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Social organization and space-use in Gunnison's prairie dog

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Summary. Social organization of the Gunnison's prairie dog, *Cynomys gunnisoni*, was studied in two populations in south-central Colorado. Gunnison's prairie dogs live in complex, interactive societies fitting current definitions of highly social ground squirrels. Members of harems ('coteries') cooperatively use and defend a common territory. Spatial overlap is extensive between the adult male(s) and adult females, and among adult females within the harem through the active season. Amicable behavioral interactions are frequent within the harem, whereas interactions between members of different harems are primarily agonistic and spatial overlap is minimal. Although their behavioral repertoire is more limited, social organization of the Gunnison's prairie dog most closely resembles that of the black-tailed prairie dog, *C. ludovicianus*. Although body size, age of first reproduction, and age of emigration differed between the two study populations (Rayor 1985a), a comparison of social traits did not reveal substantial differences.

Introduction

Interspecific differences in sociality among closely related taxa have generally been attributed to differences in habitats, resource distribution, foraging ecology, or predation (see Wrangham and Rubenstein 1986; Rubenstein and Wrangham 1986). However, several models which correlate aspects of species' life-history traits with variation in sociality have identified consistant traits associated with well-developed sociality in ground-dwelling sciurids and in canids (Armitage 1981; Bekoff et al. 1981).

In North American ground-dwelling sciurids (*Marmota, Cynomys, Spermophilus*), certain life-history traits, such as the age at which adult body weight is reached, age at first reproduction, and age of emigration, are functions of body size (Armitage 1981). Social organizations found in ground squirrels form a continuum ranging from aggregated, asocial individuals, through moderately social female kin clusters, to highly social polygynous harems (Armitage 1981; Michener 1983). The most social of the ground squirrels have relatively large bodies and typically live in environments which only allow short active seasons or which have limited nutrients (as may be the case for non-hibernating *C. ludovicianus*; Koford 1958). In these species the young remain in their natal area into their yearling summer and do not reach sexual maturity as yearlings, as in the less social, smaller species of ground squirrels (Armitage 1981; Michener 1983). Thus, in large-bodied ground squirrels, complex sociality is associated with delayed emigration of young that are unable to attain the weight needed to become reproductively mature as yearlings (Armitage 1981). A model based on life-history traits has the advantage of providing testable predictions about the sociality of unstudied species.

If life-history constraints are the basis for interspecific differences in sociality in ground squirrels, the question arises whether intraspecific variation in life-history traits will result in differences in social structure between populations. Theories of life-history have typically assumed that traits are genetically fixed (Stearns 1976), but many life-history traits have been shown to vary in response to environmental factors such as food resources (Caswell 1983; Stearns and Koella 1986; Bronson 1979; Dobson and Murie 1987). Whether the behavioral traits associated with sociality are responsive to changes in life-history traits has not been examined, but is crucial to understanding the adaptive relationship between sociality and other life-history traits.

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Gunnison's prairie dog was reported to live in 'loosely organized clans' or to be moderately social (Fitzgerald and Lechleitner 1974; Pizzimenti 1975). However, based on its other known life-history traits, Armitage's (1981) model predicted that Gunnison's prairie dogs should be highly social. The goal of this study was to describe the social organization and to determine the life-history characteristics of *C. gunnisoni* and to evaluate the predictions of Armitage's model concerning the degree of sociality based on other life-history traits in two populations of a poorly studied species. Food resources and key life-history traits related to sociality differed between the two study populations (Rayor 1985a). Prairie dogs in the poorer quality habitat, Blue Mesa (BM), grew slower, weighed less, and did not reproduce or emigrate until after the yearling summer. In contrast, animals from the better quality habitat, Quartz Creek (QC), weighed more, produced larger litters, and some yearlings emigrated or reproduced. Similar intraspecific variation in life-history traits was observed in Columbian ground squirrels, *Spermophilus columbianus* (Festa-Bianchet 1981; Dobson and Kjelgaard 1985; Dobson and Murie 1987), black-tailed prairie dogs, *C. ludovicianus* (Garrett et al. 1982), and golden-mantled ground squirrels, *S. lateralis* (Bronson 1979). However, levels of sociality have not been compared between conspecific ground squirrel populations with different life-history characteristics.

