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Agonistic Behavior in Uinta Ground Squirrels

Abstract

A modified "arena" technique was used on an unconfined population of Uinta ground squirrels (*Spermophilus armatus*) in Grand Teton National Park to study the structure of agonistic interactions. In late summer, 1969, 213 encounters were observed. Six major postural components were identified and described: initial contact, threat, attack, combat, submission, and escape. Encounters were rapid, complex, and brief; they were divided into: approach, contact, and break of contact. Flow diagrams are given for the 213 interactions. Most terminated (ca 75 percent) at the conclusion of a threat-submission interaction, but sometimes continued through fights and chases. The most severe forms of fights (locked) occurred in only 11 percent of the cases observed. The threat-submission postures permitted agonistic interactions to operate on a visual level to maintain social dominance with a minimum of physical contact.

Age and sex classes of Uinta ground squirrels have different times for entering hibernation, ranging from mid- to late summer each year (Slade and Balph, 1974; Costain, 1975, pers. comm.). Adult females disappear first, followed by males, females, and later by young of the year. Social organization at this time is in a state of flux as a result of the vacuum created by disappearing adults and maturation of young squirrels. This study examined the structure of agonistic behavior in a free-living population of Uinta ground squirrels during the terminal part of their annual above-ground activity cycle.

Study Area

This study was conducted in the northern part of Jackson Hole, Wyoming, in Grand Teton National Park. This area has been described by Reed (1952), and by Craighead and Craighead (1952). Elevation is about 1900 m. The climate is characterized by long cold winters, deep snows, a short growing season, and low mean annual temperatures. Dice (1943) classified the area into the "Mountain Biotic Province." Vegetation is a mixture of grasses, forbs, and shrubs.

Methods of Investigation

Since vegetation height and density precluded a direct investigation of agonistic interactions and their role in social organization, a modified "arena" technique (after Grubitz, 1966) was used. His closed arena involving paired squirrels was used in an investigation of agonistic behavior of six ground squirrel species. In order to draw squirrels into an area of unobscured view in this study, a food source was placed in an area of high squirrel density. The food source was a can, full of sorghum and Purina rabbit chow, buried to the level of the top of the can. Presumably this provisioning technique, similar

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to that used in numerous primate and other studies, did not alter the form of agonistic interactions although it probably did increase the frequency of such interactions. Competition over food provided an opportunity to observe agonistic interactions in a population unrestricted in its movements.

Preliminary observations located a site containing at least 13 squirrels. A catalogue of agonistic behaviors was made during June, 1969, on these 13 animals and squirrels at five other nearby locations. The principal study site was located on the periphery of Jackson Hole Biological Research Station where squirrels were somewhat habituated to humans. Park philosophy precluded individually marking squirrels. Observations were made from a blind about 4 m from the food can. Squirrels were watched at various intervals from 9 AM to 1 PM daily for 22 days (7 July to 19 August, 1969) until the last squirrel in the area disappeared below ground for the year. In 1969, Costain (1975, pers. comm.) conducting a long-term ecological study of this population, trapped the last adult male on 31 July, the last adult female on 2 August, and the last young on 24 August; the last young seen was on 30 August. Observations averaged 109 minutes each day, and 2,410 minutes for the entire study; 213 agonistic interactions were observed. An Agfa Optima 500 (55 mm lens) and a Kodak Super 8 movie camera were used to supplement observations. Supplementary observations were made at several locations in western Wyoming in the summer of 1974.

Agonistic Behavior Patterns

Agonistic behavior patterns were divided into six major components (Fig. 1). The classification scheme is an expansion of that used by Ralph and Stokes (1963) and Burns (1968); it also includes information from Grubitz (1966) and Eisenberg (1968).

Initial Contact. The first physical contact between squirrels was usually in the forms of: 1) Naso-Nasal Contact in which squirrels touch noses, vibrissae, or mouths; or 2) Naso-Anal Contact in which sniffing or licking the other squirrel's genital region was involved.

Threat. Postural components include open mouth, a semi-arched back, forelegs flexed, hind legs extended, tail held to one side, tail hairs erect and head towards the opponent.

Attack. An attacking squirrel lunges forward directly at the focus animal, usually striking the opponent with its limbs, body or teeth.

Combat. Behavior of combatant squirrels involved prolonged physical contacts; these took the forms of: 1) Locked Fights, in which squirrels oriented themselves with ventrums pressed together while rolling about biting at each other; 2) Modified Fights, in which a squirrel exhibited an attack lunge involving brief physical contact followed by immediate separation; and 3) Boxing, in which squirrels stand upright on hindlegs with forepaws held towards each other. Striking or sparring occurs.

