An Introduction to the Ethology of the Uinta Ground Squirrel (Citellus armatus)

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AN INTRODUCTION TO THE ETHOLOGY OF THE UINTA
GROUND SQUIRREL (CITELLUS ARMATUS)

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

Approved:

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Logan, Utah
1961
ACKNOWLEDGEMENT

I wish to acknowledge Dr. William F. Sigler and Dr. Fred H. Wagner for their help in initiating this research, and Dr. Allen W. Stokes for his comments and criticism of the work and drafts of this thesis.

Financial support for this research came from Utah State University, Division of University Research, Project U-137.

David F. Balph
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>The animal</td>
<td>2</td>
</tr>
<tr>
<td>The area</td>
<td>2</td>
</tr>
<tr>
<td>Annual cycle</td>
<td>2</td>
</tr>
<tr>
<td>Methods</td>
<td>3</td>
</tr>
<tr>
<td>Behavior</td>
<td>5</td>
</tr>
<tr>
<td>Maintenance behavior</td>
<td>5</td>
</tr>
<tr>
<td>Locomotion</td>
<td>6</td>
</tr>
<tr>
<td>Walking</td>
<td>6</td>
</tr>
<tr>
<td>Running</td>
<td>6</td>
</tr>
<tr>
<td>Lifting one foreleg</td>
<td>8</td>
</tr>
<tr>
<td>Causation</td>
<td>8</td>
</tr>
<tr>
<td>Function</td>
<td>8</td>
</tr>
<tr>
<td>Feeding</td>
<td>8</td>
</tr>
<tr>
<td>Elimination</td>
<td>9</td>
</tr>
<tr>
<td>Care of body surface</td>
<td>9</td>
</tr>
<tr>
<td>Dusting</td>
<td>9</td>
</tr>
<tr>
<td>Grooming</td>
<td>9</td>
</tr>
<tr>
<td>Digging</td>
<td>10</td>
</tr>
<tr>
<td>Alertness</td>
<td>11</td>
</tr>
<tr>
<td>Investigating</td>
<td>11</td>
</tr>
<tr>
<td>Causation</td>
<td>15</td>
</tr>
<tr>
<td>Function</td>
<td>16</td>
</tr>
<tr>
<td>Tailflicking</td>
<td>16</td>
</tr>
<tr>
<td>Social behavior</td>
<td>17</td>
</tr>
<tr>
<td>Agonistic behavior</td>
<td>17</td>
</tr>
<tr>
<td>Causation</td>
<td>22</td>
</tr>
<tr>
<td>Function</td>
<td>23</td>
</tr>
<tr>
<td>Attack</td>
<td>23</td>
</tr>
<tr>
<td>Threat</td>
<td>24</td>
</tr>
<tr>
<td>Section</td>
<td>Page</td>
</tr>
<tr>
<td>------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>Causation</td>
<td>25</td>
</tr>
<tr>
<td>Function</td>
<td>25</td>
</tr>
<tr>
<td>Escape</td>
<td>27</td>
</tr>
<tr>
<td>Submission</td>
<td>27</td>
</tr>
<tr>
<td>Sexual behavior</td>
<td>28</td>
</tr>
<tr>
<td>Causation</td>
<td>29</td>
</tr>
<tr>
<td>Function</td>
<td>30</td>
</tr>
<tr>
<td>Behavior of juveniles</td>
<td>31</td>
</tr>
<tr>
<td>Interspecific behavior</td>
<td>33</td>
</tr>
<tr>
<td>Badgers</td>
<td>34</td>
</tr>
<tr>
<td>Chipmunks</td>
<td>34</td>
</tr>
<tr>
<td>Humans</td>
<td>34</td>
</tr>
<tr>
<td>Pocket gophers</td>
<td>34</td>
</tr>
<tr>
<td>Weasels</td>
<td>35</td>
</tr>
<tr>
<td>Red-tailed hawks</td>
<td>36</td>
</tr>
<tr>
<td>Conclusions</td>
<td>37</td>
</tr>
<tr>
<td>Summary</td>
<td>39</td>
</tr>
<tr>
<td>Literature cited</td>
<td>41</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Uinta ground squirrel</td>
<td>4</td>
</tr>
<tr>
<td>2.</td>
<td>Utah State University Forestry Summer Camp</td>
<td>4</td>
</tr>
<tr>
<td>3.</td>
<td>Walking posture: body on ground</td>
<td>7</td>
</tr>
<tr>
<td>4.</td>
<td>Walking posture: hunched</td>
<td>7</td>
</tr>
<tr>
<td>5.</td>
<td>Walking posture: body off ground</td>
<td>7</td>
</tr>
<tr>
<td>6.</td>
<td>Digging posture</td>
<td>11</td>
</tr>
<tr>
<td>7.</td>
<td>Alertness posture: upright rest</td>
<td>12</td>
</tr>
<tr>
<td>8.</td>
<td>Alertness posture: down rest</td>
<td>12</td>
</tr>
<tr>
<td>9.</td>
<td>Alertness posture: upright intermediate</td>
<td>13</td>
</tr>
<tr>
<td>10.</td>
<td>Alertness posture: down intermediate</td>
<td>13</td>
</tr>
<tr>
<td>11.</td>
<td>Alertness posture: upright alert</td>
<td>14</td>
</tr>
<tr>
<td>12.</td>
<td>Alertness posture: down alert</td>
<td>14</td>
</tr>
<tr>
<td>13.</td>
<td>Investigating posture</td>
<td>15</td>
</tr>
<tr>
<td>14.</td>
<td>Location of main burrow entrances</td>
<td>19</td>
</tr>
<tr>
<td>15.</td>
<td>Location of female home ranges</td>
<td>20</td>
</tr>
<tr>
<td>16.</td>
<td>Location of male home ranges</td>
<td>21</td>
</tr>
<tr>
<td>17.</td>
<td>Threat posture</td>
<td>24</td>
</tr>
</tbody>
</table>
INTRODUCTION

This study describes behavior of the Uinta ground squirrel (*Citellus armatus*) in a free-living population. Its objective is to provide basic behavioral information on a small mammal which can fill in part of the gaps in our knowledge of behavior and social organization of the vertebrates. This would contribute to the long-term goal of viewing the progressive evolutionary changes in behavior from lower forms to man.

