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## AGONISTIC BEHAVIOR OF THE CALIFORNIA GROUND SQUIRREL, *SPERMOPHILUS BEECHEYI*, AT AN ARTIFICIAL FOOD SOURCE

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**ABSTRACT.**—Occurrence of agonistic behavior patterns in *Spermophilus beecheyi* at a concentrated artificial food source was studied. Our data from 851 encounters are compared with previously published information from unmanipulated populations. Eight new behavior patterns (rump block, kick, forward shove, pounce, displacement grooming, circle fight, roll fight, and boxing fight) are described.

Because of the diversity of life-styles exhibited and habitats occupied by its member species, the squirrel family Sciuridae has provided biologists with a rich source of information on the evolution of mammalian sociality. Aspects of this work with ground squirrels have been discussed by, among others, Armitage (1981) and Michener (1983). A recent volume (Murie and Michener 1984) deals extensively with the biology of ground squirrels, including sociality. Biologists generally accept, however, that successful analysis of the evolution of behavior and sociality depends upon the prior cataloging of the behavioral repertoire of each species as an ethogram (Lehner 1979). Only when the extent and context of each behavioral action is understood can its adaptiveness be fully appreciated. For this reason, many works on the behavior of squirrels have been at least partially devoted to descriptions of behavioral actions.

Among the highly social ground squirrels, agonistic behavior has received considerable attention. Descriptions of postures and actions associated with agonism have been published for several species, among them *Spermophilus undulatus* (Watton and Keenleyside 1973, Steiner 1974), *S. armatus* (Balph and Stokes 1963, Clark and Russell 1977), *S. richardsonii* (Sheppard and Yoshida 1971), *S. columbianus* (Betts 1976, Steiner 1974), and *Ammospermophilus leucurus* (Fisler 1976). For the California ground squirrel, *Spermophilus beecheyi*, Owings et al. (1977) have described many agonistic behavior patterns, and Dobson (1983) has provided information on the timing, pattern, and form of agonism in

this species. The purpose of this paper is to describe eight agonistic actions previously unreported in this species, all observed among individuals feeding at artificial, concentrated food sources; we also provide additional information concerning the context and frequency of agonistic actions previously described.

### STUDY AREA

Two populations about 880 m apart were observed in the Santa Susana Mountains, north of Chatsworth, Los Angeles Co., California, from 27 July 1975 until 29 April 1976. Site 1 was relatively flat, at the head of a steep canyon (920 m elevation); Site 2 was a south-facing hillside (985 m elevation). Predominant vegetation at both sites was wild oats (*Avena fatua*), heavily grazed by cattle. The only other vegetation was a single, small coast live oak (*Quercus agrifolia*) and a small stand of California sagebrush (*Artemisia californica*) at Site 1. Grasslands of this sort are common habitats of *S. beecheyi* in southern California. The locality studied is well within the range of *S. b. beecheyi* (Hall 1981).

### METHODS

Squirrels were live-trapped, sexed, weighed, toe-clipped for permanent identification, and dye-marked with Rodol-A. Trapping was continued sporadically throughout the study and toe-clipped animals re-dyed as necessary. Forty-eight animals (17♂, 31 ♀) were marked at Site 1, 44 (23♂, 21♀) at site 2. At Sites 1 and 2, respectively, 15 and 4

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animals were adults when first captured; all others at capture were young-of-the-year (hereafter termed young). By spring, all animals had attained adult size. No exchange of individuals between the two sites was noted.

Of the 50 observation days, 29 were in the fall prior to winter inactivity (3 September–4 December), 18 were in the spring mating, gestation, and lactation period (3 February–29 April), and 3 were in summer (13 July–19 August). Observations were made, sometimes with binoculars, from a car.

To encourage and intensify interactions, we filled four or five enclosed wooden boxes (20 × 20 × 25 cm) with seed (wild-bird mix) and placed them in various locations within the colony each observation day. Seeds fell into a 5 × 5-cm feeding tray on one side of each box where only one squirrel could feed at a time. Interactions among squirrels at each box were then recorded over a 3–4-hr period.

Most observations were made on 15 marked animals (7♂, 8♀) at Site 1 and 18 (11♂, 7♀) at Site 2; both adults and young were included. To avoid including animals of unknown biological and social status, we limited our analysis to interactions between two dye-marked squirrels. Kinship among animals was not known, but male-female pairs sometimes were identified.

## RESULTS

### New Behavioral Patterns

Behavior patterns previously unnoted in this species are described below. Where applicable, we use terminology applied by Fisler (1976).

