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Title: DYNAMICS OF A POPULATION OF BELDING'S GROUND SQUIRRELS IN OREGON

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Density, natality, survival, sex ratios, and dispersion in relation to vegetative types, were evaluated from 1802 Belding's ground squirrels, (*Spermophilus beldingi*), captured 6907 times and 902 ground squirrels collected by shooting. Density appeared to fluctuate seasonally in a similar pattern on the Harris, Big Flat, and Kurtz Study Areas. On the Harris Study Area, density during April-August ranged from 37.4 per ha on 27 April to 14.1 per ha on 29 August in 1975 and from 25.1 per ha on 13 July to 7.8 per ha on 21 August in 1976. Density on the Harris Study Area declined significantly ($P < 0.05$) by 42.2 percent between 26 May 1975 and 26 May 1976. Examination of pregnant and lactating females revealed that reproductive seasons extended from April through June.

Seasonal changes in the proportions of lactating females and yearly changes in the weights of juveniles suggested that breeding occurred 1-2 weeks earlier in 1976 than 1975. Warmer temperatures during the reproductive season in 1976 apparently advanced the onset of reproduction. Ages were determined for squirrels necropsied for reproductive evaluation by examination of the periosteum of the mandibles for adhesion lines. Ages were correctly determined for 47 of 49 "known-age" squirrels by this technique. Age-specific litter sizes were computed from numbers of viable embryos and numbers of implantation sites. Mean litter sizes were 4.4-6.4 for yearlings, 5.5-7.1 for 2-year olds, and 3.7-10.3 for 3-year old ground squirrels. Two-and 3-year old squirrels had consistently larger litters than 1-year olds. Natality was believed to increase following reductions in density through use to toxic baits. Numbers of young produced on the Harris Study Area declined from 962.8 in 1975 to 657.6 in 1976 as the result of fewer breeding females and smaller litters. Survival of adult and juvenile squirrels on the Harris Study Area from 26 May 1975 to 26 May 1976 was 30.2 percent and 6.6 percent, respectively. Poor survival of juveniles was thought to be responsible for lower densities of squirrels in 1976 and for significant changes ($\underline{P} < 0.05$) in age distributions between years. Greater proportions of 2- and 3-year old squirrels were present in 1976. Inclement weather during the reproductive season was

believed to cause low juvenile survival. Sex ratios of adults in April-June were significantly in favor of females ($\underline{P} < 0.05$) in contrast with those of juveniles which deviated less from the expected 1:1 ratio. Differential survival between juvenile males and females was thought to result in adult sex ratios that were skewed in favor of females. The average sex ratio of adults on the Harris Study Area changed significantly between years from 4.3:1 (females per male) in 1975 to 2.3:1 in 1976 ($\underline{P} < 0.05$). Greater proportions of males in 1976 were believed to result from increased survival of juvenile males during dispersal from natal burrows in 1975. Dormancy changed apparent densities, sex compositions and age structures. Oldest squirrels entered dormancy first followed by yearlings and juveniles, females preceded males. Dispersion patterns of females on the Harris Study Area were more uniform than those of males in 1975. These differences were thought to be a function of the social structure and density of the population. Males appeared to be excluded from certain habitats. Decline in density between years resulted in more uniform dispersion patterns in 1976. Distributions of squirrels on the Kurtz Study Area indicated preference for certain vegetative types and the exclusion of adult males from preferred habitat.

Dynamics of a Population of Belding's Ground Squirrels in Oregon

by

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INTRODUCTION

Belding's ground squirrels (*Spermophilus beldingi*) occur throughout Oregon east of the Cascade Mountains, except for the Columbian Basin Province, and in California, Nevada, Utah and Idaho (Hall and Kelson 1959, Bailey 1936, Turner 1972*a*). Three subspecies are currently recognized of which two, *S. b. oregonus* (formerly *S. oregonus*) and *S. b. creber*, are found in Oregon (Hall and Kelson 1959). The latter form is restricted to the extreme southeastern portion of the state (Hall and Kelson 1959).

In Oregon, Belding's ground squirrels occur at elevations of 548.6 m to 2895.6 m (1800-9500ft.) in Upper Sonoran to Hudsonian life zones but are most abundant and widespread in the Transition zone (Bailey 1936, Turner 1972*a*). Soil texture, vegetation, water and competition with other ground squirrels further restrict their distribution within the state (Turner 1972*a, b*).

Belding's ground squirrels hibernate 7-8 months each year (Bailey 1936, Grinnell and Dixon 1919, White 1972, Turner 1972*a*). Soon after they emerge from their hibernacula (January to April depending upon the elevation) Belding's ground squirrels attain breeding condition and mate (Bailey 1936, McKeever 1964). Litters of 1 to 17 young are born after a gestation period of 24-31 days (Bailey 1936, Grinnell and Dixon 1919, Howell 1938, Turner 1972 a, Sauer 1976). A single litter is produced each year (Bailey 1936, McKeever 1964, Turner 1972a). Development of young is rapid (Morton and Tung 1971, Turner 1972a). Both adults and young spend long periods of time feeding to acquire fat stores needed to survive the long dormant period (Turner 1972a, Morton 1975a). Although Belding's ground squirrels are opportunistic feeders on bulbs, roots, flowers and insects, succulent vegetation is their most abundant food source with seeds becoming increasingly important as plants mature late in the season (Bailey 1936, Turner 1972a, Morton 1975a). Dormancy occurs shortly after maximum body weight is attained (Morton et al. 1974, Morton 1975a). Belding's ground squirrels do not store food for use in winter months (Bailey 1936, Grinnell and Dixon 1919, Turner 1972a, Morton et al. 1974).

Estimates of density of populations of Belding's ground squirrels range from 32.1 to 303.7 ground squirrels per hectare (Turner 1972a, Sauer 1976). Highest densities are reported for agricultural lands, specifically alfalfa (*Medicago sativa*) fields (Turner 1972a, Sauer 1976).

Crop depredations by Belding's ground squirrels represent serious economic losses for farmers in areas where these squirrels are abundant (Bailey 1936, White 1972, Sauer 1976). In addition to consuming large quantities of forage, these ground squirrels construct burrows and mounds that damage croplands and harvesting equipment (Sauer 1976). Poisoned baits are used to reduce ground squirrel populations to diminish damages caused by these rodents (Saucer 1976, Sullins 1976).

Little quantitatively based information is available on the population biology of Belding's ground squirrels. Data are needed on density, natality, dispersal, mortality, dispersion and other population attributes to understand mechanisms by which this species maintains itself and exploits its environment .

OBJECTIVES OF THE RESEARCH

The major objective of the research was to determine demographic parameters of populations of Belding's ground squirrels over a 2-year period. The specific objectives of the study were:

1. To determine age-specific natality and age-specific mortality for populations of Belding's ground squirrels.
2. To determine seasonal and annual changes in the densities of Belding's ground squirrel populations over a 2-year period.
3. To determine changes in sex ratios and age distributions for populations of Belding's ground squirrels.
4. To determine dispersion characteristics for populations of Belding's ground squirrels.

STUDY AREAS

Two study areas were established in extreme southwestern Grant County, Oregon in 1975. A 6.9-ha study area (hereafter referred to as the Harris Study Area) was established on land administered by Oregon State University, approximately 63.4 km southwest of John Day, Oregon (R. 26E., T. 18S., Sect. 14). The second study area (designated the Big Flat Study Area) was a 9.9-ha site established on privately owned land approximately 10 km east of the Harris Study Area (R. 26E., T. 18S., Sect. 17). Field studies at the Big Flat Study Area were discontinued after 1975 because of a change in the agricultural use of the land. To replace the Big Flat Study Area, a 5.1-ha site (referred to as the Kurtz Study Area) was established in 1976 approximately 4 km southwest of the Harris Study Area on land administered by Oregon State University (R. 26E., T. 18S., Sect. 15).

The Harris Study Area was situated in a moist meadow; the natural habitat reportedly preferred by Belding's ground squirrels (Durrant and Hanson 1954). Vegetative species commonly found included Kentucky bluegrass (*Poa pratensis*), five-finger (*Potentilla gracilis*), meadow yarrow (*Achillea millefolium*), and big sagebrush (*Artemisia tridentata*). Succulent vegetation was present on the area throughout summer months. Soils ranged from deep, poorly drained silt loam to shallow shaly loam with a slope of generally less than 2 percent (W. F. Farrell, personal communication, Grant County Extension Service, 1976).

The Kurtz Study Area was located on an arid hillside. Plants tended to be clumped with intervening areas of bare soil. Prior to the study, native vegetation was removed from 48.1 percent of the study area and alfalfa established in its place. Other vegetative species commonly found on the area were: California brome (*Bromus carinatus*), cheatgrass (*Bromus tectorum*), fiddleneck (*Amsinckia intermedia*), and big sagebrush. Soils ranged from deep, well-drained loam to shallow loam and shale outcrops on a slope of 2-8 percent (W. F. Farrell, personal communication, Grant County Extension Service, 1976).

The Big Flat and Harris Study Areas appeared similar in vegetative composition. However, agricultural use of the Big Flat Study Area in 1976 prevented a survey of plant species there. No data on soil types were available for the Big Flat Study Area.

METHODS AND MATERIALS

Populations of Belding's ground squirrels were sampled by livetrapping using Tomahawk livetraps (12.7 x 12.7 x 40.6 cm and 15.2 x 15.2 x 48.3 cm) baited with oat groats. On the Harris Study Area traps were spaced at 25-m intervals in 11 rows of 12 traps each to form a rectangular grid encompassing 8.2 ha that included a 12.5-m border from which it was assumed squirrels would be captured. A similar trapping grid was established on the Big Flat Study Area with the exception that 30-m intervals between traps were used. The total area of this grid, including a 15-m border, was 11.9 ha. Traps were arranged in a square grid of 10 rows of 10 traps each with 25-m intervals between trap stations on the Kurtz Study Area. The enclosed area was 6.2 ha which included a 12.5-m border.

