LOCAL DISTRIBUTION IN A POPULATION
OF UINTA GROUND SQUIRRELS

by

Robert E. Walker

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
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in
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Approved:

Major Professor

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Logan, Utah

1968
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Robert E. Walker
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ABSTRACT

Local Distribution in a Population of Uinta Ground Squirrels

by

Robert E. Walker, Doctor of Philosophy

Utah State University, 1968

In an attempt to describe, explain, and show the demographic significance of annual variations in the nesting distribution of Uinta ground squirrels, a study was conducted during the summers of 1964 through 1967 in northern Utah. Procedures included both trapping and direct observation.

It was found that females tended to nest in open, previously inhabited, grassy areas. Males resided throughout a variety of habitats.

This typical nesting distribution was established initially in the summer by juveniles shortly after they first appeared aboveground. The extent to which the distribution was maintained the following spring depended largely upon the number of females which emerged from hibernation and the pattern in which they emerged. The number of females which appeared depended upon the previous year's breeding density and productivity. The pattern of emergence appeared to be a function of an inherent pattern of physiological arousal from hibernation and the prevailing weather conditions.
The number and sequence of emergence of females in the early spring affected breeding and social organization in a manner which limited the number of females which retained residences in the study area. This determined the actual breeding density. In addition, emergence influenced the production of offspring by altering both the breeding density and the number of non-productive females in the population.

The adaptive significance of the system and its applicability to other species are discussed.
INTRODUCTION

The term "local distribution" is defined herein as the dispersion of individuals within a population. As such, local distribution is the result of a multitude of interacting environmental and behavioral factors, both past and present.

While numerous studies of mammalian populations have described local distributions and established correlations between these distributions and specific environmental influents, few have contributed substantially to a comprehensive understanding of why the members of these populations are distributed in the manners observed or why their distributions vary from year to year. Accordingly, the study described herein is an attempt to explain annual variations in the local distribution observed in a population of Uinta ground squirrels (Citellus armatus Kennicott) from the standpoint of both their ecology and their behavior.

The study forms an integral part of a broader investigation designed to clarify the role of behavior in regulating animal numbers. The parent investigation, begun in 1964, comprises three phases, each of 4 years' duration. The first phase, completed in 1967, has been an attempt to establish norms for the population at its existing density with respect to such characteristics as behavior, demography, and habitat use. In the second phase an effort will be made to establish comparable statistics for the population at an experimentally maintained lower density, approximately 25 percent of the natural mean density. During the third phase the same parameters will be investigated as the
population is permitted to increase by removal of the induced restraints on its growth. The present study, together with two concurrent studies (Burns, 1968; Robert P. McQuivey, personal communication), is a contribution to the initial phase of the long-term investigation.

The objectives of the study are four:

1. To describe the annual distribution of the resident squirrels.
2. To determine what environmental factors are associated with this distribution.
3. To determine how this distribution is established each year.
4. To determine what effects, if any, this distribution and its establishment have on the annual breeding density and productivity of the population.

Until recently little information pertinent to the local distribution of the Uinta ground squirrel was available. Howell (1938) described the species as "... occupying a rather limited area in the mountains from southern Montana south to Utah," therein inhabiting "... dry meadows, pasture lands, and cultivated fields in high valleys ..." and ranging into "... mountain meadows nearly to timber line ...". Howell suggested, however, that these animals "... prefer moist locations near water, especially where the vegetation is rank." He further noted that "... they live in large colonies in burrows ..." and "... spend only about 5 months of the year above ground, the remaining period being spent in estivation and hibernation." He described the typical season of activity as being between early April and late August. Davis (1939), Durrant (1952), and Durrant and Hansen (1954) later reiterated these observations. However, Davis suggested that the
common association of the species with moisture is a direct result of
the coincident presence of green vegetation rather than of the water
itself.

Studies of other species of ground squirrels, particularly those
of *Citedllus beecheyi* (Evans and Holdenreid, 1943; Fitch, 1948; Linsdale,
1946; Storer, Evans, and Palmer, 1944; Tomich, 1962), *C. beldingi* (Mc-
Keever, 1963), *C. columbianus* (Manville, 1959; Shaw, 1925a, 1925b,
1925c), *C. lateralis* (McKeever, 1964), and *C. tridecemlineatus* (Criddle,
1939; McCarley, 1966; Rongstad, 1965; Wade, 1927, 1948, 1950), provided
some insight into the problem of local distribution in *C. armatus*. How-
ever, it was not until Balph and Stokes (1963) described the general
ethology of a portion of the population with which the present study is
involved that a firm foundation for the study was established. Further
information was provided when Balph and Balph (1966) described and ana-
lyzed the causes and functions of calls given by members of the same
population.

Concerning the seasonal chronology of the population, Balph and
Stokes wrote:

Ground squirrels in the study area emerged from hibernation
about April 1. Sexual activity began during the first week in
April and lasted 1 or 2 weeks. The young appeared aboveground the
last week in May. The animals began to disappear underground the
last week in July. By the second week in August nearly all were
underground for the year. (Balph and Stokes, 1963, p. 108)

The animals' compact season of activity, size, trapability, diur-
nal activity, and non-secretive behavior render Uinta ground squirrels
particularly suitable for study in the field.
PROCEDURES

This study was conducted during the springs and summers of 1964 through 1967 on 22 acres of land surrounding Utah State University's Forestry Field Station located 22 miles north-east of Logan, Utah, at an elevation of 6,300 feet (Figure 1).

The center of the study area comprised 2.6 acres of lawn and roadways around the buildings of the Station. The remainder of the area consisted of a mixture of field, brush, and forest (Figure 2).

A 40-foot grid system, designated by numbered stakes at all coordinates, was established over the entire 22 acres. This enabled observers to estimate the location of any event to the nearest one-tenth of a grid section (4 feet).

Dates of all events were recorded in terms of days since the first animal emerged from hibernation, henceforth designated as "d.s.e."

Continually throughout each field season as many members of the population as possible were captured. An effort was made to capture all individuals at least once every 10 days. Squirrels were captured in No. 2 National, and No. 1 Hav-a-hart, live-traps baited with oatmeal. In addition, juveniles were snared at the entrances to the burrows in which they were born.

Animals born in a given calendar year were considered juveniles during that year, yearlings during the following year, and adults thereafter.

For permanent identification each animal was individually toe-
Figure 1. Utah State University's Forestry Field Station (T13N-R3E, Cache County, Utah).
Figure 2. Map of the study area showing buildings, roadways, the four major vegetation types, the grid system, and seven areas selected for detailed study with their respective observation towers.
clipped when initially captured. To facilitate field recognition, each time an animal was captured its fur was marked with a coded number using black Nyanzo1 dye. With the aid of binoculars observers could read the dyed numbers at distances up to 100 yards.