Tinbergen has done much experimental work with animals, but he cautions biologists not to begin experimental work until they have a knowledge of the animals' general behavior. In his book *Social Behaviour in Animals* (1953), he states that initial behavioral research should be broad, descriptive, and observational in nature. This is necessary before attempting investigation of specific behavioral problems in order to place each behavior pattern in its proper perspective. Accordingly, this study attempts to describe the spectrum of ground squirrel activity aboveground. Further, within the limited scope of a broad descriptive study, it attempts to ascribe possible causation, function, and origin to some of these activities.

The beginner sees a welter of activities and postures in the ground squirrel. However, with time one learns that there are general patterns of behavior in the apparent chaos. A given situation, such as feeding or fighting, is sufficiently stereotyped to enable one to generalize about the activities and postures that occur. This paper presents just such
generalizations. All descriptions are of adult ground squirrels in the study area unless otherwise indicated.

The Animal

The Uinta ground squirrel is well suited for the observational approach of this study. It is a diurnal animal which inhabits open areas and is not secretive in its habits. The only major drawback is that it performs a portion of its daily activity underground.

The animal's general appearance (Figure 1) offers few clues to its behavior. It has no striking color or morphological characteristic which indicates possible behavioral function such as the modified tertiaries of the mandarin duck (Aix galericulata) (Lorenz, 1941). Other than the large foreclaws which indicate fossorial habits, the only structures of particular interest are an anal scent gland and tail hairs that are erectile.

The Area

I had two qualifications in mind for the location of a study area: a dense population of ground squirrels and an unobstructed view of their activity aboveground. I found such an area on the grounds of Utah State University Forestry Summer Camp (Figure 2), 20 miles northeast of Logan, Utah. I conducted the study on the 2 acres of lawn that surround the buildings of the camp. The ground squirrel population on the lawn varied from approximately 40 in spring to 150 after the young were born.

Annual Cycle

Ground squirrels first appeared aboveground during the first week in April. Sexual activity occurred in mid-April, and the young were born in mid-May. The young appeared aboveground about the first of June. The animals began to disappear underground the last week of July. By the second week of August nearly all were underground for the year.
Methods

The methods used in the study were directed toward observing and recording activities and postures of known individuals. I observed the animals from a portable observation tower or from the buildings. To record activities and postures, I took notes and photographs. To identify individuals, I trapped, toe-clipped, and marked them with black fur dye. Although the toe-clip was permanent, I had to reapply dye three or four times during the season. During the study I trapped 197 different ground squirrels. Of these I returned 158 to the free population and kept 39 in captivity for varying lengths of time. I used the captives to obtain a closer look at some aspects of their behavior.

The study began April 1, 1959, and terminated August 15, 1960. This period covered two complete ground squirrel seasons—a total of 8 months of aboveground activity. For seven of these months I lived at the camp and observed the animals nearly every day. These observations form the basis of this paper.

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Figure 1. Uinta ground squirrel. General color: brownish-gray. Average size in mm: length, 292; tail, 66; foot, 41; ear, 15 (Durrant, 1952).

Figure 2. Utah State University Forestry Summer Camp. T13N. R3E, Cache County, Utah.
Behavior falls roughly into two categories: maintenance behavior and social behavior. Maintenance behavior includes those functional acts necessary for the welfare of the individual such as locomotion and feeding. Social behavior includes communicative acts such as the activities in fighting and courtship.

**Maintenance Behavior**

Thorpe (1956) and Schiller (1957) indicate that instinct may play a greater role in mammalian behavior than was previously supposed. I believe this is especially true of maintenance behavior of ground squirrels. This behavior varies little between age and sex groups and is more stereotyped than social activities. I do not mean that maintenance activities are fixed-action patterns; but rather, learning is perhaps less important in maintenance than in social activities.

Precise descriptions of maintenance activities of mammals are largely lacking. This is unfortunate since many social displays may be derived from these activities (Tinbergen, 1952). Marler's (1956a) careful descriptions of the chaffinch (*Fringilla coelebs*) are a model of the care that is needed in such studies. Marler's subsequent determination of the origin of displays was possible only after his detailed study of maintenance activities. Therefore, in the next few pages I shall catalogue these activities for the ground squirrel and later attempt to show their possible influence on patterns of social behavior.
Locomotion

The movements of walking and running are relatively uniform among individuals. The animal's skeletal, muscular, and nervous organization largely predetermine the movements (Gray, 1944).

Walking

The ground squirrel walks only when moving a few feet or less; otherwise, it runs. This generally restricts walking to the vicinity of burrow entrances and to feeding activity.

The animal walks in typical quadruped fashion. One forefoot moves forward followed by the opposite hindfoot, then the other forefoot followed by the opposite hindfoot. They move in this manner with any of three different postures: (1) body on ground, (2) hunched, and (3) body off ground.

(1) Walking with the body on the ground (Figure 3) generally occurs when the animal is disturbed. The movements are rapid, jerky, and tense. There is a high probability that the animal's next activity will be escape. This is the least common walking posture.

(2) Walking while hunched (Figure 4) is most common during feeding. The posture also occurs when the weather is cold or when the animal is in an unfamiliar area. The posture is more characteristic of a subordinate animal.