The purposes of this paper are (1) to describe three major aspects of social organization in *C. gunnisoni*: harem composition, space-use, and behavioral interactions, and (2) to compare social organization between two populations that differed in key life-history traits.

Methods

Two populations of Gunnison's prairie dogs were studied in south-central Colorado from 1979 through 1981. The first study site, Blue Mesa (BM), was west of Willow Creek, near Blue Mesa Reservoir in Curecanti National Recreation Area, Gunnison County, Colorado (38°28′N, 107°06′W, elevation 2317 m). A 3.36 ha study site was chosen on the undisturbed corner of an approximately 60 ha prairie dog colony. Large areas of the colony, distant from the study site, were denuded by prairie dog grazing or disturbed by small scale human construction, and were sparsely inhabited by the prairie dogs. After the June emergence of young an estimated 1000–1500 animals lived in the entire colony, with approximately 200 individuals in the study site (Rayor 1985a, b). The second site, Quartz Creek (QC), was 48 km east of the BM site on a ranch (38°31′N, 106°40′W, elevation 2500 m). The 1.08 ha study site was a 30 to 90 m wide strip bordered by an irrigated hay meadow and hillsides. Most of the prairie dog population of approximately 125 adults and young lived within the perimeter of the site. Edible vegetation at BM was relatively sparse and there was little new growth after early July. The QC site had more abundant vegetation, and, in addition, the prairie dogs had access throughout the active season to the irrigated meadow with its ample food. The differences in diversity, quantity, and phenology of the vegetation at the two sites are described elsewhere (Rayor 1985a).

Prairie dogs were live-trapped and/or observed almost daily at BM from June through mid-August in 1979 and 1980, and from March through April 1981. Sylvatic plague (*Yersinia pestis*) killed the entire BM prairie dog colony during March and April 1981, terminating observations (Rayor 1985b). Quartz Creek animals were trapped from mid-June through August in 1980 and trapped and observed from April through August 1981. Prairie dogs were observed with a spotting scope from a car or rock outcrop at BM for 177 h, and from an 8 m tower-blind at QC for 308 h. Observations were concentrated during the animals' peak activity periods, in the morning (0600–1100 h) and late afternoon (1600–2000 h).

The periods of observation in this study did not encompass the entire active season of *Cynomys gunnisoni* in the Gunnison River Valley. The prairie dogs were reported to typically begin emergence from hibernation from mid-March to late April and the last individuals reported to immerge in mid-October (Rayor 1985b; Rayor et al. 1987). Mating occurs from mid-April to mid-May and young approximately 4 weeks old first emerged from their natal burrow between mid-June and early July (Rayor 1985a). Behavioral observations were minimal during the mating season and the first few weeks after parturition. The prairie dogs were intensively observed for the weeks prior to, and for 1.5 to 2 months after the emergence of young. Thus, conclusions about the nature of *C. gunnisoni* social organization are based on that phase of the life cycle.

Prairie dogs were captured using traps which were baited with salted oats and placed near burrow entrances where unmarked animals had been observed. Animals were trapped only in the early morning. Prairie dogs at both study sites were permanently marked with numbered fingerling fish tags in both ears. Additionally, unique marks for visual identification were painted on each animal with non-toxic fur dye. At each capture, age, sex, tag number, weight, reproductive condition, location, and date were recorded. Age classes were: young during the first summer of life; yearlings during the second summer; and adults two years old or older. Previously uncaptured prairie dogs were categorized as young or adults, with the exception of yearling females at BM. At BM the nipples of females known to be yearlings were barely visible, whereas all adult females, even nulliparous individuals, had enlarged nipples. Hence, nipple development was used to estimate the age of BM females immigrating from the surrounding colony into the study site. Kin relationships were determined primarily by trapping each litter on emergence from its natal burrow. However, a few young in harems with multiple litters were not marked before they mingled with members of neighboring litters. In those cases, maternity was retrospectively determined based on the similarity of interactions to those observed between mothers and their known offspring (Rayor 1987). The term 'harem' refers to the entire social group and is synonymous with the term 'coterie'.