Livetrapping was conducted April to August in 1975 and 1976 on the Harris Study Area, May to September 1975 on the Big Flat Study Area (alternating with trapping periods on the Harris Study Area) and May to August 1976 on the Kurtz Study Area (during the same trapping periods and on the same days as trapping on the Harris Study Area). Traps were operated on alternate weeks for approximately 5-day periods on each study area. Because livetrapping could not be conducted during inclement weather longer trapping periods were sometimes necessary. Alternate traps were set on alternate days on each trapping grid.

Ground squirrels captured on the Harris and Big Flat Study Areas were marked individually by tattooing a 3-digit number on the inside of both hind legs. Toes were removed to identify ground squirrels livetrapped on the Kurtz Study Area similar to the procedure used by Layne (1954). Sex, age, and point of capture were recorded for each individual. Ground squirrels were classified as adults or juveniles on the basis of weight, size, and pelage characteristics (Turner 1972a). Because I believed that most adults on the Harris Study Area were marked in 1975 and that few squirrels of this age class immigrated between years, unmarked adults livetrapped in 1976 were considered to be yearlings. Females were recorded as lactating if milk could be expressed from their mammae. All ground squirrels were released at their respective points of capture.

Chi-square, Z-distribution, and Student's *t* tests were used in this report. In all statistical analyses the 5 percent confidence limits were accepted as indicating significance.

Estimation of Density

Numbers of ground squirrels on each study area were estimated using the Lincoln Index (Lincoln 1930). Estimates were converted to numbers of squirrels per hectare and 95 percent confidence intervals were calculated.

Age-Specific Reproduction

Collections of adult female Belding's ground squirrels were made April-June 1975 and April-May 1976 on areas near the Harris Study Area that supported similar vegetation. Squirrels were collected where populations were not subject to control. Additional samples of adult female squirrels were obtained at the Izee ground squirrel shoot, an annual event held on Memorial Day near Izee, Oregon. These ground squirrels were collected from areas where an intensive program to reduce ground squirrel populations by use of toxic baits was initiated in 1975 and continued in 1976.

The uterus of each squirrel was excised and examined for implantation sites and developing embryos. Viable and resorbing embryos were recorded separately. Mandibles were removed and returned to Oregon State University where they were decalcified for 12 hours in a solution of 5 percent nitric acid and rinsed 12 hours in a continuous flow of water. A segment of each mandible, anterior to the molar row, was removed and cross-sectioned at 20-25 micra with a freeze microtome. Several sections were mounted on slides with albumen, stained with Papanicoloau (Harris) haematoxylin and examined under a microscope for adhesion lines (annulli) in the periosteum of the bone (Klevezal and Kleinenberg 1967).

To test if the number of adhesion lines in the periosteum was related to age in adult Belding's ground squirrels, mandibles were obtained from 49 marked squirrels on the Big Flat Study Area in 1976. Because these squirrels were marked during the 1975 trapping season their ages were known to be 1 year (marked as juveniles in 1975) or 2 years old and older (marked as adults in 1975). To determine if adhesion lines were present in juvenile squirrels, mandibles of 23 squirrels collected near the Harris Study Area and judged to be juveniles by weight and size criteria, were examined by use of the same techniques.

Estimation of Total Numbers of Offspring

Numbers of offspring were estimated for the population of ground squirrels on the Harris Study Area in 1975 and 1976. The number of adult females assumed to produce young was estimated by the formula:

$$P_t = \frac{N_t S_t}{A_t}$$

where

t = Trapping period for which estimate is desired.

P_t = Estimated number of ground squirrels of the designated sex or age class present at time t.

N_t = Estimated ground squirrel density at time t.

S_t = Number of ground squirrels of the designated sex or age group captured at time t.

A_t = Total number of squirrels captured at time t.

Time t was considered the trapping period when the proportion of lactating females was greatest. Numbers of adult females in age classes 1, 2, and 3 years were determined by multiplying the value for P_t by the proportion of females in each age category of those collected near the Harris Study Area in 1975 and 1976. Numbers of offspring were determined by summing the products of the numbers of females times the mean number of viable embryos for the respective age classes.

Survival

Annual survival rates of adult squirrels on the Harris Study Area were calculated according to the formula:

$$S = \frac{D_1}{D_2} \times 100$$

where

S = Estimated annual survival rate for squirrels of an adult sex or age class.

D_1 = Number of squirrels of an adult sex or age class alive on 26 May 1976 computed by the formula for P_t.

D_2 = Number of adult squirrels alive on 26 May 1975 computed by the formula for P_t.

Survival rates of juveniles were calculated by the same formula substituting (B) (R) for D_2 where

B = Estimated number of births for 1975.

R = Proportion of males or females; assumed to equal 0.50 for each sex.

Vegetative Survey

Major vegetative types were plotted on maps of each study area. Sampling units, each consisting of a 30.5-m (100-ft.) measuring tape strung horizontal to the vegetation and anchored at both ends with steel rods, were established in each vegetative type. Starting points and directions for each unit were obtained through use of a table of random numbers and based on trap locations within the grids. Using the point intercept method of sampling vegetation (Subcommittee on Range Research Methods 1962) a chaining pin was lowered at each 0.30-m (1-ft.) interval along the tape and the first plant species encountered was recorded. If no vegetation was present a ground surface hit (GSH) was tallied. A single hit was recorded for each drop of the pin unless shrubs were encountered in which case two hits were recorded, one for the shrub and one for the underlying vegetation or GSH. Twenty-three and 14 sampling stations were established on the Harris and Kurtz Study Areas, respectively. Distribution of sampling stations was approximately proportional to the area vegetated by each type. Because native vegetation on the Big Flat Study Area was replaced with a monoculture in 1976, no survey was conducted there.

Dispersion

Dispersion of ground squirrels in relation to vegetative types was measured by the localities where individuals were first captured during a trapping season. Expected dispersion was based on the proportion of trapping effort in each vegetative type. Chi-square and Z-distribution tests were used to determine if observed dispersion differed significantly from expected dispersion and to determine age-specific, sex-specific and year-to-year differences in dispersion patterns.

Climatological Data

Climate data were obtained from the Burns Weather Service Office located approximately 48.3 km southwest of the Harris Study Area in Burns, Oregon. Average maximum temperatures were calculated for 5-day periods, April-May 1974 and March-May 1975 and 1976. Snowfall and total moisture were determined for April and May 1974 and 1975.

RESULTS AND DISCUSSION

During this research 1802 Belding's ground squirrels were livetrapped 6907 times. For studies of natality, I shot 345 ground squirrels near the Harris Study Area, and obtained 557 additional squirrels at the shoot held near Izee, Oregon.

Density

Density fluctuated seasonally in a similar pattern on all three study areas (Table 1). Turner (1972a) suggested that the sequence of events in the life history of Belding's ground squirrels was the same for populations at different localities.

Density on the Harris Study Area exemplified the seasonal pattern of abundance of Belding's ground squirrels (Fig. 1, Table 1). In 1975, density on the Harris Study Area declined, though not significantly ($P > 0.05$), by 37.2 percent between the season high on 27 April and 11 June. Subsequently, the number of squirrels increased by 25.1 percent to 29.4 squirrels per ha on 30 June, though again the change was not significant ($P > 0.05$). Following the mid-summer peak, density declined significantly ($P < 0.05$) by 52.0 percent to its lowest level on 29 August. Minimum density was significantly lower than maximum density ($P < 0.05$) with 2.65 times more squirrels present on 26 April than on 29 August. Density

Table 1. Density estimates and standard errors of density for populations of Belding's ground squirrels on the Harris, Big Flat, and Kurtz Study Areas, Grant County, Oregon 1975-1976.

Year	Date[a]	Harris Study Area Ground Squirrels per ha ± S.E.	Big Flat Study Area[b] Ground Squirrels per ha ± S.E.	Kurtz Study Area[c] Ground Squirrels per ha ± S.E.
1975	27 April	37.4 ± 7.4		
	15 May		12.7 ± 0.9	
	26 May	28.4 ± 1.4		
	4 June		13.3 ± 0.9	
	11 June	23.5 ± 1.8		
	22 June		25.4 ± 2.1	
	30 June	29.4 ± 3.6		
	10 July		26.6 ± 3.3	
	20 July	29.3 ± 3.7		
	1 August		19.4 ± 1.5	
	13 August	23.3 ± 2.4		
	21 August		11.1 ± 1.0	
	29 August	14.1 ± 1.8		
	3 September		4.1 ± 0.9	
1976	11 April	19.2 ± 2.3		
	29 April	22.9 ± 2.8		
	15 May	22.6 ± 2.1		28.6 ± 7.5
	26 May	16.4 ± 1.1		32.2 ± 6.1
	10 June	18.1 ± 1.2		71.1 ± 20.5
	24 June	18.8 ± 1.5		79.0 ± 15.6
	13 July	25.1 ± 2.4		59.8 ± 10.3
	29 July	20.8 ± 1.5		32.5 ± 5.8

Table 1. Continued.

Year	Date[a]	Harris Study Area Ground Squirrels per ha ± S.E.	Big Flat Study Area[b] Ground Squirrels per ha ± S.E.	Kurtz Study Area[c] Ground Squirrels per ha ± S.E.
	11 August	14.4 ± 1.0		22.4 ± 5.5
	21 August	7.8 ± 0.7		13.5 ± 6.9

[a] Indicates middle day of trapping period.

[b] Livetrapping was conducted on alternate weeks with trapping on the Harris Study Area in 1975. No trapping was conducted in 1976.

[c] Livetrapping was conducted on same weeks as trapping in the Harris Study Area, May-August 1976. No trapping was conducted in 1975.

