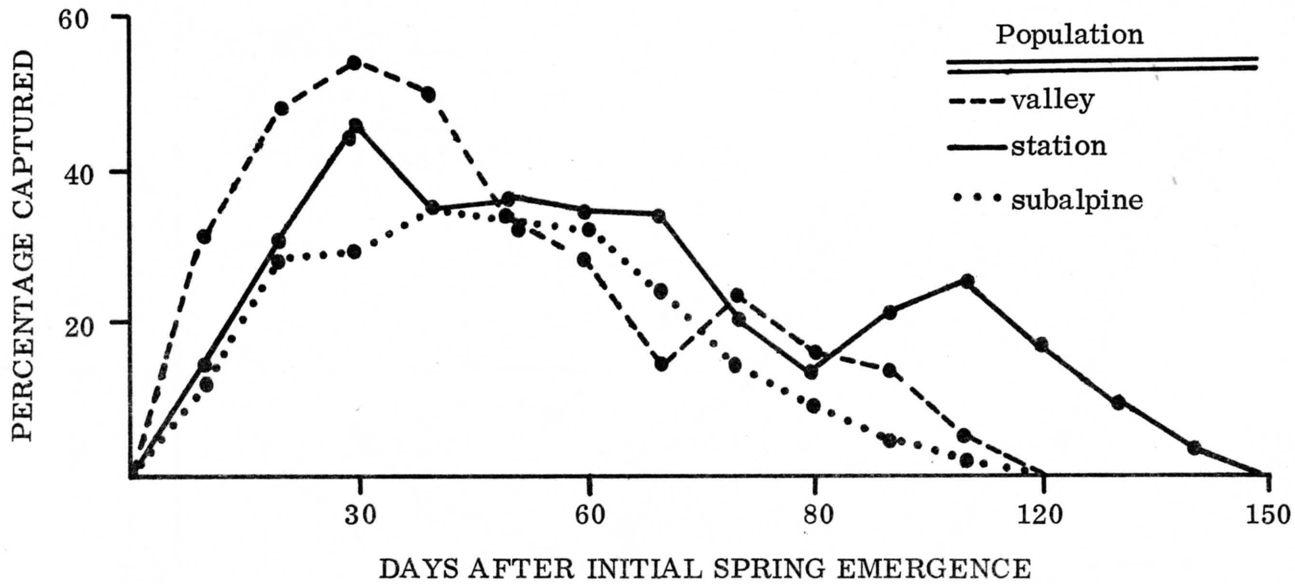
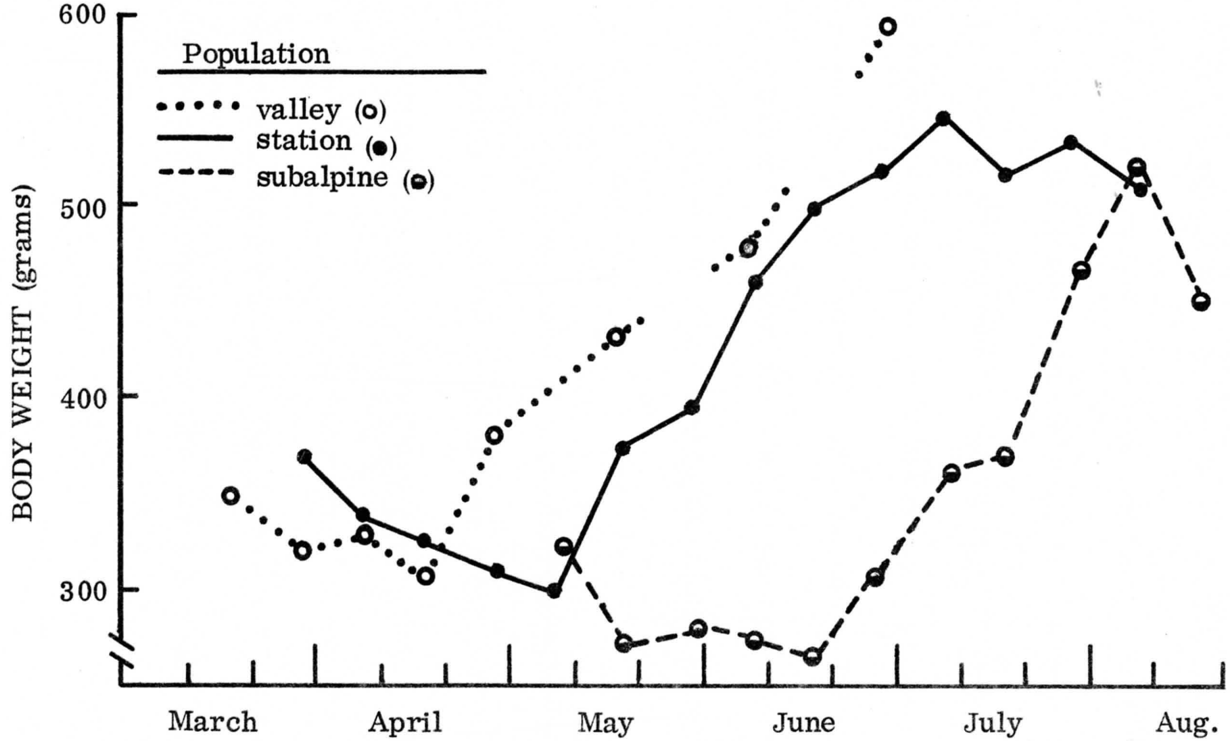


