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THE ROLE OF AGONISTIC BEHAVIOR IN REGULATION OF DENSITY IN UINTA GROUND SQUIRRELS (*CITELLUS ARMATUS*)

by

Richard J. Burns

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

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

Major Professor

Head of Department

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1968

ACKNOWLEDGMENTS

I sincerely thank Dr. A. W. Stokes for his guidance in preparing this manuscript; and both Drs. D. F. Balph and A. W. Stokes for their technical assistance, encouragement, and editorial help. Also, I thank Dr. J. B. Low for his comments on the manuscript.

This study was done as part of a team project, on the behavior and ecology of the squirrels, and I express my gratitude to all the others involved, who contributed to my work in numerous ways. To fellow students R. E. Walker and R. P. McQuivey, who supplied supporting data used in this paper, I give special mention. Finally, I am grateful to my wife, Linda, for her patience and encouragement throughout the program.

Funds were provided by grants to A. W. Stokes and D. F. Balph from the National Institutes of Health (GM-11185), and the National Science Foundation (GB-5596), and by fellowships from the National Wildlife Federation and the Society of the Sigma Xi.

Richard J. Burns

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ABSTRACT

The Role of Agonistic Behavior in Regulation of Density In Uinta Ground Squirrels (*Citellus armatus*)

by

Richard J. Burns, Master of Science

Utah State University, 1968

Major Professor: Dr. A. W. Stokes
Department: Wildlife Biology

Agonistic behavior of ground squirrels was studied for two years in north-eastern Utah at an elevation of 6,300 feet. The main objective was to determine what role agonistic behavior had in regulating density in a population. All individuals in an unconfined population were trapped, marked, and observed from towers. Detailed data on behavior and density were recorded.

Though loss from a variety of factors occurred throughout the year, agonistic behavior had an important role in regulating the population at least twice during the year. In spring some squirrels, usually yearling males and late emerging yearling females, were unable to establish territories. Breeding density was thus limited. In summer an overproduction of young was greatly reduced through aggression in, and movement of, young squirrels. This appeared to be the more important to the population in terms of numbers lost.

Agonistic behavior was influenced by density, visibility, movement, and intrusion of nonresidents on areas; by age, sex, and aggressiveness of squirrels; and by time of day and season--all probably warrant consideration in any study of agonistic behavior.

(57 pages)

INTRODUCTION

Agonistic behavior probably plays an important role in population control by influencing births, deaths, and movements. Lloyd and Christian (1967) have summarized much of the work on confined mouse populations and concluded that aggression affects birth rate mostly through physiological mechanisms.

The effect of agonistic behavior on death rate and movement, however, seems less clear. King (1955) suggested that black-tailed prairiedogs (*Cynomys ludovicianus*) forced from settled areas suffered a greater chance of dying. Armitage (1962) observed that yearling marmots (*Marmota flaviventris*) probably emigrated as a result of agonistic behavior with adults, but Bronson (1964) had good evidence that woodchucks (*Marmota monax*) dispersed during a period of declining aggressiveness. What role aggression has in controlling rodent populations, then, is still uncertain.

This study probes what role agonistic behavior has in regulating a population of Uinta ground squirrels (*Citellus armatus*). It deals with loss in the population caused by movement and mortality, which are not separated.

METHODS

Ground squirrels were studied on a 22-acre study area, during their active seasons of 1965 and 1966, at the Utah State University Forestry Field Station. The field station was 22 miles northeast of Logan, Utah, at 6,300 feet above sea level.

Squirrels were active above ground at the station from April through August. They usually emerged from hibernation about April 1, and most all but the yearling males, animals in their second season, emerged in reproductive condition. Adult males, animals in their third season or more, were aggressive toward one another at emergence, and bred both the adult and yearling females a few days thereafter. Once bred, females became intolerant of all conspecifics. Juveniles, animals born that season, usually appeared above ground during the first week in June, when they were about three weeks old. Adults began hibernating late in July, and most juveniles were hibernating by the end of August.

I was one of a team investigating the behavior and ecology of this population. We employed various methods, but here I present only those pertinent to my study of agonistic behavior.

Squirrels were trapped, checked for reproductive condition, toe-clipped for permanent identification, and marked with dye for individual recognition from a distance. The trapping and marking were intense and continuous, and all members of the population were kept recognizable throughout the active season. Most of the squirrels on the study area, since 1964, were caught as juveniles, hence the ages of most animals were known.

Behavioral data on the marked individuals were collected from six towers. Each tower overlooked a specific sample area measuring 80 x 120 feet. The entire study area was marked off in a 40 x 40 foot grid system, and locations of animals were estimated to the nearest 4 feet with the aid of the grid. The sample areas were representative of the different types of vegetation and density of squirrels on the study area. Two sample areas were on the lawn surrounding the buildings of the station where density was high. Two were in brushy areas where density was low, and two were in cover that was part lawn and part brush with intermediate density. Portions of the study area were covered by trees, but squirrels seldom used these.

Sample areas were used to measure diurnal and seasonal variations in the behavior and density of the population. The ground squirrel season was divided into 10-day periods beginning with the date of emergence of the first squirrel. Each day was divided into 3-hour intervals beginning with 6:00 a.m. and ending at 18:00 hrs 6:00 p.m. The unit of observation was a "scan." In a scan, usually taking 3-5 minutes, we recorded the number, location, and activity of each squirrel observed on a sample area. For every 3-hour interval within a 10-day period we took at least 20 scans. These scans were distributed more or less evenly throughout each 3-hour interval and 10-day period.

Immediately following each scan the social encounters that occurred on a sample area during a 5-minute period were noted. This included the location and the individuals involved. Social encounters were classified as agonistic, sexual, play, or nuzzle. In agonistic encounters we also recorded the "result" and "form" of the encounter. The results of encounters included which animal was dominant, which was subordinate, or if the encounter ended in a "stand-off," with neither animal dominant nor subordinate. The form of encounter included categories of "contact," "chase," or both. In contact, some physical contact such as wrestling or biting occurred. In chase, both animals had to move at least 3 feet in the same direction at the same time. If neither contact nor chase were involved, an encounter was still called agonistic if it contained threat postures (Balph and Stokes, 1963) or threat vocalizations (Balph and Balph, 1966).

Information was also kept on locations of squirrels and on agonistic encounters observed outside of sample areas. This was done to increase sample size on agonistic encounters, and to complete information on home ranges (i.e. . . . that area traversed by an animal in its normal activities . . . (Burt, 1943)) of individuals that lived partly or completely outside of sample areas.

From these data we determined the type of social organization in the population, i.e. whether it was territorial or hierarchical; and detected changes in the frequency, form, and result of agonistic encounters in the population and among age and sex groups. These data also provided information on the density of animals on different areas, and on the time and relative number of animals lost from the population. Other studies on the ecology and behavior of the population were conducted concurrently with this study, and some information has been drawn from them.

RESULTS

Social Organization

Reproductive season

The reproductive season lasted for about 59 days after the first squirrel emerged from hibernation (hereafter called "days after emergence" and abbreviated DAE), and included the breeding and nesting seasons. The breeding season began with emergence from hibernation and continued until about 39 DAE, when most of the females had been bred. During this period the animals engaged in a short courtship, and copulation apparently followed in a burrow (Balph and Stokes, 1963). The nesting season began soon after females were bred, and lasted until the juveniles appeared above ground at about 50-59 DAE. Since females emerged and were bred over a period of several weeks, there was considerable overlap in breeding and nesting. Females frequently gathered nest material during this period. The time periods used to define the occurrence of different behavioral characteristics of the squirrels varied with individuals and years, thus were somewhat arbitrary.

The home ranges of individuals were determined by rounding off a polygon drawn through the outside points of 90 percent of the sighted locations of individuals. Ten percent of the points, those farthest away from areas of large concentrations of points, were arbitrarily omitted because the squirrels took excursions outside the areas they usually occupied.

The areas inhabited by individuals had a definite pattern within each age and sex group, but the size and degree of overlap depended on a variety of factors (R. P. McQuivey, personal communication).

During the breeding season adult males inhabited large areas that overlapped several female burrows. Yearling males inhabited smaller areas during the reproductive season. Adult and yearling females occupied small areas associated with a specific burrow system during the nesting season. They raised their young within these systems, and the burrow opening where the young first appeared above ground was termed the "home burrow."

To find if there was some relationship between the result, location, and individuals involved in encounters, it was necessary to have some reference point to use as a basis for comparison. Activity of females was centered around a home burrow, and this burrow opening was used as a reference point. A "center of activity" was used as a reference point for males, because they sometimes used more than one burrow system.

The center of activity for males was determined by drawing a straight line through the longest axis of the areas they inhabited. A second line was then drawn, perpendicular to the first, and through the longest axis available. Where the two lines intersected was called the center of activity.