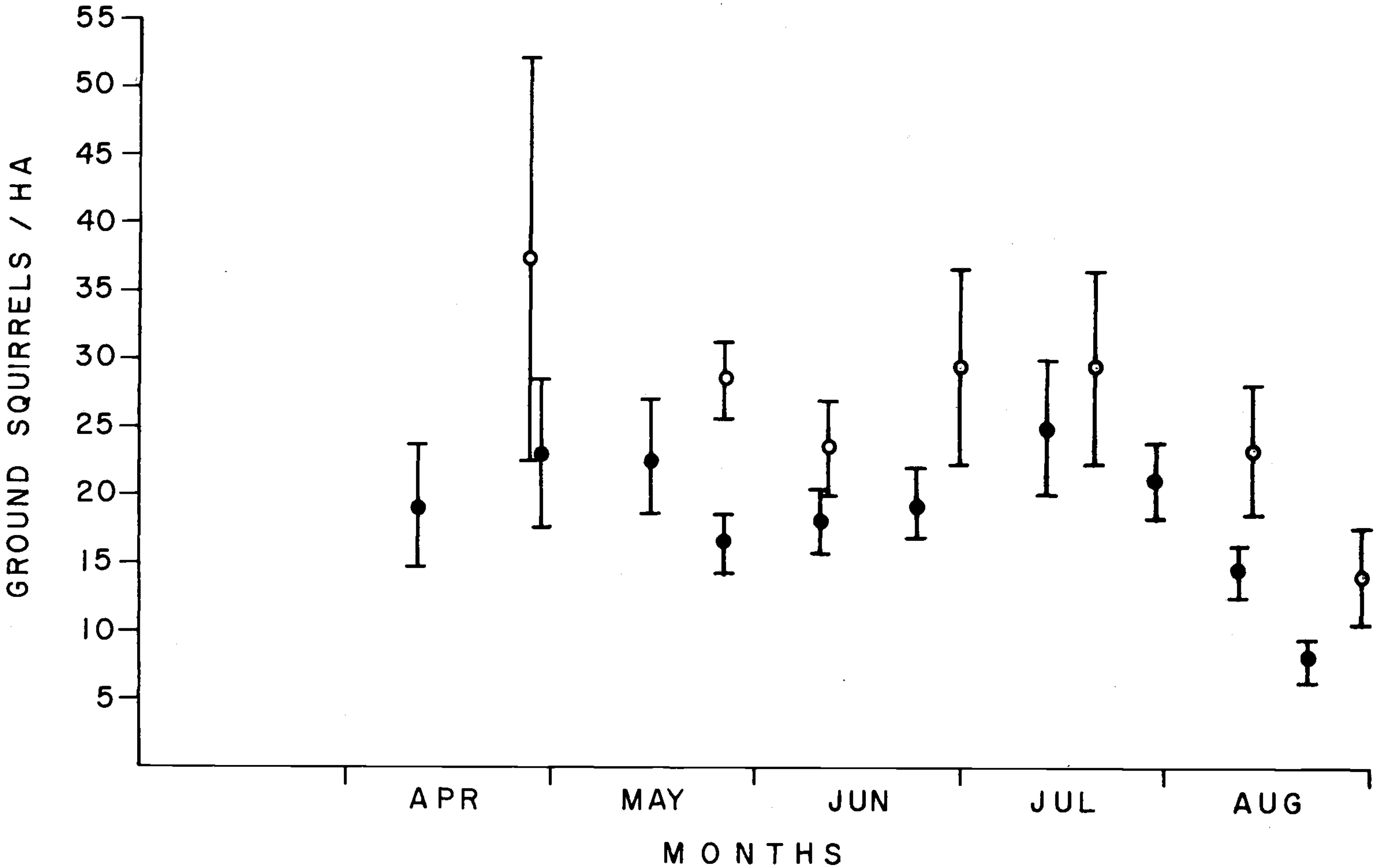

Figure 1. Estimates of density and 95 percent confidence intervals for the population of Belding's ground squirrels on the Harris Study Area, Grant County, Oregon in 1975 (open circles) and 1976 (closed circles).

changed in a similar pattern in 1976 aside from the initial increase of 19.3 percent between 11 and 29 April which was not significant ($\underline{P}>0.05$). Between 29 April and 26 May density decreased, as in 1975, by 28.4 percent, although the decline was not significant ($\underline{P}>0.05$). Succeeding estimates indicated that density increased, though not significantly ($\underline{P}>0.05$), by 53.0 percent to the season high on 13 July. As in 1975, density declined significantly ($\underline{P}<0.05$) following the mid-summer peak by 68.9 percent to the lowest density of the season on 21 August. Maximum density was significantly greater ($\underline{P}<0.05$) than minimum density with 3.2 times more squirrels present in mid-July than in late August.

Densities of ground squirrels on the Harris Study Area were generally lower in 1976 than 1975 (Fig. 1, Table 1). Estimated population size was significantly lower ($\underline{P}<0.05$) on 26 May 1976 compared with the same date in 1975. Densities were compared for 26 May because it was believed that no squirrels were dormant at that time and because recruitment of juveniles into the trappable population had not commenced.

Estimates of the numbers of ground squirrels on the Kurtz Study Area, though sensitive to changes in density, possibly were not representative of population size (Table 1). By removing toes to identify squirrels, the movements, trappability, and survivorship of marked squirrels on the area probably were affected. I observed that ground squirrels bled profusely when toes were removed, and that amputation sites were often infected when squirrels were recaptured. Consequently, density estimates, which might have been subject to error as the result of the method I used to mark squirrels, were used to indicate trends rather than absolute differences in density.

Reproductive Seasons

Reproductive seasons of Belding's ground squirrels on the Harris Study Area extended from April through June. Lactating female squirrels were livetrapped in May and June 1975 and in April, May, and June 1976 (Fig. 2). Pregnant females were collected near the Harris Study Area 17 April 1975 and 7 April 1976. Neither pregnant nor lactating females were obtained in July and August.

Seasonal changes in the proportions of lactating females livetrapped on the Harris Study Area suggested that breeding occurred 1-2 weeks earlier in 1976 than in 1975. In 1975, 80.0 percent of the females were lactating on 11 June compared with only 60.5 percent of the females on 9 June 1976 (Fig. 2). An early breeding season also was supported by comparisons of the weights of juvenile squirrels between years (Table 2); juveniles were significantly heavier ($\underline{P}<0.05$) in 1976 than on comparable dates in 1975 in all cases where sample size exceeded 10, except for weights of juvenile males on 29 August 1975 and 21 August 1976. Morton et al. (1974) attributed

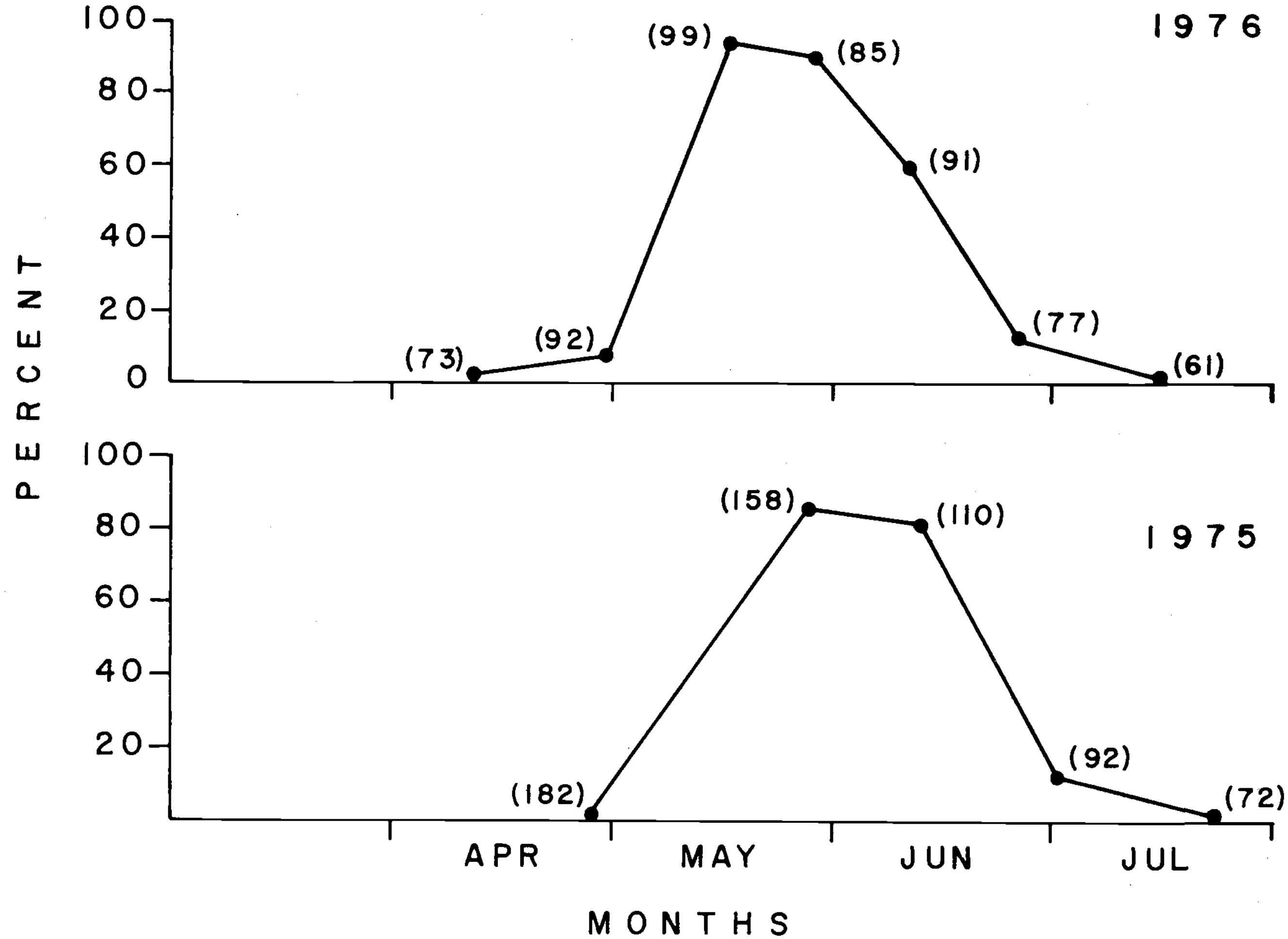

Figure 2. Seasonal changes in proportions of adult female Belding's ground squirrels lactating on the Harris Study Area, Grant County, Oregon, in 1975 and 1976 (sample sizes in parenthesis).