Figure 8. Percentage of adult and yearling ground squirrels captured each 10-day interval indicating relative duration of seasonal activity at three altitudes in 1969. Plotted values represent 3-point running averages.



No. in sample																	
valley	-	5	6	3	5	6	-	3	-	2	-	2	-	-	-	-	-
station	-	-	6	11	14	19	2	13	13	2	1	9	6	6	5	1	-
subalpine	-	-	-	-	-	-	19	12	9	11	13	12	12	8	5	3	1

Figure 9. Seasonal trends in mean weights of adult and yearling male ground squirrels in populations at three altitudes in 1969.

Emergence from hibernation in 1969

In 1969, the three populations were observed and trapped through the period of emergence from hibernation. Initial emergence occurred March 21 in the valley, March 31 at the field station, and April 28 in the subalpine population. Snow depths at initial emergence in 1969 resembled conditions in 1968 except at the lower altitude. The valley area, which was free of snow in 1968, was covered by 0.5 m of snow in 1969.

The sex and age sequence of emergence observed 1966-1967 at the field station was not evident in the valley population in 1969 (Table 6). All sex and age groups emerged simultaneously. The field station and subalpine populations, however, had similar emergence patterns in 1969. Adult males emerged first followed by the adult females. Yearling squirrels emerged last.

The emergence weights of ground squirrels varied between altitudes (Table 7). For each sex and age group, valley squirrels were heavier than their counterparts at higher elevations. The heavier weights were probably caused by the highly productive, irrigated croplands exploited by the valley population. Emergence weights of squirrels at the field station and subalpine populations were similar.

Table 6. Mean number of days after initial spring emergence that ground squirrels emerged from hibernation at three altitudes in 1969

Population =	Relative Day of Emergence					
	Valley		Intermediate		Subalpine	
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD
Adult Males	8	17 ± 7.3	7	11 ± 4.6	12	9 ± 6.3
Adult Females	8	22 ± 6.5	27	17 ± 5.3	17	14 ± 6.2
Yearling Females	8	19 ± 7.5	22	22 ± 9.2	3	19 ± 6.7
Yearling Males	14	19 ± 8.2	27	25 ± 8.8	10	17 ± 8.6

