Ethology Ecology & Evolution 3: 185-205, 1991

Social behavior and space-use of young of ground-dwelling squirrel species with different levels of sociality

L.S. RAYOR [1] and K.B. ARMITAGE

Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045, USA

Received 19 March 1990, accepted 3 January 1991

Comparisons among young of ground-dwelling squirrel species with different adult sociality indicate patterns of interaction during development that may influence the evolution of complex sociality. Social behavior and spatial overlap of weaned young with their mothers, littermates, non-littermate young, and adult conspecifics were compared among Gunnison's prairie dogs (*Cynomys gunnisoni*), yellow-bellied marmots (*Marmota flaviventris*), Columbian ground squirrels (*Spermophilus columbianus*), and thirteen-lined ground squirrels (*S. tridecemlineatus*). The adult social organization of these species differs markedly: Gunnison's prairie dogs are highly social, yellow-bellied marmots and Columbian ground squirrels are relatively less social, and thirteen-lined ground squirrels are asocial. In young Gunnison's prairie dogs, social cohesion and spatial overlap were high not only with the mother and littermates, but with all members of the harem. In yellow-bellied marmots, social cohesion occurred with all members of the matriline, but spatial overlap was less extensive than in prairie dogs. In Columbian ground squirrels, amicable social interactions of young were confined to the mother and littermates, and occurred less frequently than among the prairie dogs. Young of thirteen-lined ground squirrels interacted little and overlapped only briefly with their mothers; cohesive interactions were limited to littermates. Thus, in the more social ground-dwelling squirrel species, cohesive behaviors between mother and offspring associated with prolonged spatial overlap probably is the mechanism that establishes social groups and represents post-weaning parental reproductive investment in non-reproductive offspring. However, the tolerance and amicability of adults toward young other than their own offspring is likely a crucial step in the evolution of complex sociality.

KEY WORDS: evolution of sociality, behavior, space-use, prairie dog, ground squirrel, marmot, parental investment.

---

[1] Present address: Department of Entomology, University of Arizona, Tucson, AZ 85721, USA.

INTRODUCTION

Sociality in ground-dwelling sciurids (ground squirrels, prairie dogs, marmots) is associated with the retention of offspring within the mother's range (MICHENER 1983); in the highly social species dispersal is delayed until after the first hibernation or later and daughters may remain as adults to form matrilines (ARMITAGE 1981, 1984). It was postulated that cohesive behaviors between mother and offspring is the proximal mechanism underlying group formation (ARMITAGE 1981, MICHENER 1983). Briefly, this hypothesis states that mother:infant cohesive behaviors are prolonged, often into adulthood, in the more social species and terminate early in the first summer of life in the asocial species. Thus, full understanding of the social dynamics of ground-dwelling squirrel societies requires knowledge about behavior and space-use by the young. Comparisons of the young from species with different levels of adult sociality should indicate patterns of interaction during development that are correlated with the evolution of complex sociality in ground-dwelling squirrels. Surprisingly little work specifically examines the behavioral and spatial interactions of young (MICHENER 1981, WATERMAN 1986) and no comparative data among species are available.

ARMITAGE (1981) proposed that sociality is a means of extending reproductive investment in young beyond weaning. WASER & JONES (1983) argued that most young mammals benefit from continued residence within the natal home range past the age of independence from their parents and that such residence results in some cost to the future reproductive success of the parents. Substantial benefits may accrue to young ground-dwelling squirrels by delaying dispersal until the summer before they are reproductively mature and remaining in the relative safety of the natal area with its proven hibernaculum and warning calls of conspecifics (SHERMAN 1977, SCHWAGMEYER 1980, WASER & JONES 1983). Young that remain in or near the maternal territory appear to have a higher rate of survival than those that disperse (GARRETT 1982, WASER & JONES 1983, HACKETT 1986, VAN VUREN 1990). The value of the natal area is demonstrated by the frequent inheritance of such sites by female offspring (KING 1955, ARMITAGE 1984, HARRIS & MURIE 1984). Thus, ground squirrel sociality may be a means of directly increasing individual fitness by increasing the probability that offspring survive to reproduce (ARMITAGE 1987, RAYOR 1988).

Parental care is predicted to decrease when costs to the parents outweigh benefits to the offspring (TRIVERS 1974). In ground-dwelling squirrels, such costs may

become significant when the offspring reach reproductive maturity and have the potential to compete reproductively with their parents (ARMITAGE 1986, 1987; RAYOR 1988). Duration of parental investment in ground-dwelling squirrels is closely related to age of reproductive maturity; low sociality and early dispersal as young are typical of species that first breed as yearlings, whereas higher sociality and delayed dispersal are typical of species that first breed at 2 or more years of age (ARMITAGE 1981, MICHENER 1983). Juveniles of species that disperse later have the potential for a longer period of mother-offspring association and interaction with other conspecifics (MICHENER 1984).

We tested the general predictions that post-weaning (above ground) social behavior and space-use by young vary directly with the degree of adult sociality. Specifically, we predicted that the frequency of amicable social interactions between mother and offspring and among littermates would be higher in more social species. Second, the extent of spatial overlap was predicted to be greater and be maintained longer in more social species. Third, the cohesive behavioral interactions and spatial overlap of young with conspecifics outside the litter were similarly predicted to be more extensive as sociality increases. Finally, because females in most ground-dwelling squirrel species are the philopatric sex and more likely to be recruited into the natal population than males (HOLEKAMP 1984, ARMITAGE 1986), young males were predicted to interact less frequently and to have less space-use overlap with their mothers than young females.

Subjects

The range of adult social organizations in North American ground-dwelling squirrels forms a continuum from aggregated solitary individuals to highly social, cohesive societies (ARMITAGE 1981, MICHENER 1983). Three of the species studied were relatively social; the third was asocial. The Gunnison's prairie dog (*Cynomys gunnisoni*), the yellow-bellied marmot (*Marmota flaviventris*), and the Columbian ground squirrel (*Spermophilus columbianus*) most often reach sexual maturity as 2-year olds, and dispersal is delayed until the yearling summer (FESTA-BIANCHET 1981, FESTA-BIANCHET & KING 1984, RAYOR 1985, ARMITAGE 1986), permitting a long period of social interaction with the mother and other conspecifics (MICHENER 1984). However, the substantial differences in the adult societies of these species, suggest the value of comparing features of adult-young interactions.

Gunnison's prairie dogs (*Cynomys gunnisoni*) are among the most social of the ground-dwelling sciurids (RAYOR 1988). The social unit is a polygynous harem («coterie») in which one or more adult males and multiple females communally use and defend a common territory (MICHENER 1983 class 5, SLOBODCHIKOFF 1984, RAYOR 1988). Behavioral interactions among harem members are predominantly cohesive but are almost always agonistic toward non-harem members (RAYOR 1988). Adult males remain interactive members of the harem.

Columbian ground squirrels (*Spermophilus columbianus*) are considered to be the most social North American members of the genus *Spermophilus* (MICHENER 1983 class 3), but only moderately social relative to the highly social species of *Marmota* and *Cynomys*. The social unit is a «multiple female kin cluster» in which adult females defend quasi-exclusive territories (FESTA-BIANCHET & BOAG 1982) and neighboring females frequently are relatives (HARRIS & MURIE 1984, KING & MURIE 1985). Adult

males occupy a territory superimposed over those of several females (MURIE & HARRIS 1978).

The social unit of the yellow-bellied marmot previously was reported as a polygynous harem (ARMITAGE 1981, MICHENER 1983) but more extensive analysis indicates that the basic social unit is a matriline in which related adult females may share burrows and foraging areas with each other and with young and yearlings. A harem occurs when a male associates with one or more matrilines (ARMITAGE 1986). Social behavior among closely related matrilineal members is predominantly cohesive (ARMITAGE & JOHNS 1982).

