THE ONTOGENY OF SOCIAL BEHAVIOR
OF UINTA GROUND SQUIRRELS
by
D. Andrew Saunders

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Wildlife Biology

Approved:

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Major Professor

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Committee Member

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Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah
1970
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ACKNOWLEDGMENTS

I sincerely thank Dr. D. F. Balph for suggesting this problem and for his encouragement and advice throughout the study. I also thank Drs. A. W. Stokes, K. L. Dixon, and D. Muller-Schwarze for their help and constructive criticism.

I am one of a team of researchers who are studying the behavior and ecology of the ground squirrels, and I am grateful to the other members for their cooperation and contributions—to R. E. Walker, R. J. Burns, R. P. McQuivey, R. L. Ruff, N. A. Slade, F. Knopf, and C. Larham.

I especially want to thank Robert Walker for the memorable coffee hours we shared while discussing ground squirrels, and I shall always be indebted to Norman Slade for his optimism and aid in dealing with the statistical treatment of the data.

This study was supported by an NDEA Title IV fellowship and by the National Science Foundation (GB-5590).

D. Andrew Saunders
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ABSTRACT

The Ontogeny of Social Behavior of Uinta Ground Squirrels

by

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Utah State University, 1970

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The social behavior of juvenile Uinta ground squirrels (Spermophilus armatus) was studied for 2½ years in northeastern Utah. The purpose of the study was to describe the developing social behavior of unconfined, marked squirrels. Their behavior was recorded with motion pictures and written descriptions from the time they emerged from the natal burrow until they entered hibernation.

Three phases of behavioral development were apparent. The first phase began when the juveniles appeared above ground and ended 5 weeks later. This was a period of socialization and consisted of behavioral patterns best described as play. The second phase began abruptly with the development of intolerance and attachment to a particular site. The agonistic behavior of juveniles at this time was much the same as the adult pattern. The third phase began when they had been above ground about 8½ weeks and ended with hibernation, at about 11 weeks. During
this period juveniles combined the behavioral patterns of
the first two periods. However, they became progressively
less active as hibernation approached.

Sex was an important determinant of the developing
behavior of juveniles. Although males and females had
similar behavioral repertoires, the frequency with which
they performed specific activities often differed between
the three periods.

(42 pages)
INTRODUCTION

Biologists have been intrigued with the behavior of juvenile mammals because of its importance in providing clues as to the causes of adult behavior. Most quantitative studies have been done on young laboratory animals such as rats (Rosenblatt and Schneirla, 1962), dogs (Scott and Fuller, 1965), monkeys (Harlow, 1961), and mice (Williams and Scott, 1954). Many investigators have divided the developing behavior into discrete phases. Some have shown through deprivation experiments the functional importance of each phase to the adult (Harlow, 1961). Thus, we have some understanding of the developing behavior of domestic mammals. However, researchers have seldom attempted to quantify the juvenile behavior of wild species because of the inherent difficulties these animals pose. Of those studies that have been done, Horwich's (1967) on gray squirrels (Sciurus carolinensis) has been among the best.

Recently, more interest has developed in the social behavior of young wild mammals, because it is now recognized that this age group is primarily responsible for population dispersal. Under some conditions, dispersal can be of such proportions that it becomes the major factor regulating population density (Walker, 1968). However, little is yet known about the role of social behavior in dispersal.
More quantitative information is needed on the behavior of juveniles in wild populations.

This study attempts to contribute to our knowledge of developing social behavior of juveniles in an unconfined population of Uinta ground squirrels (*Spermophilus armatus*). The specific objectives are: (1) to describe their common postures and motor patterns, (2) to record the frequency of occurrence of these activities, and (3) to relate changes in the above to the age and sex of juveniles.
METHODS

The ground squirrels studied were juveniles of a population located 22 miles northeast of Logan, Utah, at the Forestry Field Station of Utah State University. The study site was on 2 acres of lawn that surround the buildings of the station. Balph and Stokes (1963) and Walker (1968) have described the study area and population in detail. The behavior of the ground squirrels was studied from June 10 to August 15, 1966 and 1967, and from March 31 to June 10, 1968.

Most juveniles first appeared in early June. The litters were captured as they emerged from the natal burrow and were marked with fur dye for identification. The day of first appearance, sex, sibling relationships, and female parent were recorded at this time.