Each site was divided into numbered 6 by 6 m grids. Grid locations of individual prairie dogs were recorded on emergence from the burrow in the morning, at 30 min intervals, and during focal animal observations (Altmann 1974). The sleeping burrow from which each individual emerged for the first time in the morning was recorded. Space-use analysis is based on data taken throughout the study season from three large, intensively studied harems (Penstemon-BM, Sage-BM, Ridge-QC), and three smaller, contiguous harems (Ditch, East, and New Area at QC). Space-use data from QC in 1981 are based entirely on observations (Ridge: mean observations per individual = 91, range 51–156; small harems: mean observations per individual = 47, range 27–90). Calculations of the area of home ranges at QC do not include the area of the irrigated meadow, which was used, but not defended, by all of the prairie dogs. Trap locations were combined with observational space-use data for the BM animals in 1980 to increase sample size (mean records per individual = 64, range 41–90). For no individual did the trapping data contribute more than 35% of the total space-use data at BM. Home range size (m^2) was calculated as the total number of grid squares in which each individual was observed at least once, times the area of each grid (36 m^2). Cole's coefficient of association, which is an index of domain overlap of 2-dimensional home ranges, was calculated as a weighted average of the percentage of each animal's domain that was shared by another individual (Cole 1954). The index of overlap of space-use was similar, but calculates the frequency that individuals were found in shared grids (Oosting 1956). These measures serve different functions. Space-use most accurately reflects the intensity of use in overlapping areas, whereas domain gives the total area of overlap and is a more accurate measure when there are fewer observations (e.g., for the small harems). For example, if members of one dyad were in the same grid square once and a second dyad used one grid in common twenty times, the domain overlap of the two dyads would be the same, but space-use overlap of the second dyad would be much greater. The Surface II computer program (Sampson 1975) was used to plot space-use data as three dimensional block diagrams with peak height representing the frequency of observations in each grid square (Frase and Armitage 1984).

Three aspects of *C. gunnisoni* social organization, harem composition, spatial behavior, and behavioral interactions, were compared between animals at BM and QC. When differences between sites were statistically insignificant, data were combined for further analysis as appropriate. Mean harem-composition was determined from 13 harems that were intensively observed and trapped in the second year at each site so that yearlings could be identified.

Behavioral interactions were observed using ad lib and focal animal sampling techniques (Altmann 1974). For each social interaction, the identity of the initiator and recipient, date, and location were recorded. Behaviors were later grouped into the general category of amicable or cohesive interactions ['kiss': oral-oral contact during which incisors are briefly interlocked (King 1955), greeting, play], and agonistic or aggressive interactions (chase, fight, attack). Low level agonistic interactions, such as 'open mouth threat' and spatial displacement, could not be observed reliably and were recorded infrequently; thus they were excluded from the sums of agonistic interactions. To compare the frequency of amicable versus agonistic interactions among adult and yearling age-classes in intra- and interharem interactions, all behavioral observations of identified animals in each colony were lumped for the entire season. In each age-class the proportion of the total behaviors that was agonistic was calculated for intra- and interharem interactions.

To determine whether amicable and agonistic behavioral interactions occurred randomly among all age-sex classes, a chi-square analysis (calculated from equation 7 of Altmann and Altmann 1977) was used to generate the expected rate of interactions for each dyad based on harem composition and the hours of observation of individuals within the dyad (see Rayor 1987, Appendix A). Large differences between observed and expected rates of interaction produce large 'chi-square components' that indicate a non-random distribution of interactions among one or more of the 10 possible dyads of interactants derived from the four age-sex classes, adult male and female and yearling male and female, implying that members of the dyad interacted much more or less than expected relative to their numbers in the harem. 'Chi-square components' are summed for each dyad and the total tested against the chi-square distribution. The analysis 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). This analysis is presented for the two most extensively observed harems Penstemon-BM and Ridge-QC, both of which had large numbers of adults and yearlings.

Results

Harem composition

Individual prairie dogs were considered members of the same harem by the following criteria: 1) sleeping burrows were in the same contiguous area, 2) space near the burrows was used in common, 3) for those individuals whose harem affiliation was unclear due to the location of their burrow near the border of a territory, by their association (or lack of association) with members of one harem or the other.