Each time an individual was taken record was made of its identity, location, weight (in grams), and overt reproductive condition. Males were categorized with respect to the positions of their testes, whether abdominal, inguinal, or scrotal. Females were classified according to the appearances of their nipples: (i) not visible; (ii) visible but with surrounding hair unchanged from other ventral hair; (iii) visible and with surrounding hair less dense than, or changed in color from, other ventral hair.

Seven six-grid areas, each 80 X 120 feet, representing different habitats and supporting different numbers of squirrels, were selected within the study area for detailed investigation (Figure 2). Throughout the field seasons of 1965, 1966, and 1967 observations of the activities of animals aboveground in the seven areas were made from conveniently located towers, 12 feet in height. Each of three types of data, recorded in sequences 10 to 15 minutes apart, was collected in an attempt to describe the animals' activities during each 3-hour interval within each 10-day period annually.

To begin a sequence an area was scanned, each individual present identified, and record made of its age, sex, location, and behavior. Note of the type of food eaten was made with each observation of feeding. Six major categories of food were distinguished -- grass leaves, grass seeds, forb leaves, forb seeds, sagebrush (Artemisia tridentata),
and roots. Thus, for each representative area during a specified period of time, one could determine the mean density of squirrels, age and sex ratios, relative frequencies of different types of behavior, and diet. A scan took from 1 to 3 minutes depending on the number of animals present.

For a period of 5 minutes immediately following each scan all social encounters which occurred among the squirrels in an area were described with respect to time, location, individuals involved, and type of interaction. Encounters were classified as playful, sexual, or aggressive. In the case of aggression the initiating individual was identified and the outcome recorded. This procedure provided a means of determining, for any period of time, the frequency and, in the case of aggression, success of social interactions involving different sex and age groups in different areas.

Following each 5-minute recording of encounters, data similar to those taken during scans were collected on the activities of all individuals which could be sighted from a tower. When sightings were completed a new sequence was begun.

Since it was virtually impossible to determine where an animal entered hibernation, a hibernation site was defined as the location from which an animal first emerged in the spring. Recognition of hibernation sites was facilitated by a general snow cover during the early stages of emergence. As many as possible of these sites were located and identified as to the emerging animal and its date of emergence at the outset of each field season.

A nesting site was defined according to one or more of the
following criteria: (i) the location where an animal first emerged in the morning; (ii) the location where an animal finally submerged in the evening; (iii) the location to which an animal carried nesting material; (iv) the location where an animal dug or otherwise displayed renovation of a burrow; (v) the location where a female brought her offspring aboveground for the first time. Throughout the field seasons of 1965, 1966, and 1967 all recognizable nesting sites were located and identified as to occupant and date of occupation.

Reproductive success was determined on the basis of the number of juveniles which appeared aboveground annually. Each year records were kept, wherever possible, of the number of offspring that each female in the study area brought forth from her burrow. Snaring and marking of young squirrels as they emerged, together with intensive observations of known nesting sites of females, facilitated complete litter counts and the establishment of parent-sibling relationships.

Periodically throughout 1966 the vegetation in each of the seven six-grid areas was sampled, according to the method described by Edlefsen, Cook, and Blake (1960), in order to determine the percentage of ground covered by each species of plant present. This procedure provided a quantitative measure of the available sources of food, as well as that of vegetational cover, in the same areas for which detailed information on the density, behavior, and diet of the squirrels was available.
RESULTS AND DISCUSSION

The Population

The size and discernable sex and age structure of the population during each of the four years of the study are given in Figure 3. All adults and yearlings were captured each year, as evidenced by the failure of field personnel, despite sustained effort, to observe or capture unmarked animals of either group after 50 d.s.e. Most juveniles were captured annually but a substantial number of these animals apparently left the population or died before they could be taken. Thus, while figures representing adult and yearling age classes are censuses, those referring to juveniles are estimates of their actual numbers.

As shown in Table 1, total recruitment (row 7) was estimated each year by the product of the number of productive females (row 5) and the average size of known litters (row 6). Productive females were those whose offspring appeared aboveground. Their numbers were determined by subtracting from the total number of females captured annually (row 1), first, the number which disappeared from the study area before the juveniles began to emerge (row 2), and second, the number of those remaining which failed to bring offspring aboveground as determined by direct observation of their nesting burrows or lack of change in the appearance of their nipples throughout the usual lactation period (row 4). The number of juveniles of each sex added to the population each year (rows 9 and 10) was calculated from the total number of juveniles produced on the basis of the overall sex ratio among litters of which
<table>
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<th>AGE CLASS</th>
<th>SEASON</th>
<th>1964</th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
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<tr>
<td>JUVENILE</td>
<td>1</td>
<td>243</td>
<td>268</td>
<td>247</td>
<td>223</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1964-67%</td>
<td>1965-68%</td>
<td>1966-65%</td>
<td>1967</td>
<td></td>
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<tr>
<td>YEARLING</td>
<td>2</td>
<td>80</td>
<td>87</td>
<td>86</td>
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<td>FEMALE</td>
<td>3</td>
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<td></td>
<td></td>
<td></td>
<td>44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-45%</td>
<td>-67%</td>
<td>-71%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADULT</td>
<td>4</td>
<td>50</td>
<td>23</td>
<td></td>
<td>13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5+</td>
<td></td>
<td></td>
<td></td>
<td>13</td>
<td></td>
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<tr>
<td>AD. + YLG.</td>
<td>105</td>
<td>130</td>
<td>154</td>
<td>141</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| JUVENILE | 1         | 244    | 312  | 221  | 187  |
| YEARLING | 2         | 55     | 68   | 56   |
| MALE    | 3         | 75     |      |      |      |
|        |           | -40%   | -71% |      |
| ADULT  | 4         | 21     | 9    | 13   |
|        | 5+        |        |      | 3    |
| AD. + YLG. | 75    | 76     | 110  | 92   |

Figure 3. Population of Uinta ground squirrels at Utah State University's Forestry Field Station, 1964 to 1967.
### Table 1. Estimation of annual recruitment, 1964 to 1967