Submission. Submission lacks all postural components of threat; the head may be raised or held flat against the substratum, shoulders are low, and tail is straight or slightly lifted above the substratum. The squirrel frequently remains motionless in this posture with its legs flexed and its eyes half closed.

Escape. Withdrawal from an agonistic interaction involves a rapid locomotion away

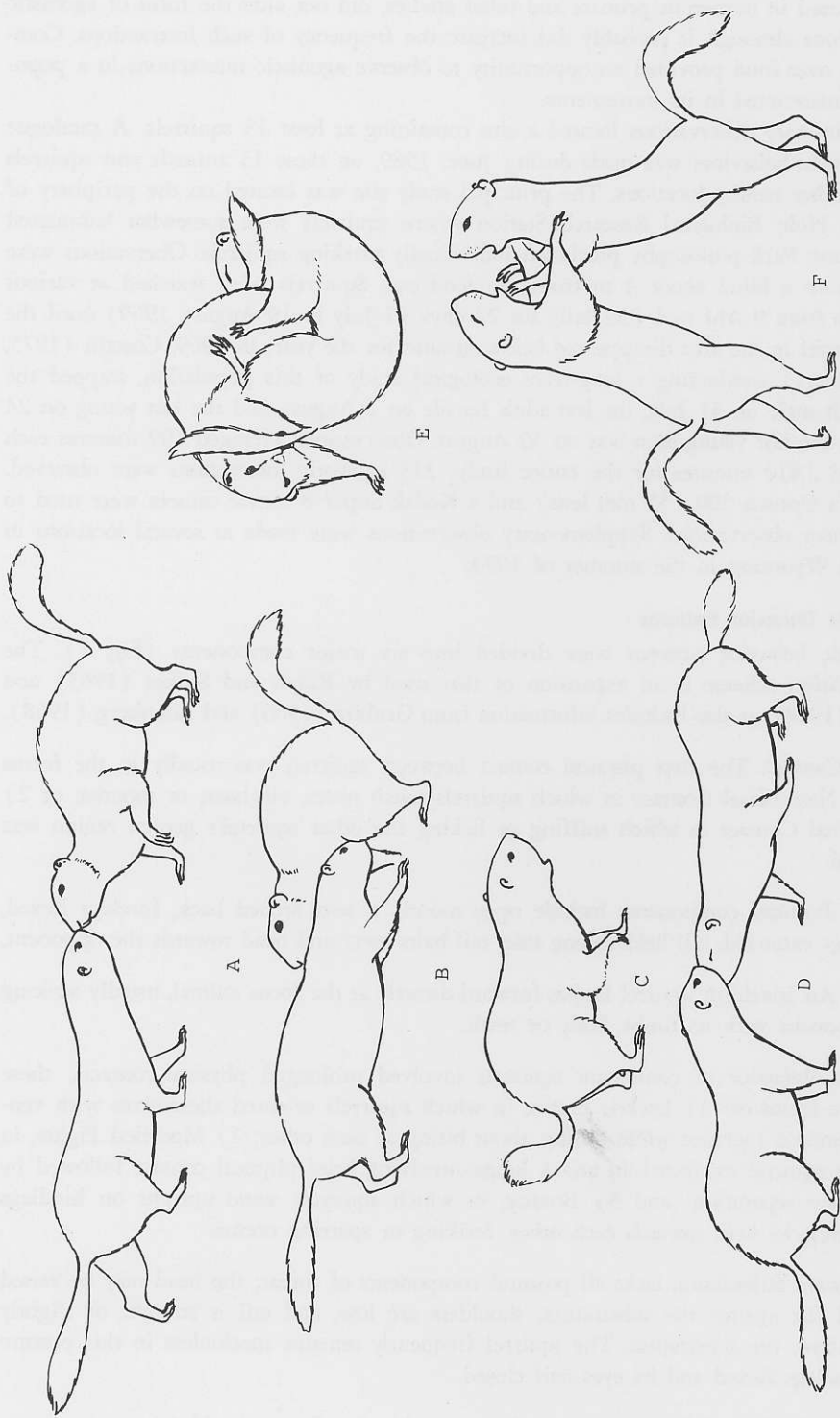


Figure 1. Postures observed in agonistic interactions among Uinta ground squirrels. A: Naso-nasal contact, B: Naso-anal (genital) contact, C: Threat, D: Dominant-subordinate interaction, E: Locked fight, and F: Boxing.

from the opponent. The retreat terminates when the escaping squirrel enters a burrow, or when it disappears into the vegetation, or when the opponent stops chasing it. Distances between squirrels is relatively uniform throughout the chase and rarely exceeds a meter.

A Generalized Agonistic Interaction

Agonistic interactions were divided into: 1) approach, 2) contact, and 3) break of contact, although in reality these form a continuum (Grubitz, 1966). Encounters are rapid, complex, and brief, usually less than a minute.

