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The Annual Demography of a Population of Antelope Ground Squirrels in Curiew Valley, Utah

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THE ANNUAL DEMOGRAPHY OF A POPULATION
OF ANTELOPE GROUND SQUIRRELS IN
CURLEW VALLEY, UTAH

by

James R. Kitts

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ABSTRACT

The Annual Demography of a Population
of Antelope Ground Squirrels in
Curlew Valley, Utah

by

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Utah State University, 1970

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The annual demography of a population of antelope ground squirrels in Curlew Valley, Utah was studied by measuring population density, natality, and mortality. Capture-recapture techniques yielded lower estimates than the Hayne strip-census. The estimates suggested 1968 was a year of population decline.

One hundred seventy-three squirrels were collected and autopsied to obtain sex ratio, age structure, natality, and mortality data. The seasonal sex ratios for adult and yearling squirrels showed 82 percent females in spring 1968, this gradually changed to 56 percent by winter. The seasonal sex ratios of the young squirrels showed 59 percent females upon emergence from natal burrows in summer 1968, increasing to 79 percent by winter.

The squirrels collected were aged by cementum annuli. The oldest were believed to be 5 years old. They composed 1.2 percent of the collection while young-of-the-year composed 38.7 percent.

The estimate of mean corpora lutea was 7.6, the mean embryo count was 7.2, and the mean post-partum placental scar count was 5.8. The mean corpora lutea count for yearlings was statistically lower than the count for adults and the mean ovulation rate for 1968 was statistically lower than the rate for 1969. An estimate of litter size from four nests gave a mean of 4.5. In 1968, the conception rate was 91 percent with yearlings comprising 75 percent of those not conceiving. In 1969, the rate was 100 percent.

Pre-emergence mortality of the young was 41 percent. Post-emergence mortality was 86 percent, and mortality, March-November, 1968 was 92 percent.

Adult and yearling spring-to-spring mortality for study area squirrels calculated from retrap data was 81 percent. Spring-to-spring mortality calculated from age distribution data and Ricker's formula was 71 percent. The spring-to-fall mortality for 1968 calculated from density estimates and age distribution data was 53 percent.

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INTRODUCTION

This research project was conducted from March, 1968 to May, 1969 as a portion of a long-range study of the population ecology of several animal species in Curlew Valley, Box Elder County, northern Utah. The antelope ground squirrel (*Citellus leucurus*) was selected for study because it is at the extreme northern edge of its range in Curlew Valley. This area of North America presents a "cold-desert" environment, and no previous studies of this species in this type of ecosystem have been published. Furthermore, the antelope ground squirrel was the only species of diurnal rodent inhabiting the sagebrush areas that was large enough and colored vividly enough to be easily recognized under unconfined conditions.

The study had one main objective: to describe the annual demography of this species in a limited area of Curlew Valley. To attain this objective, three sub-objectives were undertaken: 1) to measure population density, 2) to measure natality, and 3) to measure mortality.

LOCATION AND DESCRIPTION OF STUDY AREA

The study area was a 35-acre plot located at an elevation of 4,800 feet on the east slope of Cedar Hill, approximately 12 miles southwest of Snowville, Utah (Fig. 1). The area was accessible by truck from the Locomotive Springs Road which passed 1 mile to the east.

Utah juniper (*Juniperus osteosperma*) bordered the area to the south and west at distances of 200-500 yards. To the north and east, the vegetation of the area was continuous with an expanse of big sage (*Artemisia tridentata*) intermittently broken by rocky outcrops.

A low shrub cover of big sage dominated the area but was interspersed with various forbes and grasses. Annuals commonly emerged in late March and early April and dried by the end of July.

Gross (1967) gave a general description of the vegetation, climate, and topography of Curlew Valley.

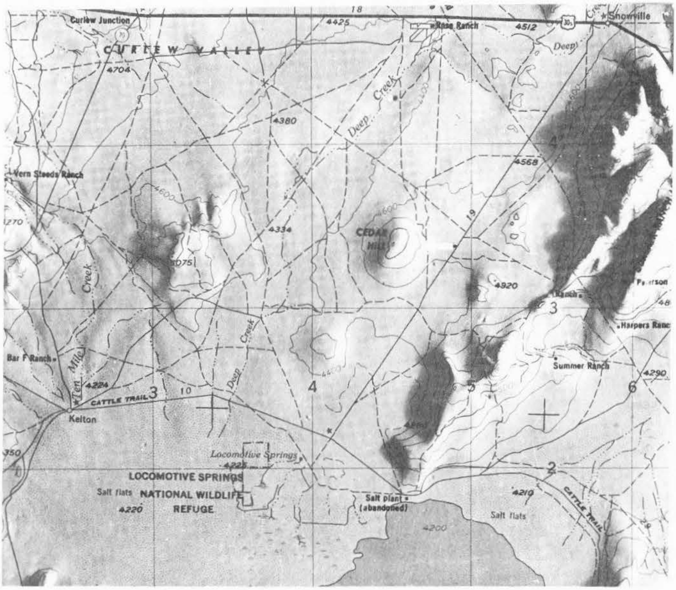

Figure 1. Relief map showing the location of the study area (arrow) in Curlew Valley.

METHODS

Measurement of Density

Absolute counts of the squirrels were not possible because of their small size, shy nature, and use of burrows. Several sampling techniques were used to determine population density during spring, summer, and fall, 1968 and spring 1969.

Capture-Recapture

First-sample techniques. For the capture phase, Sherman box traps (3 X 3 X 10 inches) were distributed on the study area in a 35-yard grid. I set 140 traps for a total of 7 trapping days per census period. Only fair-weather days were used for trapping because antelope ground squirrels are seldom active above ground during inclement weather (Hawbecker, 1953).

All traps were set and baited 1 hour after sunrise. During the summer sampling, traps were checked each day at 10:00 A.M., 2:00 P.M., and 1 hour prior to sunset. During the spring and fall census periods, traps were checked each day at noon and 1 hour before sunset. Traps were always left closed after the last check of each day. The increased trap checking during the summer was scheduled because it was feared that the heat of the day would be detrimental to any animals in the traps. Hawbecker (1958), Allred and Beck (1963), and Bradley (1967) encountered trap mortality while working with this species.

Sunflower seeds were used as bait during all trapping periods. Preliminary tests with captive squirrels indicated that they preferred sunflower seeds to rolled oats and various combinations of rolled oats, honey, and peanut butter.

Squirrels were color-marked for temporary identification during the recapture phase. The molt patterns and dye retention times were such that the same color dye was used for spring and summer captures, but a different color was used for fall captures. During the spring and summer periods, Nyanzol R (red) fur dye was mixed with a commercial cream conditioner in the proportions of 1 tablespoon of powdered dye to 2 ounces of conditioner. After the dye was applied to a squirrel's tail and rump, the squirrel was held for 10 minutes while the dye "set." The squirrel was then rinsed with warm water and released at the trap site. The dyeing procedure for fall captures was the same as for the spring except 1 ounce of black liquid hair dye was added to the dye mixture above. This was necessary because the black dye, with conditioner, did not fully color the white tail hairs of the squirrels. The animals were held 10 minutes before being rinsed and released.