<table>
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<th>1964</th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
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<tr>
<td>(1) Females captured</td>
<td>105</td>
<td>130</td>
<td>154</td>
<td>141</td>
</tr>
<tr>
<td>(2) Females which disappeared before recruitment</td>
<td>21</td>
<td>25</td>
<td>50</td>
<td>53</td>
</tr>
<tr>
<td>(3) Resident females</td>
<td>84</td>
<td>105</td>
<td>104</td>
<td>88</td>
</tr>
<tr>
<td>(4) Non-productive resident females</td>
<td>0</td>
<td>5</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>(5) Productive resident females</td>
<td>84</td>
<td>100</td>
<td>90</td>
<td>76</td>
</tr>
<tr>
<td>(6) Average litter size (Number of litters)</td>
<td>5.8</td>
<td>5.8</td>
<td>5.2</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>(20)</td>
<td>(42)</td>
<td>(44)</td>
<td>(30)</td>
</tr>
<tr>
<td>(7) Total offspring</td>
<td>487</td>
<td>580</td>
<td>468</td>
<td>410</td>
</tr>
<tr>
<td>(8) Juvenile sex ratio (Females:males)</td>
<td>40:40</td>
<td>85:99</td>
<td>104:93</td>
<td>63:53</td>
</tr>
<tr>
<td>(9) Juvenile females</td>
<td>243</td>
<td>268</td>
<td>247</td>
<td>223</td>
</tr>
<tr>
<td>(10) Juvenile males</td>
<td>244</td>
<td>312</td>
<td>221</td>
<td>187</td>
</tr>
</tbody>
</table>
all members were captured (row 8).

Prior to the appearance of the young squirrels aboveground the population totalled 180 individuals (of which 105 were females) in 1964, 206 (130 females) in 1965, 264 (154 females) in 1966, and 233 (141 females) in 1967 (Figure 3). The addition of juveniles increased these numbers by 487 animals in 1964, 580 in 1965, 468 in 1966, and 410 in 1967. Therefore, productivity, expressed as the average number of juveniles per female, fell from 4.6 in 1964 and 4.5 in 1965 to 3.0 and 2.9 in 1966 and 1967 respectively, despite a relatively unchanged average litter size over those 4 years. Hence, the major cause of the decline in productivity was the increase in the number of females which did not contribute offspring to the population—21 (20 percent) in 1964 and 30 (23 percent) in 1965, rising to 64 (42 percent) and 65 (46 percent) in 1966 and 1967 respectively.

A constant percentage of juveniles of each sex disappeared from the population each year, although the loss of juvenile males (75 to 78 percent) was consistently 10 percent greater than that of juvenile females (65 to 68 percent). The loss of older animals did not differ with sex. However, substantially greater percentages of both sexes disappeared between the springs of 1966 and 1967 than during the corresponding 1965-66 period. Reasons for the observed variations in loss will be discussed in a subsequent section dealing with the annual establishment of the nesting distribution.

The Nesting Distribution

The nesting period is the interval between the day the first
litter was born and the day the first young were observed aboveground ---about 30 to 59 d.s.e. During this period the population was relatively stable numerically and each female was associated with a single burrow. The dispersion over the study area of burrows occupied by squirrels during this period is termed the "nesting distribution."

Figures 4, 5, and 6 show the location of the most frequently used entrance to each burrow for which the occupant was identified during the nesting periods of 1965, 1966, and 1967 respectively. Entrances to the nesting burrows of all inhabitants of the lawn and the representative six-grid areas were identified annually. Less complete information on nesting was obtained for other parts of the study area.

From a comparison of the animals of each sex which nested in the central lawn area, it is evident that a greater number and percentage of females than of males inhabited the lawn annually (Table 2). Furthermore, since the lawn comprised about 12 percent of the 22-acre study area, a greater percentage of females nested there each year than would have been expected by chance, although that percentage decreased annually between 1965 and 1967. The percentages of males which inhabited the lawn suggest that the distribution of that group was not related to that of the lawn during the nesting period.

Environmental Factors Associated with the Nesting Distribution

Cover

The short grass, bare ground, and roadways which make up the lawn area constitute an open habitat with respect to vegetational cover. The remainder of the study area provides varying degrees of cover ranging
Figure 4. Distribution of the most frequently used entrances to known nesting burrows in 1965.

- Adult female
- Yearling female
- Adult male
- Yearling male
Figure 5. Distribution of the most frequently used entrances to known nesting burrows in 1966.
• Adult female
O Yearling female
X Adult male
+ Yearling male

Figure 6. Distribution of the most frequently used entrances to known nesting burrows in 1967.
Table 2. Comparison of the percentages of squirrels of each sex nesting in the central lawn area, 1965 to 1967

<table>
<thead>
<tr>
<th></th>
<th>Percentage of total population nesting on lawn</th>
<th></th>
<th>Prob. percent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1965</td>
<td>1966</td>
<td>1967</td>
</tr>
<tr>
<td>Females</td>
<td>41.5 (54/130)</td>
<td>27.9 (43/154)</td>
<td>23.4 (33/141)</td>
</tr>
<tr>
<td>Males</td>
<td>10.5 (8/76)</td>
<td>12.7 (14/110)</td>
<td>17.4 (16/92)</td>
</tr>
</tbody>
</table>

Prob. F = M < 0.005 0.005 NS
from taller grasses and forbs, through increasing densities of sagebrush and other shrubs, to aspen forest.

Few animals nested in the forested areas. The nesting distribution of squirrels over the rest of the study area, relative to the cover provided by brushy plants, is indicated by the number of residents in each of the representative six-grid areas during the nesting period each year. In 1965 females tended to occupy burrows with entrances in open areas (Figure 7). In 1966 and 1967 such a relationship was not apparent. Reasons for this will be discussed later. Cover seemed to have little influence upon the nesting distribution of males.

Food supply

Figure 8 shows seasonal changes in the diet of the squirrels according to data collected in scans over the representative six-grid areas in 1966. All sex and age groups exhibited the same dietary pattern. For 30 days after the first animals emerged from hibernation grass leaves made up over 90 percent of the squirrels' diet. The use of this component gradually decreased to 60 percent by 60 d.s.e. and 10 percent by 90 d.s.e. There were corresponding increases in the use of forb leaves, commencing 10 to 19 d.s.e., and grass seeds, commencing 50 to 59 d.s.e. From 90 d.s.e. on, forb leaves made up more than 40 percent of the diet. The intake of grass seeds rapidly declined from a high of 62 percent between 90 and 99 d.s.e. to less than 10 percent by the season's end. The latter decline was counteracted by the addition of 30 percent forb seeds to the diet and a return to the consumption of grass leaves of 15 percent. Throughout the season about 10 percent of the squirrels' diet consisted of a varying combination of sagebrush
Figure 7. Annual relationships between the number of resident females and the amount of vegetational cover provided by brushy plants in the representative six-grid areas during the nesting periods, 1965 to 1967.
Figure 8. Seasonal changes in the diet of Uinta ground squirrels according to data collected in scans over the representative six-grid areas in 1966.
leaves, roots, earthworms, soil, and foods discarded from the kitchen of the Field Station.