**RUMPBLOCK:** A shifting of the rump position by a feeding animal so as to block another individual's approach.

**KICK:** A raising of and pushing with the rear legs against the flank of another animal.

**FORWARD SHOVE:** A pushing action with the forelegs while in an upright posture.

**POUNCE:** The leaping of one animal onto another so that all four of its feet are momentarily in contact with the back of the animal being attacked.

**BOXING FIGHT:** An action in which two animals stand briefly on their hind legs, face to face, and bat each other vigorously with their forepaws.

**ROLL FIGHT:** An intense fight in which two

individuals roll over and over in a tight ball, frequently with considerable clawing and biting.

**CIRCLE FIGHT:** An intense fight in which two squirrels chase each other in a tight circle.

**"DISPLACEMENT" GROOMING:** A very brief (4–5 sec), elaborate "washing" motion, starting with a vigorous rubbing action with both forepaws on the face and ears, then proceeding rapidly down the entire body to the tail tip. Because the action appears out of context, typically interspersed among intense agonistic encounters, we interpret it to be "displacement" behavior.

### Occurrence of Behavior Patterns

Here we consider the context and frequency of occurrence of agonistic behavior patterns seen in our study. Where appropriate, we compare our findings with those of Owings et al. (1977). Data for all 851 encounters observed by us are summarized in Table 1.

**CHASE.**—As did Owings et al. (1977), we found chase the most common type of agonistic interaction (27.5% of all encounters), with males chasing more frequently than females (167 of 234 chases; 71.4%). In contrast to their findings, however, we observed males chasing females more frequently than they did other males, 1.34X as frequently among adults in spring and 1.65X as often overall. Females were the chasers 67 (28.6%) times, chasing other females 52 times, males only 15. One young female accounted for 13 of the 15 chases of seven males (six young, one adult), five of which were larger than she by 50–150 g. Two other females were also seen to chase a male once each; in one instance both animals were young, and in the other both were adults.

On seven occasions in spring, two adult males engaged in bouts of reciprocal chasing after meeting at a box. First one chased the other 2–3 m from the box. Reversing roles, the pair then ran past the box 2–3 m in the opposite direction. Typically the roles reversed repeatedly, in one case eight times, before an encounter terminated. We believe such behavior to be the result of repeated dominance reversals across a territorial boundary. As evidence, we cite the fact that such behavior could be induced only at certain locations; moving the box as little as 1 m to either side caused agonistic encounters to

TABLE 1. Frequency of behavior patterns by sex and age in dyadic encounters. All encounters involving young occurred in fall. All encounters between two adults were seen in spring, except for two rump blocks, one roll fight, and one flank push between two females, and the four male-female flank pushes in which males did the pushing. In male-female encounters, frequency of male wins and frequency of female wins, respectively, are separated by a slash. Asterisks identify newly described behaviors.

Agonistic Behavior	Age and sex									N	%
	Two adults			Two young			Adult-young				
	♂-♂	♀-♀	♂-♀	♂-♂	♀-♀	♂-♀	♂-♂	♀-♀	♂-♀ <sup>a</sup>		
Chase	32 <sup>b</sup>	25	42/1 <sup>c</sup>	26	27	54/13	5		8/1	234	27.5
Supplant	13	14	25/0	25	45	43/3	11 <sup>d</sup>	2	37/0	218	25.6
Stare			12/1		6	3/2		2	3/0	29	3.4
Rump block*		6	0/1 <sup>e</sup>		28	1/1 <sup>e</sup>				37	4.3
Kick*		2			24	1/0				27	3.2
Forward shove*					19	1/0				20	2.4
Flank push	3	4	4/4	1	37	6/3	1	13	8/0	84	9.9
Lateral approach	21	2	1/0	3	31	3/1			6/0	68	8.0
Pounce*	2		1/1							4	0.5
Boxing fight*			1/0	2	15	2/2			2/0	24	2.8
Circle fight*	1				2					3	0.4
Roll fight*	7	2	4/0	2	16	3/2			1/0	37	4.3
Displacement groom*	20									20	2.4
Cheek-back rub	30									30	3.5
Cheek rub	8									8	0.9
Dusting	8									8	0.9
Totals	145	55	90/8	59	250	127/27	17	17	65/1	851	100.0

<sup>a</sup>All encounters involved an adult male and a young female; none involving adult female and young male were seen.

<sup>b</sup>Includes 19 chases in 4 bouts of reciprocal chasing.

<sup>c</sup>Includes 4 redirected chases.

<sup>d</sup>In 2 of 11, young supplanted adult

<sup>e</sup>Female attempted to block male, but was forced out.

cease, with one male having exclusive use. This observation conforms with Dobson's (1983) finding that "dominance [is] at least partially site-specific" among adult male *Spermophilus beecheyi*.