Table 2. Means and standard errors of means of weights (in grams) of female and male juvenile Belding's ground squirrels livetrapped on the Harris Study Area, Grant County, Oregon, 1975-1976.

Year	Date[a]	Males		Females	
		Number examined	Weight (Mean $\pm$ S.E.)	Number examined	Weight (Mean $\pm$ S.E.)
1975	26 May	-	-	1	67.0
	11 June	4	82.6 $\pm$ 5.11	8	101.4 $\pm$ 7.14
	30 June	17	130.7 $\pm$ 3.85	23	122.1 $\pm$ 3.64
	20 July	21	152.2 $\pm$ 6.87	38	158.1 $\pm$ 4.18
	13 August	40	223.1 $\pm$ 4.46	57	197.1 $\pm$ 3.71
	29 August	38	233.7 $\pm$ 4.85	34	197.7 $\pm$ 3.16
1976	10 June	-	-	1	107.4
	24 June	6	141.2 $\pm$ 8.48	12	147.0 $\pm$ 7.05
	13 July	17	181.6 $\pm$ 8.12	35	172.9 $\pm$ 3.93
	29 July	23	225.1 $\pm$ 6.86	42	213.7 $\pm$ 4.30
	11 August	37	237.7 $\pm$ 4.68	37	216.5 $\pm$ 3.46
	21 August	21	237.6 $\pm$ 6.44	21	214.4 $\pm$ 4.34

[a] Indicates middle day of trapping period.

annual differences in weights of juvenile Belding's ground squirrels to variations in the timing of reproduction. Michner (1973) reported that increased temperatures accelerated breeding in Richardson's ground squirrels (*Spermophilus richardsoni*) by altering the time that they bred. Temperatures in Oregon were generally higher in March, April, and May in 1976 compared with the same period in 1975 (Fig. 3). Bailey (1936) and McKeever (1964) reported that Belding's ground squirrels bred shortly after arousal in the spring, thus warmer temperatures in 1976 probably resulted in early emergence and breeding in ground squirrels.

Age-Specific Reproductive Rates

Age Determination by Periosteal Zonation.---Of 49 ground squirrels collected at the Big Flat Study Area, the number of periosteal adhesion lines corresponded to age for 20 of 21 (95.2 percent) 1-year old squirrels and 27 of 28 (96.4 percent) squirrels that were 2 years old or older. As expected, no adhesion lines were found in the dentaries of 23 juveniles. Seemingly inconsistent with these data was the absence of detectable annulli in the mandibles of several adult ground squirrels collected near the Harris Study Area in 1975 and 1976 (Table 3). These adults were obtained in the spring, before juveniles had emerged from natal burrows, thus their ages were known to be at least 1 year. Possibly, sufficient growth of

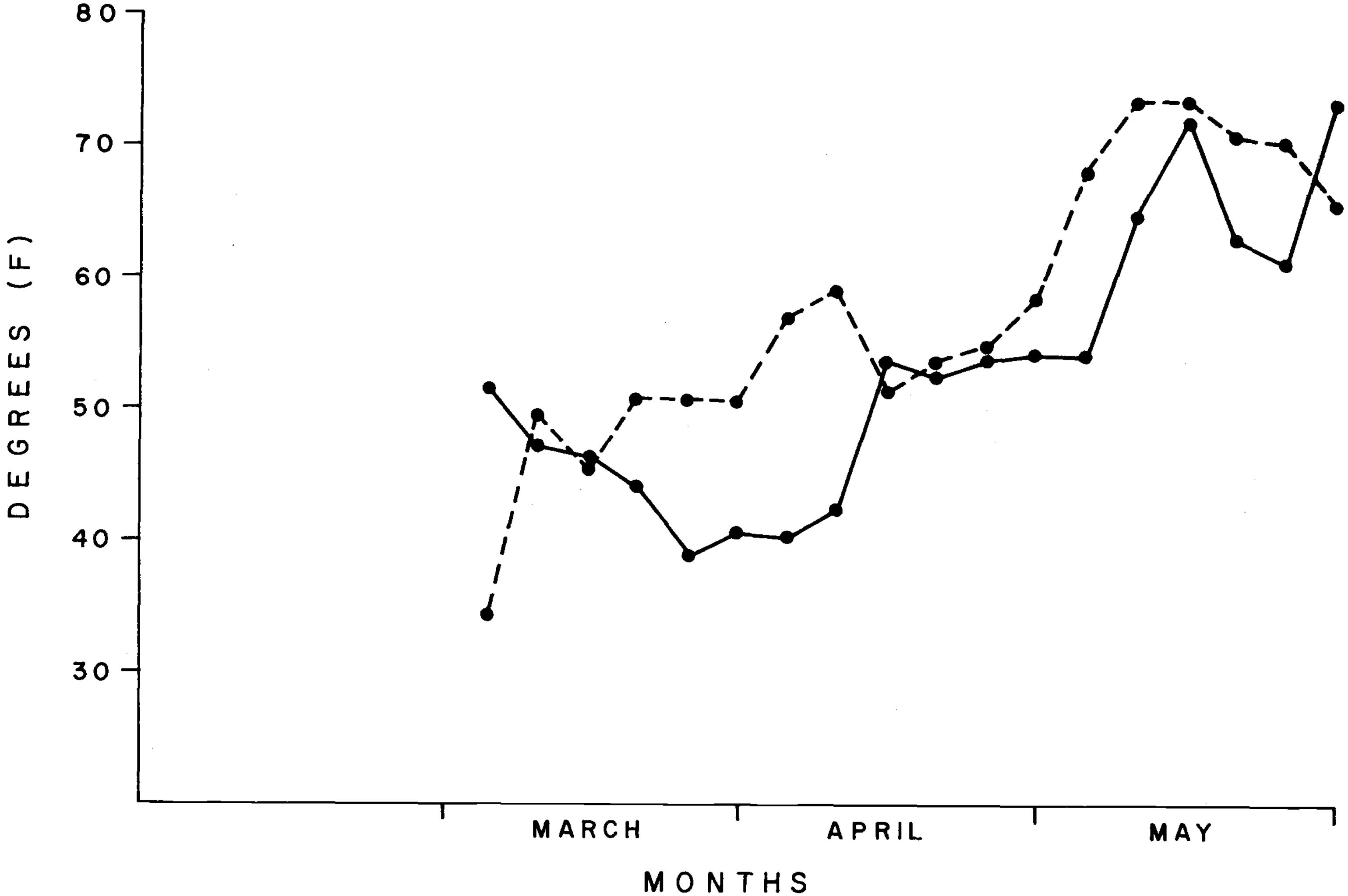

Figure 3. Average maximum temperatures (F) for 5-day periods March-May 1975 (solid line) and March-May 1976 (broken line) recorded at the Burns Weather Service Office, Burns, Oregon (U.S. Department of Commerce 1975, 1976).

Table 3. Numbers of adult female Belding's ground squirrels without observable adhesion lines and with one, two, or three adhesion lines in each collection 17 April-20 June 1975 and 7 April-31 May 1976 near the Harris Study Area, Grant County, Oregon.

Date of collection: Year	Date of collection: Day and month	Number of squirrels with 0 adhesion lines	Number of squirrels with 1 adhesion line	Number of squirrels with 2 adhesion lines	Number of squirrels with 3 adhesion lines
1975	17 April	8	10	5	
	21 April	2	11	8	1
	3 May	1	10	7	1
	10 May		11	5	
	20 June		17	8	
1976	7 April	6	6	12	
	14 April	1	12	10	1
	26 April		14	3	2
	2 May		11	14	2
	11 May		15	8	5
	18 May		10	9	2
	31 May		8	15	2

bone tissue had not occurred to distinguish adhesion lines from the outer surface of the bone in these squirrels. Klevezal' and Kleinenberg (1967) suggested that new annual layers could not be detected until they reached a certain width. The declining numbers of squirrels, without observable annulli, in successive samples each year (Table 3) probably indicated that growth of bone tissue was necessary before adhesion lines, presumably formed during winter, were detectable in all adult squirrels.

Litter sizes.---Mean numbers of viable embryos, resorbing embryos and implantation sites were computed for each age class of squirrels collected near the Harris Study Area in 1975 and 1976 (Table 4). Parous squirrels either without adhesion lines or with a single adhesion line were considered to be yearlings. To examine age-specific and year-to-year differences in reproductive rates, means were compared for samples of 10 squirrels or more using Student's *t* test; in most cases too few 3-year old squirrels were collected to allow meaningful comparisons.

Litter sizes of 2- and 3-year old squirrels were consistently larger than those of 1-year old squirrels. In 1975, mean numbers of viable embryos of 2-year old ground squirrels exceeded, but were not significantly greater, than those of 1-year old squirrels (t = 1.98, P<0.10, D.F. = 47) (Table 4). In 1976, litter sizes of 2-year old squirrels, as measured by numbers of embryos, were significantly

Table 4. Means and standard errors of means of numbers of viable embryos, numbers of resorbing embryos, and numbers of implantation sites for each age class of adult female Belding's ground squirrels collected near the Harris Study Area, Grant County, Oregon, 1975-1976.