Analysis of the locations and results of encounters for the residents of one sample area in 1966 revealed that adult males and adult and yearling females tended to be dominant in the majority of the encounters that occurred near their centers of activity (Table 1) or home burrows (Table 2). As distance increased from these central locations, however, the animals were increasingly subordinate in encounters. This was true for adult males during the breeding season, and for the females during the nesting season, especially from 30-59 DAE, though these tendencies appeared to be more significant in the females than in the adult males. Yearling males were usually subordinate. The probability of their being dominant tended to decrease with distance from their centers of activity, though the difference was not significant (Table 3).

Table 1. Effect of distance from center of activity on the results of encounters[a] in adult males during breeding, 1966[b]

Result of encounters (%)	Feet from center of activity					
	0-18	19-36	37-54	55-72	73-90	91-108
Dominant	62	77	90	63	47	33
Stand-off	38	23	10	16	32	44
Subordinate	0	0	0	21	21	22

[a] Number of encounters = 78

[b] Chi-square = 13.94 (.100 > P < .200)

Table 2. Effect of distance from home burrow on results of encounters[a] in females during nesting, 1966[b]

Result of encounters (%)	Feet from home burrow				
	0-12	13-24	25-36	37-48	49-60
Dominant	79	77	59	24	44
Stand-off	18	17	20	37	22
Subordinate	4	7	21	21	33

[a] Number of encounters = 265

[b] Chi-square = 31.96 $(P < .005)$

Table 3. Effect of distance from center of activity on results of encounters[a] in yearling males during the reproductive season, 1966[b]

Result of encounters (%)	Feet from center of activity				
	0-18	19-36	37-54	55-72	73-90
Dominant	38	24	16	14	0
Stand-off	31	15	11	14	11
Subordinate	31	61	74	71	89

[a] Number of encounters = 84

[b] Chi-square = 10.42 $(.200 > P < .250)$

The foregoing data on the areas animals inhabited and on the results of encounters indicated that the animals involved in reproducing lived in a specific area, and defended some portion of that area. They appeared, then, to be territorial. A territory is . . . any defended area . . . (Noble, 1939). Yearling males were usually not successful in defending an area.

The territorial behavior of females probably functioned partly to protect their young. This was indicated when five dead juveniles were found in the nest of a yearling female (820) soon after she was accidently killed. A neighboring adult female (24) was seen entering and leaving 820's burrow. The burrow was excavated a few hours later and each young had fresh puncture wounds on its head and neck, apparently inflicted by the incisors of another ground squirrel.

Nonreproductive season

The nonreproductive season, about 60-139 DAE, lasted from about the time juveniles appeared above ground until all animals entered hibernation.

During the nonreproductive season, adult males inhabited smaller areas than during the reproductive season, while in yearling males the situation was just the reverse. During the nonreproductive season adult and yearling females occupied areas that were sometimes larger and were usually modified to include brush cover, compared to the areas occupied during nesting. Adult males and adult and yearling females fought little at this time (data presented later) and appeared non-territorial. Most animals seemed to maintain individual distances of intolerance (Hediger, 1964, p. 111) on their home ranges, since they became aggressive toward other squirrels that approached to within 2-5 feet of them. When animals moved outside of their territories, or at times of the year when they were not territorial, they moved about freely and paid little attention to others. Aggression occurred only when a squirrel encroached upon another's territory or individual distance.

Yearling males and juveniles show some reproductive development and behavior during the nonreproductive season. In juvenile males this development usually appears very late in the year, 120-139 DAE, and is somewhat less common than in yearling males and juvenile females. In 1966 at least 62 percent of the yearling males had some testes development, beginning about 100-109 DAE. About 35 percent had testes fully descended into the scrotum and 27 percent had testes that were only partially descended from the abdomen. At this time yearling males engaged in preliminary sexual behavior with females. Juvenile females had an increasing tendency to defend a burrow, to which they carried nest material (Figure 1), and to dominate juvenile males in encounters. At the peak of carrying nest material, 90-99 DAE in 1966, juvenile females initiated 69 percent and were dominant in 86 percent of 14 encounters observed between the juvenile males and juvenile females. From these data it appears that yearling males, juvenile females, and juvenile males are territorial to some extent in the nonreproductive season.

Seasonal Changes in Agonistic Behavior

Data on seasonal changes in agonistic behavior were analyzed in three categories: the rate of encounters per individual, the form of

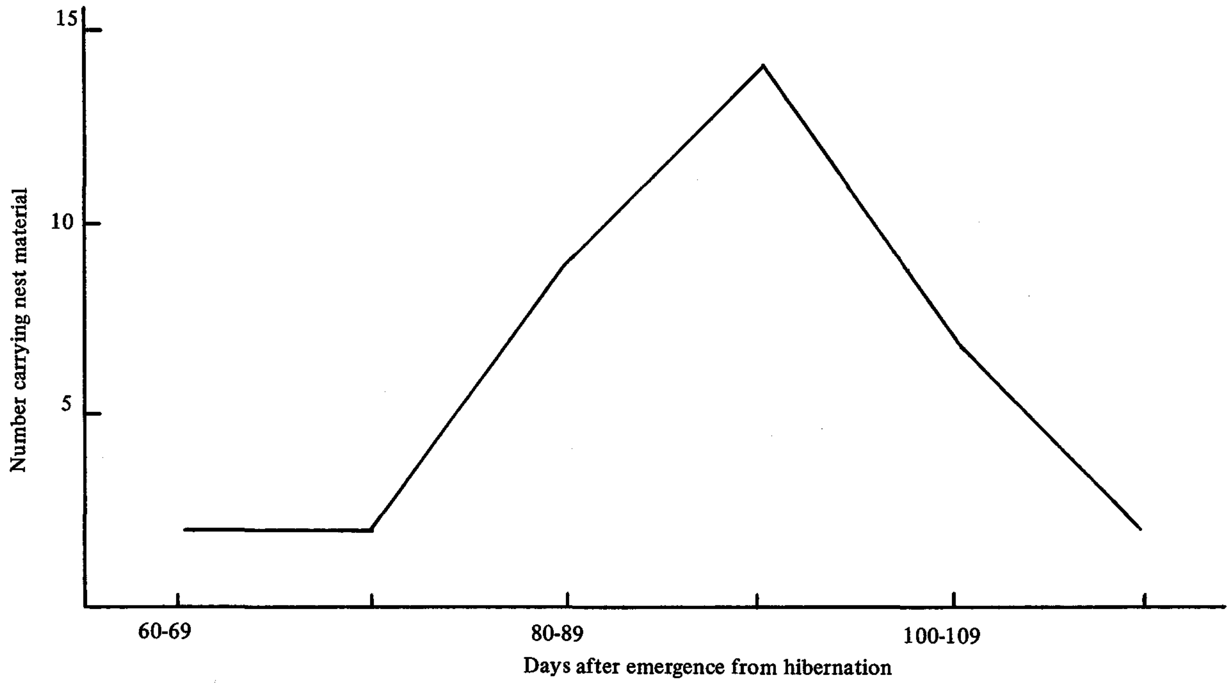

Figure 1. Seasonal changes in the number of juvenile females carrying nest material, 1966. n = 36

encounters, and the relative frequency of encounters among age and sex groups. The relative frequency of encounters among age and sex groups was also compared to an index based on a calculated, theoretical frequency of animals meeting.

The rate of encounters per observed individual (hereafter called encounter rate) probably was a better indication of social stress on the population than simply the number of encounters, which did not account for differences in density. Encounter rates were determined by dividing the number of encounters observed during a 5-minute period by the number of animals seen on the sample area immediately preceding the time period. This number of encounters per observed individual over 5 minutes was then multiplied by 12 to give an hourly rate.

The form of an encounter was probably related to the amount of associated social stress. Hence encounters were divided into three categories: high-intensity, medium-intensity, and low-intensity. In high-intensity encounters animals had body contact, wrestled, and bit each other. Medium-intensity encounters involved a chase by a dominant and escape by a subordinate. Low-intensity encounters included a threat, in posture or call, by a dominant and escape by a subordinate.

The relative frequency of encounters among different age and sex groups was compared to an index of the probability of these animals meeting. The number of encounters between individuals of a given age and sex group had little meaning unless the number of individuals of that group available to fight was known. If actual values were higher than expected values it indicated that this particular segment of the population probably had a lower threshold of aggression and, thus, a greater proportion of their meetings ended in encounters.

The relative frequency of encounters among age and sex groups depended upon the number of encounters that individuals of a group had among themselves or with individuals of other groups. The index of probability was based on the number of times animals in age and sex groups would meet assuming each observed individual on sample areas met all other individuals on sample areas one time (see Appendix for example).

The encounter rates for the entire population reached a peak in spring at about 20-39 DAE, depending on the year, and then declined. The rates increased again after the juveniles came above ground; reached a somewhat lower peak about 80-109 DAE; then declined until hibernation (Figure 2).