In four instances, a chase of an adult female by an adult male was apparently the result of redirected aggression. In each case, one of two males engaged in an agonistic encounter at a territorial boundary turned quickly to chase a female not previously involved.

**SUPLANT.**—As did Owings et al. (1977), we found supplanting—the causing of another animal to move away—to be almost as common as chasing. However, in contrast to their findings, in our study males were the most common supplanters (154 cases; 70.6%), usually of females. Females supplanted others only 64 times (29.4%); all but three of the supplanted animals were also females. No adult male was ever supplanted by a female, but twice adult males were seen to retreat at the approach of a smaller, young male.

**"BLOCKING" ACTIONS.**—A feeding squirrel tended to retain its position at a box when

approached by another animal by lifting its head and directing its gaze at the intruder (stare of Owings et al. 1977, passive displacement of Fisler 1967), by a rump block, by kicking, by a forward shove, or by a combination of these behaviors.

Stare was used to block approaching females 26 times (89.6%), males only 3 (10.4%). Eighteen times a male did the blocking, 8 times a female. A female blocked a male with a stare on only 3 occasions; in the one encounter involving two adult animals, the female was pregnant and shared a burrow with the male. Although Owings et al. (1977) reported staring among males, we saw no male-male stares.

Rump block was used exclusively by females, usually against other females. In the only two instances when a female attempted to block a male in this manner, the male supplanted the female.

On 27 of the 37 occasions when a rump block was seen, the action was followed by a kick. Twenty-six kicks were delivered by females against other females (96.3%), mainly young; only once was a male, a young, seen to



deliver a kick (3.7%) against a young female.

Frequently, forward shoves were interspersed with kicking. This action was seen 20 times, 19 of them involving two young females. All but two forward shoves occurred coincidentally with kicking.

**DISPLAYS.**—During intense agonistic encounters two animals often showed a lateral approach display (Owings et al. 1977), their bodies parallel, either head to head or head to flank, their backs arched, their heads slightly up and oriented toward the opponent, their tails elevated, and the tail hairs erect. Although Owings et al. (1977) reported such action mainly among males, of the 68 lateral approaches we saw, only 24 (35.3%) involved two males; 33 (48.5%) cases involved a male and a female, 11 (16.2%) two females.

Owings et al. (1977) reported that lateral approaches often ended in flank pushes or slams, but we found they most commonly terminated simply by separation (20 cases; 43.5%); 10 (21.7%) ended with a chase, 6 with a kick, 6 in fights (13% each), and only 4 (8.7%) in flank pushes. Furthermore, the display was not always initiated in a side-to-side orientation; 38 times (55.8%) we saw this behavior begin as two animals approached head-on, often when 3–4 m apart. Only as they closed on each other in a slow, stiff-legged gait did they assume the typical lateral position.

**PUSHES.**—Whenever two animals approached a box simultaneously, or when one tried to enter while another fed, flank pushing (side-shove match of Fisler 1976) was common. An animal at the box when the encounter began typically initiated the pushing, usually after an attempted rump block failed. Two males engaged in such matches only 5 times (6.0%) compared to 54 (64.3%) such interactions between two females and 25 (29.8%) between a male and a female. Of the 25 male-female encounters, the male retained or attained control of the box in 19 (76%). The vigorous flank slams described from film by Owings et al. (1977) were not seen.

**MARKING BEHAVIOR.**—Three behavior patterns described by Owings et al. (1977) and probably involved in scent marking occurred among our squirrels. Cheek-back rubbing was most common, with cheek rub and dusting seen only about 25% as often. All were exclusively actions of adult males in spring, usually occurring when two males met at a box on

their common territorial boundary. Typically, a lateral approach display was followed by a brief period of ambivalence as first one, then the other, approached the box. One animal would then turn away to rub either its cheek (cheek rub) or its whole side from mouth to flank (cheek-back rub) on a nearby stake or log, or in the dust (dusting). Frequently such behavior was repeated many times in succession.

In one case a cheek-back rub occurred with only one male immediately involved. While one adult male was in a trap, another advanced 5 or 6 m into the trapped male's territory where it cheek-back rubbed a stake three times before retreating.

**FIGHTS.**—Several gradations of fighting behavior occurred. Least vigorous was the pounce. Twice an adult male pounced on another adult male feeding at their common territorial boundary. In a third instance a male pounced on a female, apparently causing her to relinquish a box. In a fourth encounter a pregnant female, without obvious preliminaries, leaped onto a male (with whom she shared a burrow) while he was feeding in the grass. He gave no obvious response and continued feeding as she began feeding also.

Boxing fights occurred 24 times. This action was most common between two young (21 times; 87.5%), usually females (15 times; 62.5%). Only once did two adults, a male and a female, engage in such an action. Each encounter lasted only 3–5 sec.