The squirrels were given 2 days to resume their normal activity patterns after the 7 days of trapping and marking. The area was undisturbed during this time except for the 3 hours required to retrieve the 140 traps.

Second-sample techniques. Two methods were used to obtain recapture samples. The first involved walking transects and recording sightings of marked and unmarked squirrels; the second consisted of recording sightings at bait stations.

To determine the locations of the transects, five coordinates were selected at random from a grid map of the study area. These points were used as the starting points for the transects, each 100 yards long. The transects were oriented at right angles to the route used to check traps. Coordinates were selected at random for each of the four seasonal census periods.

Transect counts were performed for 2 days during each census period. All five transects were walked in the morning and afternoon of both days. The sequence of walking was reversed from morning to afternoon and from day to day. Transect counts began 2 hours after sunrise and ended not later than 2 hours before sunset. These times were chosen because antelope ground squirrels are most active during the most comfortable (in relation to temperature and weather) portion of the day (Bradley, 1967).

For each animal sighted, the angle from the transect baseline to the squirrel, the distance from the transect to the squirrel's position, and whether or not the squirrel was marked were recorded first. The transect number, time of sighting, and the squirrel's position when sighted (on the ground or on a shrub or rock) were recorded last.

For each of the four census periods, the locations of six bait stations were selected at random from a grid map of the study area. Each bait station consisted of a circular area 10 feet in diameter and cleared of vegetation. An 8-inch pan filled with empty sunflower seed shells (to discourage caching) was placed in the center of each bait station to be watched. Observations were made, with the aid of 10 X 50 binoculars, from a portable tower 15 feet high.

Three bait stations were watched simultaneously on the first day, and the remaining three stations of the following day.

Observation periods lasted for 2 hours in the morning and 2 hours in the afternoon. Bait stations were watched in succession, 5 minutes per station. A 5-minute rest was taken after each 15-minute sequence of observations. By this system, each bait station was observed for 1 hour throughout the day. These counts began 2 hours after sunrise and ended not later than 2 hours before sunset.

Only those squirrels that entered the cleared area were counted. Squirrels that entered the area, departed, and then re-entered without leaving the field of vision were not recounted.

Hayne Strip-Census

Enough information was collected during the transect counts to estimate population density by strip-census methods. Hayne's (1949) method, a revision of the King Method (Leopold, 1933), was selected for processing the data.

The Hayne strip-census method is based on the assumptions that each animal has a particular flushing distance and will flush only when a disturbance occurs within that distance. Flushing distance here was the distance from the observer to the animal along the line of sight, and was recorded during collection of the data. By averaging the numbers of animals seen at their individual flushing distances, a weighted mean flushing distance was obtained. This was used to determine the effective strip width. Hayne's equation is:

$$N_t = \frac{C}{2L} \left(\frac{F_1}{d_1} + \frac{F_2}{d_2} + \frac{F_3}{d_3} + \text{----} \frac{F_n}{d_n} \right)$$

where:

N_t = the population density estimate per unit area

C = the conversion factor when L and d are in different units than N_t

L = the length of the strip

F = the number of animals seen at each flushing distance

d = the individual flushing distance for each animal sighted.

Census Dates

I sampled at three periods in 1968 and one in 1969. The first period was during early spring, 1968, during the breeding season to provide an estimate of the pre-natal population density. The second census was taken immediately after the 1968 breeding season to provide a measure of reproductive output. The third census was taken during the fall of 1968, just before commencement of cold weather, to estimate fall-to-spring mortality. The last census was taken during early spring 1969. No census was scheduled for winter, 1968, because the squirrels' activity patterns are greatly restricted during winter months (Hawbecker, 1953).

Natality Measurement

Field Collections and Cursory Necropsy

Beginning in March, 1968, monthly collections of ground squirrels were made from the Curlew Valley population. Squirrels were collected during the day with a .410 shotgun and snap traps baited with peanut butter and sunflower seeds. Because of low densities, squirrels were collected primarily from areas of abundance--rocky outcrops on hill-sides and stands of juniper.

A tag containing the collection number, date, location, time of collection, air temperature, cloud cover, wind speed, vegetation in which collected, sex, and weight was attached to each squirrel. All squirrels were placed in plastic bags immediately after being collected, transported to Utah State University at the conclusion of the daily collection period, and placed in a freezer until necropsied.

Before necropsy, 15-30 squirrels were removed from the freezer and thawed for 3-5 hours. Each animal was reweighed, measured (head-body length, tail, and right hind foot), and necropsied while pinned to a 5 X 10 X 2 inch paraffin block. Entire female reproductive tracts were removed, as were the testes from the males and adrenals from both sexes. These were labeled and fixed for 24 hours in Bouin's fixative and then transferred and stored in 70 percent ethanol. Stomachs and their contents were removed, labeled, and stored in 70 percent ethanol. Mandibles, with molars intact, were removed from all squirrels, labeled, air-dryed, and stored in a jar for later use.

Laboratory Analysis

Tooth sectioning and aging. Ground squirrel young-of-the-year, hereafter referred to as young, were easily distinguished from adults and yearlings for approximately 3 months after birth by body size and dental characteristics. Criteria were available that extended the aging period to 120 days (Neal, 1965c). Counting the cementum annuli in the molar teeth was the only suitable technique for aging squirrels accurately past 4 months of age.

Van Nostrand and Stephenson (1964) were the first investigators to report the presence of tooth cementum annuli in beaver. Since that study, Adams and Watkins (1967) reported annual rings in the teeth of California ground squirrels (Spermophilus beecheyi), and Montgomery (1969) found cementum annuli in Uinta ground squirrels (Spermophilus armatus).

Air-dryed mandibles, with teeth in place, were first decalcified for 32 hours in a solution of 1 part formalin, 5 parts formic acid, and 20 parts water (Linhart and Knowlton, 1967). The third molar was then removed from the mandible with the peridontal membrane and connective tissue attached. The tooth and associated tissues were dehydrated for 15 minutes in a bath of isopropyl alcohol and glycerine mixed 8:2 respectively. Next, the tooth was cleared in two 10-minute baths of absolute ethanol and one 10-minute bath of xylene. The tooth and tissues were then infiltrated in three baths of Paraplast, 1 hour for the first bath and 2 hours for each of the next two baths. They were then embedded and longitudinally sectioned at 8 microns with these sections placed on a slide. Finally, the sections were progressively cleared with a xylene-ethanol series, stained in Harris' hematoxylin and eosine, fixed with an ethanol-xylene series, and mounted in Permount.

After the Permount dried for 36-48 hours, the slides were scanned with the aid of a 40X binocular microscope to locate the annuli. When found, the annuli were examined and counted under 100X magnification. This higher magnification was necessary because lesser annuli occasionally occurred between the rings and were not readily identifiable under 40X magnification.