Leaves of grasses, primarily Kentucky blue grass (Poa pratensis), constituted the bulk of the squirrels' diet throughout the nesting period. For several reasons this component was regarded as the primary, and preferred, source of food for the animals, provided new growth continued (and, thus, a high content of protein was maintained) and the moisture content of the leaves remained sufficiently high to satisfy the metabolic demands of the squirrels. Among those reasons were:

1. The relative consumption of grass leaves was essentially the same in all six areas studied in 1966, despite differing availabilities of that food among the areas (Figure 9).

2. Animals in five of the areas (No.'s 3 through 7) showed constant decreases in their relative consumptions of grass leaves between 50 and 89 d.s.e., 1966. In Area No. 2, however, the use of grass leaves increased rapidly from 40 percent to 70 percent after 70 d.s.e. following mowing of that area of the lawn on Day 67 and subsequent watering. This deviant pattern presumably resulted from the promotion of new growth of grass leaves by the mowing or an increase in the moisture content of the grass due to the watering.

3. In 1967 the relative consumption of grass leaves did not drop below an arbitrary 75 percent until 90 d.s.e., or June 18 as opposed to May 15 in 1966. This suggests that in the very wet season of 1967,

---

1 Observations suggest that the Uinta ground squirrel does not rely on free water for its moisture requirements; rather, it derives its moisture from its solid foods.
Figure 9. Changes in the relative consumption of grass leaves by Uinta ground squirrels in six representative six-grid areas with different relative availabilities of grasses, 1 to 9 days since initial spring emergence, 1966.
during which rainfall between April 1 and June 30 (10.0 inches) was 3.4 times that for the same period in 1966 (2.9 inches), the squirrels were able to continue eating grass leaves until new growth ceased or the existing growth dried up, about a month later than in 1966.

4. The time when juveniles appeared aboveground, and were weaned, appeared to coincide with that stage of vegetational growth when the leaves of grasses on the study area were most plentiful. In a series of colored photographs of the central portion of the study area taken in 1966, grass leaves appeared greenest and most abundant in the periods 50 to 59 and 60 to 69 d.s.e., during which virtually all the juveniles first emerged.

In 1965 nesting females were most numerous in areas where their primary source of food was most abundant during the nesting period. Accordingly, Figure 10 shows a positive relationship between the abundance of grass leaves (expressed as a percentage of the total area covered by grass) and the number of nesting females in the representative six-grid areas in 1965. The distribution of nesting males was independent of the distribution of grass.

Shaw (1925b) reported that *C. columbianus* was "... especially fond of blue grass..." and "... eagerly sought" it. He observed the highest concentrations of that species in "... blue grass sodded bottom land." In explanation Shaw wrote: "With the settling of the country, the squirrels were furnished with an abundance of plant food and at once adapted themselves to the use of ... blue grass."

**Burrows**

The existence of a burrow appeared to be a prerequisite for the
Figure 10. Annual relationships between the number of resident females and the abundance of their primary source of food in the representative six-grid areas during the nesting periods, 1965 to 1967.
establishment of residence in the study area by a Uinta ground squirrel. It was not unusual for these animals to open new entrances to old burrows from beneath the ground, especially females just prior to the emergence of their offspring. But, never in the course of this study was a squirrel observed constructing a new burrow from the ground's surface. This suggests that these animals must inhabit, or expand for their use, burrows established by their predecessors, conspecific or otherwise. Accordingly, at least on the lawn and within the representative six-grid areas where all occupied burrows were known annually, essentially the same burrows were occupied from one year to the next throughout the study.

An exception was the area of the lawn immediately west of Buildings A and B (Figure 2, page 6). Virtually no squirrels resided there prior to 1965 when the area was heavily populated by northern pocket gophers (Thomomys talpoides). Thereafter several squirrels occupied burrows in that area, while pocket gophers were all but absent as evidenced by a lack of their castings. This sequence of events and the fact that the squirrels apparently do not initiate burrows suggest that pioneer settling of a vegetationally suitable area by Uinta ground squirrels requires, and probably did require in the past, prior occupancy of that area by another burrowing species.

Previous observations of this species and of the burrowing habits of other ground squirrels lend support to this hypothesis. The common use of pocket gopher burrows by *C. tridecemlineatus* (Criddle, 1939; McCarley, 1966), *C. richardsoni* (Hansen, 1962), and *C. armatus* (Ellison and Aldous, 1952) has been reported. Referring to *C. nelsoni*, Hawbecker
(1947) stated that "... no burrow systems have been found that could be definitely assumed to be of antelope ground squirrel origin." Later Hawbecker (1953) observed that "all evidence of construction and appearance indicated that the antelope ground squirrel utilized burrows dug by kangaroo rats." In fact, he reported one observation of a squirrel forcibly ejecting a rat from its burrow. In 2 years' studying C. beecheyi, Evans and Holdenreid (1943) described the animals' digging out and reoccupying old, discarded burrows, but stated that "... no completely new burrows were observed ..." Accordingly, they noted that the squirrels tended to congregate where burrow systems were available, referring to the statement of Grinnell and Dixon (1918) that, as a result of the "... tendency to occupy certain definite tracts within a general territory to the exclusion of intervening spaces, and this without obvious reason as regards food supply and kind of soil, ... centers of population may arise through the historical circumstance of original settlement by first-comers."

Establishment of the Nesting Distribution

Dispersal of juveniles

Table 3 lists the numbers of juveniles at postnatal emergence and of resident yearlings during the nesting periods of 1965, 1966, and 1967 on and off the lawn. While the percentages of both sexes which inhabited the lawn changed markedly between their emergence as juveniles one year and their nesting as yearlings the following year, males showed greater changes than females. These changes were attributed, in part, to the dispersal of juveniles.
Table 3. Distributions of juveniles and yearlings with respect to lawn and non-lawn habitats, 1965 to 1967

<table>
<thead>
<tr>
<th>Year</th>
<th>Juveniles at postnatal emergence</th>
<th>Resident yearlings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>On lawn</td>
<td>Off lawn</td>
</tr>
<tr>
<td>1965</td>
<td>163 (61%)</td>
<td>105</td>
</tr>
<tr>
<td>Females</td>
<td>121 (49%)</td>
<td>126</td>
</tr>
<tr>
<td>1966</td>
<td>68 (30%)</td>
<td>155</td>
</tr>
<tr>
<td>1965</td>
<td>154 (49%)</td>
<td>158</td>
</tr>
<tr>
<td>Males</td>
<td>105 (48%)</td>
<td>116</td>
</tr>
<tr>
<td>1966</td>
<td>83 (44%)</td>
<td>104</td>
</tr>
</tbody>
</table>
Several weeks after appearing aboveground the majority of young squirrels abandoned the burrows in which they had been born. More juvenile males dispersed, and began to do so somewhat earlier, than juvenile females (Figure 11).