(3) Walking with the body well off the ground (Figure 5) occurs commonly when the animal is moving a lot while feeding. The posture is more characteristic of a dominant animal or an animal that is not alarmed.

Running

The ground squirrel runs when moving more than a few feet without a stop. The animal moves with a series of bounds. The running posture is nearly uniform among individuals. When an animal is not disturbed and well within its home range the tail is held high off the ground or even upright. An animal in a strange environment usually runs slowly with
Figure 3. Walking posture: body on ground. Postural components: (a) head held low, (b) trunk flat on ground, and (c) legs flexed beneath body.

Figure 4. Walking posture: hunched. Postural components: (a) head held low, (b) spinal lordosis, and (c) tail on ground.

Figure 5. Walking posture: body off ground. Postural components: (a) trunk relatively straight and parallel to ground, (b) legs partially extended, and (c) tail position varies from parallel to trunk to angled toward ground.
spinal lordosis and the tail angled toward the ground.

**Lifting one foreleg**

Lifting one foreleg often precedes locomotion of a ground squirrel. The animal lifts the foreleg as if to step forward but stops and holds it off the ground in a flexed position.

**Causation.**—Lifting the foreleg is an incomplete act of taking a step forward. It indicates the animal is about to move forward and as such appears to me to be an intention movement of locomotion. The movement is a product of two incompatible tendencies (tendency as defined by Hinde, 1955-56): to move forward and to remain. In this respect it is similar to intention movements of flight in certain passerines (Andrews, 1956).

**Function.**—Since lifting the foreleg is the first action in most locomotion, it effects a preparedness for movement. I do not know if the activity has signal value. There is no modification of lifting the foreleg as may be the case in foot tapping in deer mice (*Peromyscus maniculatus*) (personal observation).

**Feeding**

When aboveground the ground squirrel spends most of its time feeding. Feeding is most active from 1 to 3 hours after sunrise and again from 3 to 1 hours before sunset. During inclement weather feeding is more constant throughout the day beginning later in the morning and ending earlier in the evening than usual. The animal feeds while stopped or moving slowly forward. Occasionally, it may manipulate food with one or both forefeet or stand on its hind legs to reach seed heads.

Feeding postures are similar to walking postures and occur under the same conditions (see page 6). Usually, the stationary feeding posture
is the same as the walking posture that preceded the stop for feeding.

Elimination

Linsdale (1946) states that the California ground squirrel (Citellus beecheyi) defecates and urinates more often in the morning and in the same location. I did not note this pattern in the Uinta ground squirrel. However, the frequency of elimination increases during an aggressive encounter, while in a trap, or while being handled. Some experimental psychologists use the defecation rate of a rat (Rattus) as a measure of "fearfulness" (Bindra and Thompson, 1953).

Usually, the animal does not adopt a specific posture while eliminating. Other activities are not interrupted while the animal eliminates and it shows no interest in the excreted matter.

Care of Body Surface

Body care consists of dusting and grooming, and the activities do not follow one another.

Dusting

Each animal uses only one or two dusting areas. These are in loose dirt near burrow entrances. Dusting occurs most often after the peak of feeding in the morning.

The animal begins dusting by pawing a few times at the loose dirt, and then lies flat on its belly with its head on the pawed area. In this position the animal moves forward a step or two through the dirt, partially covering its head and body with dust. Often, the movement forward is with the head tilted to one side. Then the animal shakes vigorously and may repeat the activity with stretching and rolling.

Grooming

Grooming occurs anywhere in the animal's home range and consists of
washing, scratching, and mouthing or biting the fur. The animal washes by moistening either one or both wrists with the mouth, and then it draws the wrists over areas of the head and neck. It scratches nearly all lateral portions of the trunk and head with the hindfeet. The animal bites and mouths fur of the tail, legs, and ventral and lateral areas of the trunk. During the activity movements are complex and variable.

Comparing grooming behavior of Uinta ground squirrels and deer mice poses a question in my mind as to the significance of differences in behavior between the two species. Deer mice (1) wash and mouth their fur with stereotyped motor patterns that occur in sequence from head to tail (Eisenberg, 1959). (2) Washing often occurs as displacement activity (Eisenberg, 1959) as defined by Bastock, et al. (1953) and later by van Iersel and Bol (1958). (3) Deer mice are sharply bicolored, and the ventral white fur may function as a sign stimulus (Ealp and Stokes, 1960). The ground squirrel (1) does not groom in a stereotyped sequence, (2) does not groom as displacement, and (3) has no ventral sign stimulus. In deer mice one wonders if the stereotyped sequence in grooming and displacement washing evolved as a means of keeping the ventral white fur clean for its possible role as a sign stimulus.

Digging

The ground squirrel digs to open or widen old burrows or to make new ones. The activity is most common immediately after the breeding season and is more frequently done by females. Digging (Figure 6) begins with pawing at the ground with the forefeet. This action throws most of the dirt into a pile beneath the body. The animal removes the pile beneath it by pushing the dirt further back with the hindfeet. The animals uses the muzzle from time to time to loosen stones and dirt.
Alertness is a single continuum of activity that runs from rest to alert. At rest the ground squirrel is less likely to escape than at alert. The continuum occurs in either of two positions: up on hindlegs or down on four legs. The animal adopts the "upright" position anywhere and the "down" posture only when it has a clear field of vision while on four legs. The three postures that represent the continuum in either the up or down position are rest (Figures 7 and 8), intermediate (Figures 9 and 10), and alert (Figures 11 and 12). As an animal becomes more alert its posture may change from upright rest to intermediate and finally to alert (Figures 8, 10, and 12). The rest postures are common when the animal is not disturbed. It adopts the intermediate postures when disturbed such as by the appearance of a potential predator. The alert postures are held only briefly and occur just before the ground squirrel escapes.