Since cementum-annuli aging criteria have not been published for antelope ground squirrels, the criteria described by Adams and Watkins (1967) for California ground squirrels were used. The tooth cementum showed alternate dark and light layers, and the number of light rings aged the squirrels to the nearest year. Teeth annuli of squirrels believed to be 1 to 5 years old were distinct (Fig. 2).

Ovarian analysis. Corpus luteum and corpus albicans counts were used to estimate ovulation rates. Ovaries previously fixed in Bouin's solution and stored in ethanol were air-dryed for 30 seconds and weighed on a Sartoris electric balance. Because they were so small, the ovaries had to be mounted before the corpora lutea and corpora albicantia could be accurately counted.

The ovaries were dehydrated in one bath of 80 percent ethanol, one bath of 95 percent ethanol and two baths of absolute ethanol. They were then cleared in two baths of xylene, infiltrated in three changes of Paraplast, embedded, and sectioned at 10 microns. Every tenth section was mounted in series. The sections were then cleared with a xylene-ethanol series, stained in Harris' hematoxylin and eosine, fixed with an ethanol-xylene series, and mounted in Permount. Once the Permount hardened, the slides were inspected under a dissecting microscope. The corpora lutea and corpora albicantia were counted under 4X magnification.

Uterine analysis. The uterus was laid on a glass slide moistened with distilled water immediately following removal of the reproductive tract. It was then spread to display the placental scars and was examined under a 2X dissecting microscope. Scars appeared as small, dark, eliptical swellings on the uterus wall and were easily counted.

Figure 2. A photomicrograph of an antelope ground squirrel molar showing distinct cementum annuli (arrow) used in aging.

Mortality Measurement

Adult and Yearling Mortality

Because a wild animal's death is usually quite secretive, mortality rates were estimated from retrap data and age distributions in monthly collections. Ricker's (1958) formula was used to calculate a survival estimate for the study area squirrels from retrap data. This figure was subtracted from 1.00 and multiplied by 100 to obtain an estimate of the percentage mortality. Ricker's formula is:

$$S = \frac{R_x M_y}{M_x \, (R_y + 1)}$$

where:

M_x = the number of squirrels marked during the first season

M_y = the number of squirrels marked during the second season

R_x = the number of recaptures of first-season squirrels during the second season

R_y = the number of recaptures of second-season squirrels during the second season

S = the survival rate between seasons.

This formula was used to calculate adult-yearling mortality for spring-to-fall, summer-to-fall, and spring-to-spring. In addition, the fall density estimate was adjusted by excluding the percentage of young in the collection. This adjusted density estimate was then divided by the spring density estimate and the answer subtracted from 1.00 and multiplied by 100 to obtain the spring-to-fall adult mortality. An additional spring-to-spring mortality estimate was calculated independently of the estimate from the retrap data. A fall-to-spring mortality estimate was derived using the density estimates; this was then combined with the previously calculated spring-to-fall estimate using another formula from Ricker (1958):

$$a = m + n - mn$$

where:

m = the spring-to-fall mortality

n = the fall-to-spring mortality

a = the mortality for the year period.

Young Mortality

Young (squirrels under 10 months old) mortality for the study-area squirrels was estimated from retrap data in the same manner as the adult-yearling mortality. The data were not complete, and only summer-to-fall mortality could be estimated. An estimate of the pre-emergence mortality for the collected squirrels was obtained by using the difference between mean corpora lutea and mean litter counts. Post-emergence mortality for collected animals was estimated using hypothetical numbers adjusted according to the age distribution ratios and mortality estimates for adult and yearling squirrels.

RESULTS

Sex Structure

Adults

Animals 10 months old or older were classed as adults. The adult sex ratios of squirrels in the collections from September through December, 1968 (Table 1) did not differ from a 50:50 ratio at the 5 percent level ($\chi^2 = 0.36$). The ratios from early spring through summer (March-August, 1968, $\chi^2 = 14.78$, and March-April, 1969, $\chi^2 = 5.32$) were different from 50:50 at the 5 percent level.

Sex ratios of adult squirrels live-trapped on the study area are based on three sampling periods (Table 1). Sex ratios for March ($\chi^2 = 1.32$) and July, 1968 were not different from 50:50 at the 5 percent level. The November ratio was statistically different from a 50:50 ratio at the 5 percent significance level ($\chi^2 = 5.32$) and also was sharply lower than the March and July ratios: only 17 percent males. The March, 1969 census yielded only female squirrels; consequently, no meaningful sex ratio was obtained. The overall sex ratio for adult, live-trapped squirrels on the study area was 29 percent males. This, as well as the November ratio, was less than 50:50 at the 5 percent level ($\chi^2 = 5.76$).

Young

Sex-ratio estimates for young in the monthly collections were available only for the months of May-December, 1968 (Table 1). The sex ratios for May-June ($\chi^2 = 0.74$) and July-August ($\chi^2 = 1.80$), though

Table 1. Sex ratios of antelope ground squirrels in the monthly collections and live trapped on the study area during March, July and November, 1968.

Months	Collections				Live Trapped			
	Adult sex ratio males:females	Sample size	Young sex ratio males:females	Sample size	Adult sex ratio males:females	Sample size	Young sex ratio males:females	Sample size
1968								
March April	18:82	28	-----	--	33:67	12	-----	--
May June	34:66	26	41:59	33				
July August	25:75	11	37:63	20	50:50	10	43:57	7
September October November December	44:56	25	21:79	14	17:83	12	-----	--
1969								
March April	17:83	12	-----	--	-----	--	-----	--

slightly favoring females, were not statistically different from a 50:50 ratio at the 5 percent level. The ratio for September-December was different at the same significance level ($\chi^2 = 4.48$).

A young sex ratio for the study area population (Table 1) was available only for July, 1968, because the young were not available in March, and by November, the live young could not be positively distinguished from adults or yearlings. The ratio for this period was not different from 50:50 ($\chi^2 = 0.14$).

Age Structure

Monthly Collections off the Study Area

Age-structure data were grouped by months (Table 2) for three age classes: young (less than 10 months old), yearlings (10 months to 2 years), and adults (2 years and older).

Young did not emerge from the natal burrows until about the middle of May and were not available for collection earlier in the spring. Individual monthly collections from June-December, 1968 contained as high as 65 percent young (Table 2).

The pre-natal spring populations for March and April, 1968 and 1969 were divided 54 percent and 38 percent yearlings, 28 percent and 44 percent 2 year olds, and 18 percent and 18 percent 3 year olds and older. Percentages were not calculated for ages above 3 years since only 8.9 percent of the squirrels collected were 3 or older. The oldest squirrels collected were estimated to be 5 years old and they composed 1.2 percent of the entire collection.

Table 2. Percentages of young, yearling, and adult antelope ground squirrels in the monthly collections.