The reasons why juveniles dispersed are not clear. Nevertheless, available information suggests several possible explanations:

1. Juvenile dispersal was a result of the progressive expansion of individual ranges of activity until the more precocious animals, primarily males, voluntarily discontinued residence in the burrows where they were born. The average distance between the natal burrow and point of capture gradually increased during an animal's first 40 days above-ground (Figure 12). However, this distance increased at a greater rate in young males than in young females. While precocity might have been potentially advantageous to some individuals in facilitating their egress from congested areas, this behavior would, at the same time, have detached these animals from the security of their natal burrows and familiar surroundings, thus rendering them more vulnerable to exposure and predation. It seems doubtful that natural selection would have favored a type of behavior which would promote emigration from areas conducive to survival.

2. Dispersal was a necessary response to the cessation of new growth, or dehydration of existing growth, of the squirrels' primary food, the leaves of grasses. During 1966 and 1967, when dietary data were collected, juvenile dispersal occurred when the animals began to consume more forb leaves than grass leaves. However, the survival value of moving to areas which might better have satisfied the squirrels'
Figure 11. Seasonal changes in the density of juveniles in the representative six-grid areas in 1966.
Figure 12. Changes in the average distance between the natal burrow and points of capture of juveniles during their first 40 days aboveground in 1965 and 1966.
nutritional requirements would likely have been counteracted by the same mortality mentioned above. Furthermore, since the diet of juvenile squirrels did not vary with sex, movement in response to environmentally imposed dietary changes would not, in itself, explain the observed sexually differential nature of the dispersal.

3. Dispersal was an involuntary response to the intolerance of the juveniles by older animals. Sixty-two percent of 692 recorded aggressive encounters involving juveniles prior to, and during, dispersal (60 to 99 d.s.e.) in 1965 and 1966 also involved older animals. Of these 428 encounters, 248 involved juvenile females and 178 involved juvenile males. Juveniles of both sexes were generally unsuccessful when they encountered older animals. Young females submitted 89 percent of the time, young males 90 percent of the time. Therefore, while aggression of older animals towards juveniles might provide an explanation for dispersal itself, it does not seem to explain why more young males dispersed than females, unless the latter were better able to tolerate aggression than the former. No measurement of such tolerance was available.

4. Juvenile dispersal was an involuntary response to aggression among the young animals themselves, wherein females generally dominated males. Females won 74 percent of 82 decisive aggressive encounters with males recorded prior to, and during, dispersal in 1965 and 1966. Young females might have been dominant because they developed faster sexually than males. Accordingly, most yearling females emerged from hibernation capable of conception each spring, whereas males usually did not fully mature sexually until late in the summer of their second year. In
evidence, 85 percent or more of yearling females had nipples indicating conception each year, while less (and usually considerably less) than 50 percent of yearling males exhibited scrotal testes. Inherent in this, and the preceding, explanation of dispersal is the premise that each juvenile tended to remain at its place of birth. Intolerance, manifested as aggression, then operated to exclude all but one or two members of each litter, first males then subordinate females. Thus, in 1966, of 25 yearling inhabitants of the lawn whose birthplaces in 1965 were known, 96 percent had been born in, or immediately adjacent to, their existing residences. Similarly, of 16 yearlings which occupied burrows in the lawn in 1967, 94 percent were offspring of resident females of 1966.

The possible reasons for juvenile dispersal offered above are not mutually exclusive. Instead, each mechanism suggested might have operated to some extent during the study. Those mechanisms involving aggression probably would have exerted the most important influences by ultimately perpetuating those dominant individuals which remained in areas conducive to survival. However, the data suggest that animals which did eventually disperse were able to withstand aggression longer in 1967 when they were not subjected to the added nutritional stress experienced in 1965 and 1966. On the other hand, perhaps adults tolerated the juveniles longer in 1967 when green grass persisted.

Young animals, predominantly females, that were successful in retaining residences in the burrows where they were born remained there, eventually to enter hibernation. Since older animals tended to begin hibernation several weeks before juveniles, the young squirrels met
little, if any, resistance from the older ones when actually entering a burrow to hibernate.

Excluded juveniles, predominantly males, were forced to seek refuge in other than their natal burrows. Since Uinta ground squirrels apparently do not initiate burrows, the dispersing juveniles had to depend upon unoccupied burrows previously inhabited by older squirrels or other burrowing species for their winter residences. Those which acquired such refuge likely survived; those which failed probably succumbed to such factors as exposure and predation by hawks and weasels.

Consequently, prior to the onset of hibernation, a new distribution was established among the juveniles. The lawn was inhabited mostly by females successful in settling in the burrows where they were born. The remainder of the study area was occupied by similarly successful females and the squirrels which survived dispersal by virtue of having acquired vacant burrows. Assuming that dispersing juveniles of both sexes were equally vulnerable to mortality, the majority of dispersing squirrels which survived were males. Thus, in general, the distribution of the young squirrels as they approached hibernation resembled that of the older animals during the nesting period.

Emergence from hibernation

The date on which the first squirrel emerged from hibernation in the spring, and the sequence in which the rest of the population emerged thereafter, varied from year to year (Figure 13). Initial emergence occurred on April 16 in 1965. Subsequent emergence in that year was relatively synchronous in that most members of each sex and age group appeared during a relatively short period of time. In 1966 the first
Figure 13. Patterns of emergence from hibernation exhibited by Uinta ground squirrels at Utah State University's Forestry Field Station, 1965 to 1967. (Vertical lines indicate dates by which 50 percent of the members of each sex and age group had emerged.)
squirrel appeared on March 28. In general, while adults of both sexes emerged at the same time that year, yearling females emerged about 9 days later and yearling males 20 days later. The emergence of individuals within each sex and age group was asynchronous relative to 1965. In 1967 initial emergence occurred on March 21 and asynchrony was apparent, both within and among sex and age groups. Since yearlings could not be distinguished from adults in 1964, emergence patterns in that year were unknown. However, the first squirrel appeared aboveground in 1964 on April 14.