Year	Age (Years)	Numbers of pregnant females examined	Numbers of viable embryos (Mean ± S.E.)	Numbers of resorbing embryos (Mean ± S.E.)	Numbers of post-partum females examined	Numbers of implantation sites (Mean ± S.E.)
1975	1	31	5.06 ± 0.17	0.13 ± 0.06	16	4.44 ± 0.26
	2	18	5.78 ± 0.37	0.17 ± 0.09	11	5.54 ± 0.25
	3	2	6.50 ± 0.50	-	-	-
1976	1	30	4.48 ± 0.24	0.31 ± 0.12	40	5.08 ± 0.17
	2	26	5.88 ± 0.23	0.27 ± 0.14	42	5.86 ± 0.15
	3	3	3.67 ± 1.45	-	11	6.27 ± 0.27

larger than those of yearlings (t = 4.20, P < 0.01, D.F. = 53). Mean numbers of implantation sites of 2-year old squirrels were significantly greater than those of 1-year old squirrels in both 1975 and 1976 (t = 2.97, P < 0.01, D.F. = 25 for 1975; t = 3.46, P < 0.01, D.F. = 80 for 1976). Similarly, mean numbers of implantation sites for 3-year old squirrels were significantly larger than those of 1-year old squirrels in 1976 (t = 3.38, P < 0.01, D.F. = 49). No significant differences existed between the mean numbers of implantation sites of 2- and 3-year old ground squirrels in 1976 (t = 1.27, P < 0.40, D.F. = 51).

Apparently, the observed relationship between maternal age and litter size is common among sciurid rodents and other mammals. In the Uinta ground squirrel (*Spermophilus armatus*) litter size was reported to increase up to the 3rd year of life (Slade and Balph 1974). Nixon and McClain (1975) reported that litter sizes of yearling gray squirrels (*Sciurus carolinensis*) were significantly smaller (P < 0.05) than those of older females. Morton (1975*c*) reported that litter sizes of female Belding's ground squirrels that were at least 2 years old were significantly greater (P < 0.05) than those of yearlings. Nalbandov (1964) suggested that previous reproductive experience resulted in larger litters for some species of domestic animals; a similar relationship possibly existed among older Belding's ground squirrels. Because an estimated 75.8 percent (116 of 153) of the yearling females collected near the Harris Study Area and 95.2 percent (179 of 188) of those collected near Izee, Oregon in 1975 and 1976 were parous, most 2- and 3-year old ground squirrels probably were experienced breeders.

Twenty-three (3.9) percent of 595 embryos were being resorbed. No significant differences were revealed between the mean numbers of resorbing embryos for 1- and 2-year old ground squirrels ($t = 0.36$, $P > 0.50$, D. F. = 47 for 1975; $t = 0.23$, $P > 0.50$, D. F. = 54 for 1976) (Table 4).

No significant changes occurred between 1975 and 1976 in mean numbers of resorbing embryos for either 1-year old ($t = 1.32$, $P < 0.20$, D. F. = 58) or 2-year old ground squirrels ($t = 0.59$, $P > 0.50$, D. F. = 47) (Table 4).

Mean numbers of viable embryos of 1-year old squirrels declined from 5.06 in 1975 to 4.48 in 1976; however, these means were not significantly different ($t = 1.87$, $P < 0.10$, D. F. = 58) (Table 4). In contrast, mean numbers of implantation sites of 1-year old squirrels were significantly greater in 1976 ($t = 2.03$, $P < 0.05$, D. F. = 54) than in 1975 (Table 4). Numbers of viable embryos and numbers of implantation sites suggested opposite changes in litter sizes of yearlings between 1975 and 1976. Because sample sizes of pregnant ground squirrels were larger both years, mean numbers of viable embryos were considered to most likely represent changes in age-specific litter sizes between years. Litter sizes of 2-year old squirrels did not differ significantly between years as measured by mean numbers of viable embryos (*t* = 0.26, *P* >0.50, D.F. = 42) and mean numbers of implantation sites (*t* = 0.97, *P* <0.40, D.F. = 51).

Computations of natality for adult female ground squirrels obtained at the Izee ground squirrel shoot were confined to counts of implantation sites because only two pregnant females were collected (Table 5). Because of small samples sizes, analysis of age-specific and year-to-year differences in natality was restricted to 1- and 2-year old squirrels.

In 1975 and 1976, mean numbers of implantation sites of 2-year old ground squirrels were significantly greater than those of 1-year old squirrels (*t* = 2.25, *P* <0.05, D.F. = 146 for 1975; *t* = 2.48, *P* < 0.05, D.F. = 148 for 1976) (Table 5), further evidence for a direct relationship between litter size and maternal age. Comparisons of litter sizes between years indicated that mean numbers of implantation sites increased, though not significantly, for both 1-year old squirrels (*t* = 1.62, *P* <0.20, D.F. = 177) and 2-year old ground squirrels (*t* = 1.66, *P* <0.10, D.F. = 115). These increases in natality possibly were a response to a reduction in the density of ground squirrels near Izee, Oregon by use of toxic baits. Davis et al. (1964) reported that litter sizes of woodchucks (*Marmota monax*)

Table 5. Means and standard errors of means of numbers of implantation sites for each age class of Belding's ground squirrels collected near Izee, Grant County, Oregon, 1975-1976.

Age (Years)	1975 Numbers of females examined	1975 Numbers of implantation sites (Mean $\pm$ S.E.)	1976 Numbers of females examined	1976 Numbers of implantation sites (Mean $\pm$ S.E.)
1	97	6.03 ± 0.15	82	6.43 ± 0.20
2	51	6.63 ± 0.23	66	7.14 ± 0.20
3	3	8.00 ± 1.73	3	10.30 ± 2.73

increased following a decline in population density.

Total Numbers of Offspring Produced

The estimated number of young born on the Harris Study Area during the 1975 breeding season was 1.5 times greater than in 1976 with 962.8 and 657.6 young produced in the 2 years, respectively. Production declined as the result of both fewer females and smaller litter sizes. The estimated number of breeding females declined 27.2 percent from 181.2 in 1975 to 131.6 in 1976 and the mean number of viable embryos of 1-and 3-year old squirrels decreased 11.5 percent and 43.5 percent, respectively (Table 4). Average litter sizes of 2-year old squirrels increased 1.7 percent between years. The decline in the number of young born in 1976 contributed to differences in density between years during June, July, and August (Fig. 1, Table 1). In both years, increases in density during June and July resulted from the recruitment of young into the trappable population; consequently, the reduction in numbers of offspring in 1976 provided fewer juveniles for recruitment than in 1975.

Survival

Calculations of survival rates for Belding's ground squirrels on the Harris Study Area were restricted mainly to annual intervals because of the difficulty in determining precise dates that squirrels entered and emerged from dormancy. However, I have no evidence that squirrels were dormant from late April through June; consequently, survival of adults was calculated for that period. Juvenile survival from birth to maximum density of juveniles in August was not determined because it was impossible to compute the number of young dormant in August. Annual survival rates were calculated from density estimates on 26 May.

In 1975, survival of 309 adults from 27 April to 30 June was 58.8 percent compared with 71.1 percent survival of 189 adults from 29 April to 24 June 1976. These survival rates did not differ significantly ($X^2 = 1.53$, $\underline{P} < 0.25$, D. F. = 1). The annual survival rate of 234.7 adults from 26 May 1975 to 26 May 1976 was 30.2 percent. Sex-specific survival indicated that 33.6 percent of the females (60.8 of 181.2) survived the 1-year period compared with 19.1 percent of the males (10.2 of 53.5). No significant differences were found between the survival rates of adult males and adult females ($X^2 = 2.37$, $\underline{P} < 0.25$, D. F. = 1). Morton (1975a) suggested that over-winter survival was high in Belding's ground squirrels, consequently most mortality among adults on the Harris Study Area probably occurred between April and August.

Low survival of juveniles was probably the most important factor in the decline in density on the Harris Study Area between 1975 and 1976 (Fig. 1, Table 1). Of the estimated 962.8 juvenile squirrels born on the study area in 1975 only 6.6 percent reached the age of 1 year. Survival of female and male juveniles was 7.9 percent and 5.4 percent, respectively. Most mortality of juvenile Belding's ground squirrels probably occurred before young entered the trappable population, because the estimated number of offspring (117.8 squirrels per hectare) was more than 5 times greater than the maximum juvenile density (23.3 squirrels per hectare) estimated for any trapping period in June-August 1975.

Age distributions of adult female ground squirrels collected near the Harris Study Area indicated that juvenile survival probably was lower in 1975 than in 1974 (Table 6). The age composition of females collected in 1975 was significantly different from that of females collected in 1976 ($X^2 = 10.0$, $\underline{P} < 0.01$, D.F. = 2). A decline in the proportion of 1-year old squirrels from 66.7 percent in 1975 to 49.4 percent in 1976, and increases in the proportions of 2- and 3-year old ground squirrels were responsible for this difference. A similar shift to an older age distribution occurred in females collected near Izee, Oregon ($X^2 = 3.84$, $\underline{P} < 0.05$, D.F. = 1) (Table 6) which implied that the same factors influenced juvenile survival at both locations though these collection sites were 40.2 km apart.

Weather possibly adversely affected the early survival of juveniles in 1975 which resulted in low annual survival for juveniles

Table 6. Numbers of adult females in each age class of Belding's ground squirrels collected near the Harris Study Area and near Izee, Grant County, Oregon, 1975-1976 (percentages in parenthesis).

Age (Years)	Harris collection				Izee collection			
	1975		1976		1975		1976	
1	70	(66.7)	83	(49.4)	104	(65.8)	84	(54.9)
2	33	(31.4)	71	(42.3)	51	(32.4)	66	(43.1)
3	2	(1.9)	14	(8.3)	3	(1.9)	3	(2.0)

on the Harris Study Area. Inclement weather during the reproductive season might have weakened the physiological condition of pregnant females resulting in poor condition of young at the time of birth. Also, the ability of adult females to care for young might have been impaired. Analysis of weather data indicated that the reproductive season was colder and more moist in 1975 than in 1974. Average maximum temperatures were generally lower in April-May 1975 than those for the same period in 1974 (Table 7). Also, moisture received during April-May 1975 was 3.22 cm with snowfall occurring on 23 days which compared with 2.0 cm of water and 11 days of snowfall during the same period in 1974. Because most partiution and early development of young occurred in April and May, harsh weather during these months probably reduced survival of juveniles.