Months	Young-of-year	Yearlings	Adults	Sample size
1968				
March April	00	54	46	28
May June	56	14	30	59
July August	65	22	13	31
September October November December	36	38	26	39
1969				
March April May	00	38	62	16

Natality

Breeding Dates

Weights of the testes and ovaries as a percentage of the corrected body weights (i.e., weight of stomach contents deducted) were averaged by the month and plotted (Fig. 3). Testis weights were lowest from June-September. In October, they began to increase. By the end of December, the testes were well developed and had descended into the scrotum. The largest proportional weights were probably reached sometime between January and March. After March, they began to recede; and by the end of May, they were again abdominal.

The ovaries also exhibited a comparative weight change, although to a lesser degree than the testes. In general, the ovaries weighed the least during the summer months July-October. The period of high ovarian weight, December-June, corresponded to the period of high testis weight.

Neal (1965a) reported the first evidence of female Harris antelope ground squirrels (Citellus harrisi) breeding in Arizona as February 18. Female squirrels in copulating condition (with distended labia and perforate vulvae) were collected from the Curlew Valley population on March 1, 1968 and February 28, 1969. Necropsy of these squirrels and visual inspection of the uteri disclosed no implantation sites.

The 1968 conception date was derived by calculating back from the collection date of the first young. On May 5, four young squirrels were collected at a nest site. The size and activities of these squirrels at the time of capture suggested that they could not have been active above ground for more than a few days. Young antelope

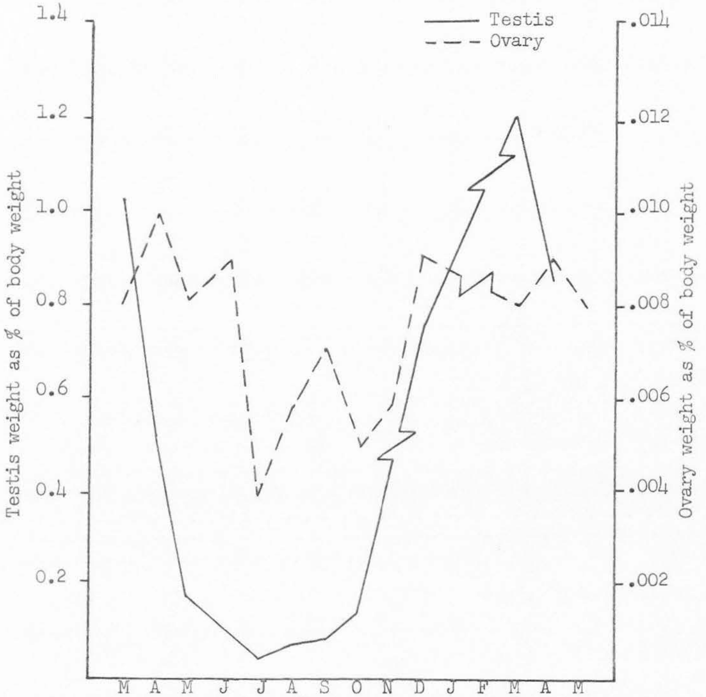

Figure 3. Monthly mean testis and ovary weights from adult antelope ground squirrels collected in 1968 and 1969.

ground squirrels are confined to the nest and burrow system for about 6 weeks after their birth (Neal, 1965c) before becoming active above ground. By subtracting 42 days (6-week burrow confinement) and the 29-day gestation period (Neal, 1965c) from May 5, an approximate conception date of February 24 was obtained. When latitudinal differences were considered, this date is in agreement with that reported by Neal (1965a).

No animals were collected after May 7, 1969, and no young were collected in 1969. The breeding date could not be substantiated by comparison with the emergence date of the first young as above.

Of the 18 adult and yearling female squirrels collected during April, 1968 and April, 1969, only one (a 2 year old) had not been pregnant. This one showed no implantation sites, and no corpora lutea were found in the sections made from her ovaries. The remaining squirrels, 12 from 1968 and 5 from 1969, had all given birth prior to April 10 (the last date in April when female squirrels were collected). The reproductive tracts of all 17 squirrels indicated that the births had been recent. The criteria used to determine this were large, flacid, heavily vasculated uteri with conspicuous longitudinal striations caused by muscular contractions following labor.

Of 13 females captured in May, 5 in June, and 3 in July, 1968, all had been pregnant. None of these squirrels bore evidence of having recently given birth. Because of this, and considering the gestation period and burrow confinement time, I believe the 1968 breeding period was concentrated about the 18-day period from February 24 to March 13.

Production of Young per Female

Ovulation rates. Ovulation rates, defined as the mean number of eggs ovulated per pregnant female collected, were estimated from the mean numbers of corpora lutea and corpora albicantia in the ovaries of 49 adult and yearling female squirrels collected from March-June, 1968, and March-May, 1969 (Table 3). The mean corpora lutea and corpora albicantia for females conceiving in the 1968 collection was 7.5, and in 1969, it was 7.6.

The mean number of eggs ovulated for all yearling and adult female squirrels collected in March-June, 1968, and March-May, 1969 was 6.8 ova in 1968 and 7.6 ova in 1969. "Student's" t test revealed a statistical difference between these two rates ($P \leq 0.01$). The mean corpus luteum and corpus albicans counts were statistically greater for female squirrels 2 years old and older (7.1) than for yearling females (6.0) for $P \leq 0.05$. This difference in reproductive potential (ova available for fertilization) was 22 percent in 1968 and 17 percent in 1969.

Conception rates. Conception rates are defined as the percentage of females in the spring population which conceived. This was determined by collections in the months of March-June, 1968 and March-May, 1969. In March, conception was recognized by pregnancy and corpora lutea; in April-June, females which had conceived were recognized by placental scars and corpora albicantia. Placental scars were used even though certain rodents can conceive and carry embryos for short periods, then resorb all of the litter without the formation of uterine scars (Conaway, 1955). All female squirrels lacking placental scars also showed no corpora albicantia.

Table 3. Monthly mean corpus luteum counts from adult and yearling female antelope ground squirrels collected in 1968 and 1969.

Months	A Mean corpora lutea per pregnant female						B Percentage of females conceiving				AxB Mean corpora lutea produced per female	
	1968	n	s	1969	n	s	1968	n	1969	n	1968	1969
March	8.4	8	1.3	8.4	5	1.5	80	10	100	5	6.7	8.4
April	7.5	11	2.9	6.8	5	1.9	85	13	100	5	6.4	6.8
May	7.3	13	1.7	7.7	4	1.7	100	13	100	4	7.3	7.7
June	6.4	5	1.3	---	-	---	100	5	---	-	6.4	---
Means	7.5			7.6			90		100		6.8	7.6

In 1968, the conception rate was 91 percent, and two of the three squirrels collected which had not conceived were yearlings. A Chi-square test revealed that conception was independent of age; although in 1969, the conception rate was 100 percent.

Litter size. Four indicators were used to determine litter size. Corpus luteum counts indicated approximate potential litter size (number of eggs available for fertilization). The mean number of embryos indicated the number of eggs fertilized, implanted, and surviving at the time of collection. In order to estimate the average number of young born, the mean number of placental scars per female that conceived was calculated. Finally, litters were counted at nest sites as a means of estimating the number of young surviving after birth.