In 1965 encounters with contacts and chases, and encounters with contacts in 1966, were most numerous on the first nine DAE, then usually decreased in number throughout the reproductive season. This type of encounter increased again after the juveniles emerged; peaked at about 60-89 DAE, depending on the year; then declined until the onset of hibernation. In 1966, however, encounters with chases remained high and relatively uniform throughout the year (Figure 3).

The rates and relative frequency of encounters for various age and sex groups shifted throughout the year. The encounter rates for adult

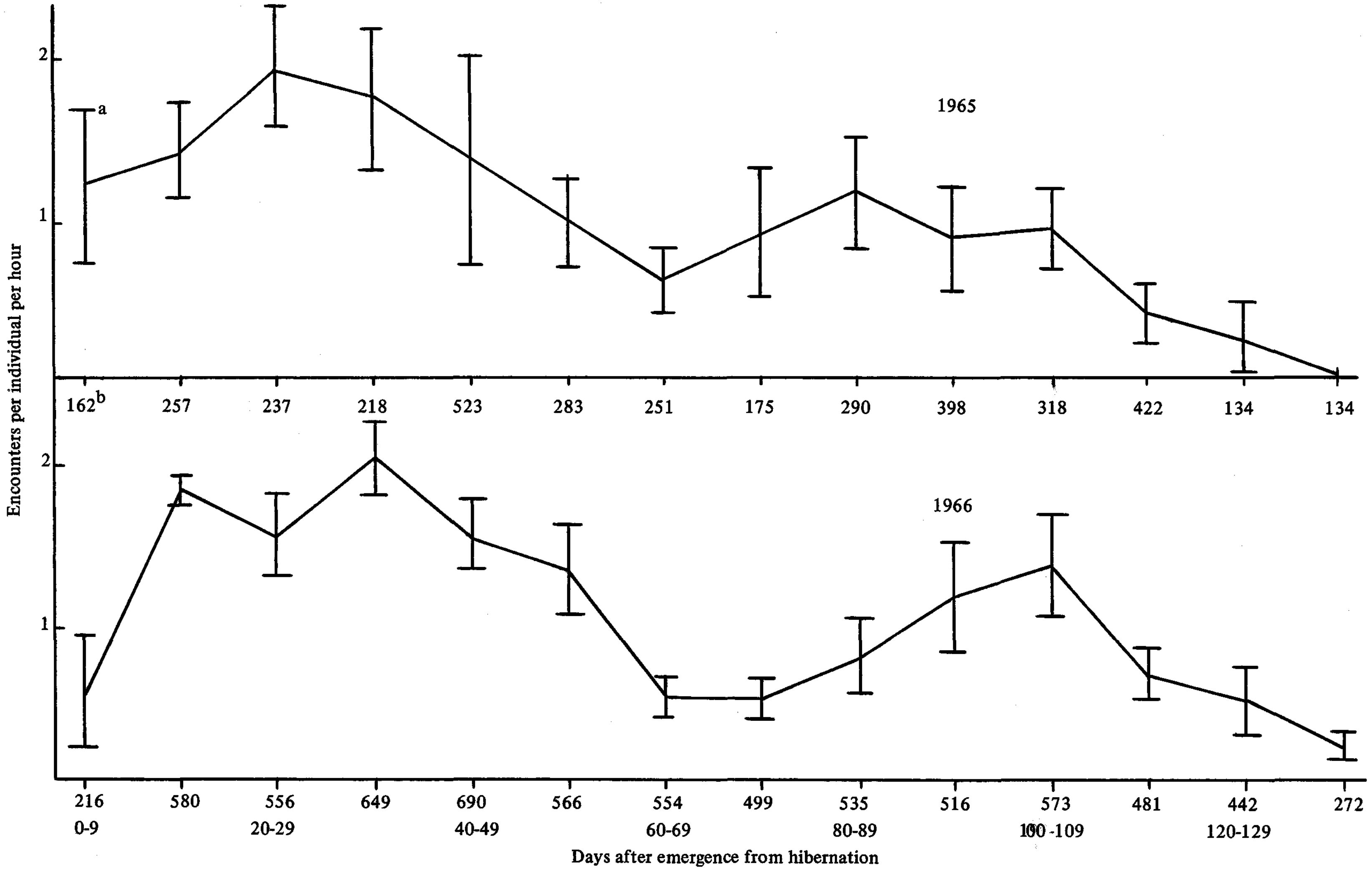

Figure 2. Seasonal changes in encounters per observed individual in the population.

[a] Standard error of the means
[b] Number of 5-minute sample periods

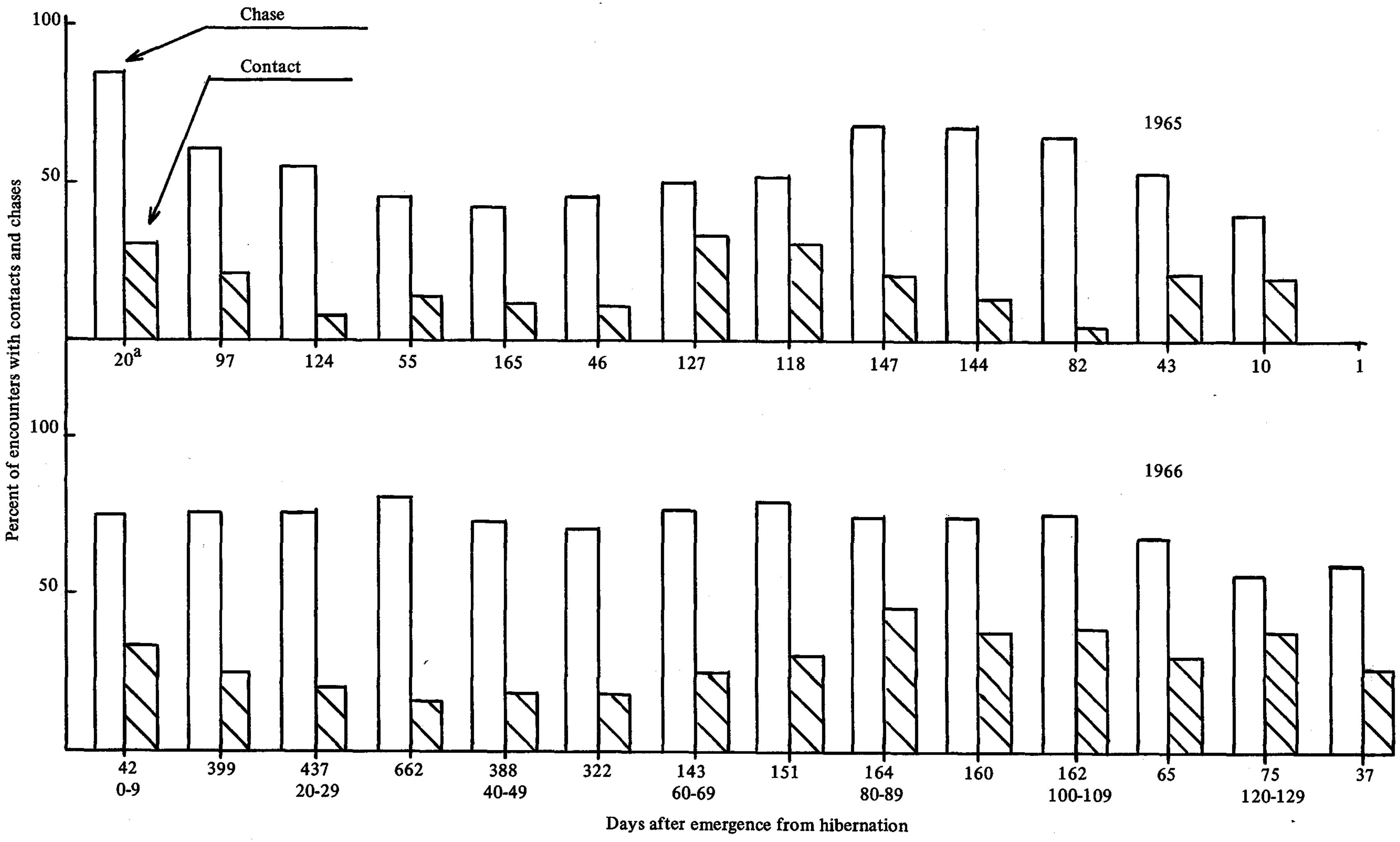

Figure 3. Seasonal changes in encounters with contacts and chases in the population.

[a] Number of observed encounters

males were highest during breeding, but increased again after the juveniles appeared above ground. Yearling males usually had lower encounter rates than adult males during breeding, but higher rates than adult males after the juveniles appeared. Juveniles had a late summer peak in encounter rates (Figure 4).

The encounter rates for females increased during breeding and remained high during nesting. The encounter rates for juvenile females appeared lower and more even through the year than the rates for juvenile males (Figure 5).