Investigating

The ground squirrel approaches unfamiliar objects with a specific movement and posture which I call investigating activity. It occurs most commonly when an animal approaches inanimate objects. An animal approa-
Figure 7. Alertness posture: upright rest. Postural components: (a) trunk upright with spinal lordosis; (b) sitting on haunches, forelegs flexed; and (c) generally relaxed.

Figure 8. Alertness posture: down rest. Postural components: (a) spinal lordosis, (b) legs flexed and beneath body, and (c) generally relaxed.
Figure 9. Alertness posture: upright intermediate. Postural components: (a) trunk upright, straight, and extended and (b) sitting on haunches to standing on hindlegs with the tail as a brace, forelegs flexed.

Figure 10. Alertness posture: down intermediate. Postural components: (a) head held high; (b) trunk straight, lower at posterior; and (c) forelegs extended, hindlegs flexed.
Figure 11. Alertness posture: upright alert. Postural components: (a) trunk upright, leaning forward; (b) sitting on haunches, forelegs extended; and (c) very tense.

Figure 12. Alertness posture: down alert. Postural components: (a) head on ground, (b) trunk pressed flat on ground, (c) legs flexed beneath body, and (d) very tense.
ching an animate object usually responds with agonistic behavior.

The ground squirrel approaches an unfamiliar object by moving forward with its forelegs while keeping its hindlegs stationary. When the body is fully extended the animal then moves forward on all four legs in a tense, slow, and hesitant manner. When the animal is not moving forward it holds a rigid posture with one foreleg raised off the ground (Figure 13).

![Figure 13. Investigating posture. Postural components: (a) neck and trunk extended and parallel to ground; (b) three legs extended, one foreleg held off ground; and (c) tail straight and parallel to trunk.](image)

_Causation_

The ground squirrel adopts investigating posture toward new objects in the environment such as a piece of paper, trap, or camera. The posture is held only briefly and is not intense. When the environment is completely strange, as with captive animals in a large observation pen, investigating activity lasts longer and the postural components are exaggerated. Therefore, one external cause of the activity seems to be unfamiliar objects.

Two tendencies involved in investigating activity are to approach and not to approach. The forward movement of the forelegs and one foreleg held off the ground represents the tendency to approach. The initial stationary position of the hindlegs, maximum extension of the body, and hesitancy of forward movement represents the tendency not to approach. If the tendency to escape is present it is at a low level. The animal
seldom flees from the object nor are there components of escape such as lowered center of gravity and flexed legs. The escape components are present in an animal approaching a trap in which it has previously been captured. In this case the approach is with the body on the ground (Figure 3), and after a few steps toward the trap an animal either turns and escapes or rushes the trap.

Function

It is characteristic of most vertebrates to explore their surroundings. Familiarity with the environment is a distinct advantage to the animal. Caution and alertness while investigating a strange environment probably has survival value.

Tailflicking

Tailflicking often accompanies movements and vocalizations of the ground squirrel. It flicks the tail in a horizontal arc, either once or a series of times at the onset of the movement or vocalization. This activity is present in some degree in most Sciuridae.

Tailflicking in the ground squirrel is not associated with any specific movement or behavioral situation. Therefore, I think it is probably a reflex not directly caused by any external or internal motivation.

If tailflicking has a behavioral function it is probably a general one for all movement. Taking a cue from Daanje (1950), tailflicking could possibly be an intention movement of a shift in the animal's position. The communication function of tailflicking may be to typify ground squirrel movement. This would enable them to identify movement as that of their own kind as distinct from that of other and potentially dangerous species.
Social Behavior

Carpenter (1942) states that "Social behavior refers to the reciprocal interaction of two or more animals and the resulting modifications of an individual's action system." The reciprocal interaction is that of stimulus and response. The social behavior of the response animal is determined by its internal state and what it perceives of the stimulus animal.

Restle's (1957) multiple-cue theory of maze learning in rats indicates that an animal relies on all its exteroceptors for perception in any given situation. However, the degree on which each is relied differs. Above-ground the ground squirrel relies mostly on sight, sound, and scent. In describing and discussing each social activity, I shall be concerned primarily with these three senses and their communicative value in social behavior.

Agonistic Behavior

Agonistic behavior refers to the activity in an aggressive encounter between two individuals. It includes attack, escape, threat, and submission. The tendencies to attack and to escape exist as the extremes of a continuum of behavior. At the extremes the relative amounts of the two tendencies differ widely, and an animal either attacks or escapes with little conflict. As the tendencies become more equal conflict arises between the two tendencies which results in threat display. In fact, Hinde (1953) states that "Only where there is conflict does display occur."

In submission the animal neither attacks nor escapes. Its posture usually does not contain any postural components of either attack or escape. If the conflicting tendencies that produce submission were attack and escape, one would think that the animal would either attack,
threaten, or escape. This does not occur—the animal either stays and adopts submission posture, or it may escape if punished too severely by an aggressor. This leads me to believe that the conflicting tendencies in submission are perhaps to stay and to escape, and that submission is not directly a part of the attack and escape continuum.

Ground squirrels exhibit agonistic behavior throughout their season of activity. Agonistic behavior differs during the breeding season (breeding season meaning time of sexual activity) from that exhibited after the breeding season. During the breeding season animals tend to move about without associating themselves with a specific area. At this time agonistic behavior is most intense between males. Since this is a part of sexual behavior, I shall describe it in more detail in that section. Here I shall describe the agonistic behavior that occurs after the breeding season.