The mean corpora lutea for pregnant females collected in 1968 was 7.5, and 7.6 in 1969 (Table 3). There was no difference between these rates ($P \leq 0.01$).

Embryos were counted from eight squirrels collected in March, 1968, and five squirrels collected in March, 1969; no difference was noted between years ($P \leq 0.05$). The combined 1968-1969 mean embryo count was 7.3. There was no statistical difference between this and the 2-year mean corpus luteum count ($P \leq 0.05$).

The mean number of placental scars per female conceiving was 5.2 in 1968, and 6.6 in 1969 (difference between years is not significant for $P \leq 0.05$). The mean for both years was 5.8. There was no difference ($P \leq 0.05$) between the mean placental scars for squirrels 1 year old (5.8) and mean placental scars for squirrels 2 years old and older (5.5). A difference did exist between the 2-year mean embryo count (7.3) and the 2-year mean placental scar count ($P \leq 0.05$).

During the 1968 spring collection, four nest sites were located (none in 1969) and the burrow systems exhaustively excavated. The entire litter was captured at each nest. The numbers of young caught were three, four, five, and six per nest. The mean litter size of young captured at the nest (4.5) was tested against the 2-year mean placental scar count (5.5), and no statistical difference existed ($P \leq 0.05$). A difference was found between nest-site litter size and the 2-year mean embryo count ($P \leq 0.05$). These data suggest a decline from potential litter size (corpora lutea) to realized litter size (young at the nest) of 40 percent.

Density

Capture-Recapture

Two recapture techniques were used to obtain separate samples. The transect and bait-station counts were taken on 4 consecutive days. These two estimates were not different within seasons ($P \leq 0.05$) and were combined by the season (Table 4). These combined data were used to calculate the combined estimates (Fig. 4).

The squirrel population on the study area rose 22 percent from the 1968 spring pre-natal density (1.8 squirrels per acre) to summer post-partum density (1.4 squirrels per acre). The censuses were arranged to sample the post-partum population after the emergence of the young but before emigration.

Table 4. Seasonal estimates of the study area antelope ground squirrel densities by the capture-recapture and strip-census techniques for 1968 and 1969.

Season	Squirrels per acre					
	Capture-recapture				Strip-census	
1968	Transects	Bait-stations	Combined	95% Confidence	Mean Est.	95% Confidence
Spring	1.1	1.2	1.2	± 0.5	1.9	± 1.1
Summer	1.2	1.5	1.4	± 0.3	3.1	± 0.7
Fall	0.7	0.9	0.9	± 0.3	1.7	± 0.6
1969						
Spring	0.5	0.7	0.5	± 0.2	2.4	± 1.1

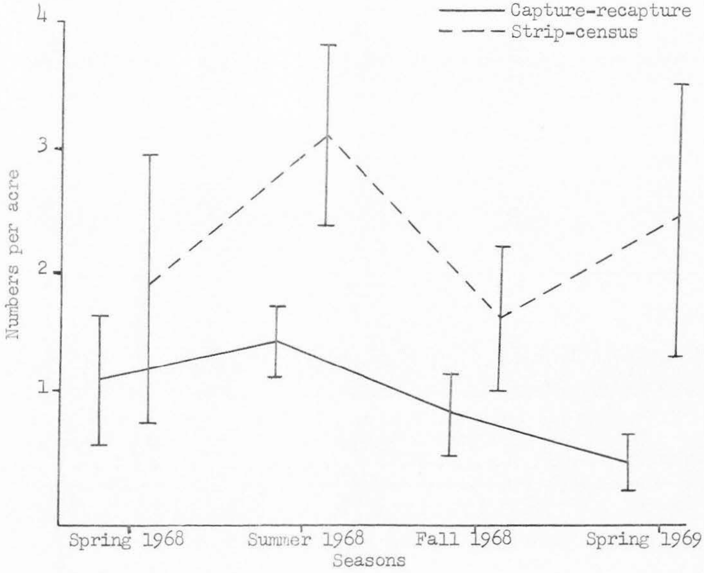

Figure 4. Seasonal estimates of the study area antelope ground squirrel densities by the capture-recapture and strip-census techniques for 1968 and 1969. Vertical lines represent 95 percent confidence intervals.

The capture-recapture census was conducted again in November, 1968 and March, 1969. Between the summer and the fall estimates, the population decreased approximately 41 percent to an estimated density of 0.9 squirrels per acre. In March, 1969, the population was estimated at 0.5 squirrels per acre, a decrease of 37.2 percent from fall, 1968, and a 54.2 percent decrease from March, 1968.

Strip-Census

The strip-census data were collected simultaneously with the transect-count data. This sampling system permitted the calculation of two morning and two afternoon estimates per census period. These were averaged to obtain a mean estimate for each of the four census periods.

The 1968 spring density was 1.9 squirrels per acre. By summer, the density had risen to 3.1 squirrels per acre, a 61 percent increase. The fall, 1968 density was estimated at 1.7 squirrels per acre, and by spring, 1969, had increased to 2.4 squirrels per acre. This constituted an increase of approximately 26 percent from spring, 1968 to spring, 1969.

Mortality

Adult-Yearling

Three methods were used to calculate mortality rates for the adult and yearling squirrels on the study area: (1) Retrap data permitted estimation of spring-to-fall, summer-to-fall, and spring-to-spring mortality (Table 5). (2) The difference between seasonal-density estimates (Table 4) adjusted according to age distribution (i.e., with young deducted from table) (Table 2) was used to calculate spring-to-

Table 5. Seasonal survival and mortality rates for antelope ground squirrels on the study area calculated from retrap data according to Ricker (1958). For derivation of values in table, see page 13.

Time Periods	M_x	M_y	R_x	R_y	S	%q
Adult and Yearling						
Spring-to-Fall	12	12	2	4	.400	60
Summer-to-Fall	17	12	2	2	.471	53
Spring-to-Spring	12	7	1	2	.194	81
Young						
Summer-to-Fall	8	5	3	2	.625	38

fall mortality (53 percent). This latter value is not statistically different from the 60 percent estimated through capture-recapture. (3) Ricker's (1958) formula a = m + n - mn (m was spring-to-fall mortality, n was fall-to-spring mortality) was used to estimate an additional spring-to-spring mortality rate (71 percent). This value is not statistically different from the 81 percent mortality estimated from retrap data.

As an additional check on the mortality for populations over the valley as a whole, a life-table (Table 6) was constructed using the animals from the spring, 1968 collection. When the yearling age class is discounted, the mean, annual mortality rate for ages 2-5 is 60 percent.

Young

Young mortality is often considered in two categories, prenatal and postnatal (Newson, 1964; Gross, 1967). Actual prenatal mortality was not estimated because no near-term fetuses were found in the pregnant squirrels collected. These categories were not suitable for antelope ground squirrels since the young were not available for collection until they were at least 6 weeks old. Consequently, prenatal mortality estimates were extended to include deaths during this period and were termed pre-emergence mortality.