Encounters among adult males were high for the first 19 DAE, and greatly exceeded the probability of adult males meeting. Thereafter, encounters among adult males were few (Table 4).

Encounters among adult females and between adult and yearling females, were highest during nesting and usually somewhat surpassed the probability of these animals meeting at this time. After the young appeared, however, encounters among these females were few, though they remained somewhat above the probability of their meeting. Encounters among yearling females were most frequent and surpassed the probability of the animals meeting about the time the young appeared (Table 4).

Yearling males fought little among themselves. The frequency of encounters exceeded the expected values for these animals meeting mostly in the nonreproductive season, when the yearling males showed adult-like territorial behavior. Encounters between yearling males and

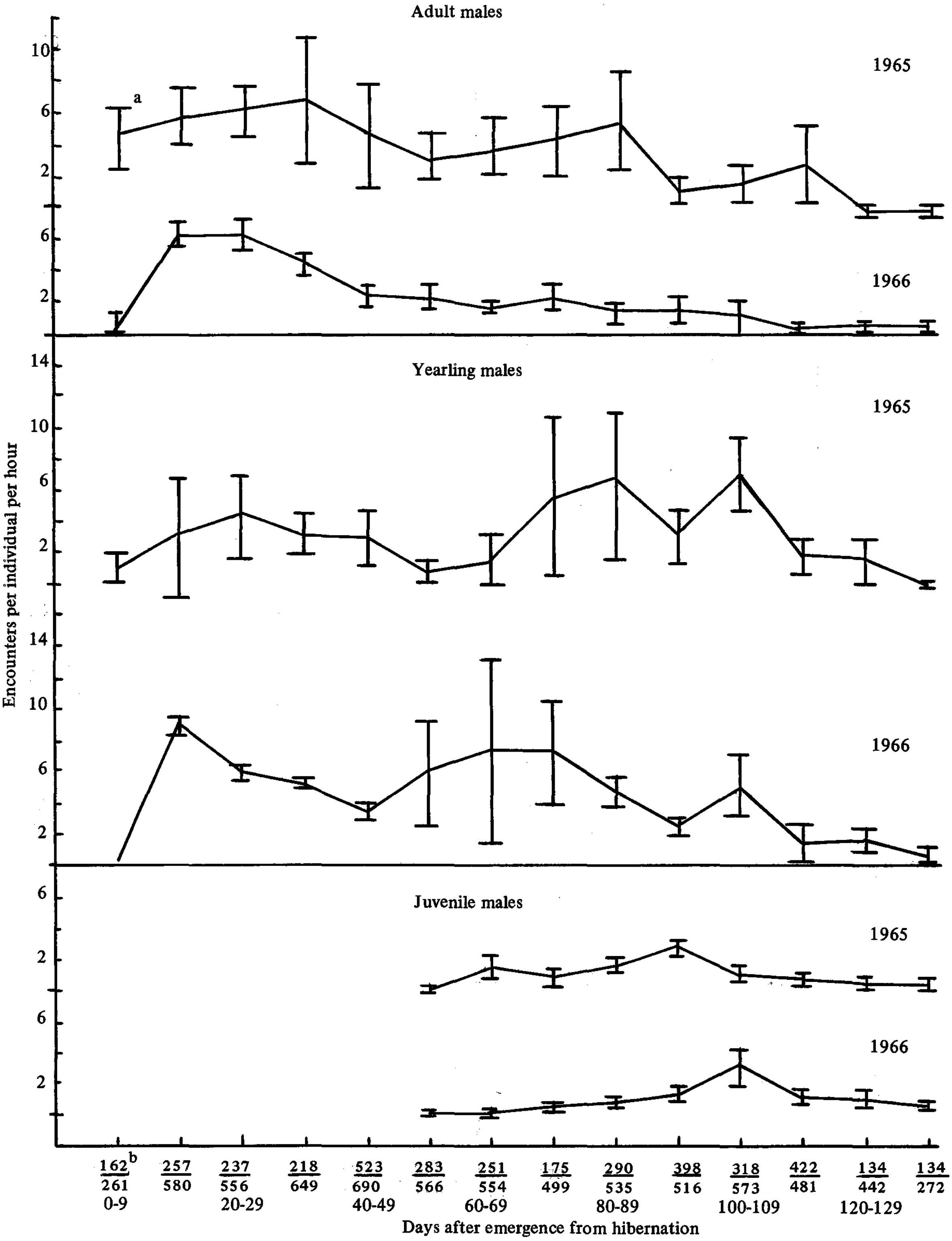

Figure 4. Seasonal changes in encounters per observed male in the population.

[a] Standard error of the means

[b] Number of 5-minute sample periods $\frac{1965}{1966}$

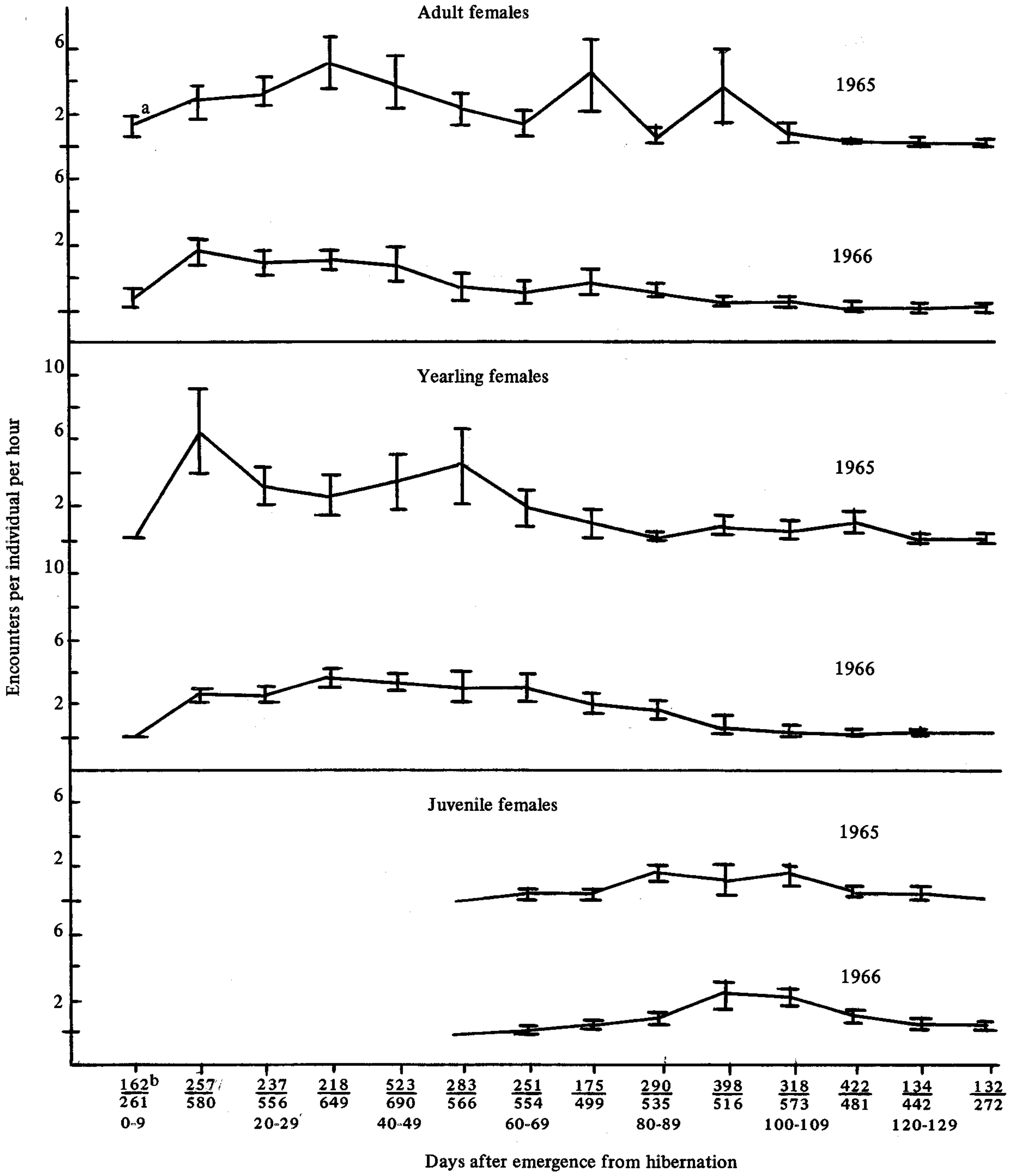

Figure 5. Seasonal changes in encounters per observed female in the population

[a] Standard error of the means

[b] Number of 5-minute sample periods $\frac{1965}{1966}$

Table 4. Relative frequency of encounters compared to the index of probability of animals meeting (%)