Table 7. Emergence weights of ground squirrels at three altitudes in 1969

Population =	Emergence Weights (grams)					
	Valley		Intermediate		Subalpine	
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD
Adult Males	8	358 ± 37.3	7	300 ± 35.4	12	310 ± 40.6
Adult Females	8	355 ± 43.1	27	274 ± 40.8	17	288 ± 43.0
Yearling Males	14	294 ± 46.6	27	252 ± 37.7	10	218 ± 38.0
Yearling Females	8	274 ± 55.1	22	221 ± 31.9	3	231 ± 37.6

DISCUSSION

The Annual Cycle

Reproductive activities of Uinta ground squirrels commence shortly after spring emergence. Adult males emerge first and breed females as the females emerge. Soon after conception, females become intolerant of conspecifics and defend nesting areas near the hibernation burrows. In years when the sequential emergence is pronounced, adult females emerge, breed, become aggressive, and establish territories before most yearling females emerge. Upon emergence the yearling females are then forced into marginal habitats. In years when squirrels of all sex and age groups emerge more synchronously, adult and yearling females emerge, conceive, and become intolerant simultaneously and have an equal opportunity of establishing in preferred nesting areas. As a result, defended nesting areas are smaller and the density of reproductive females much higher in preferred nesting areas than when emergence is asynchronous. Thus, the sex and age sequence of arousal from hibernation is one of the mechanisms through which behavior operates to regulate nesting dispersion in the station squirrel population (Walker 1968).

The longer the breeding season the greater was post-emergence weight loss of adult males. In 1967, adult males probably emerged near the time they aroused. These males bred adult and yearling females as the females emerged over the following 30-40 days. The adult males lost body weight during that period. In 1965, adult males aroused but failed to emerge until after most females had also aroused. Adult males and all females emerged synchronously and most breeding activity was completed within two weeks. Because of the synchronous emergence and short breeding season, adult males began to gain weight soon after emergence in 1965. Delayed emergence in 1965 had virtually no effect upon the time that adult males commenced metabolic preparation for the subsequent estivation-hibernation period. Mean body weights of adult males were lowest about May 1 each year.

Post-emergence weight losses of adult males appeared the result of increased activity during breeding. Adult males ranged over much larger areas during breeding than later in the season (Burns 1968). The leveling off of mean female weights appeared the result of an initial loss at parturition and increased energy demands during lactation.

Most yearling males did not develop scrotal testes or exhibit sexual behavior in 1965 or 1966. Mean body weights of yearling males increased slightly during breeding those years. In 1967, however, about 50 percent of the yearling males had scrotal testes (Walker 1968) and mean weights decreased during breeding.

Most adult and yearling ground squirrels attained maximum seasonal body weight during July each year. Although some squirrels at the field station immerged soon after attaining a peak weight, many remained above ground for up to 30 additional days. Occassional squirrels lost substantial body weight before immergence. Thus, the attainment of maximum body weight did not appear to be a stimulus for immergence, just as some laboratory studies have shown (Pengelley 1968).

At the field station, the time that a ground squirrel immerges may be related to survival of estivation-hibernation in two ways. Firstly, immergence late in the summer allows animals more time to gain weight and thus guarantee sufficient fat reserves to last 8-9 months of torpor. Secondly, late immergence may increase the probability that a squirrel will be detected by badgers (Taxidea taxus). Badger predation was the major mortality factor on the field station population during the inactive season (Slade 1972). This predation was most intense September-November each year. Squirrels that were active later each season may have been more susceptible to predation. The more recent activities would give their burrow entrances the appearance of heavier use than burrows of squirrels that had been in torpor 2-4 weeks. Whereas squirrels that immerge early have less metabolic reserve to withstand prolonged torpor, those immerging later probably receive the brunt of the badger predation.

Selective pressure on squirrels immerging late was not evident in the other two populations. Badger predation occurred in late June and early July as juveniles were first emerging above ground in the subalpine population (Knopf and Balph 1969) and not until late winter in the valley (unpublished observations).