As a conclusion for the project, a collection was to be made of the study area squirrels on 3 consecutive days using snap traps. The same array of traps was used as for the live-trapping, with peanut-butter and sunflower seeds used as bait. The purpose of the collection was to provide reproductive data from the study area squirrels for

Table 6. Time-specific life table for adult and yearling squirrels collected in March, April and May, 1968.

x Age in Years	l_x Number alive at beginning of age interval	d_x Number dying in age interval	q_x Mortality rate for squirrels alive at beginning of age interval
0.8-2.0	18	3	17
2.0-3.0	15	9	60
3.0-4.0	6	4	67
4.0-5.0	2	0	0
5.0-older	2	2	100
Totals and Mean	43	18	42

comparison with data from squirrels collected throughout Curlew Valley. The traps were set and checked for 6 consecutive days; no squirrels were caught.

Pre-emergence mortality, from ovulation through emergence of the young from their burrows, was 40 percent in 1968 for the collected squirrels [mean corpora lutea (7.5) minus mean litter size (4.5) divided by mean corpora lutea (7.5)]. This included the loss of ova, loss of embryos, and loss of young before emergence.

Post-emergence mortality in 1968 was calaulated as follows (representation in Table 7). The percentages in each age class in the July and August, 1968 collection (Table 2) were taken as absolute numbers in a hypothetical population. The adult and yearling values were reduced by 53 percent (summer-to-fall adult-yearling mortality estimate from Table 5), providing hypothetical fall survivors in these age classes of 10 and 6 respectively (Table 7), or 16 total.

Returning to the age structure data we find (Table 2), the ratio of young to combined adults and yearlings to be 36 to 64. If this ratio is used to estimate the absolute number of young surviving in the hypothetical population we have 36/64 as x/16 or 9 young (Table 7). With 65 young alive in July-August, the summer-to-fall, young mortality is 65 minus 9 divided by 65 or 0.86 or 86 percent.

Mortality of young, (a) from conception to November, 1968, was 92 percent as calculated from the Ricker (1958) formula, $a = m + n - mn$ (m was pre-emergence mortality, n was post-emergence mortality). First year mortality estimated by Hawbecker (1958) was 80 percent for Nelson antelope ground squirrels. Post-emergence mortality for the study area squirrels (37.5 percent) from June-November, 1968, estimated from retrap data (Table 5), is considerably different from the 1968 post-emergence mortality estimate (86 percent) derived from the age distribution data. It was not used to calculate total mortality because it could not be established that differential emigration did not occur between summer and fall and this would have affected the estimates.

Table 7. Estimation of summer-to-fall, 1968 mortality in young ground squirrels. See text for explanation.

	Young-of-year	Yearlings	Adults
1. July-August, 1968 population (from Table 2)	65	22	13
2. Deduct 53 percent mortality (from Table 5)		10	6
		16 (Yearlings + Adults)	
3. September-December, 1968 population composition (from Table 2)	36	38	26
		64 (Yearlings + Adults)	
4. Determine September-December number of young by proportion $\frac{36}{64} = \frac{x}{16}$	9		
5. Estimate of summer-to-fall young mortality $\frac{65 - 9}{65}$	0.86		

DISCUSSION

Sex Structure

Neal (1965b) listed by sex, 103 Harris antelope ground squirrels collected in southern Arizona from July, 1961 through July, 1962. This permitted calculation of sex ratios for his collection (Table 7). The ratios for only one of the five groupings differed from a 50:50 ratio: the September-December group showed a ratio of 70 percent males. This is in direct contrast to the results of this study since in none of the groups is the percentage of males greater than 50 percent. Hawbecker (1958) listed a sex ratio (obtained by live trapping) of 57 males to 43 females. He stated that the estimate was biased since males were caught first and scared females from the traps.

The sex ratios for the young squirrels collected shortly after emergence from the natal burrows was 41 percent males to 59 percent females. The percentage of males dwindled consistantly throughout the remainder of the year to 21 percent males 6 months after emergence. Nine months after emergence, the ratio was reduced to 17 percent males to 83 percent females. Evans and Holdenried (1943) reported the same phenomenon in Beechy ground squirrels (Citellus beechi), although the reduction of males was not so pronounced. Rongstad (1965) also reported a low percentage of young, male, thirteen-lined ground squirrels (Citellus tridicemlineatus) during late summer: 28 percent males to 72 percent females.

Table 8. Sex ratios of Harris antelope ground squirrels collected in Arizona from July 1961 through July 1962 (Neal, 1965b).

Months	Adult sex ratios		Sample size
	% males	% females	
January February	61.0	39.0	23
March April	46.0	54.0	24
May June	35.0	65.0	17
July August	33.0	67.0	9
September October November December	70.0	30.0	30
Totals	53.0	48.0	103

Adult sex ratios for the collected animals changed from a low percentage of males in the spring, 18 percent males, to a ratio of 44 percent males to 56 percent females. This condition, an excess of female animals, appears normal in many mammal populations although it has not been thoroughly studied (Lack, 1954, pp 111-113).

The March-April, 1968 and 1969 sex ratios from my collections (Table 1) show lower percentages of males than does the March-April ratio obtained from Neal's data. One possible explanation for this is that collecting by shooting may not give a random sample with respect to sex during the early spring months. Of 28 squirrels I collected in March-April, 1968, 23 were females and 17 of these were shot on the ground; only 6 were taken on elevated surfaces such as shrubs or rocks. During the same period, only five males were collected, but all were shot on elevated surfaces. The March-April, 1969 collections show similar results, although the numbers are less. Of 10 females collected, 8 were shot on the ground. Only two males were collected, but both were shot on elevated surfaces.

These locations at the times of collection suggest that males spend more time above the ground surface than do females. Because of this and the squirrel's keen eyesight, males would be considerably more difficult to stalk and shoot.

Litter Size

A mean litter size (young born alive) within the range of 4.5-5.5 young is lower than the litter size (6.5) reported by Neal (1965a) for Harris antelope ground squirrels. Lord (1960), in his study of litter size and latitude, used 7.0 as the typical antelope ground squirrel litter size and concluded that latitude has no effect on litter size in ground squirrels. Rongstad (1965) found a lower-than-expected litter size (when compared with litter size of the same species from southern latitudes) for thirteen-lined ground squirrels in southern Wisconsin. He suggested the possibility of a negative correlation between litter size and latitude.

Neal (1965a) did not define litter size, but rather he listed means for post-partum placental scars, birth records of captive female squirrels, and embryo counts. His "average of young born" is the average of all these plus a mean of 6.4 young from the autopsy records of another investigator. His assumption, that placental scars, embryos, fetuses, and young born alive are equal units to be grouped for a litter size estimate, seems unwarranted in view of Conaway's (1955) discussion of placental scar formation.