The typical harem in *C. gunnisoni* is composed of one adult male, one or more adult females, associated yearlings, and young of the year (Table 1). Harem membership remained stable for adults, and young through the yearling summer, throughout the years of the study.

Peripheral animals living outside the borders of established harem territories were common. These animals lived alone or near several other individuals, but rarely interacted with each other or members of the harem. Some of these animals came from neighboring harems that had disbanded. Social interactions in two BM harems, each with several litters in 1979, were disrupted in 1980 when the mothers did not survive the

Table 1. Composition of nine 1980 Blue Mesa and four 1981 Quartz Creek harems in which yearlings could be identified and all individuals were known to be residents

Age-sex	Mean	Range	Individuals
Blue Mesa			
Adult male	1.2	0–2	11
Adult female	3.0	1–5	27
Yearling male	1.3	0–3	12
Yearling female	2.0	1–4	18
Litters per harem	1.5	0–4	14
Quartz Creek			
Adult male	1.3	1–2	5
Adult female	2.8	1–4	11
Yearling male	3.0	1–8	12
Yearling female	1.3	0–4	5
Litters per harem	2.0	0–5	8

Table 2. Percent spatial overlap between individuals in each age-sex dyad at each site

	Domain		Space-use				*P*	*P*	
	intraharem		intraharem		interharem		BM vs QC	Intra vs Inter	
	BM	QC	BM	QC	BM	QC		BM	QC
A♂:A♂	16 (1)	27 (1)	9	10	9±5 (2)	0 (1)	–	–	–
A♂:A♀	41±12 (12)	33±19 (13)	34±19	29±22	11±11 (12)	1±2 (5)	<0.02	<0.0004	<0.01
A♀:A♀	41±16 (12)	39±25 (10)	28±14	28±22	12±9 (16)	3±3 (6)	<0.02	<0.0009	<0.014
A♂:YL♂	38±25 (2)	32±19 (6)	20±14	18±13	1 (1)	2±3 (6)	–	–	–
A♂:YL♀	47±16 (4)	42±15 (8)	35±20	23±15	11±9 (2)	0 (1)	–	–	–
A♀:YL♂	23±15 (4)	34±13 (13)	16±18	25±15	6±8 (4)	4±10 (24)	–	–	<0.004
A♀:YL♀	44±19 (8)	34±13 (16)	40±20	18±16	12±10 (8)	1±1 (5)	<0.02	<0.01	–
YL♂:YL♂	–	45±17 (7)	–	30±20	–	4±8 (9)	–	–	<0.002
YL♂:YL♀	39±34 (2)	45±12 (10)	30±29	36±24	–	0 (2)	–	–	–
YL♀:YL♀	30 (1)	37±15 (8)	24	19±13	–	–	–	–	–

Overlap is presented as $\bar{x} \pm$SD. When only two individuals in a given age-sex class overlapped, only the mean is given. The number of dyads compared is given below each overlap measure. Sample size is identical for intraharem domain and space-use. Domain is the total area of overlap, while space-use assesses the frequency of use of common grid squares. Domain, which always exceeded space-use overlap, is only shown for intraharem comparisons. Interharem space-use compared overlap between individuals of one age-sex class in one harem and those from a class in another harem, for those dyads that could be compared. The difference between interharem overlap between sites, and intra- and interharem overlap was tested by the Mann-Whitney *U* test when there were five or more observations. Note that at QC where most individuals from different harems did not overlap, the standard deviation is larger than the mean. Harems used for analysis were Sage and Penstemon at BM, and Ridge, East, Ditch, and New at QC. Ridge was omitted from interharem analyses

winter. The surviving adult male(s) and yearlings continued to live in the same territory, but did not interact as a cohesive social unit. In both cases, some of the yearlings moved into those burrows in their natal territory that bordered a neighboring harem, although their movements into and interactions with harem members were minimal. Such individuals account for many of the peripheral animals.

Spatial patterns within the harem

Areas of individual home ranges did not differ significantly between sites, sexes, age groups, or members of large versus small harems (Mann-Whitney, all $P > 0.08$). Median home range area was 774 m^2 (range 504–972 m, $n = 14$) at BM and 684 m^2 (range 324–1476 m^2, $n = 26$) at QC.