Approaches. Most agonistic interactions started when a squirrel approached an animal eating at the food can. The approaching squirrel frequently moved in a slow, jerky locomotion; tail movements took no apparent pattern as squirrels approached. When the approach was from a postero-lateral to posterior direction relative to the squirrel at the food can, the eating squirrel sometimes whirled around to face the oncoming animal. The approaching squirrel, if unchallenged, moved directly to the food can and the two animals began eating side-by-side. An agonistic behavioral sequence usually ensued if a challenge by either squirrel was given; these sequences comprised some or all of the behavioral categories defined above.

Contact. Initial contact generally consisted of either a Naso-Nasal or Naso-Anal posture. A few instances were observed in which two squirrels approached head on and moved side-by-side, each facing head-to-tail. Other types of contact sometimes followed, including Combat behavior involving Locked Fights, Modified Fights, and Boxing. Any interaction may have exhibited all or part of these behavior patterns.

Break of Contact. Termination of contact occurred when one squirrel turned and ran (Escape), usually being chased. The pursuing squirrel persisted in the chase only a short distance before returning to the food can or to other activities.

Agonistic Behavioral Sequences

A flow diagram showing the sequences of 213 agonistic interactions is given in Figure 2. Initial contacts were either Naso-Nasal (25 percent), Naso-Anal (36 percent), or Neither (40 percent). The "Neither" category included a situation in which one squirrel was eating at the food can and another squirrel approached and immediately began eating.

After the initial contact, one of the squirrels usually threatened the other (54 percent), submitted (27 percent), or escaped (19 percent). If one squirrel threatened the other, the interaction usually continued. If one squirrel submitted, the agonistic encounter was terminated: the two squirrels ate side-by-side, or if one squirrel escaped, the remaining one stayed and ate alone.

When interactions continued, some squirrels responding to the threat submitted (16 percent), some type of combat ensued (54 percent), or one of the squirrels escaped (30 percent) (Fig. 3). If one squirrel submitted or escaped, this terminated the interaction. Combat took the form of locked fights (39 percent), modified fights (35 percent), or boxing (26 percent). The interaction may then have terminated if one or both squirrels began eating (11 percent). If one squirrel escaped (89 percent), however, the encounter ended with that individual's retreat (71 percent) or with the other ani-

mal giving chase (30 percent). In half of the locked fights and all boxing bouts, vocalizations were heard. Chases (N=16) seldom persisted over 5 m (N=2).

Contacts and Responses

The types of initial contact varied slightly, but differences were not significant. Responses also varied. A threat, as opposed to submission or escape, most often ensued

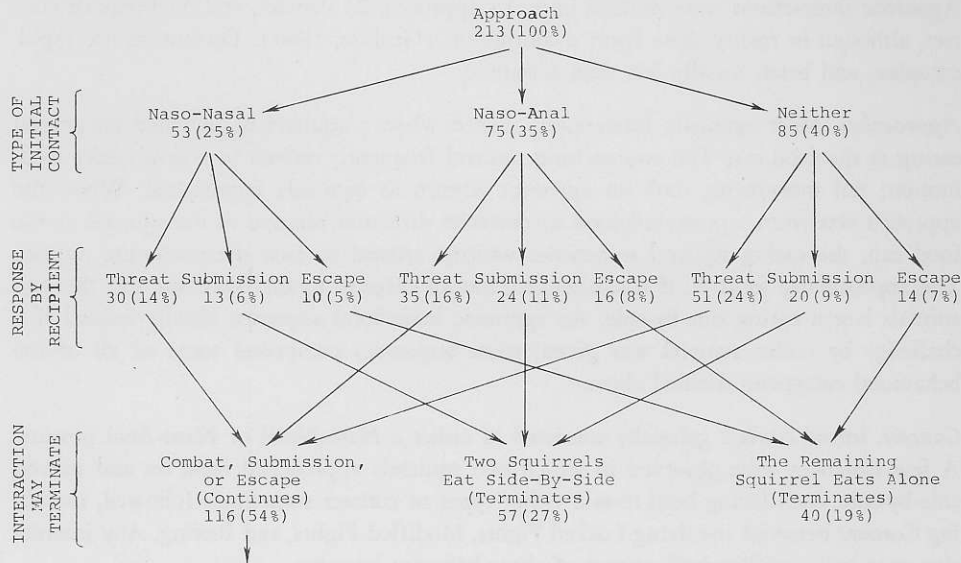


Figure 2. Flow diagram showing the behavioral sequences comprising agonistic interactions in the Uinta ground squirrel.