Limited observations of thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) were included because of the value of contrasting the behavior of an asocial species with the three more social species. Thirteen-lined ground squirrels live in aggregations, but are essentially asocial (MCCARLEY 1966). The social unit may be considered to be a «single family kin cluster» because the home ranges of mothers and adult daughters may overlap (MICHENER 1983 class 2, VESTAL & MCCARLEY 1984). Home ranges of adult males spatially overlap those of adult females (SCHWAGMEYER & BROWN 1983, pers. obs.), but male-female interactions are minimal after courtship (WISTRAND 1974). Young disperse within a few weeks after emergence and females first breed as yearlings (MCCARLEY 1966).

STUDY SITES AND METHODS

Study sites and litters observed

Two populations of Gunnison's prairie dog were studied by L.S. Rayor in south-central Colorado from 1979 through 1981; during 1981 mother-offspring dynamics were the central focus of the study. The primary site for study of the young was Quartz Creek (QC), a 1.08-ha strip along an irrigated hay meadow northeast of Parlin, Colorado, USA (38°31'N, 106°40'W, elevation 2500 m). Supplementary observations were made at a 3.36-ha site near Blue Mesa Reservoir (BM) (38°28'N, 107°06'W, elevation 2317 m), 48 km west of the QC site. Prairie dog study sites and vegetation are described elsewhere (RAYOR 1985). Each site was divided into numbered 6 by 6 m grids. Prairie dogs were live-trapped and observed almost daily from March through August 1981 at QC, and in June through August 1979 and 1980 at BM. Behavioral interactions and spatial patterns of young were analyzed for eight litters containing 59 young ($\bar{x}$ littersize ± SD = 7.4 ± 1.7) from three harems («Ridge» and «East» at QC in 1981, «Aster» at BM in 1980). Generalizations from litters from all years of the study and from harems other than those closely analyzed are included where appropriate. In the East harem, mothers 917 and 921 weaned litters in the same burrow, so that discrimination between litters was impossible. Mother 917 died in a trap 4 days after young first emerged; her young remained associated with 921. The two litters of East young were treated as littermates for the analyses. Three mothers (807, 813, 843) were killed by predators during mid-July, 4 weeks after the young had emerged.

Columbian ground squirrels were studied at the Dyson Creek site by L.S. Rayor, a 0.76-ha grassy meadow in southwestern Alberta, Canada, (50°37'N, 114°40'W, elevation 1570 m), from June through early August 1983. The study area is described by FESTA-BIANCHET (1981); the site was gridded in 10 by 10 m quadrats. Analysis is based on eight litters containing 36 young (4.5 ± 0.7). One mother (4767) was killed by a predator 14 days after young emerged.

Thirteen-lined ground squirrels were observed at two locations at the Billard Airport in Topeka, Kansas, USA (39°04'N, 95°37'W, elevation 280 m), from June through early August 1982 by L.S. Rayor. Both sites were on grassy lawns mowed weekly. Only three litters were observed sufficiently for analysis, limiting the conclusions which can be made about this species. Mother 1031 and six young lived on a 0.94-ha lawn. Mothers 1033 and 1007 with eight and six offspring,

respectively, lived on a 0.65-ha strip of lawn. Mother 1033 was killed on the 2nd day after the young emerged. Both areas were partitioned into 15.2 by 15.2 m grids.

Behavioral and space-use data for the yellow-bellied marmot from four colonies in the East River Valley, Colorado (see ARMITAGE 1974, 1986 for description of study sites, field methods, and marmot biology) were collected by K.B. Armitage from 1972-1989 as part of a long-term study of factors affecting lifetime reproductive success of males and females of this species.

Grid sizes were chosen to reflect the ability of the observer to determine location precisely in each habitat, or to use the grid system already in place (Dyson Creek). The overlap method used for analysis was determined post hoc. As a result of using different grid sizes, space-use patterns were not compared between species.

All study animals were permanently marked with numbered fingerling fish tags inserted in both ears. Brightly colored flagging or discs were attached to the tags in *S. columbianus* and *S. tridecemlineatus*. Additionally, unique marks for visual identification were painted on each animal with non-toxic fur dye. Maternity was determined by trapping each litter on emergence from its natal burrow.

Above-ground actions of prairie dogs were observed with a spotting scope from a 8-m tower-blind at QC for 260 hr and from a car or rock outcrop at BM for 150 hr after young emerged. Columbian ground squirrels were observed for 100 hr from a 2-m tower, and thirteen-lined ground squirrels were observed for 51 hr from a car. Marmots were observed for more than 300 hr each year. Observations were concentrated during the morning and late afternoon when the animals were most active. Grid locations of visible animals were recorded at 15 min intervals throughout observation periods. Behavioral interactions were observed using ad libitum and focal sampling techniques (ALTMANN 1974).

Behavioral analysis

For each behavioral interaction, the identities of the initiator and recipient, date, and grid location were recorded. Behaviors were later grouped into the general categories of amicable, cohesive interactions [greetings involving naso-oral contact or a brief interlocking of incisors known as «kissing» (KING 1955), play, allogroom] or of agonistic interactions (chase, fight, attack). Play was defined as vigorous, apparently purposeless motor activity, in which motor patterns from other contexts were used in modified forms and altered temporal sequences (from BEKOFF & BYERS 1981). Social play with other individual(s) was typically initiated by a mouth-spar (NOWICKI & ARMITAGE 1979, JAMIESON & ARMITAGE 1987) and characterized by frequent role-reversals and rough-and-tumble behaviors. Behavior was analyzed between young and all animals with whom the young could interact, including their mother, littermates, non-littermate young, yearlings, and other adults. Because interactions of young prairie dogs with non-harem members were infrequent, agonistic, and resemble those of adults with non-harem members (RAYOR 1988), only behavioral interactions that occurred between members of the same harem are included.

To determine whether amicable or agonistic behavioral interactions occurred randomly among all age-sex classes, a chi-square analysis (calculated from equation 7 of ALTMANN & ALTMANN 1977, see RAYOR 1987) was used to generate the expected rate of interactions for each dyad adjusted for the group (population, harem, or litter) composition and the hours of observation of individuals within the dyad. Large differences between observed and expected rates of interaction produce large «chi-square components» that indicate a non-random distribution of interactions, implying that members of the dyad interacted much more or less than expected relative to their numbers in the group. The «chi-square components» are summed for all dyads and the total tested against the chi-square distribution. Large «chi-square components» that contributed over 10% of the total chi-square value were considered to be biologically significant. The advantage of this analysis is that it takes into account (1) the demography of the social environment and (2) changes in that demography (e.g., loss of individuals from predation or dispersal). For example, for a litter with five young males and one young female, if the mother responded to her offspring according to their frequency in the litter, mother-son interactions should outnumber mother-daughter interactions without indicating any maternal preference for sons over daughters. When necessary information about the participants of an interaction was unknown (e.g. the sex of an offspring interacting with its mother), it was

omitted from the appropriate analysis. As a result, observation numbers for a given dyad may differ between tables.

The age-sex classes that young yellow-bellied marmots interacted with were calculated for litters from three sites. No chi-square analysis was done on the behavioral data for marmots.