The juveniles were observed from vantage points on the lawn through the day and nearly every day they were active above ground. Records were made with movie cameras and written descriptions of social encounters as they occurred. An attempt was made to obtain information on three facets of encounters. As the encounter began, the identity of the participants, the distance at which they first appeared to respond to each other, and the environmental situation were noted. During the encounter, the
sequence, frequency, and type of postures and motor patterns that occurred were recorded. At the end of the encounter the distance the participants were apart was recorded and dominance and subordinateness were assigned, if the interaction ended in one juvenile chasing the other away.
RESULTS

Ground squirrels were born about May 1 and remained underground for approximately 3 weeks. Just prior to their emergence, the female parent often opened several small burrow entrances from underground some distance from the major entrance to the burrow. The juveniles generally appeared at one of these small entrances. One after another of the litter emerged during the day to stand upright beside the entrance. The entire litter, which averaged about six young, usually appeared within 2-3 days.

For the first 3 days, juveniles had few and brief social encounters. The most common form was when one juvenile placed its forefeet on another while standing upright in a group around the burrow entrance. Occasionally one moved a short distance from the group and touched noses or mouths with others of the litter when it returned. By the end of the first week, social encounters were frequent, sometimes long, and involved many different postures and motor patterns. At this time they rapidly expanded their home ranges and began to meet juveniles of other litters. From the middle of June through August many juveniles disappeared from the population through dispersal and mortality (Walker, 1968). The frequency of encounters
per juvenile per hour decreased through the summer months (Burns, 1968). They began to hibernate in August and most were underground by September 1.

During the study I recorded 891 samples of juveniles in 425 social encounters involving 120 individuals.

**Postures and Motor Patterns in Social Encounters**

An analysis of film taken early in the study indicated that juvenile squirrels commonly exhibited seven postures and motor patterns during their social interactions. Thereafter, emphasis was placed on recording encounters in terms of the frequency and form of these activities as a function of the participants' age and sex.

**Kissing**

Kissing was nose-nose contact between squirrels (Figure 1). During contact, their mouths were sometimes partially opened, one or both had their heads tilted, and they sometimes moved forward to touch the other's cheek with their nose. Adults very seldom kissed, and then only during the breeding season (Balph and Stokes, 1963).

The frequency of kissing changed with age \((P < 0.001.\) All statistical tests are chi-square applied to the numeric data.). It was the most common activity from 0-20 days since first appearance above ground (hereafter abbreviated D.A.), decreased after this time, but increased just prior to hibernation (Table 1). There was no significant
Table 1. Percentage of each age and sex exhibiting various activities during social encounters

<table>
<thead>
<tr>
<th>Days since emergence</th>
<th>Kissing</th>
<th>Sparring</th>
<th>Grasping</th>
<th>Biting</th>
<th>Mounting</th>
<th>Tail fan</th>
<th>Chase</th>
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<td>0  0</td>
<td>0  0</td>
<td>67  0</td>
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</tr>
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difference between males and females in the frequency of kissing nor in the changes that occurred with age.

**Sparring**

Sparring was the interplay of forelimbs in mutual boxing and pushing. Adults sparred only during courtship behavior when males attempted to make contact with females.

Juveniles began sparring about the second week (Table 1). As the season progressed sparring became faster, more forceful, and was more frequently accompanied by squeals. Males sparred more than females ($P < 0.025$) and the frequency varied with age ($P < 0.001$). Females sparred about the same amount through the season ($P < 0.7$). The activity was relatively more common in male-male encounters than in male-female or female-female encounters ($P < 0.01$).

**Grasping**

In grasping, the forelimbs of one squirrel were placed around the body of another, but without mounting. Adults grasped one another while rolling about during intense fights.

The frequency of grasping quickly increased and then gradually declined through the season (Table 1). The change with age was significant for males and females ($P < 0.001$). There was no significant difference between the sexes in the frequency of the behavior ($P < 0.3$).
**Biting**

In biting, one juvenile secured a hold on another with its teeth. The activity varied in intensity and form with age. Young squirrels did little more than mouth the fur of another during an encounter. Older squirrels bit forcefully and often elicited squeals.

Juveniles bit at nearly all ages (Table 1). The frequency of biting did not change significantly with age for males \( (P < 0.1) \) or females \( (P < 0.9) \). Nor was there a difference between the sexes in the amount of biting or the age at which it was done.