After the breeding season females become more intolerant of other individuals (especially males) and settle down to specific areas of the lawn. Intolerance tends to space the centers of activity of females on the lawn (Figure 14), and since females are dominant at this time, males are forced off the lawn (Figure 14). Neighboring animals establish social rank (Figure 14) which does not change as the animals get further from their centers of activity and closer to that of their neighbors. Home ranges overlap (Figures 15 and 16) and are not defended. Rather, each animal is intolerant of another within what Hediger (1942) calls the individual distance. This distance of intolerance moves with animals and is not associated with a specific location as Yerger (1953) found it was in chipmunks (Tamias striatus). After ground squirrels chase off intruders, they do not return to where the chase began. Marler (1956b)
Figure 14. Location of main burrow entrance and dominance relationships after the breeding season of individual Uinta ground squirrels. Arrows indicate dominance, and "-1-" indicates neither dominant.
Figure 15. Location of home ranges of female Uinta ground squirrels after the breeding season. Home ranges were determined by observation of marked individuals.
Figure 16. Location of home ranges of male Uinta ground squirrels after the breeding season. Home ranges were determined by observation of marked individuals.
states that individual distance in the chaffinch varies with sex, behavior, and the individual intruder. This is also true of ground squirrels. Intolerance is greater between animals of widely separated social status and less when they are feeding or alert.

An aggressive encounter begins by one or both animals approaching the other. Social status and learning determine the manner in which they approach and their subsequent response. In an initial encounter or one between animals of nearly equal rank the approach is with components of threat behavior (page 24). The result is usually a fight or threat. If a chase occurs both animals have components of threat. Animals of widely separated status have little or no components of threat and their response is to attack or escape without threat. Learning hastens the subsequent response. For example, the more often a subordinate escapes from a dominant, the more quickly it responds with escape when the dominant approaches.

As the year progresses agonistic behavior occurs less frequently. However, the decrease is gradual and the behavior continues until the animals go underground for the year.

Causation

When two ground squirrels come together agonistic behavior often occurs. One external cause of this behavior seems to be the sight of other animals within the individual distance they defend. Since intolerance varies with sexual activity and pregnancy, one internal cause may be dependent on fluctuating endocrine levels. Two external factors that decrease the frequency of agonistic behavior as the year progresses are learning and a decrease in the population. Subordinate animals learn to avoid dominants, and dominants habituate to others of nearly equal rank.
Mortality among ground squirrels is high during the summer; therefore, the probability of animals encountering each other decreases.

Function

Agonistic behavior in many animals functions to establish territory. Most researchers accept Noble's (1939) definition of territory as any defended area. Emlen (1957), in his critique of the territory concept, rejects it as being a defended area and warns against using stereotyped definitions. He views territory as only a place where an animal is dominant. I accept Emlen's views on this matter and shall not attempt to fit the descriptions of individual distance and social rank of ground squirrels into any concept of territory.

The function of territory is to space the home ranges of animals. Individual distance in the ground squirrel after the breeding season serves the same function and does so selectively. Females are spaced on the lawn, and males are forced off the lawn. This is of probable survival value to young as well as adults. Spacing may decrease fighting and disturbance to the young. Further, the lawn is better habitat than areas peripheral to it both for food availability and protection from predation. Animals on the lawn have the advantage of unobstructed vision and many burrow entrances for escape.

Since attack and escape are a continuum of behavior, elements of threat occur in most encounters. However, for the sake of simplicity, I shall describe attack and escape as they occur at the ends of the continuum and describe threat separately.

Attack

Attack includes both fighting and chasing. In fighting animals look together, roll over and over, and bite each other. Contact lasts only a
few seconds at the most and results in no apparent injury. It terminates in either threat or chase. Chasing begins as one animal turns to escape. The act of turning and running seems to elicit chase from the dominant. Locomotion by the dominant animal is the same as rapid running (page 6). Chase varies from a few feet to over 100 feet and usually ends when the dominant stops chasing. Both animals then return to other activities.

Threat

In threat ground squirrels face each other and exhibit characteristic movements, sounds, and posture. Usually, the only locomotion is a rapid and jerky step or two toward or away from the other animal. When animals are nearly in contact, occasionally one places a forefoot on the other or pushes at it, but they do not stand upright and spar. During the encounter they adopt a threat posture (Figure 17). When facing each other in this posture either animal may growl or chatter its teeth together. Before or after exhibiting threat posture either animal may growl, teeth chatter, or give the chirp or churr call.

![Figure 17. Threat posture. Postural components: (a) head held low, mouth open; (b) trunk anterior low to ground, spinal lordosis; (c) forelegs flexed, hindlegs extended; (d) tail held to one side, tail hairs erect; and (e) anal papillae protruded.](image)

Threat terminates in a fight, chase, or when one animal moves off. Generally, the animal that stays is the one whose forepart of the body was held lower and hindpart of the body was held higher during the encounter.
When an animal moves off it does so with a slow, tense walk similar to the hunched walking posture (Figure 4). If the animal moves rapidly it is attacked.

Stokes (in press) states that in blue tits (Parus caeruleus) at a feeding station some threat represents a conflict between the tendencies to attack and stay. When a feeding bird (usually the dominant) is approached by another bird, the feeding bird usually does not attack but has the tendency to stay, threaten, and continue feeding. Ground squirrels (usually the dominant) adopt this "stay-threat" when approached while occupied with maintenance activities, and subordinate animals may adopt it after a chase. In both cases the animals have the tendency to remain fixed. Stay-threat differs from threat described on page 24 in three ways. (1) An animal displaying stay-threat may give high-pitched squeak sounds. (2) It does not move toward or away from the intruder. (3) The escape of an intruder does not elicit chase.

Causation.—When one animal attacks and the other escapes with little hesitancy, there is little threat. If the animals are more hesitant in their response, there is more threat. If the animals neither attack nor escape, threat display is most intense. Therefore, threat seems to be the product of a conflict between the tendencies to attack and to escape.