My data indicate a mean embryo count of 7.3 (n = 13 females) and Neal's (1965a) data agree with 7.3 (n = 7 females). Neal shows a mean placental scar count of 6.3 (n = 11 females); my data yield a mean of 5.8 (n = 38 females). The average number of young alive at the nest also is lower in this study with 4.5 (n = 4 litters) as opposed to 6.0 (n = 2 litters) for Neal.

Density

In order to obtain valid results from the capture-recapture census, five assumptions must be met (Ricker, 1958). (1) All marked individuals must remain identifiable through the census period. (2) There must be no differential natural mortality. (3) Equal vulnerability to recapture must exist for marked and unmarked animals.

(4) One sample (either capture or recapture) must be taken at random. (5) Immigration, emigration, and recruitment must be negligible between marking and recapture.

Assumption (1) was not violated; the squirrels retained the dye marking throughout each census period. Assumption (2) was considered valid because the mortality rates from the monthly collection and the estimates for the study area squirrels were statistically equal and no mortality was traced to mishandling during the capture phases of the study. To insure the validity of point (3), recapture techniques were different from capture methods. Point (4) was valid because the transects and bait stations were located at random for each seasonal census period. Point (5) could not be validated, but the effects from violation of the assumption were minimized by reducing the time between capture and recapture, and by arranging the censuses so recruitment did not occur during a census period.

As with the capture-recapture census, certain assumptions must be met to obtain reliable results from the Hayne strip census: (1) Animals flush at various distances. (2) The animals (with regard to flushing distance) are scattered over the study area at random. (3) The weighted average flushing distance is a good estimate of the true average flushing distance of the animals throughout the population.

Assumption (1) was true during this study. The mean flushing distance for 82 sightings was 16.4 yards with a range of 4-36 yards. By far, the most frequent distances were between 9 and 12 yards (Fig. 5).

In theory, if animals are evenly distributed throughout an area, the average of a distribution of the sighting angles will be approxi-

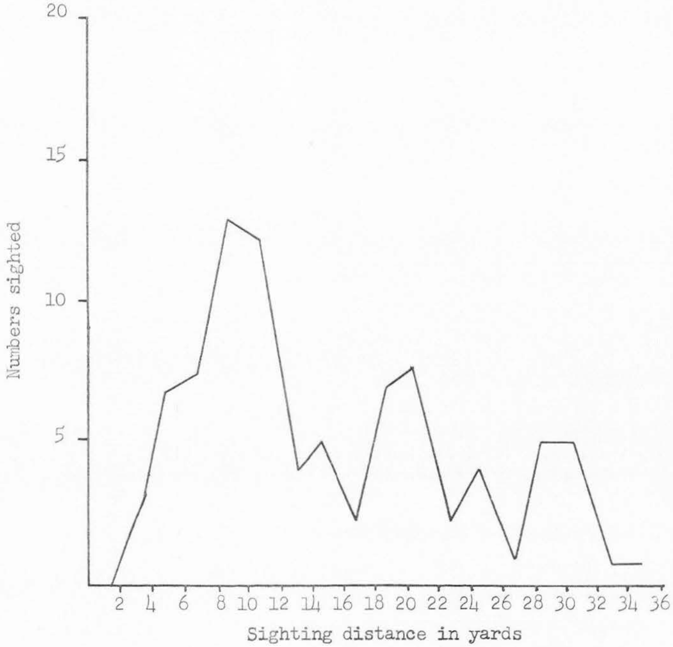

Figure 5. Sighting distances of 82 antelope ground squirrels sighted on the study area during the seasonal censuses.

mately 33 degrees regardless of the flushing distances (Hayne, 1949). A goodness-of-fit Chi-square test revealed the sighting angles recorded for the study area squirrels were significantly less than 33 degrees for all seasons. Not only were the sighting angles small ($\bar{X}$ = 21°), but the lateral distances were short ($\bar{X}$ = 4.6 yards), suggesting the possibility of the squirrels not being scattered at random throughout the area (Fig. 6), thereby violating assumption (2). A possible explanation is that the squirrels were able to anticipate the census route from noises made by the investigator. Squirrels with lateral distances over 4.6 yards would have wide enough sighting angles at their flushing distances to be content to remain still and attract little attention. Conversely, those squirrels with short lateral distances would flee and attract attention.

Assumption (3) cannot be substantiated because there was no way to be certain each squirrel was seen as it flushed. Many could have traveled some distance before being seen. Furthermore, there was no way to eliminate the possibility of a recount. Some of the unmarked squirrels could have been recounted at various distances. One animal recounted with a short flushing distance will raise the population estimate proportionately more than one animal recounted with a long flushing distance.

Flyger (1959) used several methods to estimate gray squirrel (Sciurus carolinensis) population densities and concluded trap-sight data were least biased. Edwards and Eberhardt (1967) were satisfied to use the capture-recapture technique with sightings of dye-marked animals as a means of establishing cottontail rabbit (Sylvilagus floridanus) densities. Robinette et al. (1956) found the Kelker Belt

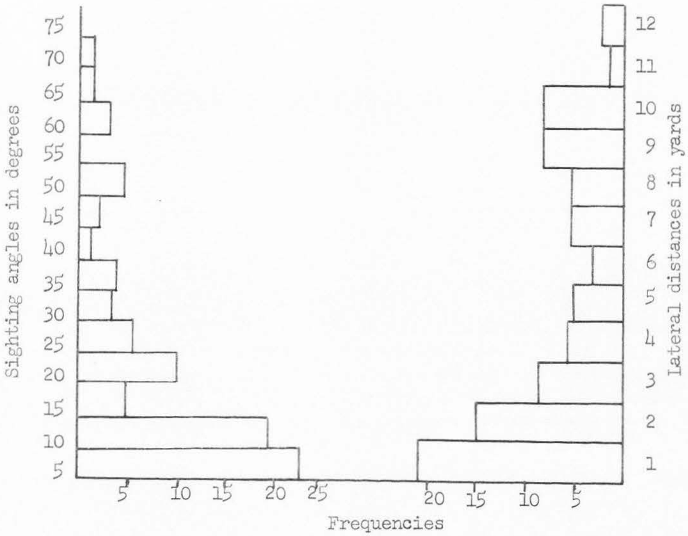

Figure 6. Sighting angles and lateral distances for the squirrels sighted on the study area during the seasonal censuses.

Transect the most accurate strip census technique. It was not used here because the data were insufficient to establish seasonal belt widths. Hayne's (1949) method was selected and, because of my field experiences and the biases explained previously, I believe the capture-recapture estimates best reflect the squirrel densities from March, 1968 through April, 1969.

I located only one reference that reported antelope ground squirrel densities (Bradley, 1967). Densities in southern Nevada were given as 16.5 squirrels per square mile in the summer and 90 squirrels per square mile in the fall. These figures suggest an increase of approximately 446 percent from summer to fall. Bradley (1967) listed no causes for this increase but did mention that the young began entering the population in July and August and presumably the rise could be attributed to recruitment.