Individuals in encounters	Days after emergence from hibernation													
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Adult males vs.	65[a]	17	5	1	1	1	0	1	0	0	0	0	0	0
Adult males	11[b]	5	3	2	1	1	0	0	1	0	0	0	0	0
Adult females vs.	23	25	20	11	8	7	8	5	2	1	1	0	0	0
Adult females	32	22	16	9	8	8	2	1	3	0	0	0	0	0
Adult females vs.	3	12	14	14	9	12	9	3	2	2	2	0	0	0
Yearling females	8	7	12	10	8	8	2	1	0	1	1	0	0	0
Yearling females vs.	1	5	10	9	12	24	9	2	1	0	0	0	0	0
Yearling females	3	8	10	14	12	12	2	2	0	2	1	0	0	0
Yearling males vs.	0	1	1	4	3	1	1	2	3	2	3	1	1	0
Yearling males	0	0	3	3	4	4	0	0	0	1	1	1	0	0
Yearling males vs.						0	2	9	7	6	5	14	16	3
Juvenile females						0	4	3	4	5	5	5	3	5
Juvenile females vs.						0	0	4	16	29	18	13	16	10
Juvenile females						0	4	9	10	19	19	29	33	28

[a] Percent of total encounters in the population, 1965 and 1966

[b] Percent of total probability of animals meeting, 1965 and 1966

juvenile females were relatively high, and almost always exceeded the expected value for meeting, from 70 DAE until hibernation, when juvenile females also showed adult-like territoriality. Juvenile females fought most, and the frequency of their encounters surpassed the probability of the females meeting on 90-99 DAE. This was at the peak of carrying nest material. The number of encounters then declined and fell below the expected value for juvenile females meeting (Table 4). For a similar comparison of all age and sex groups see the Appendix.

Changes in Agonistic Behavior With Area

The study area supported different densities of squirrels and different vegetative covers, and these seemed to affect agonistic behavior. High density usually occurred on lawn sample areas where visibility was good, and low density in brushy sample areas where vision was obstructed. The encounter rate was higher on high-density areas than on low-density areas (Figure 6). Encounters with contacts and chases, however, were more numerous on low-density areas (Figure 7), hence, aggression was more intense in form with low density.

The amount of intrusion by nonresidents was also different on areas of low and high density, especially among the juveniles. A greater proportion of nonresident juveniles was observed on low-density than on high-density areas (Table 5). This did not appear to be true of adults and yearlings for most of the year, however (Table 6). A resident juvenile was defined as one born on or within 40 feet of a sample area, and a

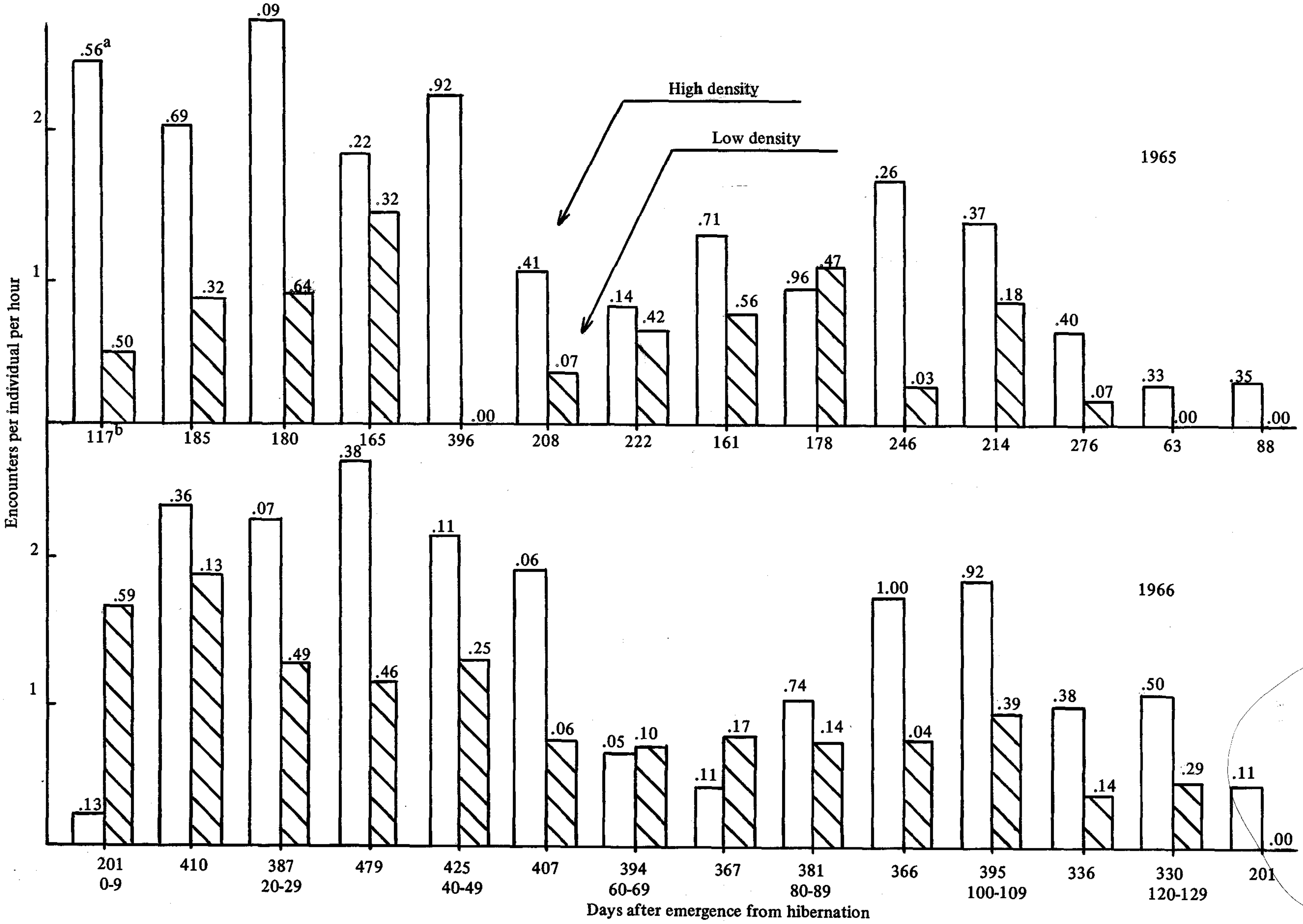

Figure 6. Differences in encounters per observed individual on high and low density sample areas.
[a]Standard error of the means
[b]Number of observed encounters