**Mounting**

Mounting was the placing of forelimbs around another juvenile from above and behind (Figure 2). Usually the squirrels remained upright, but sometimes they fell on their sides when the activity was intense. Mounting between adults was not seen during this study. Presumably, most copulations occurred underground (Balph and Stokes, 1963).

Juveniles began mounting each other several days after emerging from the natal burrow. The activity disappeared after 35-39 D.A. except for three occurrences during 70-74 D.A. (Table 1). Males mounted more than females \( (P < 0.001) \). Further, the behavior occurred more frequently in male-male encounters and less frequently in male-female and female-female encounters than expected by chance \( (P < 0.01) \).
Figure 2. "Mounting"
Tail fanning

Tail fanning was the pilo-erection of tail hairs (Figure 3). The variable position of the tail and the extent to which the hairs were erected resulted in many forms of the activity. Adults fanned their tails in agonistic encounters (Balph and Stokes, 1963) and when handled (Balph, 1968). The activity was a major component of threat.

Juveniles fanned their tails at all ages (Table 1). Males increased the activity as they grew older ($P < 0.001$), but females did not ($P < 0.4$). There was no significant difference in the frequency of tail fanning between the sexes and between the various sex combinations in encounters.

Chase

Chase was the active (running) pursuit of another squirrel. The speed and distance of chases increased as the juveniles grew older but decreased just prior to hibernation. Chases were frequent and conspicuous in adult agonistic behavior (Burns, 1968).

Juveniles chased each other more as they grew older ($P < 0.001$), especially males (Table 1). The relative number of chases for males and females was about the same ($P < 0.6$). However, male-male and female-female encounters contained fewer chases and male-female encounters contained more chases than expected by chance ($P < 0.01$).
Figure 3. "Tail fanning"
Combinations of activities

Juveniles often exhibited several of the above activities in a single encounter. Eight of the 21 possible two-activity combinations occurred in frequencies not attributable to chance. The paired behaviors were kissing-sparring, kissing-chasing, sparring-grasping, sparring-mounting, grasping-mounting, mounting-biting, mounting-chasing, and kissing-mounting. The frequency of these activities was greater for males and less for females than expected ($P<0.05$).

As the season progressed, squirrels were less apt to combine several activities in an encounter (Table 2. $P<0.025$) and more apt to display a simple tail fan or chase (Table 1). As this perhaps suggests, encounters became more brief and less complex as the juveniles grew older.

Interaction Distances

The distances at which juveniles initiated and terminated encounters changed with their age ($P<0.001$). They responded to one another at close distances until 35-40 D.A. when there was a sudden increase in the distance (Figure 4). The initiation distance decreased sharply at the end of the season. The distance between juveniles at the end of the encounter increased rather steadily as they grew older (Figure 4). Juveniles of all ages separated at distances greater than the distance at which they
Table 2. Frequency that various paired activities occurred together in same social encounter as juveniles grew older

<table>
<thead>
<tr>
<th>Paired activities</th>
<th>Days since appearance</th>
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<td>Kissing-tail fan</td>
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<tr>
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<td>Sparring-grasping</td>
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</tr>
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<td>Sparring-mounting</td>
<td>46</td>
</tr>
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<td>Sparring-tail fan</td>
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</tr>
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<tr>
<td>Biting-chasing</td>
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</tbody>
</table>
Figure 4. Average distance juveniles were apart when they initiated and terminated social encounters as the season progressed.
responded to each other. This suggests that the activity in the encounters served to separate squirrels in space.

**Sex Relationships**

The sex of juveniles influenced the probability of interaction with other juveniles. A greater proportion of males took part in encounters than females \((P < 0.001)\). However, neither sex strongly selected partners for an encounter on the basis of sex \((P < 0.20)\).

**Sibling Relationships**

The probability of a juvenile interacting with siblings varied as they grew older \((P < 0.001)\). Young juveniles were more apt to have social encounters with siblings (Figure 5). As the squirrels spent less time in the vicinity of the natal burrow, they were more apt to encounter juveniles of other litters. Thus, the decrease in probability of sibling encounters after about 30 D.A. was a function of dispersal rather than the selection of non-siblings.