Sex Ratios

Sex ratios of ground squirrels livetrapped on the Harris Study Area were determined for each trapping period in 1975 and 1976 (Tables 8 and 9). Separate sex ratios were computed for each discernible age class. Chi-square analysis was used to determine if ratios deviated significantly from the expected 1:1 ratio. All sex ratios were expressed as numbers of females per male.

Sex ratios of adults in April, May, and June were believed to represent the sex composition of the population when no ground

Table 7. Averages of maximum daily temperatures (F) over 5-day periods April-May 1974 and April-May 1975 recorded at the Burns Weather Service Office, Burns, Oregon (U.S. Department of Commerce 1974, 1975).

Period	Average maximum temperatures	
	1974	1975
1 April- 5 April	48.6	40.0
6 April-10 April	52.0	42.4
11 April-15 April	56.0	53.4
16 April-20 April	58.0	52.2
21 April-25 April	56.8	53.0
26 April-30 April	58.8	53.4
1 May- 5 May	66.8	53.4
6 May-10 May	68.6	64.6
11 May-15 May	55.4	71.8
16 May-20 May	49.6	63.0
21 May-25 May	70.8	61.4
26 May-31 May	70.5	72.7

Table 8. Numbers of male and female Belding's ground squirrels, sex ratios, and calculated chi-square values between observed and expected numbers based on an equal sex ratio for juveniles and adults livetrapped on the Harris Study Area, Grant County, Oregon, 1975.

Date[b]	Adults			Juveniles		
	Sex ratio (Females:Males)		X^2 [a]	Sex ratio (Females:Males)		X^2 [a]
27 April	182:38	(4.8:1)	94.2*	-		-
26 May	164:48	(3.4:1)	63.5*	1:0		-
11 June	120:25	(4.8:1)	62.2*	8.4	(2.0:1)	1.3
30 June	99:20	(5.0:1)	52.4*	23:17	(1.4:1)	0.9
20 July	72:19	(3.8:1)	30.9*	38:21	(1.8:1)	4.9*
13 August	22:21	(1.0:1)	-	57:43	(1.3:1)	2.0
29 August	3:5	(0.6:1)	0.5	36:44	(0.8:1)	0.8

[a] Tests for significant deviation from expected 1.0:1.0 ratio.

[b] Indicates middle day of trapping period.

* ($\underline{P} < 0.05$, D.F. = 1).

Table 9. Numbers of male and female Belding's ground squirrels, sex ratios, and calculated chi-square values between observed and expected numbers based on an equal sex ratio for juveniles and adults (yearlings, adults 2-years old and older, and adults of all ages) live-trapped on the Harris Study Area, Grant County, Oregon, 1976.

Date[b]	Adults of All Ages			Juveniles			Yearlings			Adults 2 Years Old and Older		
	Sex ratio (Females:Males)		X^2[a]	Sex ratio (Females:Males)		X^2[a]	Sex ratio (Females:Males)		X^2[a]	Sex ratio (Females:Males)		X^2[a]
11 April	73:42	(1.7:1)	8.4*	-		-	30:22	(1.4:1)	1.2	43:20	(2.2:1)	8.4*
29 April	92:36	(2.6:1)	24.5*	-		-	38:24	(1.6:1)	3.2	54:12	(4.5:1)	26.7*
15 May	101:42	(2.4:1)	24.3*	-		-	44:31	(1.4:1)	2.2	57:11	(5.2:1)	31.1*
26 May	88:32	(2.8:1)	26.1*	-		-	34:23	(1.5:1)	2.1	54:9	(6.0:1)	32.1*
10 June	93:37	(2.5:1)	24.1*	1:0		-	39:24	(1.6:1)	3.6	54:13	(4.2:1)	25.1*
24 June	77:37	(2.1:1)	14.0*	12:6	(2.0:1)	2.0	33:26	(1.3:1)	0.8	44:11	(4.0:1)	19.8*
13 July	61:40	(1.5:1)	4.4*	35:17	(2.1:1)	6.2*	26:30	(0.9:1)	0.3	35:10	(3.5:1)	13.9*
29 July	34:45	(0.8:1)	1.5	42:24	(1.8:1)	4.9*	14:35	(0.4:1)	9.0*	20:10	(2.0:1)	3.3
11 August	8:21	(0.4:1)	5.8*	39:39	(1.0:1)	0.0	5:20	(0.2:1)	9.0*	3:1	(3.0:1)	1.0
21 August	1:15	(0.1:1)	12.2*	21:21	(1.0:1)	0.0	1:15	(0.1:1)	12.2*	-		-

[a] Tests for significant deviation from expected 1.0:1.0 ratio.

[b] Indicates middle day of trapping period.

* ($\underline{P} < 0.05$, D.F. = 1)

squirrels were dormant. In these 3 months, sex ratios were significantly in favor of females both in 1975 and 1976 (Tables 8 and 9). Turner (1972a) reported unbalanced sex ratios for adult Belding's ground squirrels.

Sex ratios of juveniles deviated less from the expected 1:1 ratio than those of adults (Tables 8 and 9). The sex ratios of 121 juveniles collected near Izee, Oregon, in 1975, and 125 collected in 1976 were 1.2:1 and 1.1:1, respectively. Neither of these ratios were significantly different from an expected 1:1 ratio ($X^2 = 0.67$, $P > 0.50$, D.F. = 1 for 1975; $X^2 = 0.39$, $P > 0.75$, D.F. = 1 for 1976). Morton et al. (1974) reported an equal number of males and females among 672 juvenile Belding's ground squirrels.

Differences between sex ratios of adults and juveniles indicated that differential mortality occurred between sexes. Turner (1972a) suggested that unbalanced sex ratios of adult ground squirrels resulted from the emigration and subsequent mortality of juvenile males. Because juvenile females remained near natal burrows until the following spring, they were not subject to the mortality that dispersing juvenile males were (Turner 1972a). Sex-specific dispersal was reported for several species of ground squirrels (Evans and Holdenried 1943, McCarely 1966). Concerning the Richardson's ground squirrel, Michner and Sheppard (1972) stated, "Adult females tend to ignore and reject their own male young, at the same time engaging in more neutral and cohesive contacts with their female young". They noted that this behavior might help explain sex-specific dispersal in Richardson's ground squirrels.

Sex ratios of ground squirrels captured on the Kurtz and Big Flat Study Areas (Tables 10 and 11) indicated that differential mortality between female and male juveniles also occurred on these areas.

To compare sex ratios of adults between years, a single average sex ratio was computed for adults in 1975 and for each age class of adults in 1976 including yearlings, squirrels 2-years old and older, and all adults collectively. Each mean sex ratio was calculated from the numbers of adult squirrels captured on the Harris Study Area in trapping periods in April, May and June in 1975 and 1976. Chi-square analysis was used to test for significant year-to-year variations in sex ratios.

The average sex ratio of adult squirrels changed significantly between years ($X^2 = 5.2$, $\underline{P} < 0.05$, D.F. = 1), from 4.3:1 in 1975 to 2.3:1 in 1976. However, the mean sex ratio of squirrels that were 2-years old or older in 1976, 4.0:1, was not significantly different from the sex ratio of adults in the previous year ($X^2 = 0.23$, $\underline{P} > 0.75$, D.F. = 1). This suggested that sex ratios among adults differed between years because of a large proportion of males in the yearling age class. The average sex ratio of yearlings, 1.4:1,

Table 10. Numbers of male and female Belding's ground squirrels, sex ratios, and calculated chi-square values between observed and expected numbers based on an equal sex ratio for juveniles and adults livetrapped on the Kurtz Study Area, Grant County, Oregon, 1976.

Date[b]	Adults Sex ratio (Females:Males)		Adults X^2 [a]	Juveniles Sex ratio (Females:Males)		Juveniles X^2 [a]
15 May	51:27	(1.9:1)	7.4*	-		-
26 May	74:30	(2.5:1)	18.6*	-		-
10 June	59:24	(2.5:1)	14.8*	19:23	(0.8:1)	0.4
24 June	44:11	(4.0:1)	19.8*	70:55	(1.3:1)	1.8
13 July	12:14	(0.9:1)	0.2	79:62	(1.3:1)	2.1
29 July	0:4		4.0*	60:36	(1.7:1)	6.0*
11 August	0:2		2.0	31:38	(0.8:1)	0.7
21 August	-		-	11:20	(0.6:1)	2.6

[a] Tests for significant deviation from expected 1.0:1.0 ratio.

[b] Indicates middle day of trapping period.

* ($\underline{P} < 0.05$, D.F. = 1).

Table 11. Numbers of male and female Belding's ground squirrels, sex ratios, and calculated chi-square values between observed and expected numbers based on an equal sex ratio for juveniles and adults livetrapped on the Big Flat Study Area, Grant County, Oregon, 1975.

	Adults			Juveniles		
Date[b]	Sex ratio (Females:Males)		X^2 [a]	Sex ratio (Females:Males)		X^2 [a]
15 May	38:31	(1.2:1)	0.7	-		-
4 June	109:30	(3.6:1)	44.9*	-		-
22 June	99:27	(3.7:1)	41.1*	41:52	(0.8:1)	1.3
10 July	59:16	(3.7:1)	24.6*	60:56	(1.1:1)	0.1
1 August	27:21	(1.3:1)	0.8	73:64	(1.1:1)	0.6
21 August	4:9	(0.4:1)	1.9	13:23	(0.6:1)	2.8

[a] Tests for significant deviation from expected 1.0:1.0 ratio.

[b] Indicates middle day of trapping period.

* ($\underline{P} < 0.05$, D.F. = 1).

differed significantly from the adult sex ratio of 1975, 4.3:1 (X^2 = 11.9, $P < 0.01$, D.F. = 1). These results indicated that differential mortality between male and female juveniles was less in 1975 than in preceding years. Slade and Balph (1974) observed that survival of juvenile male Uinta ground squirrels increased following a reduction in population density. They suggested that juvenile males dispersed shorter distances over more familiar areas, thus reducing their vulnerability to predation and accidents. In a similar manner, greater survival of juvenile male Belding's ground squirrels, during dispersal from natal burrows, probably occurred in 1975 as a result of the decline in population density on the Harris Study Area between 1975 and 1976 (Fig. 1, Table 1).