At present the specific factors responsible for year to year variations in the initial date, and subsequent synchrony, of emergence from hibernation are unknown. Investigators of other species of ground squirrels have suggested the relevant importance of temperature and moisture (Criddle, 1939; Shaw, 1925c), the thawing of frozen ground (Rust, 1946; Wade, 1950), the melting of snowpack (McKeever, 1963, 1964; Mullally, 1953), and various combinations of these factors associated with differences in elevation (Fitch, 1948; McKeever, 1963; Moore, 1937; Mullally, 1953; Storer, Evans, and Palmer, 1944). McCarley (1966) justifiably denied the influence of temperature or frost melt upon the emergence of *C. tridecemlineatus* in northern Texas. It does, however, seem certain that some component of spring weather plays a leading role in determining the pattern of emergence of Uinta ground squirrels.

Unfortunately, quantitative records of spring weather conditions were not available for the study area, nor for any comparable area in the vicinity. Nevertheless, qualitative information on temperature,
precipitation, and cloud cover taken daily throughout the study sug-
gests that late, synchronous patterns of emergence were associated with
late springs, while early, asynchronous patterns occurred in years with
early springs.

Physiological arousal from hibernation in this species, under some
intrinsic control, likely occurs in a characteristic, although overlap-
ping, sequence--adult males followed by adult females, yearling fe-
males, and yearling males respectively. When spring weather conditions
are favorable for the commencement of activities aboveground when the
squirrels arouse, the animals' sequence of emergence closely resembles
that of their physiological arousal, as it did in 1967 and, except for
adult males, in 1966. However, under more severe spring conditions,
which were exemplified in 1965, animals which arouse early, despite
their increased metabolic activity, remain underground until conditions
improve, whereupon all aroused animals emerge at essentially the same
time. The remainder conform to the sequence of emergence determined by
their order of arousal.

A comparison of the average weights of the first 25 individuals of
each sex and age group which appeared in 1965 and 1966 (Table 4) sug-
gests that the longer an aroused animal was held underground by incle-
ment spring weather, the more weight it lost because of its increased
metabolism and inability to obtain food.

Breeding

Most adult male Uinta ground squirrels emerged from hibernation in
breeding condition. Annually 90 percent or more of these animals exhi-
bited scrotal testes upon emergence (Figure 14). By mid-May the testes
Table 4. Differences between 1965 and 1966 emergence weights based on the first 25 individuals of each sex and age group captured each year

<table>
<thead>
<tr>
<th></th>
<th>Emergence weight (grams)</th>
<th>Percent difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1965</td>
<td>1966</td>
</tr>
<tr>
<td>Adult males</td>
<td>302</td>
<td>348</td>
</tr>
<tr>
<td>Adult females</td>
<td>254</td>
<td>273</td>
</tr>
<tr>
<td>Yearling females</td>
<td>201</td>
<td>205</td>
</tr>
<tr>
<td>Yearling males</td>
<td>235</td>
<td>227</td>
</tr>
</tbody>
</table>
Figure 14. Spring changes in the reproductive conditions of adult and yearling males, as reflected by the percentages of each group exhibiting scrotal testes in 1965, 1966, and 1967.
of virtually all adult males had regressed to inguinal or abdominal positions. Only a few of the earliest appearing yearling males displayed scrotal testes and regression in these animals occurred even earlier than in adults.

Adult and yearling females were bred primarily, if not exclusively, by adult males within a few days of the females' emergence from hibernation. In 1965 and 1966 the initially high frequency of sexual encounters decreased to zero by mid-May (Figure 15), following essentially the same course as the regression of testes in adult males. Furthermore, a positive correlation existed between the dates of initial appearance of females in the spring and the dates on which their respective litters appeared aboveground, about 53 days later (Figure 16). The gestation period of the species is probably near 27 days, while observations suggest that juveniles tended to remain in their mothers' nests for about 24 days after birth.

Social organization among females

After conceiving, females became intolerant of all conspecifics. Consequently, such activities as communal feeding, commonplace at the outset each spring, were restricted to areas, like that immediately south of Building D (Figure 2, page 6), which annually lacked burrows and, thus, pregnant females. The latter began to defend areas around

1Although the exact gestation period of the Uinta ground squirrel is unknown, those of several other species of the genus Citellus have been determined and suggest the probable period for C. armatus: C. beecheyi, 30 days (Grinnell and Dixon, 1918); C. columbianus, 24 days (Shaw, 1925b); C. douglasi, 25 to 30 days (Edge, 1931); C. lateralis, 28 days (McKeever, 1964); C. parryi, 25 days (Mayer, 1953); C. tridecemlineatus, 27 to 28 days (Bridgewater, 1966; Wade, 1927).
Figure 15. Changes in the frequency of sexual activity in the springs of 1965 and 1966.
Figure 16. Relationship between the emergence of females from hibernation and the subsequent appearance of their respective offspring aboveground, 1965 to 1967.

\[ r = 0.913 \ (P < 0.001) \]
the burrows in which they would eventually bear their offspring. In most cases (80 percent of 64 females of which both hibernation and nesting sites were known) these were the same burrows from which they had emerged in the spring.

As intolerance intensified some females abandoned the burrows in which they had hibernated. Some of these were able to establish residences elsewhere in the study area. The remainder disappeared from the population.

The earlier a female emerged from hibernation, the more likely she was to remain in the burrow where she had spent the winter (Table 5). A female which emerged early, conceived early, and became intolerant early found relative ease in driving later-appearing, simultaneously non-aggressive animals from the vicinity of her burrow. Hence, if two females which had hibernated in adjacent burrows emerged some days apart, the earlier animal tended to nest there while the later animal tended to move. On the other hand, if both females appeared aboveground on the same day, both tended to remain.

Apparently a type of social rank existed among initially neighboring females and its clarity varied from year to year according to the annually differing patterns of emergence from hibernation illustrated in Figure 13 (page 35). In the late spring of 1965 (and presumably in 1964), when all females appeared at about the same time, relative social equality existed, both within and between age groups. Conversely, in 1966 and 1967, when emergence was asynchronous and most adult females appeared aboveground and conceived before yearlings, dominant-subordinate relationships were clearer and, in general, adults
Table 5. Dependence of the residential success of females upon their time of emergence from hibernation in 1965 and 1966

<table>
<thead>
<tr>
<th>Day of emergence (d.s.e.)</th>
<th>Percentage of emerging females which nested at hibernation site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1965</td>
</tr>
<tr>
<td>1 to 9</td>
<td>82 (58/71)</td>
</tr>
<tr>
<td>10 to 19</td>
<td>80 (32/40)</td>
</tr>
<tr>
<td>20 to 29</td>
<td>61 (11/18)</td>
</tr>
</tbody>
</table>
dominated yearlings.