Many species of ground squirrels are distributed across altitudinal clines in the western United States. Population activities such as spring emergence from hibernation and appearance of young above ground tend to occur later in the year at higher elevations (McKeever 1964; Manville 1959; Mullaly 1953; Moore 1937; Shaw 1921). However, lack of information about immergence times of those populations has fostered the belief that duration of seasonal activity is shorter at alpine elevations. My data indicate that length of the active season is independent of altitude for Uinta ground squirrels.

The longer season of activity at the field station in 1968 appeared atypical for that altitude. Ground squirrels on the periphery of the study area were active above ground for much shorter periods. The cultivated lawn at the field station was a preferred habitat of the squirrels (Walker 1968) and supported high ground squirrel densities. I have no indication how these densities or the human activity on the area may have affected the duration of activity above ground. Apparently, such a disturbed lawn area is the only habitat that another estivator, the thirteen-lined ground squirrel (S. tridecemlineatus), occupies in the arid, extreme southern portions of its geographic range (McCarley 1966).

Evidences of Endogenous Periodicity

Possible manifestations of an endogenous timing mechanism were observable at two points in the annual cycle of Uinta ground squirrels, arousal from hibernation and the initiation of male body weight gains. At the field station, arousal occurred about mid March and the start of weight increase about May 1 every year.

Many species that hibernate exhibit an overlapping sex and age sequence in appearing above ground in the spring (Iverson and Turner 1972; Yeaton 1972; McKeever 1964; Snyder and Christian 1960; Manville 1959; Alcorn 1940; Wade 1927; Shaw 1925). Only twice has field data been obtained that indicate the sequence occurs in arousal from torpor. Esmagelov (1955) found that adult male sand gophers (S. maximus) on Barc-Kelmes Island arouse first each spring, followed by the adult females, yearling females and, late in the spring, yearling males. Further, he emphasized the role of spring weather in regulating the emergence times of the adult animals. In describing a similar sequence of emergence in the Uinta ground squirrel at the field station, Walker (1968) compared the weights of squirrels at emergence in early and late springs to show that arousal of each sex and age group likely occurred about the same date annually. This is consistent with observations in the laboratory that arousal is the most accurately dated event in the annual cycle of golden-mantled ground squirrels (S. lateralis. Heller and Poulson 1970).

The valley and subalpine populations also appeared to arouse about the same time each year. Within a given year however, squirrels at high elevations aroused later than those at low elevations. Squirrels in the valley aroused in early March each year. Squirrels at the subalpine area aroused in late April--as reflected by a sex and age sequence of emergence at that population. Since the populations were not considered genetically isolated, this temporal shift was interpreted as evidence that endogenous timing mechanisms of the species are entrained to the environmental conditions encountered at the respective altitudes.

Male squirrels at the field station began to gain body weight about May 1 each year. Initiation of gains occurred approximately four weeks after arousal from hibernation, but independent of the time of emergence above ground. Recent studies of woodchucks in environmental chambers also reported synchronized initiation of annual body weight gains (Davis 1970). However, the synchronization was for both males and females and was independent of the time that they aroused from torpor. I believe the yearly synchrony in male Uinta ground squirrels has no direct relationship to an endogenous rhythm. Rather, the synchrony only reflects the completion of breeding activities.

The Role of Exogenous Factors

Numerous investigators have speculated that increasing ambient temperatures, melting snow, or thawing of the soil may trigger spring emergence in ground squirrels (McKeever 1964; Mullally 1953; Wade 1950; Shaw 1925). The alleged emergence clue differs in widely-distributed species. The thirteen-lined ground squirrel, for example, ranges from central Alberta to Arizona and southeastern Texas (see Folk 1963). Wade (1950) related emergence of the species to thawing of the soil in Nebraska. However, this clue is not present at emergence in Texas (McCarley 1966). McCarley (1966) found no association between ambient temperature and the time of emergence of the species in Texas. In general, spring weather conditions are highly variable within the range of the species.

Neither the identity nor manner of influence of the exogenous clues regulating time of emergence of Uinta ground squirrels is obvious. Walker (1968) felt that time of emergence at the field station is influenced by the general climatic conditions in the spring. However, the very different environmental conditions (as indexed by snow depths) encountered at emergence at different altitudes indicate that Uinta ground squirrels may use different environmental clues at each area.