**Dominance Relationships**

Juveniles did not exhibit dominance relationships in many encounters, especially from 0-35 D.A. Some encounters contained no activities deemed aggressive. Others contained such behavior, but participants displayed dominant
Figure 5. Deviations from numbers expected by chance of juveniles that interacted with siblings as the season progressed.
and subordinate patterns within the same encounter. Such reversal of roles is common in the behavior of many young mammals.

In those encounters where social status was established, males were dominant less frequently from 0-25 D.A. and more frequently thereafter than expected by chance (Figure 6A. P < 0.001). The frequency of females being dominant was about as expected by chance and remained the same through the season (Figure 6B). The above differences between males and females were significant (P < 0.05).

Juveniles did not seem to form lasting dominance relationships. A squirrel dominant to another in an encounter might have been subordinate to the same individual on the next encounter. The exception was from 40-60 D.A. when they behaved much like adults establishing territories in spring (Walker, 1968). The juveniles began localizing their activity near a specific burrow, gathering nest material (Burns, 1968), and giving the aggressive "chirp" vocalization (Balph and Balph, 1966). During this time they frequently initiated encounters and were usually dominant over other squirrels that approached their burrow. Both sexes displayed this behavior, and seldom did one individual maintain the activity more than a few days.
Figure 6. Deviations from numbers expected by chance of males (A) and females (B) that were dominant in encounters as the season progressed.
DISCUSSION

The juveniles were about 24 days old when they first appeared above ground. From that time until most entered hibernation (0-80 D.A.), many of their activities formed continuums of developing behavior. However, some data and qualitative observations suggest that the squirrels' first season of activity could be divided into three general phases.

Phase I was from 0-35 D.A. During this phase juveniles initiated an encounter most frequently with a kiss. If they did not immediately separate after nose-nose contact, the participants began other activities such as biting, grasping, sparring, chasing, tail fanning, and mounting. The most conspicuous behaviors of the first phase were kissing, sparring, and mounting.

Kissing was of several seconds duration and usually involved an investigation of the nose, mouth, and cheek areas. Apocrine glands are present in the cheeks of Uinta ground squirrels (D. F. Balph, personal communication). These and other glands along the lips may provide olfactory clues to convey information concerning the identity of the participants.

Sparring was not rapid among juveniles from 0-10 D.A., and encounters sometimes ended after this activity. Older
juveniles sparred vigorously when they faced each other, and one would attempt to move behind the other to mount. Sparring occurred most frequently when one male interacted with another. I think this was because both animals would attempt to mount, and to keep from being mounted. Other young rodents also spar. Horwich (1967) reported that young gray squirrels pawed during encounters. He thought that this was mild defensive behavior.

During the first phase, males persistently attempted to mount in an encounter. Mounting was repulsed by sparring, grasping, biting, or moving away. Males frequently ran after the squirrel that tried to leave during an encounter. Females were relatively passive and were chased by males. This probably explains the differences in frequency of the chase between the sexes. Females sometimes mounted in an unusual way. Instead of first orienting to the rear by grasping or biting the fur of the neck and then grasping, as the males did, females leaped into the air and came down on the back of another participant. However, females also mounted in a manner that was identical to that of the males.

Phase II began abruptly at about 40 D.A. and lasted about 20 days. The characteristics of this phase were: (1) increased activity within their home range; (2) gathering nest material, carrying it to a burrow, and restricting activities to the vicinity of the burrow; (3) frequently adopting an upright alert posture while calling at other animals; and (4) a general increase in intolerance (Figure 4).
Most encounters of the second phase began when one juvenile approached the area where another juvenile had carried nest material into a burrow. The intruder and the resident sometimes stood upright and chirped at each other. In these encounters, chirping seemed to have the same function as in adults (Balph and Balph, 1966) in that it served to inhibit the approach of another juvenile. If the intruder did not move away at the call, the resident immediately attempted to drive it away. During the chase, the resident carried its tail vertically, the intruder horizontally. Occasionally, both animals gave the tail fan while running. The intruder sometimes stopped after being chased some distance and threatened the resident. The resident then usually returned to his area. If contact resulted, biting occurred, but it never seemed to cause serious injury.

The encounters of the second phase were similar to those of adults engaging in agonistic behavior. These patterns were not restricted to a specific sex. They could have been an expression of territoriality because of the localization of aggressive encounters.