Dormancy

Seasonal changes in the numbers of dormant individuals was a major factor affecting the density, sex composition and age structure of the trappable population of Belding's ground squirrels on the Harris Study Area.

Changes in the proportions of dormant squirrels resulted in both decreases and increases in the numbers of active squirrels on the Harris Study Area. In both 1975 and 1976, dormancy was believed to be a contributing factor to the decline in apparent density in late July and August (Fig. 1, Table 1). Comparisons of densities on 29 August 1975 and 11 April 1976 revealed that more ground squirrels were present when squirrels emerged from dormancy in the spring than in late summer of the preceding year. Although this difference was not significant (*P* > 0.05), it indicated that dormancy probably contributed substantially to the lower measured density in August. Similarly, the apparent decrease in density in August of 1976 probably also was related to dormancy. In 1976, the increase in density in the trappable population between 11 April and 29 April, although not significant (*P* > 0.05), probably was the result of squirrels emerging from dormancy (Fig. 1, Table 1). Morton (1975 *a*, *c*) reported that Belding's ground squirrels emerged from dormancy over a span of several weeks, thus squirrels that were dormant on 11 April probably were active on 29 April.

Dormancy also resulted in seasonal changes in the apparent sex composition of ground squirrels on the Harris Study Area. In both 1975 and 1976, the proportion of females in the adult population declined in July and August (Tables 8 and 9). Because the sex composition of the adult cohort did not change appreciably between years, sudden increases in female mortality could not explain this decrease. Possibly adult females entered dormancy sooner than adult males as suggested by Turner (1972*a*). Similarly, juvenile females probably entered dormancy before juvenile males as indicated by the decreasing proportion of females in successive trapping periods each year

(Tables 8 and 9). Morton et al. (1974) reported that juvenile females preceded juvenile males into dormancy.

Seasonal changes in apparent age ratios also appeared to be related to dormancy. Among adults, the proportion of squirrels in the trappable population that were at least 2-years old decreased sharply in August 1976 (Table 12). Probably older adults entered dormancy earlier than yearlings, resulting in the observed changes in age ratios. Age ratios of the trappable population of adults and juveniles also declined sharply in August (Table 12). Adults might have entered dormancy before juveniles as was observed in other populations of Belding's ground squirrels (Turner 1972a, Morton 1975a).

Dispersion in Relation to Vegetative Types

Vegetative Survey.---Five different vegetative types were discernable on the Harris Study Area (Table 13). Vegetative type 1 was comprised of approximately 2.0 ha of open meadow with Kentucky bluegrass (*Poa pratensis*) being the most numerous plant species. Unlike type 1, the 0.56 ha area of vegetative type 2 contained scattered patches of big sagebrush (*Artemisia tridentata*) in addition to open meadow. Most of vegetative type 3 was flooded periodically by an irrigation ditch, consequently this was the wettest vegetative type on the study area. The largest percentage of

Table 12. Age ratios of Belding's ground squirrels livetrapped on the Harris Study Area, Grant County, Oregon, 1976.

Date[a]	Age ratios (Ground squirrels at least 2 years old: Yearlings)		Age ratios (Adults:Juveniles)	
11 April	63:52	(1.2:1)	-	
29 April	66:62	(1.1:1)	-	
15 May	68:75	(0.9:1)	-	
26 May	63:57	(1.1:1)	-	
10 June	67:63	(1.1:1)	130:1	(130:1)
24 June	55:59	(0.9:1)	114:18	(6.3:1)
13 July	45:56	(0.8:1)	101:52	(1.9:1)
29 July	30:49	(0.6:1)	79:66	(1.2:1)
11 August	4:25	(0.2:1)	28:78	(0.4:1)
21 August	0:16	(0.0:1)	16:42	(0.4:1)

[a] Indicates middle day of trapping period.

Table 13. Numbers of sampling hits on plant species and numbers of ground surface hits (GSH) in each vegetative type on the Harris Study Area, Grant County, Oregon (percentages in parenthesis).

Category	Vegetative Types 1		2		3		4		5	
Plant species										
Poa pratensis	317	(52.8)	110	(50.2)	68	(34.7)	32	(5.7)	346	(33.9)
Potentilla gracilis	69	(11.5)	3	(1.4)	10	(5.1)	3	(0.5)	26	(2.5)
Agropryron spicatum	39	(6.5)	7	(3.2)	15	(7.6)	3	(0.5)	15	(1.5)
Antennaria sp.	36	(6.0)	2	(0.9)	-		-		19	(1.9)
Juncus balticus	24	(4.0)	-		34	(17.3)	5	(0.9)	13	(1.3)
Achillea millefolium	19	(3.2)	13	(5.9)	2	(1.0)	6	(1.1)	63	(6.2)
Koelaria cristata	19	(3.2)	-		-		9	(1.6)	11	(1.1)
Carex sp.	12	(2.0)	1	(0.4)	14	(7.1)	-		14	(1.4)
Fragaria virginiana	7	(1.2)	1	(0.4)	-		1	(0.2)	12	(1.2)
Festuca idahoensis	4	(0.7)	-		-		12	(2.1)	2	(0.2)
Arnica chamissionis	3	(0.5)	-		-		4	(0.7)	9	(0.9)
Artemisia tridentata	-		22	(10.0)	-		50	(8.9)	222	(21.8)
Cirsium arvense	-		3	(1.4)	-		-		2	(0.2)

Table 13. Continued.

Category	Vegetative Types 1		2		3		4		5	
Scirpus cespitosus	-		-		4	(2.0)	-		-	
Chrysothamnus sp.	-		-		-		18	(3.2)	10	(1.0)
Sitanion hystrix	-		-		-		5	(0.9)	-	
Stipa occidentalis	-		-		-		2	(0.4)	19	(1.9)
Bromus tectorum	-		-		-		1	(0.2)	-	
Lupinus leucophyllus	-		-		-		-		2	(0.2)
Sidalcea sp.	-		-		-		-		1	(0.1)
GSH	51	(8.5)	57	(26.0)	49	(25.0)	410	(73.1)	234	(22.9)
Totals	600	(100.0)	219	(100.0)	196	(100.0)	561	(100.0)	1020	(100.0)

sedge (*Carex* spp.) and rush (*Juncus* spp.) species were found on this type which was 0.52 ha in size. Vegetative type 4 was 0.81 ha and was largely devoid of vegetation, with soil that was mainly shallow and rocky. Kentucky bluegrass and big sagebrush were the most abundant plant species on this area. Vegetative type 5 was the largest type, 2.53 ha, and contained the most abundant and widespread stands of big sagebrush. The remaining 0.44 ha of the study area consisted of a narrow road and two small streams that crossed the area.

Four vegetative types were distinguishable on the Kurtz Study Area (Table 14). Vegetative type 1 was 0.62 ha and consisted of several native plant and shrub species of which the most abundant were big sagebrush and blue-bunch wheat grass (*Agropyron spicatum*). Vegetative type 2 covered 1.61 ha. Vegetation was very sparse and limited mainly to scattered clumps of crested wheat grass (*Agropyron cristatum*) and big sagebrush. Vegetative type 3 comprised 0.40 ha and was principally California brome (*Bromus carinatus*). Vegetative type 4 was 2.43 ha. Native vegetation was removed from this area previous to this study and alfalfa established in its place. Several species of forbs also were present including cheatgrass (*Bromus tectorum*), fiddleneck (*Amsinckia intermedia*) and pennycress (*Thalspi arvense*).

Table 14. Numbers of sampling hits on plant species and numbers of ground surface hits (GSH) in each vegetative type on the Kurtz Study Area, Grant County, Oregon (percentages in parenthesis).

Category	Vegetative Types							
	1		2		3		4	
Plant species								
Artemisia tridentata	29	(12.1)	86	(17.5)	-		-	
Agropyron spicatum	14	(5.8)	-		-		-	
Chrysothamnus sp.	11	(4.6)	6	(1.2)	-		-	
Eriogonum sp.	9	(3.8)	-		-		-	
Potentilla gracilis	7	(2.9)	-		6	(6.0)	-	
Lomatium grayi	7	(2.9)	-		-		-	
Poa pratensis	6	(2.5)	-		10	(10.0)	-	
Agropyron cristatum	6	(2.5)	23	(4.7)	-		-	
Achillea millefolium	1	(0.4)	-		-		-	
Purshia tridentata	1	(0.4)	-		-		-	
Stipa occidentalis	1	(0.4)	-		-		-	
Carex sp.	1	(0.4)	-		-		-	
Sitanion hysterix	-		4	(0.8)	-		-	

Table 14. Continued.

Category	Vegetative Types							
	1		2		3		4	
Bromus carinatus	-		-		63	(63.0)	36	(5.2)
Amsinckia intermedia	-		-		-		53	(7.6)
Bromus tectorum	-		-		-		61	(8.8)
Medicago sativa	-		-		-		152	(21.8)
Phacelia sp.	-		-		-		1	(0.1)
Polygonum aviculare			-		-		1	(0.1)
Rumex sp.	-		-		-		3	(0.4)
Thlaspi arvense	-		-		-		36	(5.2)
GSH	147	(61.2)	373	(75.8)	21	(21.0)	354	(50.8)
Totals	240	(100.0)	492	(100.0)	100	(100.0)	697	(100.0)

Distribution of Captures.---In 1975, the distribution of female ground squirrels on the Harris Study Area, according to the locations where each female was captured, did not differ significantly from expected based upon the trapping effort in each of the five vegetative types (X^2 = 7.91, $P < 0.10$, D.F. = 4 for adults; X^2 = 6.66, $P <$ 0.25, D.F. = 4 for juveniles) (Table 15). Only in vegetative type 3 were the proportions of females significantly less than expected (Z = 2.22, $P < 0.05$ for adults; Z = 2.06, $P < 0.05$ for juveniles). Type 3 was often flooded, consequently squirrels avoided this area. Unlike dispersion among females, distributions of male ground squirrels were significantly different from expected in the five vegetative types (X^2 = 14.7, $P < 0.01$, D.F. = 4 for adults; X^2 = 16.1, $P < 0.01$, D.F. = 4 for juveniles) (Table 15). The proportion of adult males was significantly less than expected in type 1 (Z = 2.39, $P < 0.01$) and type 3 (Z = 1.92, $P < 0.05$) and was significantly greater than expected in type 5 (Z = 3.04, $P < 0.01$). Juvenile males were located in type 1 in significantly greater numbers than expected (Z = 3.67, $P < 0.01$).