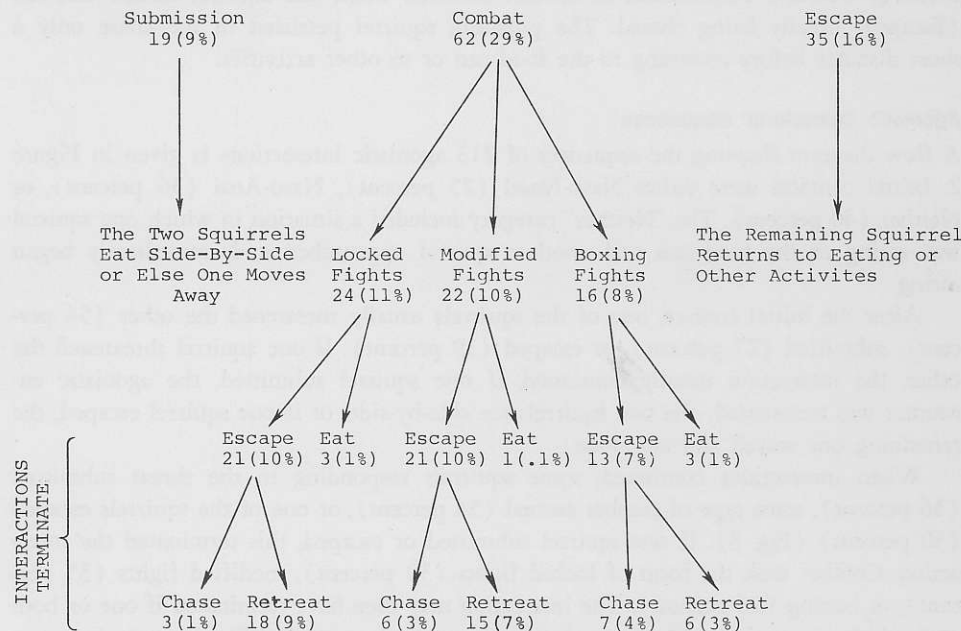


Figure 3. Flow diagram showing the behavioral sequences most agonistic interactions took in Uinta ground squirrels, if they did not terminate at an early "stage" shown in Figure 1.

after the initial contact; this difference was significant ($X^2=16.2$, 2df; $p=.001$). Threats most often led to combat (62 percent) rather than submission (16 percent) or escape (22 percent); this difference was also significant ($X^2=24.1$, 2 df; $p=.001$). Combative behavior took three forms (Fig. 2); differences were not significant. These interactions terminated in either an escape by one squirrel, which may be chased (29 percent) or both squirrels starting to eat; differences between escaping and eating were significant ($X^2=27.6$, 1df; $p=.001$).

Discussion

Agonistic interactions are highly variable in Uinta ground squirrels. Usually encounters terminated at the conclusion of a threat-submission interaction, but sometimes continued through fights and chases. About one-fourth of all interactions involved combat; the most severe form of fights (locked) occurred in only 11 percent of the cases observed. The outcome of most combats was apparent when one squirrel retreated. Dominance-subordinance hierarchies were established with little overall physical contact and possible injury to each other.

Since ground squirrels are diurnal, a large part of agonistic behavior is based on visual exchanges of information between potential opponents (Grubitz, 1966). Perhaps most individuals were littermates or neighbors and had probably encountered each other numerous times and in a variety of circumstances before our study. The food can "arena" probably served only to intensify the agonistic interaction rate among these young squirrels.

Burns (1968) found that, in the same season as our study, most Uinta ground squirrels in his Utah population seemed to maintain individual distances of tolerance; they became aggressive towards other squirrels that approached to within 0.6-1.5 m of them. Large numbers of young Uinta ground squirrels disappeared from his population during this season. Burns noted that the period of disappearance is characterized by instability in the population resulting from: 1) development of sexual behavior; 2) increased aggression in one-year-old males and young females; and 3) increased movement by young that were lost during this period when young females dominated over males. This disproportionate disappearance seemed directly related to aggression on the part of young females in the Utah population. Presumably this fact has adaptive significance in that young females consequently remained in areas that already had proved themselves to be consistently productive environments. When these young females then emerged from hibernation the following spring, they would already inhabit such an area.

The complex sequence of agonistic behavior patterns served to establish or reinforce social dominance among Uinta ground squirrels. The threat-submission postures permitted the interactions to operate on a visual level to maintain social dominance with a minimum of physical contact.

Acknowledgments

We would like to thank Cheryl Hughs for the drawings and Denise Casey, Brent Costain, and Don Streubel for their critical advice on the manuscript. A grant from the Marsh Fund of the National Academy of Sciences gave us the opportunity to complete this paper. The Department of Zoology, University of Wisconsin, provided facilities. Dr. L. Floyd Clarke, Director of the Jackson Hole Biological Research Station, provided space at the station.

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Received January 5, 1976

Accepted for publication March 2, 1976