In addition to climatic factors, behavior associated with competition may influence the date that some squirrels arouse (Slade 1972). Male Uinta ground squirrels that are born into a low-density population may arouse and emerge simultaneously with adult males the subsequent year. They also behave sexually like adult males. Such early arousal of yearlings probably reflects reduced social harassment of the males during their juvenile season.

At the field station, the chronology and duration of squirrel activity above ground varied significantly between years. The seasons of 1965 and 1967 were of similar length although the former began three weeks later in the spring. The season of 1966 commenced intermediate to 1965 and 1967 but terminated earliest and was shortest. Such variation in the timing of seasonal activities indicated that environmental conditions influenced the chronology of not only emergence but also immergence of the population.

Many studies have investigated the roles of various environmental parameters on the time that an animal begins torpor. Pengelley (1967, p. 25) summarized that "Environmental temperature, photoperiod, food, water and access to a means of locomotor activity have all been shown to have an influence on the time sequence of hibernation . . ." Hudson and Bartholomew (1964) and Shaw (1925) emphasized the role of dessication of the vegetation and thereby restriction of the food supply as the ultimate factor influencing immergence of estivators in the wild.

Uinta ground squirrels at higher elevations did tend to disappear as the vegetation dried each season. Squirrels in the valley, however, resided along the periphery of irrigated croplands--a food source that remained succulent long after immergence. Further, squirrels in the valley experienced high midday temperatures from late May until they immerged. High ambient temperatures cannot be tolerated by the squirrels. Animals left exposed to the sun in traps died within 10-15 minutes. These observations, coupled with the many incidences of squirrels becoming torpid when accidently left in a trap overnight, indicate that immergence may be a generalized response to stressful situations.

Interaction of Endogenous and Exogenous Controls

Temporal organization of the seasonal activities of Uinta ground squirrels best follows the interpretations of annual rhythmicity proposed by Heller and Poulson (1970) in studies of other ground squirrels and chipmunks (Eutamias spp.). Environmental stimuli appear to act constantly either to shorten or lengthen a particular phase (reproduction, hibernation, etc.) of the cycle and thereby synchronize activities with periodic phenomena in the environment. These exogenous phasers make adjustments in the annual cycle but have no influence on the underlying rhythm.

The chronology of Uinta ground squirrel activities appears the result of such an interaction between endogenous timing mechanisms and immediate environmental conditions. Selective pressures seem to have favored preparation for general seasonal conditions, while maintaining the flexibility to synchronize precisely the activities of the animal with intraseasonal changes in the environment.

Initiation of the underlying annual rhythm probably occurs in the late spring or early summer when a hibernator is homeothermic (Hoffman 1964a, b). Heller and Poulson (1970) consider resetting of the annual rhythm to occur earlier in the spring, at the onset of breeding condition. Among Uinta ground squirrels, however, more than 90 percent of the adult males emerged in breeding condition annually (Walker 1968). Even in 1967 when emergence approximated arousal date, most males had scrotal testes at emergence. Thus, initiation of the breeding condition appeared to commence prior to arousal.

The annual periods of golden-mantled ground squirrels tend to be less than one year (Pengelley and Fisher 1961; Pengelley and Kelly 1966; Heller and Poulson 1970; Blake 1972). A rhythm of approximately 11 months may provide a margin of safety which enables animals to compensate for abnormally early seasons and thereby synchronize the annual cycle with fluctuating environments (Blake 1972). Such a margin of safety in the annual cycle of Uinta ground squirrels occurs at emergence from hibernation. However, in the Uinta ground squirrel, the exception seems to be the abnormally late season rather than the abnormally early season. Emergence of the early-arousing sex and age groups may be delayed 4-6 weeks after arousal in seasons of late springs without apparant detrimental effects upon the chronology of subsequent phases in the annual cycle. The selective advantage of early arousal/emergence for the adult squirrels is that in early springs, they (the proven breeders) have the opportunity to become established in preferred nesting habitats prior to emergence of the yearling animals (Walker 1968). A margin of safety at emergence guarantees that these proven breeders have the metabolic reserves to compensate for late springs and thus remain in the breeding population.