Phase III contained the remaining days of activity above ground before hibernation, 68-80 D.A. During this phase, territorial-like behavior ceased and juveniles spent less time near a specific burrow. Encounters sometimes started with the kiss which was followed by a chase
that ended in the entrance to a burrow. Here the pursuer
was occasionally repelled by sparring that was accompanied
by one or both of the animals squealing. Mounting
occurred, but infrequently.

Sex was an important determinant of developing
behavior for the juvenile Uinta ground squirrel. The
sexes differed in the frequency they would perform certain
activities. For adult deer mice (*Peromyscus maniculatus*),
Eisenberg (1962) found that frequencies of aggressive
patterns were more characteristic of males. However, no
motor pattern was restricted to a specific sex; this was
also true for the juvenile ground squirrel. This is not
surprising in view of descriptions of behavior of other
young vertebrates. For instance, mounting, which is
characteristic of males, has been reported for both sexes
of young cattle (Brownlee, 1954) and young antelope
(*Antilocapa americana*) (Prenzolow, Gilbert, and Glover,
1968). Collias (1944, p. 102), in discussing the relation­
ship of hormones to aggressive behavior in vertebrates,
stated, "Sex merely defines two modalities of behavior pat­
terns as well as of morphology and appearance; either males
or females may at times exhibit behavior typical of the
opposite sex."

Young male ground squirrels began more encounters
than females. Horwich (1967) reported that young male
gray squirrels also initiated more sexual play encounters
than young females.
The social behavior changed or developed with age. Perhaps these could be related to the developmental periods recognized for other animals. Two of four periods, "socialization" and "juvenile," described by Williams and Scott (1954) for house mice (Mus musculus) and used by Horwich (1967) for gray squirrels, are applicable. However, the use of these periods and strict comparisons with other rodents are difficult because of the different ecological setting of Uinta ground squirrels, i.e., hibernating rodent active for only a short period of each year. Furthermore, development was traced from emergence and not from birth.

Juvenile ground squirrels showed only limited social interactions for the first few days above ground. Possibly, the behavior selected for quantification began before the animals came above ground. Several factors could have inhibited social behavior at emergence. Weaning may have depressed social interactions as in laboratory mice (Bolles and Woods, 1964). Secondly, the strange surroundings could have elicited alarm or exploration that inhibited social behavior. However, the fact that juveniles appeared "awkward" in their first interactions suggests that most activities (grasping, mounting, biting, tail fan, and chase) originated after emergence.

The socialization period for house mice (12-25 days) began when their eyes opened. The period contained
"violent flurries of escape behavior ... the beginning of weaning ... with animals remaining near if not in actual contact." (Williams and Scott, 1954, p. 100).

For gray squirrels (Horwich, 1967), the socialization period was the time when social behaviors were emerging (41-70 days). Since the eyes of juvenile ground squirrels were fully opened when they emerged and weaning occurred at this time as well as flurries of escape behavior, the period of time from just prior to emergence and through 10 D.A. could be considered the socialization period. However, many of the encounters of Phase I involve prolonged contact; perhaps this phase could be viewed as an extended socialization period.

The juvenile period for house mice extends from weaning to sexual maturation (26-40 days). During the corresponding juvenile period for gray squirrels, the remaining social behaviors emerged while others underwent quantitative changes (70-335 days). Mice fought during the juvenile period, but only rarely during the period of socialization. On this basis, the second and third phases of ground squirrels could be encompassed in the juvenile period because aggressive encounters were numerous during this time.

Some qualities of the behavior that occurred during the first phase were like those described for play (Beach, 1945; Meyer-Holzapfel, 1956; Loizos, 1966; Marler and
Hamilton, 1966). Firstly, the over-all effect of the encounters was not "serious," i.e., encounters did not have an immediate biological function such as the procurement of resources or the establishment of dominance relationships. Though squirrels tended to separate at greater distances after an encounter (Figure 4), their activities during the encounter did not appear to be specifically distance-increasing. Also, there was no rigid sequence of behaviors within an encounter, and some, e.g., mounting, were repetitive.