Space-use overlap

For *Cynomys gunnisoni*, *Spermophilus columbianus*, and *S. tridecemlineatus* home-range size was calculated as the area of the grid squares in which an individual was observed at least once. This method should tend to underestimate total home range size compared to other methods because grids where the individuals were not observed were not counted, even if the «unoccupied» grid was surrounded by «occupied» grids. Sexual differences in home range size were tested by the 2-tailed Mann-Whitney U test. The index of space-use overlap (OOSTING 1956: 77-78) was calculated as a weighted average of the percentage of each animal's domain shared by another individual, taking into account the frequency of occurrence in shared areas. Because space-use includes the frequency with which an area is used, it most accurately reflects differential use in overlapping areas. Within litters, space-use overlap of male and female young was compared individually with all other littermates and with their mother for each period. Within-litter overlap comparisons were standardized using each litter's emergence date as day 1. For comparisons of overlap between litters, spatial data for entire litters were lumped for each period. Because litters emerged at different times, overlap between litters was compared for the same dates rather than for the number of days post-emergence. By so doing, the contemporaneous spatial behavior of members of different litters could be compared. Space-use data for the mothers were analyzed separately from those of their young. Differences between maternal overlap with sons and daughters were tested by 1-tailed Mann-Whitney U for each period. The indices of space-use overlap between sibling dyads within the litter were analyzed by Kruskal-Wallis tests for each period. Space-use overlap for *Marmota flaviventris* was calculated identically, but because the time periods calculated were not the same, direct comparisons with the other species were not made. Dispersal was defined as permanently leaving the natal home range or, for prairie dogs, the natal harem (HOLEKAMP 1984).

RESULTS

Behavioral interactions within the litter

Young Gunnison's prairie dogs interacted frequently and amicably with their mothers and all other members of their harem during their first summer (Fig. 1). Mothers and other harem members tolerated play nearby and the persistent attempts of young to initiate interactions. Amicable interactions between mother and offspring included frequent «kiss» greetings (KING 1955), occasional allogrooming, and mother-young play. Nuzzling and nursing attempts by the young occurred frequently but were excluded from the analysis because the mothers were recipients of, but not participants in the interaction. The relatively infrequent agonistic interactions with the mother were primarily in response to persistent nursing or play attempts by the young.

Young yellow-bellied marmots interacted only amicably with their mothers and other members of the maternal matriline (Fig. 1). The young initiate interactions with the mother. Mother-offspring amicable interactions include solicitation greetings, allogrooming, and naso-oral contact. The adult members of a matriline and all the young may behave as one social group. For example, in 2 years at Marmot Meadow colony, litters were intermingled in the burrow system prior to emergence. All of the social interactions ($n = 39$) of the young with adults and yearlings were amicable; 25

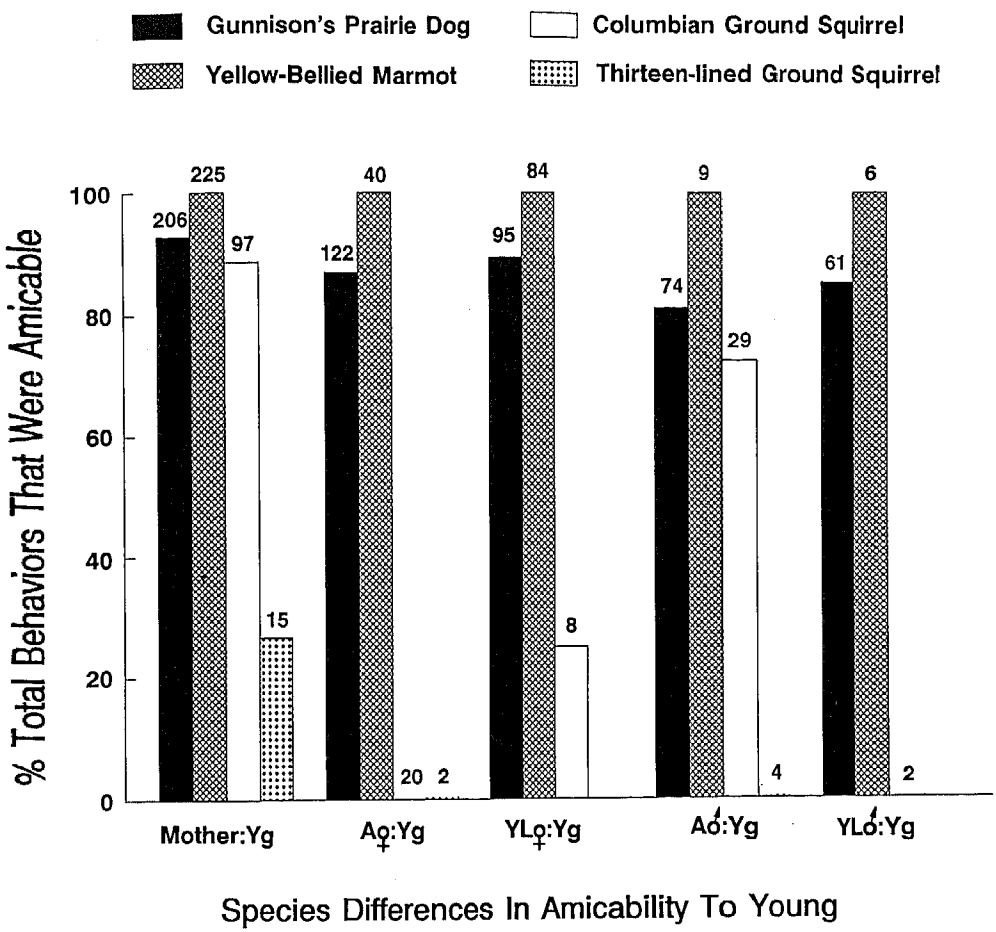

Fig. 1. — Percentage of behavior with young (Yg) that is amicable within each dyad for all three species. Total interactions in each dyad are shown above each column. A♀ = adult females other than the mother; YL = yearling; A♂ = all males including the father. Yearling thirteen-lined ground squirrels were considered to be adults. Marmot data from Picnic Colony 1975-1988.

occurred with the three maternal females, 11 occurred with yearling females, and two were with a yearling male. There was no evidence that the adult females discriminated among young (ARMITAGE 1986). Of 66 social interactions among young, 53 were amicable greetings and 13 were play. Agonistic interactions among littermates or burrowmates have never been observed (ARMITAGE 1982).

Columbian ground squirrel young interacted amicably with their mother (Fig. 1) and littermates. Although young initiated interactions with their mothers, young were not as persistent as prairie dog young. Mother-offspring amicable interactions included nose-to-nose and mouth-to-nose greetings (STEINER 1975), occasional «kissing», allogrooming, and nuzzling and nursing attempts. Agonistic interactions between mother and young were infrequent.

Table 1.

Distribution of amicable behavioral interactions of young (Yg) Gunnison's prairie dogs with their mothers, littermates (LM), non-littermate young (NLM), non-mother adults (A) and yearlings (Yl) of each sex. E = Expected; O = Observed. Components of the chi-square for a given dyad that contributed a large portion of the total chi-square (*) were considered biologically significant. The first five females were members of Ridge harem; East harem contained two intermingled litters. There were no yearlings in the Aster harem. In Aster, young interacted with the presumed father (^{F}) and a visiting adult male (^{V}).

	Mother 807		Mother 905		Mother 813		Mother 843		Mother 915		East		Aster	
	E	O	E	O	E	O	E	O	E	O	E	O	E	O
Mother:Yg	4.0	34*	2.6	31*	2.7	34*	2.6	16*	2.5	25*	24.0	43*	6.6	8
LM	27.2	56*	5.2	14*	9.9	18	8.9	20*	14.8	33*	120.4	110	32.9	34
NLM	149.9	65*	61.9	29*	94.0	41*	101.8	57*	79.3	46*	—	—	—	—
A♀:Yg	15.6	24	5.7	2	8.2	11	7.7	14	5.1	4	25.5	34	14.6	17
Yl♀:Yg	19.7	43*	5.7	9	13.1	14	10.7	13	10.4	6	—	—	—	—
A♂:Yg	14.4	4	5.2	0	7.5	7	4.1	17	3.4	4	25.5	11*	^{F}7.3	13*
Yl♂:Yg	5.3	10	1.4	3	3.6	14*	3.1	2	2.5	0	25.5	23	^{V}14.6	4*
χ^2	350		351		426		150		246		27.1		12.9	
P	<0.005		<0.005		<0.005		<0.005		<0.005		<0.005		<0.025	

The three thirteen-lined ground squirrel mothers appeared to avoid their offspring actively and rebuffed attempts of the young to initiate interactions. Only four of the 15 mother-offspring interactions observed were amicable (Fig. 1, Table 3).