Function.—The function of threat is the same as that for fighting. It usually results in keeping animals at a distance from one another. However, threat is a more advanced form of behavior. It involves less energy and risk of injury than fighting yet accomplishes the same result.

From a functional point of view threat posture divides the body into anterior and posterior parts. The anterior part contains the components of: head held low, trunk low to ground, and forelegs flexed. These components
are the same as those in walking or feeding with the body on the ground (Figure 3) and down alert posture (Figure 12). In each case they occur in a posture which indicates readiness to move rapidly. The posterior part contains the components of: trunk high off the ground, hindlegs extended, tail held to one side, and tail hairs erect. From the frontal view this increases the apparent size of the animal and may function to intimidate another animal. Therefore, the entire posture seems to be a compromise between the "need" for rapid movement in any direction represented by the anterior part of the body and the "need" for an enlarged appearance to intimidate represented by the posterior part of the body.

Basically, the functions of stay-threat and threat are the same. Both tend to keep an intruder at a distance. When a feeding animal displays stay-threat toward an intruder, the intruder usually moves off. This enables the animal to continue feeding undisturbed. When a subordinate animal retaliates with stay-threat, it decreases the chance of further attack by the dominant.

Many rodents stand upright while threatening. Crowcroft (1955) suggests that the enlarged appearance of a shrew (Sorex araneus) standing upright functions as intimidation. However, ground squirrels do not stand upright in threat behavior. Perhaps this is because it would appear similar to alertness postures (Figures 7, 9, and 11). The survival value of alertness postures is probably great enough to prevent the development of components that might be confused with them.

The role of scent and sound in an aggressive encounter presents an enigma. Ground squirrels have an anal scent gland and protrude the papillae in threat, but I do not know if scent is given off. Sounds do not seem to be specifically associated with dominance or subordinance.


Escape

The escaping animal merely runs from the approaching animal. It runs the same way as the attacker except the tail is sometimes held closer to the ground. The escaping animal does not enter a burrow but continues to run from the attacker. The escaping animal regulates its speed to maintain a short distance between itself and the attacker. Rarely is it overtaken.

Escape terminates in stay-threat by the subordinate or the dominant stops chasing. Stay-threat by the subordinate occurs under the same conditions as Clarke (1956) describes for retaliation in the vole (Microtus agrestis). The chased animal stops, faces the attacker, and threatens. When the dominant ceases to chase, the subordinate ceases to escape. Often the subordinate adopts the upright intermediate posture (Figure 9) after a chase.

Submission

When an animal is attacked and does not or can not escape, it may exhibit submission. I did not see this behavior in the ground squirrel. The habitat offers ample opportunity to escape, and the escaping animal is always successful in doing so.

Hinde (1955-56) describes submission posture in finches (Fringillidae) as being similar to postures given when cold, sick, or at rest. In the ground squirrel this posture is down rest (Figure 8). Occasionally, a subordinate animal that is approached by a dominant adopts this posture and remains motionless. However, when the dominant gets close the subordinate escapes. Occasionally, a captive animal also remains motionless as I approach it in the pen. As I draw closer it begins to close its eyes. However, the animal escapes before I can touch it.
Sexual Behavior

Sexual behavior begins about 1 week after ground squirrels appear in the spring and lasts for 2 or 3 weeks. During the first week animals are aboveground most of their time is spent feeding, and they show little interest in each other. The first evidence of sexual activity is the development of agonistic behavior in the population—especially between males. Then differences in behavior develop between males and females.

Males range over a wide area and are very active. Many of their movements are rapid, jerky, and tense. Most male activity consists of feeding, dusting, calling, and agonistic behavior. They often feed with the body on ground posture (Figure 3). Males dust by pawing at the ground a few times and then wiping the side of the head in the pawed area. This differs from dusting described on page 9 in that their bodies are not on the ground, and the activity occurs anywhere on the lawn. Calling by males is similar to the chirp call except it is higher pitched, shorter in duration, and has a bell-like quality. This call occurs only during the breeding season and only by males. Dominant males call more frequently than subordinates, and the call is usually not answered. Agonistic behavior between males is intense and usually involves fighting and chasing.

Females are less active than males and do not range over as much area. Their activities during and after the breeding season are similar except they are less aggressive during the breeding season.

A week after sexual activity starts the males begin to approach females with either a rapid or slow movement. In the rapid approach a male assumes the body on ground posture (Figure 3) and takes a few rapid steps toward the female. The male stops a few feet from the female and either escapes or rushes her. This activity is similar to an animal
approaching a trap in which it has been previously captured (page 16).
If the male rushes he attempts to strike the female with his forefeet or
bite her before escaping. The male often repeats the activity, and it is
accompanied by components of threat. The female responds to this approach
by remaining motionless in the down rest posture (Figure 8) with the tail
hairs erect. The female stay-threatens and may bite the male when he makes
contact. The activity sometimes ends in a chase by either the male or the
female.

In the slow approach to a female the male does not threaten. He
assumes the body on ground posture (Figure 3) except the trunk is held
slightly off the ground. The male then moves slowly but steadily toward
the female and partially closes his eyes as he gets closer. The animals
make contact by touching noses or mouths, and then they nuzzle each other.

King (1955) describes touching mouths together in prairie dogs (Cynomys
ludovicianus) as "kissing" and suggests it functions as tactile recogni-
tion. The female responds to the slow approach with less threat than to
the rapid approach and does not bite the male. This activity sometimes
results in the male chasing the female.

When a male chases a female sometimes the chase ends in a burrow
entrance immediately below the surface of the ground. One of the animals
(probably the female) gives the high-pitched squeak call. Although I
have not seen copulation, I suspect it occurs at this time. Most of the
burrow entrances are large enough for the activity to occur in them.