Three features characterize the use of space within a harem of *Cynomys gunnisoni*. First, home range of an adult male extensively overlaps those of adult females and other harem members (Table 2, Fig. 1). Second, home ranges of adult females within the harem extensively overlap one another. Third, spatial overlap of individuals that are members of the same harem (intraharem) is typically much greater than overlap with members of other harems (interharem) (Table 2).

Animals using the same burrow entrance were considered to share the burrow system. Adult males in approximately half of the harems shared sleeping burrows with one or more adult females through the season. Of the 9 (56.2%) adult males sharing burrows with adult females (at least after emergence of young), 10 (90.9%) of the females had litters in the same burrow. Of 67 adult females, only two pairs shared sleeping burrows, one at each site. In both cases, each female of the pair raised a litter. Adult females often slept with their litters or yearling offspring, or with an adult male, in various permutations. One burrow was shared by a yearling mother, her litter, the litter's grandmother, and an adult male. In another, a yearling brother and sister lived with their mother and her subsequent litter. Of the 39 yearlings whose harems included other known yearlings, 43.6% shared a burrow with at least one other yearling haremmate.

Space-use overlap by regular burrowmates (56.7±10.4%), with the sites combined, was significantly greater than overlap between non-burrowmates within the same harem (21.8±14.6%, Mann-Whitney, $P < 0.0001$). Overlap among burrowmates was almost identical between sites (Mann-Whitney, $P > 0.97$, BM $n = 8$, QC $n = 13$). However, individuals in the BM harems overlapped more with non-burrowmates from the same harem (24.8±13.4%, $n = 38$), than did those at QC (20.4±14.9%, $n = 79$, Mann-Whitney, $P < 0.051$). Defense of burrows from other harem members was not observed postemergence of young (when most observations were made), and harem members apparently had access to all areas and

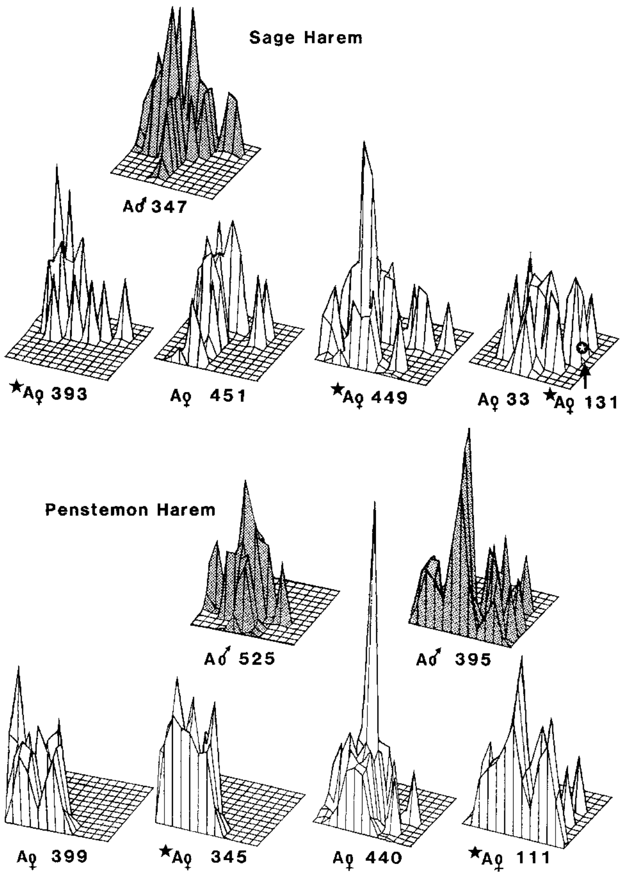

Fig. 1. Computer generated plots of the use of space by each adult in the neighboring Sage and Penstemon harems at Blue Mesa in 1980. Peak heights represent the frequency of observation in each 6 m square grid. The same total 72 m square area is shown for both harems. The two harems are viewed from the western edge of Penstemon. Age, sex, and individual numbers are given below each plot. Females with litters are starred. Adult female 131 was seen too infrequently to plot, * indicates her burrow

burrows. Although not quantified, harem members often foraged in close association, within 0.5 m of one another.