Throughout the course of this study, no drastic seasonal density changes were encountered. Density estimates for spring and fall were as much as 4.7 times higher than on Bradley's area. Young squirrels began emerging from natal burrows in May, and recruitment continued through June. A period of low productivity occurred in 1968 when an average of only 4.5 young survived at the nest. The density estimates from the capture-recapture census show a declining population from spring, 1968 to spring, 1969.

Because the study area was located in ideal habitat, i.e., on a sandy hillside close to dense juniper stands, the densities listed may not be representative of the densities in lesser habitat throughout Curlew Valley. I believe they do represent the squirrel densities in similar habitat within Curlew Valley.

Mortality

Adult-Yearling

The mean, annual mortality rate (Table 6) for adult squirrels (2 years and older) in the spring collection is slightly lower than the spring-to-spring mortality estimated for the study area squirrels by Ricker's formula (Table 5). These rates are in agreement with the 60 percent annual mortality rate reported by Hawbecker (1958) for well established, adult, Nelson antelope ground squirrels.

The percentages of yearlings in the 1968 and 1969 spring collections, 54 percent and 38 percent respectively, reflects low post-emergence survival of young. When compared with the adult percentages, the ratios of yearlings:adults are not statistically different at the 5 percent level. A pre-natal spring ratio of adult:yearling Uinta ground squirrels of approximately 50:50 is not unusual during periods of high population density (D. F. Balph personal communication). The first-year mortality rate for squirrels collected in the spring of 1968 (Table 6) seems too low. I believe this is because yearlings were disproportionately represented either through bias in the collecting method or because of some selective mortality within the ground squirrel population that affected the older animals in that year. King (1955) found in a population of black-tailed prairie dogs (*Cynomys ludovicianus*) the survival rate was higher for adults than juveniles. Rongstad (1965) reported this situation in a population of thirteen-lined ground squirrels as did Amend (1970) for a population of Uinta ground squirrels.

Young

The summer-to-fall mortality calculated from retrap data (Table 5) is considerably lower than the mortality rate calculated by the difference between the summer and fall age distributions. The 1968 fall age distribution showed 36 percent young. By spring, 1969, these squirrels would be classed as yearlings; the percentage of yearlings in the spring, 1969 collection was 38, suggesting a constant mortality rate through winter in all age classes. The age distribution figures indicate a mortality rate of approximately 86 percent for the young from midsummer through fall. This seems reasonable since this would be the period when the young are most active above ground and most susceptible to avian and non-fossorial predators.

Predation

Potential predators including coyotes, badgers, weasles, rattlesnakes, ravens, owls, hawks, and eagles regularly traveled through or over the study area. It is not likely that coyotes contributed heavily to the squirrel mortality. Ferrel et al. (1953) found no antelope ground squirrel remains in 813 coyote stomachs collected in California. Further, no antelope ground squirrel remains were found in coyote stomachs collected in Curlew Valley and Box Elder County, Utah from 1967-1969 (F. W. Clark personal communication).

Badgers are known to prey on ground squirrels (Snead, 1942; Thomas, 1963; Jense, 1968) and, in the sandy soil of the study area, would have little difficulty capturing them. However, no fresh badger diggings were found on or near the area during the study. Only one weasel was caught on the area and appeared to have entered the trap in search of or in pursuit of a pocket mouse, the remains of which were in the trap with the weasel. Kangaroo rats, pocket mice, and deer mice were all abundant on the area and seem more appropriate prey even though Hawbecker (1953) lists weasels as predators on Nelson antelope ground squirrels.

Evans and Holdenried (1943) found rattlesnakes responsible for a portion of the mortality of young Beechy ground squirrels. Only one rattlesnake was found on the study area, but, since they are most active at night, the probability of finding them was small. They could have been a factor contributing to the low number of young appearing on the area in 1968.

During the spring and early summer, several days were spent watching the study area from a blind in a nearby juniper. No avian predators were observed taking squirrels. Frequently, ravens, hawks, and eagles were active over the area while squirrels were about. Hawbecker (1953) found antelope ground squirrels had no fear of eagles.

Population Trend

The capture-recapture estimates (Fig. 4) suggest 1968 was a year of population decline. This decline resulted from several factors: (1) during the 1968 breeding season ovulation per female squirrel was low--6.8 ova as opposed to 7.6 in 1969; (2) mean litter size as recorded at the nest was unusually low for a species of ground squirrel--4.5 young, indicating high young mortality in that year; (3) there was low post-emergence survival of 1968 young as shown by the low percentage of yearlings in the spring, 1969 collections--38 percent as compared with 54 percent in spring, 1968; (4) low spring, 1968 to spring, 1969 survival of adults and yearlings (Table 5).

I can suggest no single cause for higher mortality rates during 1968. The climatic conditions were such that vegetation production was relatively high. Rainfall in 1968 was above average and early spring temperatures were mild. These conditions point to what should have been a period of population increase.

SUMMARY

The objectives of this study were to measure (1) population density, (2) natality, and (3) mortality. Two census methods were used to obtain seasonal density estimates. The capture-recapture techniques yielded lower estimates than the Hayne strip census. However, the strip census was biased. The two capture-recapture techniques gave statistically equal results and therefore the data were combined and used to calculate a third estimate. This was considered the best estimate of seasonal squirrel densities.

A total of 173 antelope ground squirrels were collected and autopsied to obtain data on sex ratios, age structure, natality, and mortality. The sex ratios agreed in part with the sex ratios from live trapping in the study area. They were not in harmony with ratios from data collected in Arizona by Neal (1965a).

No data are known to have been published on the age structure of a population of antelope ground squirrels. The squirrels collected were aged by the number of cementum annuli in the molars. The oldest squirrels were believed to be 5 years old and comprised only 1.2 percent of the collection, while young comprised 38.7 percent.

The estimate of mean corpora lutea was 7.6, the mean embryo count was 7.2, and the mean post-partum placental scar count was 5.8. The mean corpora lutea count for yearlings was significantly lower than the count for adults, and the mean ovulation rate for 1968 was statistically lower than the rate for 1969. An estimate of litter size from four nests gave a mean of 4.5 which is lower than other

investigators have found. In 1968, the conception rate was 91.3 percent with yearlings comprising 75 percent of those not conceiving. In 1969, the rate was 100 percent on a small sample of 14 squirrels.

Young mortality was calculated from ovulation through emergence (a period of 77 days) and from emergence through 10 months. Minimum pre-emergence mortality was 41 percent, minimum post-emergence mortality for collected squirrels was 86 percent, and minimum mortality, March-November, 1968, was 92 percent.

Adult-yearling mortality was calculated seasonally as well as annually. Spring-to-spring mortality for study area squirrels calculated from retrap data was 81 percent. Spring-to-spring mortality calculated from age distribution data and Ricker's formula was 71 percent. Spring-to-fall mortality for 1968 was calculated from density estimates and age distribution data (53 percent). The mortality for the collected squirrels as calculated from the life-table was 60 percent for squirrels aged 2-5 years.

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