LITERATURE CITED

Alcorn, J.R. 1940. Life history notes on the Piute ground squirrel. J. Mammal. 40:160-170.

Aschoff, J. 1963. The ecological significance of circadian rhymicity. Proc. XVI Internat. Congr. Zool. 4:341-345.

Aschoff, J. (Ed.). 1965. Circadian Clocks. North-Holland Publishing Co., Amsterdam. 479 p.

Balph, D. F. and A. W. Stokes. 1963. On the ethology of a population of Uinta ground squirrels. Am. Midland Natural. 69:106-126.

Bartholomew, G. A. and J. W. Hudson. 1960. Aestivation in the Mohave ground squirrel, _Citellus mohavensis_. Bull. Mus. Comp. Zool. Harvard. 124:193-208.

Blake, B. H. 1972. The annual cycle and fat storage in two populations of golden-mantled ground squirrels. J. Mammal. 53:157-167.

Bruce, V. G. 1960. Environmental entrainment of circadian rhythms. Cold Spring Harbor Symp. Quant. Biol. 25:29-48.

Burns, R. J. 1968. The role of agonistic behavior in regulation of density in Uinta ground squirrels (_Citellus armatus_). Unpublished MS thesis. Utah State Univ., Logan, Utah. 57 p.

Davis, D. E. 1967. The annual rhythm of fat deposition in woodchucks (_Marmota monax_). Physiol. Zool. 40:391-402.

Davis, D. E. 1970. Failure of schedule of torpor to alter annual rhythm of appetite of woodchucks (_Marmota monax_). Mammalia 34:542-544.

Enright, J. T. 1970. Ecological aspects of endogenous rhythmicities, pp. 221-238. _In_ R. F. Johnston (Ed.). Annual review of ecology and systematics, Vol. I. George Banta Co., Inc., Palo Alto, California.

Esmagelov, M. E. 1955. About the hibernation of sand gophers (Citellus maximus Pall.) on the island Barc-Kelmes. Zool. Zhur. 34:454-459. (In Russian)

Folk, G. E., Jr. 1963. Hibernation and reproduction of animals, pp. 703-714. In S. W. Tromp (Ed.). Medical biometeorology (Weather, climate and the living organism). Elsevier Co., Amsterdam.

Heller, H. C. and T. L. Poulson. 1970. Circannian rhythms II. Endogenous and exogenous factors controlling reproduction and hibernation in chipmunks (Eutamias) and ground squirrels (Spermophilus). Comp. Biochem. Physiol. 33:357-383.

Hoffman, R. A. 1964a. Speculations on the regulation of hibernation. Ann. Acad. Scientiarum Fennicae, Ser. A, IV. 71:199-216.

Hoffman, R. A. 1964b. Terrestrial animals in cold: hibernators, pp. 379-403. In D. B. Dill (Ed.). Handbook of Physiology sec. 4: Adaptation to the environment. Amer. Physiol. Soc., Washington, D. C.

Hudson, J. W. and G. A. Bartholomew. 1964. Terrestrial animals in dry heat: estivators, pp. 541-550. In D. B. Dill (Ed.). Handbook of physiology sec. 4: Adaptation to the environment. Amer. Physiol. Soc., Washington, D. C.

Iverson, S. L. and B. N. Turner. 1972. Natural history of a Manitoba population of Franklin's ground squirrel. Canad. Field Natural. 86:145-149.

Kavanau, J. L. 1967. Behavior of captive white-footed mice. Science 155(3770):1623-1639.

Knopf, F. L. and D. F. Balph. 1969. Badgers plug burrows to confine prey. J. Mammal. 50:635-636.