The social environment of young in a species that aggregates extends beyond their mother and littermates to encompass other adults, yearlings, and young in the vicinity. However, among young prairie dogs and Columbian ground squirrels amicable interactions occurred significantly more than expected with their mothers and with littermates than with other dyads (Tables 1, 2). Thirteen-lined ground squirrels interacted more than expected with littermates, but not with their mother or other adults (Table 3). Young yellow-bellied marmots interacted only amicably with their mothers and other members of the matriline.

A bias toward more frequent interactions among littermates and with the mother may be due to the greater proximity of these individuals, permitting more opportunities to interact. To determine whether behavioral patterns within the litter were nonrandom, amicable interactions that occurred between mothers and offspring and among littermates were extracted from the total interactions of the young with all animals and reanalyzed. In six of seven prairie dog litters, mothers interacted amicably more frequently than expected with their offspring (all significant $\chi^2 \geq 12.8$, $df = 1$, $P < 0.005$). In other words, young interacted more with their mother than with littermates. In contrast, mothers in all six Columbian ground squirrel litters interacted amicably consistently less often than expected ($\chi^2 \geq 6.2$, $P < 0.025$), as did one of three thirteen-lined ground squirrel mothers ($\chi^2 = 10.8$, $P < 0.005$). In the other two thirteen-lined litters the rate of amicable interactions of the mother with her offspring did not differ from that expected.

Table 2.
Amicable behavioral interactions of young Columbian ground squirrels with all animals with whom the young could interact. See Table 1 for key to details.

	Mother 8115		Mother 4792		Mother 4767		Mother 4953		Mother 4795		Mother 4784	
	E	O	E	O	E	O	E	O	E	O	E	O
Mother:Yg	3.7	39*	3.3	13*	0.5	10*	4.2	13*	2.2	4*	1.6	3*
LM	7.4	80*	6.7	55*	2.0	20*	6.2	63*	3.8	34*	3.2	25*
NLM	81.7	9*	56.8	19*	25.6	9*	98.6	45*	27.7	8*	22.7	6*
A♀:Yg	16.4	0*	11.8	0*	5.0	0	12.5	0*	4.3	1	4.8	0
Yl♀:Yg	7.3	1	6.7	1	2.4	0	8.3	0	4.4	0	—	—
A♂:Yg	7.3	1	6.7	4	2.4	0	5.0	16*	4.4	2	1.6	0
Yl♂:Yg	6.1	0	—	—	1.0	0	4.2	2	2.2	0	—	—
χ^2	1148		420		363		614		266		168	
P	<0.005		<0.005		<0.005		<0.005		<0.005		<0.005	

Table 3.
Distribution of amicable and agonistic interactions of young thirteen-lined ground squirrels with their mothers and other adults. When interactions were too infrequent to analyze, only the observed values are recorded. Mother 1033 was killed on the young's 2nd day above ground. See Table 1 for details.

	Mother 1033				Mother 1031				Mother 1007	
	Amicable		Agonistic		Amicable		Agonistic		Amicable	Agonistic
	E	O	E	O	E	O	E	O	O	O
Mother:Yg	3.3	2	0.7	0	5.3	2	2.1	7*	0	4
LM	34.2	55*	7.8	9	13.3	38*	5.4	1	7	4
A♀	9.7	0	2.2	0	10.7	0	2.1	3	0	1
A♂	9.7	0	2.2	4	10.7	0	4.3	3	—	—
χ^2	32.7		4.6		69.1		15.3			
P	<0.001		>0.1		<0.001		<0.001			

Intralitter interactions also were analyzed to examine differences in maternal interactions with sons versus daughters and among sibling dyads (Tables 4-6). In five of six litters, prairie dog mothers interacted with their offspring of each sex relative to their proportion in her litter (Table 4). In the sixth, young males were more interactive with their mother than expected. Columbian ground squirrel mothers interacted more with daughters in two litters, but no sexual preference was apparent in the other three litters (Table 5). In the thirteen-lined ground squirrels (Table 6) maternal interactions with offspring were observed too infrequently for preferences for either sex to be apparent.

Table 4.

The distribution of amicable behavioral interactions between sons and daughters and among sibling dyads in Gunnison's prairie dog litters. Symbols represent young sons (♂) or daughters (♀). See Table 1 for details.

	Mother 807		Mother 905		Mother 813		Mother 844		Mother 915		East	
Dyad	E	O	E	O	E	O	E	O	E	O	E	O
Mother:♂	8.3	8	11.6	11	6.5	4	2.3	6*	14.9	17	30.6	25
Mother:♀	6.7	7	17.4	18	16.5	19	4.7	1*	7.1	5	12.4	18
χ^2	0.03		0.05		1.3		8.7		0.9		3.5	
P	>0.5		>0.5		>0.1		<0.005		>0.1		>0.05	
♂:♂	13.0	18	1.4	1	1.2	1	0.84	1	13.4	16	45.7	42
♂:♀	26.6	20	8.4	9	8.8	7	5.8	6	17.5	15	44.0	45
♀:♀	8.4	10	4.2	4	7.9	10	9.3	9	2.1	2	6.2	9
χ^2	3.8		0.16		0.94		0.07		0.86		1.6	
P	>0.1		>0.9		>0.5		>0.9		>0.5		>0.1	

Table 5.

Distribution of amicable behavioral interactions between sons and daughters and among sibling dyads in Columbian ground squirrel litters. See Table 1 for further details.

	Mother 8115		Mother 4792		Mother 4767		Mother 4795		Mother 4784	
Dyad	E	O	E	O	E	O	E	O	E	O
Mother:♂	25.8	15*	10.4	6	6.0	7	2.2	2	1.8	2
Mother:♀	17.2	28*	2.6	7*	4.0	3	1.8	2	2.2	1
χ^2	11.3		9.3		0.42		0.04		0.67	
P	<0.005		<0.005		>0.5		>0.97		>0.5	
♂:♂	24.3	37*	33.0	33	8.0	12	3.4	8*	4.7	1
♂:♀	48.6	38	22.0	22	11.0	8	8.8	4	4.7	7
♀:♀	8.1	6	—	—	1.0	0	1.8	2	1.6	3
χ^2	9.4		0		3.8		8.8		5.2	
P	<0.025		<0.99		>0.1		<0.025		>0.05	

Prairie dog young did not interact selectively with brothers or sisters (Table 4). In two Columbian and two thirteen-lined ground squirrel litters, male-male dyads interacted (primarily play) more than expected (Tables 5, 6). No sexual differences in the infrequent agonistic behavior were observed among young in the four species. Agonistic interactions within litters were infrequent in all four species and insufficient for statistical analysis.

Table 6.
Distribution of amicable and agonistic interactions between sons and daughters and among sibling dyads within thirteen-lined ground squirrel litters. See Tables 1 and 3 for more information.