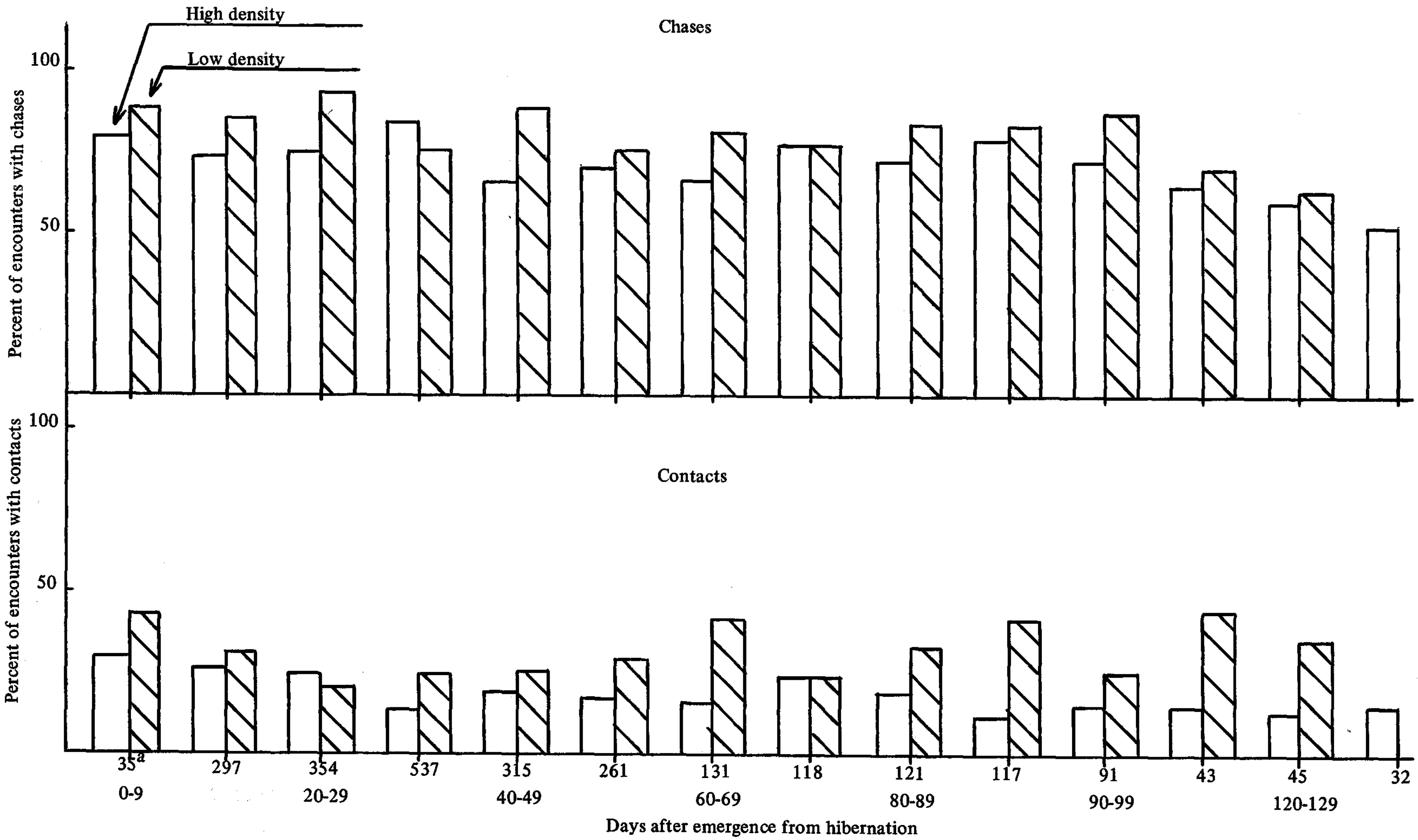

Figure 7. Differences in encounters with contacts and chases on high and low density areas, 1966.

[a] Number of encounters observed

Table 5. Differences in observations of nonresident juveniles[a] on areas with different densities, 1966[b]

Density of sample area	Days after emergence from hibernation						
	70-79	80-89	90-99	100-109	110-119	120-129	130-139
High	4(%)[c]	7	11	15	4	11	26
Low	3	20	31	51	47	56	56

[a] Total number of observations of juveniles = 4,763

[b] $T = 3.28$ $(P < .025)$

[c] Percent of observations that were nonresidents

Table 6. Differences in observations of nonresident adults and yearlings[a] on areas with different densities, 1966[b]

Density of sample area	Days after emergence from hibernation							
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79
High	1(%)[c]	13	9	13	8	7	9	7
Low	54	42	11	7	5	7	9	11

[a] Total number of observations of adults and yearlings = 5,578

[b] $T = 1.41$ $(.200 > P < .400)$

[c] Percent of observations that were nonresidents

resident adult was defined as one with its home burrow on or within 40 feet of a sample area. All others were considered nonresidents of that area.

Areas with high density probably had more frequent encounters per individual because animals had a greater chance of meeting. Less intensive forms of aggression could have resulted from good visibility permitting animals to avoid known dominants, and from less intrusion by nonresidents. Residents usually attacked a nonresident on sight.

Areas with low density probably had fewer encounters per individual because there was less chance of animals meeting. More intense forms of aggression could have occurred because animals met unexpectedly, at close range because of poor visibility and because of more intrusion from nonresidents.

High-density areas, therefore, appeared more stable socially. A more rigid social structure forced by density may lower fighting (Lloyd and Christian, 1967). In squirrels, greater density appeared to increase social stability by limiting the amount of intrusion from nonresidents, thus producing lower intensity in encounters. It would, however, be difficult to tell if the animals were under more stress on areas with high or low density.

Daily Changes in Agonistic Behavior

Encounter rate through the day varied with the time of season. In spring the rate for the population was lower in the mornings and evenings, when density was highest; and high at midday, when density was lowest. In late summer the encounter rate was higher in the mornings and evenings and lower at midday (Figure 8). Aggression was similar both years, but in 1966 the comparable daily pattern occurred 10 days later than in 1965.

There were apparently two variables causing seasonal differences in encounters--the aggressiveness of the squirrels, and a conflict between aggression and feeding behavior. Fighting in a potentially aggressive situation may be suspended if the animals have a strong tendency for an activity incompatible with aggression (Marler, 1957). In spring when squirrels were aggressive, a strong tendency to feed in the mornings and evenings apparently interfered with agonistic behavior, and animals fought less even though density was highest then. At midday when animals fed little, the aggressiveness was manifested and encounters per individual were frequent. In late summer when animals were less aggressive, encounters were few during the midday hours when density was low. With the variable of feeding, there are probably at least two phenomena operating to decrease aggression. Feeding animals tend to move less, and lowered aggression may result from a conflict with feeding behavior and from a decreased tendency to move.

Population Regulation

The population was regulated by a variety of factors acting at different times and to different degrees. The role of agonistic behavior in regulating the population appeared important at least twice during the

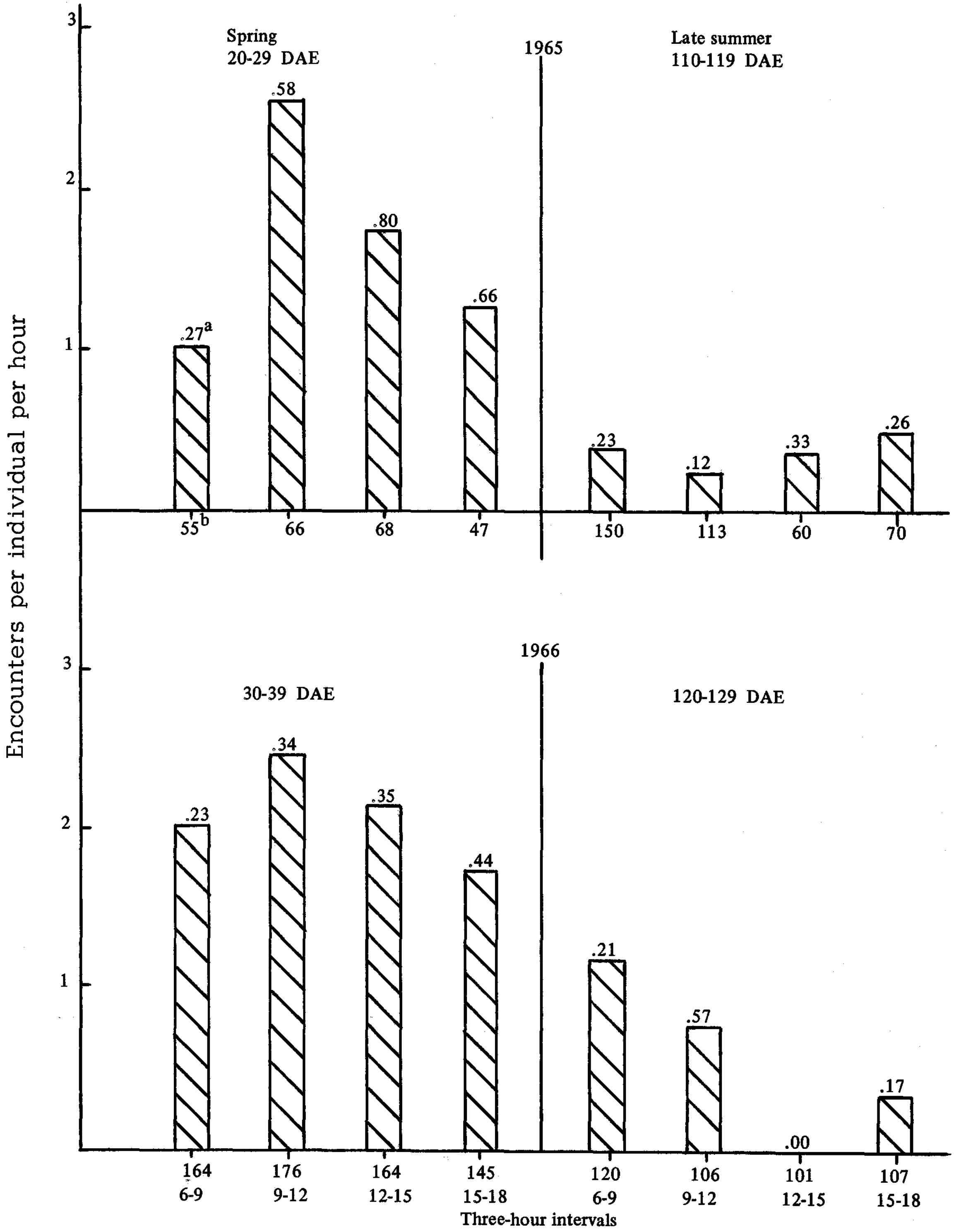

Figure 8. Diurnal changes in encounters per observed individual in the population.

[a] Standard error of the means

[b] Number of 5-minute sample periods

squirrels' active seasons.

Some animals were lost in spring. Though the mortality was higher about 30-49 DAE (Table 7), the difference was not significant. The loss during each 10-day period is expressed as a percent of the total number of adults and yearlings in the population. An animal was considered lost from the population when it was known to have died or moved outside the study area or was no longer seen or trapped. The time of loss was the last time the animals were seen or trapped on the study area.