The effects of these social relationships among females, with respect to their resultant nesting distribution, were illustrated in several sets of data presented earlier. The figures given in row 2 of Table 1 (page 12) indicate that about twice as many females disappeared from the population in the early springs of 1966 and 1967 as in the late springs of 1964 and 1965. Expressed as percentages of the total numbers of females in the population annually, 20 percent disappeared in 1964 and 19 percent in 1965, while 32 and 38 percent disappeared in 1966 and 1967 respectively. Data presented in Table 2 (page 18) show that, although 42 percent of the females nested in burrows in the central lawn area in 1965, only 28 percent did so in 1966 and 23 percent in 1967. Similarly, in the late spring of 1965 many females were able to establish themselves residentially in open, grassy areas, while in the early springs of 1966 and 1967, when the animals emerged over several weeks, fewer nested in these apparently preferred areas (Figure 7, page 20, and Figure 10, page 25).

**Determination of Breeding Density and Productivity**

**Breeding density**

Andrewartha and Birch (1954) emphasized that distribution and abundance are different aspects of the same phenomenon. Accordingly, the present attempt to explain local distribution would be incomplete without an accompanying explanation of population size, particularly of the annual breeding density.

In dealing with the breeding density of Uinta ground squirrels,
perhaps it is best to focus upon the females since they determine the productivity of the population, the males being promiscuous. Data pertinent to the annual establishment of the breeding density of females are given in Table 6. A constant percentage of the female breeding density (row 4) plus its female offspring (row 5) was lost from the population between the time of recruitment one year and that of emergence from hibernation the following year. Therefore, the number of females which emerged each spring (row 2) was dependent upon the number of females in the population immediately subsequent to recruitment the previous year (row 6). However, the actual breeding density of females in the spring (that is, the number of resident females) appears to have depended upon both the number of females which emerged from hibernation and their pattern of emergence. The latter largely determined the percentage of emerging females which disappeared from the population (row 3) prior to that year's production of offspring, in the manner diagrammed in Figure 17.

**Productivity**

Productivity decreased from 4.6 and 4.5 offspring per female in 1964 and 1965 respectively to 3.0 in 1966 and 2.9 in 1967. (See page 13.) Several mechanisms effected the observed reduction. Each was related, in part at least, to annually varying patterns in which the animals emerged from hibernation.

Figure 18 illustrates the mechanisms influencing annual productivity, using the dates of initial emergence as indices of spring conditions. With increasingly earlier springs, and thus increasingly pronounced dominant-subordinate relationships among females, decreasing
Table 6. Numerical changes in the female population relative to establishment of the annual breeding density

<table>
<thead>
<tr>
<th></th>
<th>1964</th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Initial emergence</td>
<td>Apr. 14</td>
<td>Apr. 16</td>
<td>Mar. 28</td>
<td>Mar. 21</td>
</tr>
<tr>
<td>(2) Emerging females</td>
<td>105</td>
<td>130</td>
<td>154</td>
<td>141</td>
</tr>
<tr>
<td>(3) Females which disappeared</td>
<td>21</td>
<td>25</td>
<td>50</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>(20%)</td>
<td>(19%)</td>
<td>(32%)</td>
<td>(38%)</td>
</tr>
<tr>
<td></td>
<td>-60%</td>
<td>-59%</td>
<td>-60%</td>
<td>-59%</td>
</tr>
<tr>
<td>(4) Resident females</td>
<td>84</td>
<td>105</td>
<td>104</td>
<td>88</td>
</tr>
<tr>
<td>(Breeding density)</td>
<td>(Breeding density)</td>
<td>(Breeding density)</td>
<td>(Breeding density)</td>
<td>(Breeding density)</td>
</tr>
<tr>
<td>(5) Female offspring</td>
<td>243</td>
<td>268</td>
<td>247</td>
<td>223</td>
</tr>
<tr>
<td>(6) Total females after recruitment</td>
<td>327</td>
<td>373</td>
<td>351</td>
<td>311</td>
</tr>
</tbody>
</table>
Figure 17. Diagrammatic representation of the annual variation in spring expulsion of late-emerging females.
Figure 18. Mechanisms responsible for annual variations in productivity.
percentages of females were able to settle in the central lawn area. Conversely, while the percentage of females settling in marginal habitats within the study area remained unchanged, progressively larger percentages of females disappeared from the population before the juveniles began to appear aboveground. Also, of the females which were permanent residents of the area, greater percentages failed to produce litters in years with early springs than in years with late springs.

Of course, barren females and females which disappeared from the study area prior to the emergence of the juveniles failed to add offspring to the population. A productive female which resided in the study area contributed offspring according to her age and the habitat in which she lived (Table 7). On the whole, adult females produced larger litters than yearling females. Similarly, litters born on the lawn were larger than those born elsewhere. Consequently, in late springs, when a greater proportion of resident females inhabited the preferred habitat, productivity was greater than in early springs when the majority of residents inhabited marginal areas.
Table 7. Average sizes of litters borne by adult and yearling females in lawn and non-lawn areas in 1965, 1966, and 1967

<table>
<thead>
<tr>
<th></th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Yearling</td>
<td>Adult</td>
</tr>
<tr>
<td>Lawn</td>
<td>6.5 (16)</td>
<td>5.2 (10)</td>
<td>5.9 (15)</td>
</tr>
<tr>
<td>Non-lawn</td>
<td>5.9 (11)</td>
<td>4.8 (5)</td>
<td>5.7 (7)</td>
</tr>
</tbody>
</table>

*Number of litters in sample.
GENERAL DISCUSSION

In the thirteen-lined ground squirrel in northern Texas, "population size was mostly regulated by dispersal of the juvenile part of the population in late summer and early fall. Additional adjustment of population size and sex ratio through dispersal and mortality occurred in the spring" (McCarley, 1966). A similar situation was evident in the present population of Uinta ground squirrels. The typical nesting distribution and breeding density were established in two distinct steps. The first, effected by the sexually differential dispersal of a majority of the juveniles several weeks after their initial appearance aboveground, left a preponderance of young females in the proven successful nesting areas of their female parents. The second adjustment involved yearling and adult females shortly after their emergence from hibernation in the spring. It was a result of further dispersal by the later-emerging, and thus socially inferior, animals and left dominant, earlier emergents at the sites of previously successful production.