As the breeding season wanes females become more intolerant and males
cease to approach them.

Causation

Early sexual behavior of males develops without any behavioral
changes in the females or any manifestation of interest in them. Therefore, I suspect male behavior is not caused by any external stimuli but rather by the endocrine system.

Males begin to take interest in females without behavioral changes on the part of females or any physical contact with them. Since there is no dimorphism in ground squirrels, sex recognition and stimulation at this time must be by scent. I do not know what determines which of the two ways the males will approach females. The initial behavior of the females to both approaches is the same. This indicates that the method of approach is not determined by visual stimuli.

Function

Four activities characterize the early sexual behavior of males: feeding, dusting, calling, and aggression. Since the manner and degree to which males perform these activities are unique to the breeding season, it is likely they have sexual function. The anal region is in contact with the grass in the body on ground posture (Figure 3). Wiping the side of the head occurs frequently and anywhere in the area. Both these activities may function to spread scent. However, both males and females use the body on ground posture after the breeding season, and gross examination of the head region of males reveals no glandular development for scent. Kilham (1958) and Hazard (1960) suggest that calls are used by pikas (Ochotona princeps) and squirrels (Sciuridae) respectively in territorial behavior. The high-pitched chirp call and aggressive behavior of male ground squirrels may serve the same function. A male sometimes chases other individuals away from a specific burrow entrance and gives the call while doing it. However, this is not common. Perhaps the high population density makes conditions atypical for manifestations of territoriality.
The rapid approach of a male toward a female results in a chase, or the male moves off after a time if the female remains motionless. Perhaps the male attempts to incite the female to chase with the rapid approach.

Usually, the female defends an individual distance. Even during the breeding season a male intruder is generally met with hostility. However, when a male uses the slow approach she permits contact. This leads me to believe that the posture and movements of the slow approach have an appeasing function. The posture contains no components of threat and the movements are slow. Further, I have seen a dominant animal approach a feeding subordinate in the same manner. The subordinate may threaten to some extent but does not bite the dominant. The dominant, using the slow approach, pushes the subordinate away and takes over the feeding site. Had the dominant animal rushed the subordinate a fight would have ensued before the subordinate moved off. Here again the slow approach seems to have appeasing function.

Behavior of Juveniles

Juvenile ground squirrels appear aboveground about 2 weeks after they are born. Their activity for the first few weeks is as follows: On the first day two or three young of the litter appear at the same burrow entrance. They are out only briefly and restrict their activity to within a few feet of the entrance. On the second day the entire litter appears at the same entrance. During the day young gradually extend their range from the burrow entrance to a radius of 15 or 20 feet. Some of them begin using other entrances to the same burrow system. The young walk slowly with hunched posture (Figure 4) when moving away from the entrance. Often, one of the young turns and runs for the entrance for no apparent reason. This engenders escape from other members of the litter. Other activities
at this time are feeding, giving the chirp call, and alertness. When the litter is grouped around the entrance in upright posture (Figures 7, 9, and 11), they often place their forefeet on each other. Other than this activity young show little interest in each other.

As the first week progresses juveniles extend their range and take more interest in each other. Agonistic behavior begins to appear in the form of biting and pushing each other. Then young begin displaying traces of threat by erecting the tail hairs and opening the mouth.

By the middle of the second week juveniles range as far as adults and behave as adults. However, juvenile agonistic behavior differs in some respects from that of adults. Young often begin an encounter by kissing and nuzzling each other. Encounters last longer and often stop and resume again. The young remain together after the encounter and return to other activities. Since agonistic behavior of juveniles does not result in separating the young, it does not function as it does in adults. I suspect that the activity in young enables them to develop a proficiency in agonistic behavior.

By the end of the second or third week most of the litter no longer associate themselves with a specific burrow. They range over a wider area than the adults and sometimes move to other areas of the lawn. The young that remain last at the original burrow are the runts and others that develop slowly. By this time agonistic behavior is less frequent and more like the adult pattern.

For the first few weeks juveniles and adults show little interest in each other. There is no maternal care of the young aboveground. The only direct benefit the young derive from adults is a warning of potential danger. The young respond to the chirp and churrr calls of adults with
alertness or escape. Occasionally, adults attack and chase young. Adults display no threat in the attack. Only after the young are 6 or 8 weeks old do young and adults threaten each other. At this time it is difficult to distinguish juveniles from adults either by size or behavior.

Interspecific Behavior

The response of ground squirrels to individuals of other species seems to be determined by whether or not the other species is potentially dangerous to them. This appears to be related to the size of the other species. Individuals of other species smaller than ground squirrels are either attacked or ignored. Individuals of larger species elicit alertness, threat, or escape from ground squirrels.

When a ground squirrel sights a larger animal (e.g. man, dog, mink, or cat) at a distance, it adopts the upright or down intermediate posture (Figures 9 and 10) and usually gives the chirp or churr call. Other ground squirrels respond with the same posture but do not call. The churr call is less common and has less effect on the population. If the larger animal remains at a distance, ground squirrels return to other activities but remain alert. If the larger animal is partially hidden or suddenly disappears, ground squirrels become more alert, calling is louder and more frequent, and they attempt to stand up higher. If the larger animal approaches, calling continues and they adopt the upright or down alert posture (Figures 11 and 12). As the larger animal comes closer, the ground squirrels run for a burrow and either enter or stop and adopt the upright or down alert posture beside the entrance. Escape is usually not accompanied by threat components. When the animals are in the down posture beside the burrow, they often move closer to the entrance in the body on ground posture (Figure 3). The movements at this time are jerky and tense.
When a larger animal appears suddenly close at hand, the ground squirrels immediately escape toward a burrow. Escape is often accompanied by the high-pitched squeak and erect tail hairs of threat behavior. If the ground squirrels do not enter the burrow, their behavior is the same as when the larger animal comes closer.