Three harems, Penstemon-BM, Ridge-QC, and Activity-BM, had two resident males. In these harems, the adult males were never observed to interact with one another or to be in the vicinity of one another, although their space-use patterns overlapped (Table 2). Adult male 525 immigrated into the Penstemon-BM harem on 1 July 1980 and apparently displaced the original harem male, 395, who subsequently restricted his movements to a smaller area on the western edge of the harem territory (Fig. 1). Females did not overtly alter their patterns of space-use in response to the new male. Similarly, in Ridge harem at QC, as one adult male increasingly shifted his activity outside the communal territory, the second adult male expanded his range of activity to encompass that vacated by the first male. In the 1979 Activity harem, the two males avoided each other and by 1980 one of the two males and an adult female moved to a nearby unoccupied area and established a new harem. Although mean overlap of spatial domain for the other age-sex dyads ranged from 30% to 47%, intraharem adult male domain overlap was only 27% at QC and 16% at BM (Table 2). Space-use overlap was notably low at 9.2 to 9.6% for these adult males.

Because either few observations or low population density could affect the documentation of spatial overlap, overlap patterns of three small harems were compared to the larger Ridge harem at QC. The large Ridge harem territory encompassed 2,340 m^2 and in June, 12 adults and yearlings were residents, the small harems encompassed $1,344 \pm 245$ m^2 with 6.3 ± 3.2 residents. Among those age-sex dyads which could be compared for space-use overlap, none in the three small harems differed from its counterpart in the larger harem (all $P > 0.24$). Hence data from all four QC harems were combined. Similarly, with the one exception discussed below, domain and space-use overlap of intraharem age-sex dyads did not differ between BM and QC harems (Table 2, Mann-Whitney, all $P > 0.19$).

The exception is significant because it is related to life-history differences between the sites. Space-use overlap of adult and yearling females was significantly less at QC than at BM (Table 2, Mann-Whitney, $P < 0.009$). Only two large harems, Ridge-QC and Penstemon-BM, of the six used to analyze spatial patterns, had both adult and yearling females. Examination of these harems illustrates the elements that differed. Ridge was composed of four adult females, three with litters, and four yearling females, two with litters. Of the four yearling females only one shared a burrow; she weaned a litter in the burrow she shared with her mother, who did not reproduce that year. Penstemon consisted of four adult females with three litters and three yearling females (one was killed by a badger early in the summer and was excluded from space-use calculations) which shared burrows with adult females. The primary difference was that BM yearling females were sexually immature, whereas, QC yearlings were sexually mature (Rayor 1985a) and, thus, potential competitors with the adult females (Armitage 1986).

Spatial patterns between harems

Interharem spatial overlap of individual home ranges was significantly less than intraharem spa-

Table 3. The proportion of agonistic behavioral interactions observed in adult (A) or yearling (YL) dyads within and between harems at the two study sites

	A:A		A:YL		YL:YL	
	QC	BM	QC	BM	QC	BM
Intraharem *N*	0.51 (41)	0.43 (49)	0.45 (75)	0.45 (62)	0.31 (163)	0.38 (16)
Interharem *N*	1.00 (16)	0.93 (40)	0.90 (31)	0.80 (35)	1.00 (21)	0.25 (4)

When only agonistic behaviors were observed the proportion equalled 1.0. The total interactions observed for each dyad are given below each proportion. Data from all 4 harems at QC and 7 at BM were combined for each site. The proportion of agonistic interactions within age-dyads did not differ between sites (Mann-Whitney *U*, $P > 0.2$), but interharem interactions were significantly more agonistic than intraharem interactions (Wilcoxon, $P < 0.03$)

tial overlap (Table 3). Even overlap with intraharem non-burrowmates was much greater than overlap between individuals from neighboring harems. Ridge harem, which was only slightly contiguous with Ditch harem and whose members had virtually no overlap with other harems, was omitted from measures of such overlap at QC.