	Mother 1033				Mother 1031				Mother 1007	
	Amicable		Agonistic		Amicable		Agonistic		Amicable	Agonistic
	E	O	E	O	E	O	E	O	O	O
Mother:♂	—	1	—	—	—	1	3.5	4	0	1
Mother:♀	—	1	—	—	—	1	3.5	3	0	3
χ^2								0.1		
P								>0.5		
♂:♂	17.1	30*	3.2	2	4.8	13*	—	0	0	0
♂:♀	25.7	15*	4.8	5	14.4	11	—	0	0	0
♀:♀	5.1	3	1.0	2	4.8	0*	—	0	1	1
χ^2	15.0		1.5		19.6					
P	<0.005		>0.1		<0.005					

Behavioral interactions outside the litter

Prairie dog and Columbian ground squirrel young interacted amicably less often than expected with non-littermate young (Tables 1, 2). However, of the amicable interactions that occurred among all young prairie dogs, 64.6±8.4% (n=379) involved non-littermate young, whereas significantly fewer (21.1±10.2%, n=397) of the Columbian ground squirrel amicable interactions involved non-littermates (Mann-Whitney, $P<0.01$). The percentage of all young-young agonistic interactions that were with non-littermates (68.8±14.9%, n=47 prairie dogs; 81.4±22.2%, n=24 Columbians) did not differ between species (Mann-Whitney, $P>0.2$). None of the thirteen-lined ground squirrel litters in this study overlapped in space.

The relationship between non-mother adult and yearling behavior with young was strikingly different among species. More than 85% of the interactions between young and non-mother prairie dog adults and yearlings were amicable (Fig. 1). However, adult female and yearling Columbian ground squirrels were primarily agonistic toward non-offspring (Fig. 1). Only adult male Columbians were amicable toward young. The source of agonistic interactions with young also differed between the species. Aggression toward prairie dog young was primarily in response to the young persistently bothering the adults or attempting to suckle (including mothers other than their own, non-lactating females, or adult males). Among Columbians, the adults typically initiated aggression when young approached too closely. Although encounters were infrequent, thirteen-lined ground squirrel non-mother adult females and males were only agonistic toward young (Fig. 1).

The role of adult males in Gunnison's prairie dog and Columbian ground squirrel societies differs markedly in interactions with the young. Some Gunnison's prairie dog males both responded to and initiated amicable interactions with the young. The

significance of presumed paternity and shared space on adult male prairie dog behavior was illustrated in the «Aster» harem at Blue Mesa in 1980 (Table 1). An adult male from a neighboring harem was tolerated in Aster's territory by the resident adults (atypical adult behavior, RAYOR 1988). Young from the Aster litter approached both males and attempted to initiate kisses and play with each. The resident, presumed father, kissed and initiated gentle play (N = 4 bouts) with the young (Table 1) and he permitted youngsters to play over and around him as he foraged and was observed to seek out contact with his offspring. In contrast, the visiting adult male snapped at and attacked youngsters who attempted to initiate interactions with him (Table 1). Adult male Columbian ground squirrels responded amicably to greetings from the young, but mostly ignored them or initiated sexual behavior.

Adult and yearling Gunnison's prairie dogs played with the young at both study sites in all years of the study. To the best of our knowledge, no other adult ground squirrel was reported to play regularly with young. Play between young and older animals involved play solicitation, gentle wrestling, pouncing, rearing, and other typical elements of young-young play (STEINER 1971). Adults also reared up on their hind feet, walked several steps, and slowly pounced on the young. The two yearling mothers played in 24.0 ± 2.8% of the amicable interactions with their offspring; the seven adult mothers played in 7.0 ± 2.8% of the interactions. Of the total amicable interactions with young for each age-sex group, adult females other than the mother played in 7.5% (play bouts N = 8) of their interactions; adult males 8.3% (N = 5); yearling females 28% (non-reproductive N = 17, reproductive N = 7); and yearling males 5.8% (N = 3).

Spatial patterns

Intralitter

Use of space by young of the four species was similar at weaning, but diverged as the young matured. Young from newly-emerged litters remained together in a tight group for the first several days but gradually they began to forage independently and progressively farther from the natal burrow. Home-range sizes of the young peaked in week 2 for thirteen-lined, and in weeks 3-4 for Columbian ground squirrels, and in weeks 5-6 for prairie dogs (Table 7). The prairie dog colony at QC (used exclusively for the space-use analysis) was composed of discrete, defended harem territories that were separated from an irrigated field by a large ditch (see RAYOR 1985, 1988). Members of all harems foraged in the irrigated field. As young prairie dogs matured and were able to jump or swim across the ditch, they foraged increasingly in the field. Young prairie dogs rapidly used their entire harem territory, but because positions were not recorded in the irrigated field, the home range measure does not accurately reflect the expanding space-use of the young prairie dogs. Home range sizes did not differ between sexes for any period for any of the species (Table 7).

Mean space-use overlap decreased between Columbian and thirteen-lined ground squirrel mothers and their offspring over the course of the summer (from 63.7 ± 2.9 to 36.2 ± 4.9% by week 5, 6; 36.4 ± 5.5 to 12.0% with daughters and 0% with sons by week 3, respectively), but there was little overall decrease among the prairie dogs (52.3 ± 2.5 to 50.2 ± 3.0% by week 5, 6). Although young prairie dogs foraged over an ever larger range as the summer progressed, surviving mothers and most young continued to sleep in the natal burrow, thereby maintaining high spatial overlap. Only

Table 7.

Home range size (m^2) of young for three of the species during each time period after emergence from the natal burrows ($\bar{x} \pm SD$). Weeks 1 and 2 were combined for the prairie dogs, indicated by *. Home range sizes differed only between sexes in thirteen-lined ground squirrels during week 2 by the Mann-Whitney U test.

	Prairie dogs		Columbian		Thirteen-lined	
	Male	Female	Male	Female	Male	Female
Week 1:						
Home range			382.3 ± 209.8	420.0 ± 220.1	533.6 ± 156.6	515.5 ± 154.7
N young			17	10	10	9
Observ./yg			13.7 ± 7.7	16.9 ± 7.9	28.5 ± 13.3	23.0 ± 15.1
Week 2:						
Home range	235.6 ± 74.4*	246.0 ± 82.4*	313.3 ± 91.5	333.3 ± 86.6	951.2 ± 277.7	773.3 ± 284.1
N young	11	12	15	9	10	9
Observ./yg	11.8 ± 4.3	12.8 ± 3.7	6.5 ± 2.0	7.0 ± 2.1	26.4 ± 12.6	18.5 ± 4.6
Weeks 3,4:						
Home range	317.4 ± 95.0	298.3 ± 89.8	627.3 ± 261.1	566.7 ± 377.7	762.3 ± 258.1	894.8 ± 411.3
N young	11	14	11	6	7	7
Observ./yg	12.8 ± 3.9	13.9 ± 4.0	12.8 ± 6.0	11.3 ± 6.1	13.8 ± 6.8	11.3 ± 5.8
Weeks 5,6:						
Home range	330.0 ± 117.0	313.7 ± 131.0	571.4 ± 205.4	560.0 ± 219.1		
N young	12	7	14	5		
Observ./yg	14.2 ± 3.7	13.8 ± 4.6	9.2 ± 3.3	8.8 ± 3.5		
Weeks 7,8:						
Home range	226.3 ± 92.3	262.3 ± 79.7				
N young	7	7				
Observ./yg	12.6 ± 3.6	12.4 ± 4.2				
Weeks 9-11:						
Home range	261.0 ± 79.8	259.2 ± 58.3				
N young	4	10				
Observ./yg	13.5 ± 4.1	12.5 ± 3.3				

two young females (of 217 young from 41 litters studied) were known to emigrate from their natal harem. No Columbian ground squirrel young dispersed, but as both mothers and offspring increased their range and many young began to sleep apart from their mothers, space-use overlap decreased. In the two thirteen-lined ground squirrel litters with extant mothers, one mother moved away from the natal burrow 10 days after the young emerged; in the second litter five of six young dispersed or disappeared by 3 weeks post-emergence. Overall, seven of 19 thirteen-lined ground squirrel young disappeared from their natal area by 3 weeks post-emergence.

Space-use by young yellow-bellied marmots was similar to that of the prairie dogs in that young and mothers continue to use the same home burrow throughout the summer. For three colonies of marmots, space-use overlap between mothers and young averaged 47.2% (N = 75 young) for the 6 weeks post-emergence. The overlap

of adult females with unrelated young, calculated only for those situations in which an unrelated female lived near enough so that space-use overlap could occur, averaged 6.5% (N = 38). For each of the three colonies, the range of space-use overlap values for mother-young did not overlap that for unrelated-adult-female with young.