The concept of play may be of value in explaining and describing the behavior of some animals. In this study it could be used to describe much of the activity of the first phase. The vagueness of the term play has been recognized and criticized (Beach, 1945; Schlosberg, 1947; Berlyne, 1960; Marler and Hamilton, 1966; Muller-Schwarze, 1968). Indeed, Marler and Hamilton (1966, p. 175), in discussing play, state "more observation and experiment are needed before the proper questions can be asked." The vagueness stems from using a single term to describe not only different types of behavior; i.e., exploratory, solitary, and social phenomena; but also different types of motor patterns and postures within a single category. This multitude of behavior is reflected in Welker's definition of play:

activities that move the organism or its parts through space such as running, jumping, rolling, and somersaulting, pouncing upon and chasing objects or other animals, wrestling, and vigorous manipulation of body parts or objects in a variety of ways. (Welker, 1961, p. 175)
Although some behavior of ground squirrels during the first phase could be considered play, it should also be viewed as part of an ontogeny, a continuum of developing behavior, in which juveniles perceive one another, approach or avoid, and behave in a manner that facilitates or inhibits contact. This behavior consists of a limited number of activities—motor patterns and postures—that resemble those of the adults. The occurrence of these activities can be described in terms of frequencies that change with sex and age.

Perhaps the causal factors of the developing social behavior of the squirrels could be evaluated as Schlosberg (1947) proposed for play, i.e., in terms of stimulus-response properties, changing responsiveness to stimuli, and learning; or by the processes that Welker (1961) suggested: heightened interest in novel stimuli, habituation of interest with continued exposure, and recovery of response. The abruptness of the transition from the first to the second phase indicates some changes in the internal environment that merit further study, e.g., hormone levels.

The factor(s) that caused the change in behavior between the first two phases might also be responsible for the dispersal of juveniles from the population. Juveniles at about the same age changed remarkably in a few days from relatively tolerant, social animals to very intolerant, aggressive ones that restricted their fighting to a small
area. The numbers of juveniles that move before becoming aggressive relative to those that are forced to move as a result of aggression must be known before the relationship between the changes in behavior and dispersal can be established. My observations suggest that in most cases movement preceded aggression and that few animals were displaced as a result of aggression.

Finally, before the adaptive value or dispersal mechanisms of any of the behavior described in this study can be determined, the dispersion and reproductive success of the juveniles as mature members of the population must be examined. For instance, it may be that frequency of contact with other juveniles influences or is indicative of an animal's ability to maintain a territory and reproduce when an adult. Possibly, the frequency of performance of a single activity such as mounting contributes to the ability of an individual to compete for resources.

The social behavior of other young spermophiles may be similar in form and development. Although their social interactions have not been quantified, qualitative descriptions indicate activities like those of the Uinta ground squirrel. For instance, young California ground squirrels (Spermophilus beecheyi) (Linsdale, 1946), begin encounters with nose-nose contact. Nose-anal contact sometimes occurs next. After nosing, wrestling occurs.
Several grips or procedures seem to be standard: (1) a shoulder or hip grip from the back made with the forefeet that are frequently shaken off but may be repeated by the aggressor, (2) a head-to-tail circling, both suddenly jumping and turning and thus trying to get to the shoulder of the other from the back. This usually ends in mid-air with the animals locked belly-to-belly, (3) a head-to-tail clinch starting when one tries for a hip hold on the other and the second retaliates by taking a hold. (Linsdale, 1946, p. 350)

Later during the summer, juveniles fought in a manner identical to that of adults.

For 13-lined ground squirrels (*Spermophilus tridecemlineatus*), W. R. Knight (personal communication) observed brief sparring, nosing, wrestling, and short chases by young during their play. They also showed adult-like patterns of aggression later in the summer. For the same species, Johnson (1931, p. 285) reported "... that sexual development was proceeding for some of the males 'rode' females when 34 days old and later," and McCarley (1966) observed "mock fighting" between young 13-lined ground squirrels.

From these descriptions and the information provided by this study, it may be that the early social interactions of the ground squirrels represent developing social behavior that is composed of adult-like motor patterns and postures. Continued study is necessary before it can be determined if there are differences in behavior due to sex and if there are general phases of development for the juveniles of all species. Further quantification of developing behavior by spatio-temporal analysis should reduce accounts
of play to detailed, meaningful descriptions. These will permit continued reappraisal and comparisons useful in establishing principles of behavioral development.

Balph, D. F. 1969. Associate Professor of Animal Behavior, Department of Wildlife Resources, Utah State University, Logan, Utah. Personal communication, September 15.


Knight, W. R. 1969. Professor of Psychology, Department of Psychology, Hiram College, Hiram, Ohio. Personal communication, May 15.


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