Table 7. Loss of adults and yearlings[a] from the population,[b] 1965 and 1966[c]

	Days after emergence from hibernation							
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	Total
Animals lost (%)	1	5	5	8	9	5	6	39

[a] Total number lost = 185

[b] Number of adults and yearlings in the population = 470

[c] $F = 1.21 \quad (P < .250)$

Some of the loss to adults and yearlings that occurred in spring was related to agonistic behavior. I witnessed a good example of this when agonistic behavior of at least four territorial adult females (36, 167, 468, and 601) apparently forced two yearling females (742 and 745) from the territories of the adults. During a 16-day period, 16-32 DAE, the adults dominated the yearlings in 30 of the 31 observed encounters that occurred between them. Yearling 745 finally established herself at the edge of the older females' territories after carrying nest material to, digging at, or spending the night in at least seven different burrows. Yearling 742 subsequently disappeared after carrying nest material to at least three different burrows (R. E. Walker, personal communication).

Dispersal in marmots in spring was associated with changes in home range and with avoidance of dominants by subordinates (Armitage, 1965). The mechanism of loss in ground squirrels appeared similar, and apparently operated mostly on animals unable to establish themselves territorially such as yearling males and late emerging yearling females.

Many juveniles were lost from about 70-109 DAE (Table 8). In this time span in 1966, the average number of juveniles seen per sample area decreased from over 2.0 to about 0.7 (R. E. Walker, personal communication). At the same time, encounter rates for juveniles increased from about 0.5 to over 2.0 encounters per hour on the same areas (Figures 4 and 5). Also at this time juveniles were much more mobile, apparently exploring their environment and expanding their home ranges or moving out altogether. Thereafter, the encounter rates for juveniles decreased, and the density of juveniles remained relatively constant until hibernation.

Hence, it seems likely that much of the dispersal of well over half of the juveniles in this 40-day period was related to aggression. Aggression, then, appeared to be an important means of population regulation, especially in juveniles, but also in adults and yearlings.

Table 8. Loss of juveniles[a] from the population,[b] 1966

	Days after emergence from hibernation							
	60-69	70-79	80-89	90-99	100-109	110-119	120-129	Total
Animals lost (%)	3	9	16	7	13	7	6	62

[a] Total number lost = 290

[b] Number of juveniles in the population = 468

DISCUSSION

Social Organization

The Uinta ground squirrels involved in reproduction defend territories during the reproductive season (Tables 1 and 2). Adult males have large territories during the breeding season that may include the home burrows of several females. The males are very aggressive toward all other males at this time. A male presumably breeds the females on his territory soon after the females emerge from hibernation. Territories apparently reduce interference with breeding, and larger territories may increase the number of females a male can breed, thus favoring aggressiveness in males.

Adult and yearling females become intolerant of all other squirrels when bred, and defend smaller territories than males. These include a home burrow where the young are raised. This, plus the fact that territorial behavior ends when the juveniles appear above ground (page 6), and that juveniles apparently killed by another squirrel were found in an unprotected nest (page 10), indicate that one function of female territoriality is to protect the young.

Calhoun (1952) found that social stability favored reproduction by facilitating breeding and decreasing mortality of young rats (_Rattus norvegicus_). The same probably applies to ground squirrels. Territorial behavior localizes individuals and to some extent spaces them. This apparently limits interference with breeding and nesting thus favoring reproduction.

Hinde (1956) suggested that territoriality in birds may reduce the time they spend in fighting, and this also appears true of territorial behavior in the squirrels. As female territories become established there are fewer encounters per individual in the population (Figure 2), and the encounters that do occur are less intense in form (Figure 3). This is probably the result of animals' becoming familiar with their neighbors and learning territorial areas.

Some adults and yearlings disappear during the reproductive season (Table 7), and the aggression inherent in establishing territories causes part of the loss. Yearling males that are not territorial, and females unable to establish a territory for themselves (pages 28 and 29), are probably the animals most affected.

Yearling males are not involved in breeding and are not successful in defending a territory (Table 3). After the breeding and nesting seasons the adult males and reproducing females no longer defend a territory. Hence, squirrels tend to defend territories only when the defense has a biological function, i.e. in males enhancing the opportunity to breed females, and in females protecting the young.

Some yearling males and juvenile females show adult-like territorial behavior in the nonreproductive season (pages 10 and 11; Figure 1). These individuals will breed the following year, when having a territory is biologically functional. Their behavior, then, is similar to that of some birds that take up a temporary territory prior to their first breeding season, i.e. Canada geese (Branta canadensis) (Martin, 1964). Martin suggested that this may reduce . . . territorial friction associated with nesting . . . in the following spring. Being dominant in aggression also reinforces fighting behavior, and individuals, used to dominating others, fight savagely and efficiently (Scott, 1958, p. 19). Success in aggression during the nonreproductive season may enhance the chances of the yearling males and juvenile females in defending a territory successfully the following spring.

Juvenile males, do not breed the next spring, hence, have no apparent "need" to prepare for competition with adults, and do not show territoriality in late summer to the extent shown by yearling males and juvenile females.

Large numbers of juveniles disappear from the population in the nonreproductive season (Table 8). The time of loss is characterized by instability in the population due to development of sexual behavior and increased aggression in yearling males and juvenile females (pages 10 and 11), and increased movement by juveniles that are expanding their home ranges (page 29). About twice as many juvenile males as juvenile females are lost during the period when juvenile females dominate juvenile males (R. E. Walker, personal communication). This disproportionate disappearance appears to be directly related to aggression on the part of juvenile females. Older animals, except yearling males, do not participate in this aggression to any extent (Appendix). It appears that once an animal has bred its territory is secure. Adults are usually able to prevent successful invasion of younger animals. Loss of juveniles appears to be influenced almost entirely by the behavior of the juveniles themselves.

Density of animals must be contained to keep them from overexploiting the resources in their environment (Wynne-Edwards, 1962, p. 7). Agonistic behavior in the ground squirrels has this role, though it is not the sole regulator of the population. Other limiting factors are death during hibernation, predation and disease, and decreased recruitment of juveniles caused by an interaction between behavior and weather (R. E. Walker, personal communication). The causes of loss are interrelated; the relative significance of each cause of loss is difficult to ascertain, and this loss varies with density, weather, and probably other variables. Nevertheless I have shown that the squirrel population is partly regulated by agonistic behavior at least twice during the squirrels' active season. The time of loss and relative numbers lost seem to follow a biologically functional pattern. Losses are greatest after the juveniles become active, when the population is highest, and lower in the spring after density has been reduced.

The squirrel population is relatively stable, and its control is similar to that found in red grouse (Lagopus lagopus) (Jenkins, Watson, and Miller, 1963). In grouse, territorial behavior in fall largely determines the size of the breeding population, with surplus animals forced out. In spring there is another adjustment based on the surviving birds and the effects of winter on the habitat.

In the squirrels the upper limit of density seems to be set by territorial intolerance related to burrows. Food appears more than adequate. The number of juveniles produced far surpasses the number that can breed within the study area. The surplus is removed by a variety of mortality factors, but to a large extent in summer by agonistic behavior and movement of juveniles. How many actually breed the following spring depends on over-winter survival and spring weather, but is finally determined by the number of animals able to defend a territory.

Factors Affecting Agonistic Behavior

This study revealed that agonistic behavior in ground squirrels was influenced by a variety of factors that probably affect all populations where animals fight. The density, visibility, movement, and intrusion of nonresidents on an area (Tables 5 and 6; Figures 6 and 7); the age, sex, and aggressiveness of individuals involved (Figures 4 and 5; Appendix); and the time of day and season (Figures 2, 3, and 8), all played a part in determining the frequency, and the intensity of form, of agonistic encounters.

These factors can be divided into three categories that may well be examined in any study of agonistic behavior. First, factors influencing the probability of animals meeting or detecting one another, such as density, movement, and visibility on areas. Second, factors that determine whether or not agonistic behavior results when individuals are aware of each other, for example, the aggressiveness of the individuals involved, or the location where they meet. Third, the outcome of an encounter, should one occur, i.e. the dominant-subordinate relationship and the intensity of form in the encounter. One could also analyze these factors in groups that have some homogeneity in agonistic behavior, i.e. age or sex groups, or both, in order to best relate them to the population.

This type of comprehensive approach is important now, and will probably be more so in the future. With wild animals under increasing pressure from an expanding world population, more detailed research will be necessary, not only in agonistic behavior, but in all phases of behavior and population ecology, for more intensive management and control of animals.

SUMMARY

Agonistic behavior of Uinta ground squirrels was studied in 1965 and 1966 at the Utah State University Forestry Field Station, 22 miles northeast of Logan, Utah, at 6,300 feet above sea level. The main objective was to determine what role agonistic behavior had in regulating density in the population.