In ground-dwelling squirrel species with moderate to low sociality, young males disperse farther from the natal area than young females and are almost never recruited into the natal social group (e.g., SCHMUTZ et al. 1979, HOLEKAMP 1984). In species with higher sociality, including Gunnison's prairie dogs, Columbian ground squirrels, and yellow-bellied marmots, males do not disperse until the yearling summer (ARMITAGE 1974, FESTA-BIANCHET & KING 1984, HOLEKAMP 1984, RAYOR 1985, this study). Therefore, differences in maternal spatial overlap with young sons and daughters would be expected to be more pronounced in less social species. However, in the more social species, there might be early evidence of greater maternal spatial overlap with young daughters. In the two thirteen-lined ground squirrel litters with surviving mothers, only one of seven young females and none of the five males remained near their mother by the 3 week. No sexual difference in mother-offspring space-use overlap could be detected for any period during the study for prairie dogs or Columbian ground squirrels (all Mann-Whitney $P > 0.05$). For yellow-bellied marmots, the mean space-use overlap for mothers with sons (35.7%, N = 71) was significantly less than that for mothers with daughters (40.1%, N = 69) (Mann-Whitney $P = 0.025$). There were no differences in spatial overlap among dyads of male-male, male-female, and female-female young during any period for the prairie dogs or ground squirrels (Kruskal-Wallis, all $H > 3.0$, $P > 0.05$), except for prairie dogs during weeks 5-6 ($H = 6.34$, $P < 0.05$) when male-female overlap was low and for Columbian ground squirrels during week 1 ($H = 6.9$, $P < 0.05$) when male-female overlap was low and female-female overlap was high.

Percent space-use overlap among littermates decreased rapidly in thirteen-lined ground squirrels [88.9 ± 18.9 ($\bar{x} \pm$ SE) week 1, 60.1 ± 27.0 week 2, 58.2 ± 32.3 week 3, and 30.4 ± 32.4 week 4], but more slowly among prairie dog and Columbian littermates (Table 8).

Interlitter

Litters of Gunnison's prairie dogs within a harem mingled more quickly and overlapped more with other litters than did Columbian ground squirrel litters (Table 8). Only during the first 2 weeks after emergence did prairie dog littermates overlap significantly more with each other than they did with non-littermates; thereafter, overlap between littermates and non-littermates in the same harem could not be distinguished (Table 8). However, Columbian ground squirrel littermates overlapped significantly more with each other than with non-littermates until 5 or 6 weeks after emergence (Table 8).

Rates of litters mingling can not be attributed solely to differences in the spacing of burrows or to differences in grid size (6 × 6 m for prairie dogs; 10 × 10 m for Columbian ground squirrels). The average distances between natal burrows of the litters used in the space-use analysis was not significantly different (prairie dogs 23.2 ± 10.4 m, n = 10; Columbians 22.6 ± 11.6 m, n = 21; Mann-Whitney). Given equivalent distances between natal burrows, when grid sizes are larger, individuals are anticipated to overlap more with one another because it is more likely that an

Table 8.

Space-use overlap (mean ± SD) between littermates (LM) and non-littermate (NLM) young within a species over the summer. Means were calculated from the mean for each litter and SD from the difference between litter means, not individual overlap scores. The probability that space-use overlap between littermate and non-littermate young within a species did not differ was tested by the Mann-Whitney U test for each period (* significant value). Prairie dog position were combined for weeks 1 and 2.

	Prairie dog			Columbian		
	LM	NLM	*P*	LM	NLM	*P*
Week						
1	60.1 ± 10.4	17.0 ± 7.4	0.002*	73.5 ± 10.7	3.2 ± 5.5	0.003*
2				61.1 ± 14.3	15.8 ± 17.1	0.001*
3, 4	32.9 ± 5.7	40.4 ± 16.4	0.426	51.3 ± 15.8	14.9 ± 15.8	0.003*
5, 6	40.3 ± 9.9	32.6 ± 21.0	0.426	33.5 ± 12.3	22.9 ± 15.9	0.129
7, 8	40.2 ± 17.7	18.3 ± 12.1	0.052			
9-11	30.7 ± 14.8	17.9 ± 16.1	0.230			

individual will enter the larger area. Contrary to expectations, prairie dogs showed greater overlap than Columbians, indicating that more extensive prairie dog overlap is a real phenomenon. However, the area which encompassed the burrows of focal litters was somewhat larger for Columbian ground squirrels (1,800 m²) than prairie dogs (1,080 m²).

The degree of space-use overlap (calculated for the entire season) varied considerably for yellow-bellied marmot young from different litters within a matrilineal group. In three colonies, River in 1986 and 1987, Marmot Meadow in 1980 and 1981, and Picnic in 1976, 1978, and 1989, two or more litters either occupied the same burrow at weaning or intermingled so quickly at emergence from the natal burrow that maternity could not be assigned and no pattern in space-use overlap could be detected that permitted the assignment of young to litters. In other words, all the young behaved as one social group. At River in 1985, four litters intermingled soon after litter identity was known. The mean space-use overlap of littermates did not differ significantly from that of non-littermates (Mann-Whitney, $P=0.13$). However, when the data were reanalyzed with space-use calculated for each individual marmot rather than with the mean for the litter, the space-use overlap of two litters was significantly higher for littermates than their overlap with each of three groups of non-littermates (Mann-Whitney varied from 0.00003 to 0.03). The space-use overlap among members of the other two litters did not differ between littermates and non-littermates (Mann-Whitney $P=0.33$). Two litters at River in 1988 also varied in patterns of space-use; members of one litter overlapped more with littermates (41.7%) than with non-littermates (31.7%) (Mann-Whitney $P=0.0007$) whereas members of the other litter overlapped equally with littermates (37.3%) and non-littermates (31.7%) (Mann-Whitney $P=0.2$). At Picnic in 1989, six litters were produced in one matrilineal group consisting of a mother and her five adult daughters. The mother, her 4-year old daughter and a 2-year-old daughter had their litters in a common burrow system and young nursed more than one female (K.B. ARMITAGE & G. GURRI-GLASS, unpub-

lished data). Two 3-year old sisters shared a common burrow system with their litters and a 2-year old had her litter in a burrow distinct from her mother and sisters. Each of the two combined litters was treated as a single unit. Space-use overlap among young of the two 3-year old sisters averaged 50.5% and was significantly greater than the overlap with the young of the three-litter burrow ($\bar{x} = 5.7\%$) or with young from the single-female burrow ($\bar{x} = 1.2\%$) (Mann-Whitney $P < 0.00003$). Likewise, the space-use overlap among the young of the three-litter burrowmates and among the young of the single-female litter was greater than the space-use overlap of young between the two groups (Mann-Whitney $P = 0.025$).

Burrows of two of the thirteen-lined litters were 30 m apart, but no spatial overlap was observed.

DISCUSSION

Mother-offspring relationships vary with adult sociality; little amicable behavior characterizes those relationships in the asocial thirteen-lined ground squirrel whereas predominantly amicable behavior characterizes mother-offspring relationships in the three more social species. The major difference among the social species is in the relationships among non-littermate young and between young and females other than their mother. In the most social of those species, Gunnison's prairie dog, amicable behavior between young and other members of the population and the intermingling of young from different litters occurs to a greater extent than in the other two social species. If social tolerance by and prolonged extensive spatial overlap of young with parents are fair measures of reproductive investment in immature offspring that may increase offspring survival (ARMITAGE 1981, WASER & JONES 1983), then young of more social species receive greater parental investment than those of less social species.