Sex-specific dispersion patterns appeared to be common among species of ground squirrels (Quanstrom 1971, Slade and Balph 1974, Morton 1975b). In adult Uinta ground squirrels, sex-specific dispersion possibly resulted from interactions between males, who were subordinate to females, and territorial females (Slade and

Table 15. Numbers of Belding's ground squirrels livetrapped and numbers expected (in parenthesis) on the basis of trapping effort in each vegetative type on the Harris Study Area, Grant County, Oregon, 1975: only first captures were used in this analysis.

Category	Vegetative Types									
	1		2		3		4		5	
Adult females	61	(68.4)	19	(18.5)	6	(14.8)	41	(35.1)	117	(107.2)
Adult males	11	(20.7)	6	(5.6)	0	(4.5)	11	(10.6)	46	(32.5)
Juvenile females	36	(30.8)	9	(8.3)	1	(6.7)	19	(15.8)	45	(48.3)
Juvenile males	41	(24.9)	7	(6.7)	4	(5.4)	6	(12.8)	31	(39.1)

Balph 1974). This resulted in males avoiding areas where females were abundant. Morton (1975b) suggested that male Belding's ground squirrels were forced from certain habitats as the result of antagonism between squirrels of different sexes. Consequently, adult Belding's ground squirrels probably exhibited the same female-male dominance behavior as Uinta ground squirrels (Slade and Balph 1974) and Richardson's ground squirrels (Michner 1973). As a result, females probably had highest priority in habitat selection. Turner (1972a) suggested that neither sex was dominant in adult Belding's ground squirrels. However, his conclusions were based upon observations of only two adult males, and he presented no data to substantiate his claim.

Uniform distribution of adult females, in regard to the five vegetative types (Table 15) suggested that, with exception of type 3, preference for available vegetative types by females was not different. Distributions of adult and juvenile female squirrels were expected to coincide because juvenile females resided near natal burrows during their first winter (Turner 1972a). Distributions of males probably represented exclusion from certain habitat types. As density increased on specific areas, males might have been forced into other, less suitable habitats. Unequal dispersion of adult and juvenile males possibly indicated incompatibility between these age groups. Antagonistic behavior of adult males toward juvenile males was reported in Columbian ground squirrels (*Spermophilus columbianus*) and Arctic ground squirrels (*Spermophilus undulatus*) (Steiner 1972).

Analysis of first captures of ground squirrels on the Harris Study Area in 1976 revealed no significant differences between expected numbers of squirrels in each of the five vegetative types and the distributions of adult females ($X^2 = 9.22$, $P < 0.10$, D.F. = 4), juvenile females ($X^2 = 6.12$, $P < 0.25$, D.F. = 4), adult males ($X^2 = 2.94$, $P < 0.75$, D.F. = 4), and juvenile males ($X^2 = 4.11$, $P < 0.50$, D.F. = 4) (Table 16). Only the proportion of adult females in vegetative type 3 was significantly less than expected ($Z = 2.54$, $P < 0.01$). Although the distributions of adult and juvenile males did not deviate significantly between years ($X^2 = 6.79$, $P < 0.25$, D.F. = 4 for adults; $X^2 = 7.93$, $P < 0.10$, D.F. = 4 for juveniles), they indicated a definite shift to more uniform dispersion in 1976. Possibly the reduced density in 1976 (Fig. 1, Table 1) allowed males to move into habitats where formerly they were excluded.

Distributions of female ground squirrels and juvenile male ground squirrels by first capture, in the four vegetative types on the Kurtz Study Area, differed significantly from expected based upon the proportion of trapping effort in each vegetative type ($X^2 = 49.3$, $P < 0.01$, D.F. = 3 for adult females; $X^2 = 20.4$, $P < 0.01$, D.F. = 3 for juvenile females; $X^2 = 12.3$, $P < 0.01$, D.F. = 3 for juvenile

Table 16. Numbers of Belding's ground squirrels livetrapped and numbers expected (in parenthesis) on the basis of trapping effort in each vegetative type on the Harris Study Area, Grant County, Oregon, 1976: only first captures were used in this analysis.

Category	Vegetative Types									
	1		2		3		4		5	
Adult females	57	(55.8)	11	(15.1)	3	(12.0)	33	(28.6)	95	(87.4)
Adult males	23	(28.0)	10	(7.6)	4	(6.1)	17	(14.4)	46	(43.9)
Juvenile females	29	(24.1)	4	(6.5)	5	(5.2)	18	(12.4)	30	(37.8)
Juvenile males	17	(15.7)	4	(4.2)	0	(3.4)	7	(8.0)	28	(24.6)

males) (Table 17). Adult females, juvenile females and juvenile males were present in significantly greater proportion than expected in type 4 (Z = 4.14; Z = 4.45; Z = 3.40; respectively, $\underline{P} < 0.01$) and in significantly less proportion than expected in type 2 (Z = 6.89; Z = 2.79; Z = 2.42; respectively, $\underline{P} < 0.01$). These results suggested that ground squirrels preferred vegetative type 4 and tended to reject type 2 as suitable habitat. Preference for type 4 might be expected because alfalfa fields were reported to be favored habitats of Belding's ground squirrels (Turner 1972a). Low density of vegetation on type 2 probably precluded extensive use of this area by ground squirrels. Unlike the distributions of other groups of squirrels, the distribution of adult males was not significantly different from expected ($X^2 = 7.34$, $\underline{P} < 0.10$, D.F. = 3) (Table 17). Males also differed from other squirrels in that they were found in significantly greater proportion than expected in type 1 (Z = 2.06, $\underline{P} < 0.05$) and they showed no preference for type 4 (Z = 0.03, $\underline{P} < 0.98$). These data suggested that adult males were excluded from certain habitats as density increased on preferred areas.

Table 17. Numbers of Belding's ground squirrels livetrapped and numbers expected (in parenthesis) on the basis of trapping effort in each vegetative type on the Kurtz Study Area, Grant County, Oregon, 1976: only first captures were used in this analysis.

Category	Vegetative Types							
	1		2		3		4	
Adult females	32	(24.5)	7	(46.1)	18	(11.5)	87	(61.9)
Adult males	18	(11.2)	13	(21.1)	6	(5.3)	29	(28.4)
Juvenile females	23	(31.4)	41	(59.2)	11	(14.8)	110	(79.6)
Juvenile males	25	(29.4)	40	(55.4)	11	(13.8)	97	(74.4)

CONCLUSIONS

Although it is obvious that the dynamics of populations of Belding's ground squirrels probably were not fully understood because of the limited time span of this investigation, information obtained provided insights to the population biology of this species. Populations of Belding's ground squirrels appeared to be limited in size by the physical resources of their environment. Alteration of density of ground squirrels appeared to invoke density-dependent responses.

Vegetation probably was an important factor affecting the density of populations of Belding's ground squirrels. Nonuniform distributions of females and juvenile males on the Kurtz Study Area (Table 17) suggested that different vegetative types supported different numbers of ground squirrels. Because of this relationship, changes that alter the vegetative composition might be associated with changes in the density of squirrels. On the Kurtz Study Area a portion of the vegetation was altered from native plant species to predominantly alfalfa (Table 14). The strong preference of females and juvenile males for this type (Table 17) suggested that density was increased on that area by the change in vegetation. Similar findings by Turner (1972a) indicated that agricultural practices that provided for increased amounts of succulent vegetation also resulted in greater densities of ground squirrels.

Changes in mean numbers of offspring produced per female possibly was a density-dependent response of Belding's ground squirrels. Between 1975 and 1976, the litter sizes of females collected near Izee, Oregon, increased (Table 5) possibly in response to a presumed decline in density on the area through the use of toxic baits. This relationship suggested that a reduction in population size might be at least partially compensated for by improved reproductive performance. Litter sizes, as measured by numbers of viable embryos, did not increase with the decline in density on the Harris Study Area between 1975 and 1976 (Fig. 1, Table 1). Possibly, the increase in available resources was relatively small for squirrels that remained after the reduction in density, or declines in the amounts of physical resources occurred between years such that natality remained near the maximum allowed by the environment.

Another density-dependent response of Belding's ground squirrels appeared to be differential survival of juvenile males. Survival appeared to increase following the reduction in population density on the Harris Study Area between 1975 and 1976 (Fig. 1, Table 1). Improved survival of juvenile males would tend to increase density on areas where the numbers of squirrels was reduced.

A third density-dependent response of Belding's ground squirrels was that at high population levels (Fig. 1, Table 1) certain sex and age groups were excluded from various vegetative types (Table 15). In contrast, these groups of squirrels did not appear to be forced from those habitats (Table 16) at low population levels (Fig. 1, Table 1).

Survival of juvenile Belding's ground squirrels appeared to be an important factor that affected the density of Belding's ground squirrels. Poor survival of juveniles was believed to be the major cause of the decline in density of the Harris Study Area between years (Fig. 1, Table 1). Inclement weather during the breeding season was suspected to be the reason for low survival of juveniles. Consequently, weather probably contributed to the decline in density on the study area. However, the influence of weather on survival also appeared to increase the reproductive potential of the population by causing a shift to an older age distribution (Table 6). With greater proportions of older females that were capable of producing larger litters (Table 4) the mechanism for rapid recovery of density through increased natality was provided.

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