Marked individuals, of known ages and sexes, in an unconfined population, were observed from six towers overlooking specific sample areas with different densities and vegetative covers. Data on the number, location, and activity of all animals on the sample areas were related to changes in frequency, intensity of form, and dominant-subordinate patterns in agonistic encounters. These data permitted us to determine relationships between agonistic behavior, establishment of a social organization, and times and relative numbers of animals lost in the population.

All individuals involved in reproduction were territorial during the reproductive season; adult males during breeding, and adult and yearling females during nesting. A minor reduction related to agonistic behavior occurred at this time, and appeared to affect mostly females unable to establish a territory and yearling males who were not territorial.

Yearling males and juvenile females showed territoriality during the nonreproductive season. The juveniles were also expanding their

home ranges at this time, and the population appeared unstable. The major reduction in population numbers related to agonistic behavior also occurred during the nonreproductive season. It affected mostly juveniles, and especially juvenile males, who were dominated by juvenile females at the time of loss.

An overproduction of juveniles in summer is greatly reduced through agonistic behavior in, and movement of, young squirrels. Other mortality also occur in fall and winter, but breeding density in spring is finally determined by the number of animals able to establish territories.

Agonistic behavior in the population was influenced by a variety of variables. These included the density, visibility, movement, and intrusion by nonresidents on sample areas; the age, sex, and aggressiveness of individuals; and the time of day and season. These factors all warrant consideration in any study of agonistic behavior.

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APPENDIX

Table 9. Relative frequency of encounters compared to the index of probability of animals meeting[a] (%)

Individuals in encounter	Days after emergence from hibernation 0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Adult males	50[b]	5	2	1	0	1	0	0	0	1	0	1	1	0
	9[c]	2	4	1	0	1	0	0	2	0	1	0	0	0
vs.														
	81[d]	30	9	2	2	1	0	2	0	0	0	0	0	0
Adult males	13[e]	9	3	3	3	2	1	0	0	0	0	0	0	0
Adult males	33	19	16	12	6	7	9	0	2	1	0	0	0	0
	26	11	15	8	5	7	2	1	5	0	0	0	0	0
vs.														
	14	31	25	11	10	7	8	10	2	1	2	0	0	0
Adult females	39	33	17	11	12	10	3	1	1	1	1	0	0	0
Adult males	2	3	5	2	2	3	1	5	0	2	2	0	0	0
	1	1	2	2	2	3	0	0	1	0	2	0	0	0
vs.														
	3	3	6	15	8	6	4	5	8	5	2	0	0	0
Yearling males	8	4	3	8	8	6	1	0	1	2	2	0	0	0

Table 9. Continued

	Days after emergence from hibernation													
Individuals in encounter	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Adult males	7	14	19	14	5	11	5	2	2	1	3	1	0	0
	16	10	15	11	6	7	1	1	0	1	2	0	0	0
vs.														
	0	10	9	14	13	13	14	4	3	4	1	0	0	0
Yearling females	0	5	10	10	10	10	3	1	1	2	1	0	0	0
Adult males						0	1	2	1	1	2	2	0	0
						1	2	2	10	1	5	2	0	0
vs.														
						0	1	3	1	7	4	4	0	0
Juvenile males						0	2	2	11	3	7	3	0	0
Adult males						0	0	1	9	4	2	2	0	0
						0	2	2	11	3	7	3	0	0
vs.														
						0	1	2	4	7	9	0	0	0
Juvenile females						0	3	2	3	4	5	1	0	0

Table 9. Continued

Individuals in encounter	Days after emergence from hibernation 0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Adult females	0	5	7	10	12	9	8	2	0	1	0	0	0	0
	18	18	14	11	12	12	5	3	3	0	0	0	0	0
vs.														
	0	10	11	4	5	7	6	2	0	0	0	0	0	0
Adult females	28	29	21	9	11	8	7	1	1	1	0	0	0	0
Adult females	2	7	7	16	20	8	12	8	1	2	0	0	0	0
	1	4	4	7	12	10	2	2	1	0	0	0	0	0
vs.														
	3	4	3	16	15	10	9	10	12	1	1	0	0	0
Yearling males	11	7	8	14	14	13	9	1	2	2	1	0	0	0
Adult females	2	31	19	24	30	32	11	3	0	0	0	0	0	0
	22	34	28	30	29	26	7	6	0	1	0	0	0	0
vs.														
	0	8	24	11	20	21	17	7	3	1	1	0	0	0
Yearling females	0	10	24	17	18	21	6	2	2	2	1	0	0	0

Table 9. Continued

Individuals in encounter	Days after emergence from hibernation													
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Adult females						0	6	2	1	1	1	0	0	0
						2	14	10	10	1	1	0	2	0
vs.														
						0	4	6	1	2	0	0	0	0
Juvenile males						0	9	7	7	4	2	0	0	0
Adult females						0	6	2	1	1	1	0	0	0
						1	11	10	12	2	1	1	2	0
vs.														
						0	4	3	5	2	0	0	0	0
Juvenile females						0	8	6	6	6	5	0	0	0
Yearling males	0	2	1	4	3	0	1	3	2	1	3	0	0	0
	0	0	0	1	3	2	0	0	0	1	1	0	0	0
vs.														
	0	0	1	5	4	3	2	1	4	3	3	2	2	0
Yearling males	1	0	7	5	4	7	1	0	1	2	2	2	1	1

Table 9. Continued

	Days after emergence from hibernation													
Individuals in encounter	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Yearling males	0	4	12	4	9	8	2	5	6	7	8	0	0	0
	1	4	4	9	14	11	1	2	0	3	2	0	0	0
vs.														
	0	2	3	15	13	13	13	6	8	4	5	4	2	0
Yearling females	0	1	5	13	11	12	3	1	2	4	3	2	1	0
Yearling males						0	2	10	5	5	6	6	12	0
						1	3	3	2	4	5	4	2	5
vs.														
						0	1	8	9	8	4	23	20	6
Juvenile males						0	5	4	6	6	5	7	4	6
Yearling males						0	2	11	20	4	19	12	19	0
						1	2	3	3	9	8	5	2	5
vs.														
						0	2	5	14	16	24	25	17	20
Juvenile females						0	4	4	5	10	13	16	13	11

Table 9. Continued

Individuals in encounter	Days after emergence from hibernation													
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Yearling females	2	10	11	13	13	23	7	2	0	0	0	0	0	0
	6	16	14	20	17	14	2	3	0	2	2	0	0	0
vs.														
	0	1	10	6	11	16	12	3	2	0	0	0	0	0
Yearling females	0	1	7	8	7	10	3	1	1	2	1	0	0	0
Yearling females						0	8	11	4	3	1	0	0	0
						2	10	10	0	5	7	1	0	0
vs.														
						0	1	7	8	7	3	2	0	0
Juvenile males						0	9	9	7	6	4	3	2	0
Yearling females						0	9	9	10	6	4	0	0	0
						0	7	10	0	14	10	1	0	0
vs.														
						0	1	7	7	3	0	0	3	0
Juvenile females						0	7	8	6	9	10	7	7	0

Table 9. Continued

	Days after emergence from hibernation													
Individuals in encounter	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Juvenile males						0	11	3	2	3	2	5	15	0
						0	9	8	8	4	8	13	20	23
vs.														
						0	0	3	0	3	3	8	12	3
Juvenile males						0	7	13	12	5	3	5	4	10
Juvenile males						0	0	7	12	14	22	49	38	0
						0	14	18	21	25	23	40	45	45
vs.														
						0	0	4	5	12	27	25	27	46
Juvenile females						0	11	24	21	16	17	26	26	38

Table 9. Continued

Individuals in encounter	Days after emergence from hibernation 0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139
Juvenile females						0	1	8	27	43	24	19	15	0
						0	5	8	12	25	17	29	26	22
vs.														
						0	0	1	5	16	13	8	18	20
Juvenile females						0	4	10	9	13	21	30	40	34

[a] Probability of animals meeting if each observed individual on sample areas met all other observed individuals on sample areas one time. Example, if sample areas contained 3 adult males (X) and 6 adult females (Y) the probability for:

adult males meeting adult males = $\frac{(X \times X-1)}{2} = \frac{3 \times 2}{2} = 3$

adult females meeting adult females = $\frac{(Y \times Y-1)}{2} = \frac{6 \times 5}{2} = 15$

adult males meeting adult females = $X \times Y = 3 \times 6 = 18$

Total meetings = 36

Then the percent of total probability for: adult males meeting adult males = $\frac{3}{36} = 8\%$

adult females meeting adult females = $\frac{15}{36} = 42\%$

adult males meeting adult females = $\frac{18}{36} = \underline{50\%}$

Total percent = 100%

[b] Percent of total encounters in the population, 1965

[c] Percent of total probability of animals meeting, 1965

[d] Percent of total encounters in the population, 1966

[e] Percent of total probability of animals meeting, 1966

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