In Gunnison's prairie dogs frequent amicable interactions and prolonged maternal tolerance appear to reinforce the mother-offspring bond. Young prairie dogs are socially integrated into the dynamics of harem life. Play, which serves a strong cohesive, socially bonding function in mammals (BEKOFF 1978), occurs not only among young, but also among harem adults and young. Spatial overlap is sustained between mother and young, and because the harem territory is used in common, members of different litters within the harem mingle extensively. The amicable characteristics of interactions of young with their mothers and other harem-members resemble those of adult intraharem social interactions (RAYOR 1988).

Columbian ground squirrels are quite social relative to other members of the genus *Spermophilus* (ARMITAGE 1981, MICHENER 1983). However, in comparison to the Gunnison's prairie dog; mothers and offspring were less interactive; other adults and yearlings were intolerant of young; interlitter interactions were agonistic; and spatial overlap between litters increased more slowly. Cohesive behavior and, perhaps most importantly, tolerance of the young occurred only with mothers and adult males, which have a high probability of being the father of many of the young living near him (MURIE & HARRIS 1978). Thus, non-reproductive young are able to remain in the maternal home range with minimal conflict with their parents. However, because this tolerance is not exhibited by neighboring non-mother adults and non-littermates, the development of more complex sociality is constrained.

Yellow-bellied marmots were classified as less social than Gunnison's prairie dog

and more social than the Columbian ground squirrel (ARMITAGE 1981, MICHENER 1983, RAYOR 1988). The space-use patterns and social behavior of the young are consistent with this classification. Thus, young marmots were amicable with all adult females in the matrilines and interlitter social behavior was amicable with all young produced in the same matriline. However, intermingling of litters did not occur to the same extent in marmots as in the prairie dogs and play rarely occurred between young and adults (NOWICKI & ARMITAGE 1979).

Thirteen-lined ground squirrels are largely asocial; limited observations suggest that above ground mother-offspring interactions were almost non-existent and little social cohesion or tolerance occurred between mother and young. Because the mothers avoided the young and many young disappeared by their 3 week above ground, spatial overlap was minimal and decreased rapidly as the young matured. Littermates interacted cohesively and remained in association for a longer period than mother and young, but even those associations began to dissolve by 3 weeks post-emergence.

The trends found in this study generally concur with less detailed observations from other ground-dwelling squirrel species. Interactions of asocial or low social young with non-littermates and non-mothers differ markedly from those in the social species. In the asocial golden-mantled ground squirrel, *Spermophilus lateralis*, maternal interactions with young were agonistic or neutral, whereas all interactions with non-offspring were agonistic (FERRON 1985). Interactions within the litter prior to dispersal were primarily cohesive, but agonistic with non-littermates and other age-sex classes. Young Wyoming ground squirrels, *S. elegans* (MICHENER 1983 class 2) show similar patterns, but interactions with the mother are more amicable in the month between emergence and dispersal (PFEIFER 1980). Young Richardson's ground squirrels, *S. richardsoni* (MICHENER 1983 class 2) exhibit frequent amicable interactions among family members, but are agonistic with other conspecifics (MICHENER 1981). For the first 4 weeks post-emergence the average distance between littermates increased, indicating decreasing space-use overlap, and dispersal occurred by 9-10 weeks.

Young Gunnison's prairie dogs were more interactive in this study (RAYOR 1985, 1988), than in other studies of this species. FITZGERALD & LECHLEITNER (1974), who reported that adult Gunnison's prairie dogs have low sociality, found that «Pups were never observed attempting to play with adult males, and greeting behaviors between adult males and pups were uncommon... Few attempts at care-soliciting or play were initiated between young and the adult females, and no pups were observed attempting to nurse». In contrast, in both populations in this study interactions of the young with both adult males and females were frequent and amicable. Nuzzling and attempts to suckle the mother persisted for at least 4 weeks post-emergence. Above-ground nursing was observed 15 times, the last occurring approximately 2 weeks after emergence. Additionally, groups of young occasionally mobbed mothers and attempted to nurse. Mothers usually responded by snapping at or running away from the young. However, two sons of a three-legged female repeatedly chased and knocked her down, then sought her nipples. FITZGERALD & LECHLEITNER's (1974) population was in the midst of a plague outbreak and social interactions may have been severely disrupted. Our observations of young Gunnison's prairie dog behavior and interactions with non-mother adults in the harem most closely resemble those reported for young black-tailed prairie dogs, *C. ludovicianus* (KING 1955).

Sex differences between offspring in behavior, maternal association, and movement patterns occur in many ground-dwelling squirrel species (e.g., MICHENER 1981, HOLEKAMP 1984, VESTAL & MCCARLEY 1984). However, of the traits evaluated in this study, the only consistent sexual difference among young was that Columbian and thirteen-lined brothers interacted amicably (played) more than sisters or brother-sister dyads. No sex differences in behavioral interactions with mothers were observed during the first summer. Although space-use overlap was greater between yellow-bellied marmot mothers and daughters than between mothers and sons, there is no evident biological significance for this statistical significance. If sons are avoiding their mothers and daughters are not, then brother-sister space-use overlap should be significantly less than overlap between sisters, which it is not. The lack of conspicuous sex differences in Columbian young contrasts with WATERMAN's (1986) results. In her population young males played less frequently than did females, and females interacted more often with their mother. Differences in our results are probably due to the variables measured and the method of analysis.

Why were sex differences not observed in this study? Young Gunnison's prairie dogs, Columbian ground squirrels, and yellow-bellied marmots remain near the mother and do not disperse until at least their yearling summer (FESTA-BIANCHET & KING 1984, RAYOR 1985, ARMITAGE 1986). Because the mother gains direct fitness from both sons and daughters, it is to her advantage to increase the probability that all of her offspring survive to reproductive age. Similarly, young of both sexes may benefit from maintaining maternal association and remaining in the territory. The lack of sex differences in behavioral interactions between siblings may indicate that divergence in behavior develops later in social species.

Some yearling females reproduced in or near their natal area in one prairie dog population (2/5 yearling females at QC, 0/15 at BM), and the Columbian ground squirrel site (4/12 yearling females in 1983). Early reproduction was probably due to the unusually high quality of both habitats (FESTA-BIANCHET 1981, RAYOR 1985). RAYOR (1988) did not find differences in social behavior between populations with and without yearling females breeding. RAYOR predicted that high sociality, including the benefits of increased tolerance and spatial overlap of adults with young, would not decrease unless the typical age of sexual maturity decreased and reproductive competition with parents outweighed the benefits of cooperation. The small number of yearling mothers were presumed not to affect patterns of interaction. Data from litters of both yearling prairie dog mothers, and space-use data from one yearling Columbian mother were included in this analysis.

We suggest that social tolerance and extensive spatial overlap between ground-dwelling squirrel parents and offspring are important features of parental investment in the more social ground squirrel species. Further, social tolerance by adults of young, other than their own offspring, may be a necessary step for the evolution of complex sociality.

ACKNOWLEDGEMENTS

Most of this research is part of a dissertation submitted in partial fulfillment of Ph.D. requirements at the University of Kansas by L.S. Rayor. Special thanks go to the Paul Vader family who kindly allowed the study of prairie dogs on their Quartz Creek ranch in Colorado, to D.A. Boag

who permitted L.S. Rayor to live at the University of Alberta's R.B. Miller Biological Station in the Sheep River Wildlife Sanctuary in Alberta, and to D.A. Boag, M. Festa-Bianchet, W. King, and J.O. Murie who graciously allowed study of the Columbian ground squirrels at the Dyson Creek site and provided background information on individual animals. We thank the staff at the Phillip Billard Airport in Topeka, Kansas for their cooperation. Marmot research was conducted at the Rocky Mountain Biological Laboratory, Gothic, Colorado and supported by NSF grants GB-32494, BMS 74-21193, DEB 78-07327, BSR 81-21231, and BSR 86-14690. R. Gonzalez assisted with trapping and observations in 1981. D. Van Vuren wrote the computer program to analyze spatial overlap. Discussions with and review of the manuscript by R.S. Hoffmann, G.R. Michener, C. Gilbert, D. Van Vuren, and B.M. Vestal were invaluable. The research was financed by a University of Kansas Graduate School Summer Fellowship to L.S. Rayor, and by University of Kansas General Research Fund grants No. 3336 and 3788 to K.B. Armitage

REFERENCES

ALTMANN J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.