Both roll and circle fights were usually intense, often involving clawing and biting. Roll fights, the more common of the two, occurred among both mature and immature animals. In 2 of the 10 roll fights between a male and a female (both young), the female won the encounter and retained the box.

Of the 68 fights of all sorts, roll fight and boxing fight were most common (54.3% and 35.3%, respectively); pounce accounted for only 5.9% of the fights and circle fight only 4.5%. Forty-six (67.6%) fights were between two young animals, and 33 (48.5%) involved two young females.

**DISPLACEMENT GROOMING.**—This action was seen only during high-intensity encounters between adult males on territorial boundaries. It was observed in six encounters and in each was repeated many times. Each

time the behavior was seen it was interspersed among bouts of lateral approach, flank push, fights, and marking behavior. Typically a male would break off an agonistic encounter, engage in displacement grooming, then either renew the encounter with its adversary or mark a nearby stake.

We occasionally shifted the action from one member of a dyad to the other by moving the feeding box 0.5–1 m toward the territory of the animal that had previously been "grooming." Consequently, our subjective opinion is that the grooming animal is the one most "ill at ease" at the moment. We have not seen such action among adult males in any other context, nor among females or immature males.

#### DISCUSSION

Our study differs from that of Owings et al. (1977) in that most interactions we saw took place at a concentrated food source. Presumably the level of antagonism at such a locale is higher than among individuals interacting where resources are more widely scattered. This difference in procedure probably accounts for most of the differences observed in frequency and context of behavior patterns. It probably also accounts for our observations of several previously unreported fight patterns and displacement grooming, thereby allowing an extension of the ethogram for *Spermophilus beecheyi*.

Some behavior patterns, (e.g., chase, supplantation, flank push, lateral approach) are common to both sexes and all ages. Indeed, if one assumes a 1:1 ratio among the sexes in the populations, the frequency of occurrence of the first two behaviors approximates the 1:2:1 ratio expected on the basis of likelihood of male-male, male-female, or female-female contacts. The frequencies of occurrence of the flank push and lateral approach, on the other hand, are clearly skewed, the former much more common among females than males, the latter mainly utilized when the two animals are of the same sex.

Other behaviors are more restricted in occurrence. Almost half of the fights were between young females, perhaps animals still sorting out hierarchical relationships. Stare and rump block were never seen between two males of any age, although both were common

when two females or a male and a female interacted. Kick and forward shove, typically associated with stare and rump block, were almost totally restricted to young females. They occurred only rarely in a young male-female encounter and never between two males of any age. Among adult males, the more intense agonistic action of lateral approach appears largely to replace the milder actions of rump block, stare, kick, and forward shove, although it is not restricted to this context.

Four behavior patterns—displacement grooming and three marking actions—occurred only during intense boundary interaction between two adult, territorial males. Owings et al. (1977) also reported cheek rub and cheek-back rub to be mainly a male action, although they saw these actions among females occasionally. The predominance of marking actions among males is not surprising since such actions are presumed to be related to identification and reinforcement of territorial boundaries; evidence that adult males are territorial during the breeding season is strong, but clearcut indications of territoriality among females is lacking (Dobson 1983). The role of displacement grooming is not clear.

As evidenced by the "winner" in all categories of agonistic behavior but one (rump block), male dominance is characteristic in this species, even among young and among adults in the nonbreeding season. This conforms generally with the findings of Dobson (1983) and Fitch (1948). Male dominance may be related both to sex-related hormonal differences and to the generally larger size of males. However, the possibility that factors other than sex and size are also involved is suggested by the fact that among Richardson's ground squirrels (*S. richardsonii*) the larger males do not dominate females after the breeding season (Michener 1983). Even in the California ground squirrel male dominance is not invariable, as indicated by a young female that at various times chased seven different males, all but two larger than she, and by a pregnant female that attacked a larger male in whose territory she lived (her mate?) with apparent impunity on a few encounters. Clearly the degree of aggressiveness among females differs and may temporarily be increased relative to certain males during

pregnancy. Dobson (1983) also found females to occasionally dominate males, at least non-resident ones.

Our observations also confirm the findings of Dobson (1983) that male California ground squirrels frequently are territorial, at least during the breeding season. Using artificial food sources, we had no difficulty identifying the territorial borders between adjacent males and found them to be stable throughout the breeding period. We suggest that this technique, though manipulative, may prove useful with other squirrels for verifying the existence of territoriality and for delineating boundary locations.

Finally, we note that the majority (92%) of the agonistic encounters seen appear to involve little energy output and entail little physical risk. The four fight categories, those behaviors presumed bioenergetically most expensive and potentially most harmful, comprised only 8% of the encounters observed.

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