Not only does the situation considered herein parallel that reported in other ground squirrels, but bears some resemblance to that described for the red grouse (*Lagopus lagopus*) in Scotland by Jenkins, Watson, and Miller (1963). In both species, rather than a gradual decline between the time of recruitment and the subsequent nesting period, two rather abrupt declines were separated by periods when numbers and distribution were relatively constant. In both species the primary decline resulted from the expulsion of subordinate juveniles, leaving a
potential breeding population concentrated in the preferred nesting areas. In red grouse this potential, or maximum, breeding density comprised the number of territorial males which the late summer food supply would support. In the ground squirrel the potential breeding population was set by the number of females which the existing burrows would accommodate. In both species the second change in numbers and distribution resulted primarily from the expulsion of surplus animals in the spring. Annually variable winter weather depleted the grouse's food supply. According to Jenkins et al., the birds assessed this depletion and reduced their numbers accordingly through intolerance, in the general manner postulated by Wynne-Edwards (1962). Uinta ground squirrels, too, appear to have reduced their numbers and adjusted their local distribution in accordance with weather conditions. But, an active assessment of the resultant nutritional resources by the animals was neither apparent nor necessary. More simply, adjustment seemed to be an inherent social response to the squirrels' pattern of emergence from hibernation.

One might speculate that the system employed by the squirrels has evolved to limit the production of young in a manner which minimizes unnecessary expenditure of reproductive energy by the population (Figure 19). Spring weather conditions evidently tend to influence the population such that late springs result in relatively high recruitment and early springs in relatively low recruitment due to the lack of production by late-emerging females. At the same time, spring conditions influence growth of the squirrels' food supply. Generally, in years of early springs the phenology of Kentucky blue grass is advanced in
Figure 19. Diagrammatic representation of the suggested relationship between the emergence of females from hibernation, the production of offspring, and the phenology of Kentucky blue grass in the study area.
comparison with years of late springs. In either case the quantity and quality of the squirrels' primary source of food evidently begins to deteriorate about 9 weeks after initial spring emergence. Thus, young first appearing aboveground after this critical period for grass growth (that is, the offspring of females which emerge from hibernation late) would, if born, be subjected to inferior nutrition and their probability of survival reduced. Perhaps, then, there is some advantage to the population in a system whereby late-emerging females do not reproduce and, thereby, conserve energy which would otherwise be wasted, for the most part, in the form of doomed offspring.

Irrespective of such a behavioral regulatory mechanism attuned to an annually fluctuating environmental situation, recruitment by the Uinta ground squirrel provides a surplus of young animals each year. From this surplus a portion of the future breeding stock can be drawn. While dispersal of many juveniles in the late summer eliminates some and predation by badgers (*Taxidea taxus*) over winter removes others, still a surplus of young females remains to be added to the older animals the following spring. This remaining surplus is apparently eliminated through social strife in the spring.

In general, annual fluctuations in the resultant resident female population, and the productive members thereof, are determined by variations in spring dispersal, the extent of which is contingent upon spring weather conditions and the resultant patterns of emergence of the females from hibernation. Hence, the size and distribution of the breeding population tends to fluctuate in accordance with spring weather conditions, this notwithstanding the effects of the size of the
emerging population.

The phenomenon described herein for the Uinta ground squirrel may well occur in a number of other species. Certainly one might expect weather to similarly influence other hibernators which compete for space after emerging in the spring. And, it is not difficult to imagine a similar mechanism operating in territorial, migratory birds, where inclement weather along their migration route in some years could cause a delay, and thus congestion, in the otherwise sequential return of males to the breeding grounds. In fact, it seems reasonable to suggest that a situation paralleling that observed in a single population of ground squirrels could occur in any group of animals in which there were a sufficient number of those individuals which determine the breeding density to create competition for space, and in which the basically staggered arrival of those individuals on the preferred breeding areas was vulnerable to the potentially deterrent effect of some environmental factor such as weather.
SUMMARY AND CONCLUSIONS

The study described herein was an attempt to explain the local distribution of the resident members of a population of Uinta ground squirrels on the basis of both their ecology and their behavior. The investigation was conducted on 22 acres of land in northern Utah during the springs and summers of 1964 through 1967, when the annual population comprised in excess of 600 individuals.

The objectives of the study were:

1. To describe the annual distribution of the resident squirrels.
2. To determine what environmental factors were associated with this distribution.
3. To determine how this distribution was established each year.
4. To determine what effects, if any, this distribution and its establishment had on the annual breeding density and productivity of the population.

Field procedures employed throughout each of the animals' seasons of activity included continuous trapping, time-controlled observations of animals in representative areas within the study area, identification of residential burrows, and determination of litter sizes. During one season a quantitative analysis of the vegetation in each of the representative areas was also made.

The results of the study may be summarized as follows:

1. Resident females tended to concentrate on the 2.6 acres of lawn which made up the central portion of the study area. Males resided over
2. The area of apparent preference by females was characterized by a lack of vegetational cover, an abundance of the squirrels' primary source of food during the reproductive period, and numerous burrows.

3. The typical nesting distribution was established annually in two distinct steps.

4. The first step consisted of the sexually differential dispersal of a majority of the juveniles several weeks after their initial appearance aboveground in the early summer. This dispersal was attributed primarily to aggression among the juveniles themselves and among the juveniles and older animals. It resulted in a preponderance of dominant young females in the already proven nesting areas of their female parents.

5. The second step involved the disappearance from the study area of an annually varying number of late-emerging females. This loss was precipitated by the intolerance of earlier-emerging, pregnant females.

6. The number of females which emerged from hibernation each year was directly related to the number of female residents of the previous year plus their female offspring.

7. The number of females which retained residences in the study area each year, and the residential distribution thereof, depended upon both the number which emerged from hibernation and the pattern in which they emerged.

8. Variations in the pattern in which animals appeared aboveground in the spring appeared to be a result of the effects of spring weather conditions upon a characteristic, endogenously controlled sequence of
physiological arousal from hibernation.

9. Productivity in years with late springs, in terms of the number of offspring per female which emerged, was nearly double that in years with early springs. This discrepancy was attributed to increases in the percentage of emerging females which disappeared prior to recruitment, and in the percentage of resident females which failed to produce litters, in years with early springs.

10. Consequently, both the number of females which emerged from hibernation and the consequences of the pattern in which they emerged contributed to determining the total number of offspring produced each year.

The system whereby the annual breeding density and productivity were determined in this population may have evolved to minimize unnecessary expenditure of energy in the production of late-appearing offspring whose chances of survival would be reduced by a deteriorating food supply late in the season.

A similar system might occur in other species, particularly migratory birds, in which the sequence of arrival on the breeding areas of those individuals which determine the breeding density is subject to the compressing effect of some environmental factor such as weather.


Shaw, W. T. 1925c. Duration of the aestivation and hibernation of the Columbian ground squirrel (Citellus columbianus) and sex relation to the same. Ecology 6(1): 75-81.


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