ALTMANN J. & ALTMANN S. 1977. On the analysis of rates of behavior. *Animal Behaviour* 25: 364-372.

ARMITAGE K.B. 1974. Male behaviour and territoriality in the yellow-bellied marmot. *Journal of Zoology, London* 172: 233-265.

ARMITAGE K.B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48: 36-49.

ARMITAGE K.B. 1982. Social dynamics of juvenile marmots: role of kinsip and individual variability. *Behavioral Ecology and Sociobiology* 11: 33-36.

ARMITAGE K.B. 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability, pp. 377-403. In: Murie J.O. & Michener G.R., Edits. Biology of ground-dwelling squirrels. *Lincoln: University of Nebraska Press.*

ARMITAGE K.B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies, pp. 303-331. In: Rubenstein D.I. & Wrangham R.W., Edits. Ecological aspects of social evolution. *Princeton: Princeton University Press.*

ARMITAGE K.B. 1987. Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends in Ecology and Evolution* 2: 279-284.

ARMITAGE K.B. & JOHNS D.W. 1982. Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. *Behavioral Ecology and Sociobiology* 11: 55-63.

BEKOFF M. 1978. Social play: structure, function, and the evolution of a cooperative social behavior, pp. 367-383. In: Burghardt G.M. & Bekoff M., Edits. The development of behavior: comparative and evolutionary aspects. *New York: Garland Press.*

BEKOFF M. & BYERS J.A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological hornet's nest, pp. 296-337. In: Immelmann K. et al., Edits. Behavioral development. The Bielefeld Interdisciplinary Project. *Cambridge: Cambridge University Press.*

FERRON, J. 1985. Social behaviour of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Canadian Journal of Zoology* 63: 2529-2533.

FESTA-BIANCHET M. 1981. Reproduction in yearling female Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology* 59: 1032-1035.

FESTA-BIANCHET M. & BOAG D.A. 1982. Territoriality in adult female Columbian ground squirrels. *Canadian Journal of Zoology* 60: 1060-1066.

FESTA-BIANCHET M. & KING W.J. 1984. Behavior and dispersal of yearling Columbian ground squirrels. *Canadian Journal of Zoology* 62: 161-167.

FITZGERALD J.P. & LECHLEITNER R.R. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. *American Midland Naturalist* 92: 146-163.

GARRETT M.G. 1982. Dispersal of black-tailed prairie dogs in Wind Cave National Park, South Dakota. *M.S. Thesis, Iowa State University, Ames.*

HACKETT D.F. 1986. Dispersal of yearling Columbian ground squirrels. *Ph.D. Dissertation, University of Alberta, Edmonton.*

HARRIS M.A. & MURIE J.O. 1984. Inheritance of nest sites in female Columbian ground squirrels. *Behavioral Ecology and Sociobiology* 15: 97-102.

HOLEKAMP K.E. 1984. Dispersal in ground-dwelling sciurids, pp. 297-320. In: Murie J.O. & Michener G., Edits. The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality. *Lincoln: University of Nebraska Press.*

JAMIESON S.H. & ARMITAGE K.B. 1987. Sex differences in the play behaviour of yearling yellow-bellied marmots. *Ethology* 74: 237-253.

KING J.A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contributions of the Laboratory of Vertebrate Biology Michigan* 67: 1-123.

KING W.J. & MURIE J.O. 1985. Temporal overlap of female kin in Columbian ground squirrels (*Spermophilus columbianus*). *Behavioral Ecology and Sociobiology* 16: 337-341.

MCCARLEY H. 1966. Annual cycle, population dynamics and adaptive behavior of *Citellus tridecemlineatus. Journal of Mammalogy* 47: 294-316.

MICHENER G.R. 1981. Ontogeny of spatial relationships and social behaviour in juvenile Richardson's ground squirrels. *Canadian Journal of Zoology* 59: 1666-1676.

MICHENER G.R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids, pp. 528-572. In: Eisenberg J.F. & D.G. Kleiman, Edits. Advances in the study of mammalian behavior. *American Society of Mammalogy Special Publication* No. 7.

MICHENER G.R. 1984. Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality, pp. 81-107. In: Murie J.O. & Michener G.R., Edits. The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality. *Lincoln: University of Nebraska Press.*

MURIE J.O. & HARRIS M.A. 1978. Territoriality and dominance in male Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology* 56: 2402-2412.

NOWICKI S. & ARMITAGE K.B. 1979. Behavior of juvenile yellow-bellied marmots: play and social integration. *Zeitschrift für Tierpsychologie* 51: 85-105.

OOSTING H.J. 1956. The study of plant communities, 2nd Ed. *San Francisco: W. H. Freeman and Co.*

PFEIFER S.L. 1980. Demographic and behavioral influences on juvenile Wyoming ground squirrel dispersal. *Ph.D. Dissertation, University of Colorado, Boulder.*

RAYOR L.S. 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Canadian Journal of Zoology* 63: 2835-2840.

RAYOR L.S. 1987. Social dynamics of the Gunnison's prairie dog, with a comparison of the behavior of prairie dog and Columbian and thirteen-lined ground squirrel young. *Ph.D. Dissertation, University of Kansas, Lawrence.*

RAYOR L.S. 1988. Social organization and space-use in Gunnison's prairie dog. *Behavioral Ecology and Sociobiology* 22: 69-78.

SCHMUTZ S.M., BOAG D.A. & SCHMUTZ J.K. 1979. Causes of the unequal sex ratio in populations of adult Richardson's ground squirrels. *Canadian Journal of Zoology* 57: 1849-1855.

SCHWAGMEYER P.L. 1980. Alarm calling behavior of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus. Behavioral Ecology and Sociobiology* 7: 195-200.

SCHWAGMEYER P.L. & BROWN C.H. 1983. Factors affecting male-male competition in thirteen-lined ground squirrels. *Behavioral Ecology and Sociobiology* 13: 1-6.

SHERMAN P. 1977. Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.

SLOBODCHIKOFF C.N. 1984. Resources and the evolution of social behavior, pp. 227-251. In: Price P.W. et al., Edits. A new ecology: novel approaches to interactive systems. *New York: John Wiley & Sons, Inc.*

STEINER A.L. 1971. Play activity of Columbian ground squirrels. *Zeitschrift für Tierpsychologie* 28: 247-261.

STEINER A.L. 1975. «Greeting» behavior in some Sciuridae, from an ontogenetic, evolutionary and socio-behavioral perspective. *Naturaliste Canadien* 102: 737-751.

TRIVERS R.L. 1974. Parent-offspring conflict. *American Zoologist* 14: 249-264.

VAN VUREN D. 1990. Dispersal of yellow-bellied marmots. *Ph.D. Dissertation, University of Kansas, Lawrence.*

VESTAL B.M. & MCCARLEY H. 1984. Spatial and social relations of kin in thirteen-lined and other ground squirrels, pp. 404-423. In: Murie J.O. & Michener G.R., Edits. The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality. *Lincoln: University of Nebraska Press.*

WASER P.M. & JONES M.T. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology* 58: 355-390.

WATERMAN J. 1986. Behaviour and use of space by juvenile Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology* 64: 1121-1127.

WISTRAND H. 1974. Individual, social, and seasonal behavior of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *Journal of Mammalogy* 55: 329-347.