Manville, R. H. 1959. The Columbian ground squirrel in northwestern Montana. J. Mammal. 40:26-45.

McCarley, H. 1966. Annual cycle, population dynamics and adaptive behavior of Citellus tridecemlineatus. J. Mammal. 47:294-316.

McKeever, S. 1964. The biology of the golden-mantled ground squirrel. Ecolog. Monogr. 34:383-401.

Moore, A. W. 1937. Some effects of altitude and latitude on the Columbian ground squirrel. J. Mammal. 18:368-369.

Mullally, D. P. 1953. Hibernation in the golden-mantled ground squirrel, Citellus lateralis bernardinus. J. Mammal. 34:65-73.

Pengelley, E. T. 1967. The relation of external conditions to the onset and termination of hibernation and estivation, pp. 1-29. In K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schonbaum, and F. E. South (Eds.). Mammalian Hibernation, Vol. III. Oliver and Boyd, London.

Pengelley, E. T. 1968. Interrelationships of circannian rhythms in the ground squirrel, Citellus lateralis. Comp. Biochem. Physiol. 24:915-919.

Pengelley, E. T. and K. C. Fisher. 1961. Rhythmical arousal from hibernation in the golden-mantled ground squirrel, Citellus lateralis tescorum. Canad. J. Zool. 39:105-120.

Pengelley, E. T. and K. H. Kelley. 1966. A "circannian" rhythm in hibernating species of the genus Citellus with observations on their physiological evolution. Comp. Biochem. Physiol. 19:603-617.

Shaw, W. T. 1921. Moisture and altitude as factors determining the seasonal activities of the Townsend ground squirrel in Washington. Ecology 2:189-192.

Shaw, W. T. 1925. The duration of estivation and hibernation of the Columbian ground squirrel (Citellus columbianus) and sex relation to the same. Ecology 6:75-81.

Slade, N. A. 1972. Population ecology of Uinta ground squirrels. Unpublished PhD Dissertation. Utah State Univ., Logan, Utah. 50 p.

Snyder, R. L. and J. J. Christian. 1960. Reproductive cycle and litter size of the woodchuck. Ecology 41:647-656.

Sollberger, A. 1965. Biological rhythm research. Elsevier Publishing Co., Amsterdam. 461 p.

Squires, V. R. 1971. Temporal patterns of activity in a small flock of merino sheep as determined by an automatic recording technique. Anim. Behav. 19:657-660.

Wade, O. 1927. Breeding habits and early life of the thirteen-striped ground squirrels, Citellus tridecemlineatus (Mitchell). J. Mammal. 8:269-276.

Wade, O. 1950. Soil temperatures, weather conditions, and emergence of ground squirrels from hibernation. J. Mammal. 31:158-161.

Walker, R. E. 1968. Local distribution in a population of Uinta ground squirrels. Unpublished PhD Dissertation. Utah State Univ., Logan, Utah. 71 p.

Yeaton, R. I. 1972. Social behavior and social organization in Richardson's ground squirrel (Spermophilus richardsonii) in Saskatchewan. J. Mammal. 53:139-147.

VITA

Fred L. Knopf

Candidate for the Degree of

Master of Science

Thesis: Annual Periodicity in a Free-Living Hibernator, the Unita Ground Squirrel

Major Field: Ecology

Biographical Information:

Personal Data: Born at Aurora, Ohio, 6 June 1945, son of Fred M. and Mary E. Knopf; married Suzanne E. Field 1 September 1968; one child--Jennylene Elizabeth.

Education: Attended elementary school in Aurora, Ohio; graduated from Aurora High School in 1963; received the Bachelor of Arts degree from Hiram College (Ohio), with a major in biology and minor in general science in 1967; completed requirements for the Master of Science degree in ecology at Utah State University in 1973.

Professional Experience: 1967-1968, 1971, research assistant, Department of Wildlife Science, Utah State University; 1969-1970, biological research assistant, United States Army Research Institute of Environmental Medicine, Natick, Massachusetts.