The following are descriptions of the relationships between ground squirrels and six other species that inhabit the area.

**Badgers**

Badgers (*Taxidea taxus*) dig into ground squirrel burrows leaving a mound of loose soil beside an enlarged burrow entrance. Ground squirrels do not avoid or show special interest in these entrances. Since badgers are largely nocturnal, I was unable to observe their responses to each other.

Seton (1928) and others say that badgers dig into burrows to capture ground squirrels. I consider this ineffective on the lawn because it is pervaded with burrows and entrances which offer ample opportunity for ground squirrels to escape. However, on three occasions I noted badger activity that may have been an effective means of predation. I reported this as underground concealment, which may function as "ambush" for ground squirrels (*Balph*, in press).

**Chipmunks**

Chipmunks (*Eutamias minimus*) are abundant in the area but usually avoid close proximity with ground squirrels. As long as chipmunks stay 5 or 10 feet away, ground squirrels ignore them. If the chipmunks come closer, they are sometimes attacked. Attack consists of several rapid steps toward the chipmunk or a short chase. In neither case is there threat by the ground squirrel. The immediate response of the chipmunk is to escape.
This does not increase the intensity of the attack.

**Humans**

In early spring ground squirrels are prone to escape from me. As the season progresses, they become habituated to my activity. If I make no sudden movement, they will tolerate me within a few feet. This does not represent a modification of their behavior—merely a higher threshold of alert and escape tendencies.

When handled, ground squirrels exhibit many components of agonistic behavior. These include biting, erect tail hairs, protruded anal papillae, all five sounds, and elimination. After release, animals often run 10 to 15 feet, adopt the upright intermediate posture and remain for a minute or until I make a movement. They usually do not call after release.

**Pocket Gophers**

Northern pocket gophers (*Thomomys talpoides*) and ground squirrels are numerous on the lawn. However, their respective niches provide little opportunity for them to be in competition. Most pocket gopher activity is in the top 1 foot of soil. Burrow systems of ground squirrels are at the 2- to 4-foot level. The only contact I observed between the two species was on two occasions when ground squirrels ate dead pocket gophers.

**Weasels**

Ground squirrels ignore long-tailed weasels (*Mustela frenata*) when the weasels are in full view on the lawn. However, if weasels are in the cover or partial cover at the edge of the lawn, ground squirrels sometimes adopt the upright intermediate posture (Figure 9) and chirp. I have never seen agonistic behavior toward weasels except by juveniles. On one occasion a juvenile chased a weasel. The attack included the erect tail hairs of threat. On another occasion a juvenile was attacked by a weasel. The
juvenile's response was stay-threat. The juvenile succeeded in defending itself in this manner for about 1 minute before I intervened.

**Red-tailed Hawks**

The response of ground squirrels to red-tailed hawks (*Buteo jamaicensis*) is the same as that to other larger species. Ground squirrels do not have a specific call for avian predators as reported for California ground squirrels (Fitch, 1948). They do respond to the shadow of a hawk moving on the lawn, but it is similar to the sudden appearance of a larger animal. I saw three cases of predation on adult ground squirrels by hawks—all in sage-grass areas a short distance from the lawn.
CONCLUSIONS

Knowledge of an animal's behavior can best be assessed by the ability to predict a response under given conditions. Ethologists believe that this knowledge can best be gained through the study of cause, function, and origin of behavior patterns. To a large extent, ethologists working on wild vertebrates have confined their research to birds and have given little attention to mammals. The consensus is that avian behavioral response is relatively stereotyped. Birds rely most heavily on the optic and auditory exteroceptor systems—both of which man is best equipped to study. On the other hand, mammalian behavioral response is more varied. Mammals rely on more exteroceptor systems, and this tends to make research more complex. For these reasons many researchers are inclined to think that the techniques and approach used by avian ethologists cannot be applied to mammals.

This study of the Uinta ground squirrel has convinced me that the ethological techniques and approach can be used for the study of this mammal. Further, the behavior principles developed by avian ethologists apply to ground squirrels. Although the behavioral responses of ground squirrels are more varied than those of lower forms, they are not as varied as one might suspect from casual observation. In any case, the variability does not invalidate the ethological approach. Components of posture in the ground squirrel such as tail hairs erect or mouth open are no different than components such as fanned tail or open beak in a bird as far as signal
value is concerned. All that is needed in the study of mammals is more quantitative data to handle the variability and a few techniques to investigate the tactile and chemical senses.
The objective of this study was to describe the behavior of Uinta ground squirrels in a free-living population. Within the scope of a descriptive study an attempt was made to ascribe causation, function, and origin of some of the behavior. The methods used in the study were directed toward observing and recording the activities of known individuals.

The activities of adult ground squirrels were divided into maintenance and social behavior. Maintenance behavior included locomotion, feeding, elimination, care of body surface, digging, alertness, investigating, and tailflicking. Each of these activities were described as to movements, postures, and sounds.

Social activities included agonistic and sexual behavior. The movements, postures, and sounds of these activities were described, and their possible role in social communication was discussed.

Juvenile behavior was described from the time the young appeared aboveground to the time they behaved as adults.

The behavior of ground squirrels to six sympatric species was described. The response of ground squirrels to other species seemed to be determined by the relative size of the other species; hence, their potential danger to ground squirrels.

The conclusion reached from this study was that the techniques and approach used by avian ethologists can be used on a wild mammal such as
the ground squirrel. Further, mammalian behavioral response is more stereotyped than was previously thought.
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