In all age-sex groups that could be compared, interharem overlap was greater at BM than at QC (Table 2). However, the importance of this test is confounded because at BM space-use was measured only in Sage and Penstemon harems whose common border was not delimited by physical barriers. I inadvertently increased interharem overlap by regularly setting baited traps at a major burrow system, located just inside the Penstemon territory near the border with Sage, thus attracting the Sage animals. Sage and Penstemon harem members overlapped the most of any harems observed in this study. Interharem overlap for other BM harems appeared more similar to that observed at QC, but sample sizes were too small to analyze overlap. Non-residents occasionally foraged in adjoining territories, but not with the persistence or to the extent seen among Sage and Penstemon prairie dogs.

Most harem territories were separated by physical barriers such as areas of dense sagebrush, *Artemisia frigida*, or rock outcrops, or had relatively small areas of abutment. The neighboring Sage and Penstemon harems were somewhat unusual in being situated in a large open area with no clear physical barriers between them. Yet it was evident that a definite boundary existed through the center of the area for the prairie dogs (Fig. 1). For example, adult female 393 from the Sage harem was never observed to cross the boundary. Animals that wandered into the Penstemon area, primarily to reach baited traps, always provoked active agonism from Penstemon residents. Sage adult female 449, who had the most overlap into Penstemon (Fig. 1), was particularly persistent and aggressive and was the source of many agonistic interharem interactions.

At QC the irrigated meadow served as a foraging 'sink' that was not available at BM. Prairie dogs at QC were more likely to move into the lush meadow to forage than into another harem's territory. However, to reach the irrigated meadow, individuals from New Area had to pass north through East and/or Ditch harems and many East animals entered the meadow by crossing northwest through Ditch.

Young from different litters within the same harem mingle and play with one another by three weeks after emergence from the natal burrow (Rayor 1987). Most young continued to sleep with their mothers in the natal burrow or elsewhere if she moved to another burrow, but during the day the young associated freely with other harem members. Spatial and behavioral patterns of young Gunnison's prairie dogs are examined extensively in Rayor (1987).

Behavioral interactions within harems

Interactions within the harem tend to be amicable, whereas behavioral interactions between members of different harems are primarily agonistic (Table 3). Social interactions within two of the large harems, Ridge-QC and Penstemon-BM, represent typical intraharem behavior of the prairie dogs at both sites. There was no difference between the frequency of amicable or agonistic behavior within the harems, if a ratio of 50:50 is assumed (BM $\chi^2 = 0.02$, QC $\chi^2 = 2.14$, both n.s.). However, behavioral interactions did not occur in proportion to the frequency at which members of age-sex classes occur in the population (Table 4). For example, in both harems, adult females were less amicable and more agonistic with each other than expected (Table 4). Adult females tolerate the close association (within 0.5 m) of other females foraging nearby and spatial overlap among adult females was extensive (Table 2). In Ridge harem the extent of agonism is inflated because 12 of the 13 agonistic interactions occurred within 1 h in July when the three neighboring females were highly agitated, possibly due to a long-tailed weasel, *Mustela frenata*, entering burrows in that area.

Table 4. Intraharem behavioral interactions in age-sex dyads in the Ridge harem at Quartz Creek in 1981, and in the Penstemon harem at Blue Mesa in 1980

	Quartz Creek				Blue Mesa			
	Amicable		Agonistic		Amicable		Agonistic	
	Expect	Observe	Expect	Observe	Expect	Observe	Expect	Observe
A♂:A♂	1.5	0	0.5	0	0.6	0	0.6	0
A♂:A♀	8.4	5	6.3	2	6.3	4	6.5	3
A♀:A♀	5.4	2	2.0	13*	5.6	0*	5.8	9
A♂:YL♂	2.9	0*	2.2	13*	1.6	3	1.6	5*
A♂:YL♀	8.9	6	6.7	2	4.0	5	4.2	2
A♀:YL♂	5.7	4	4.3	4	3.7	2	3.8	5
A♀:YL♀	15.0	11	11.3	0*	9.6	14*	9.8	9
YL♂:YL♂	0.5	10*	0.2	6*	–	–	–	–
YL♂:YL♀	5.8	12*	4.3	3	2.4	6*	2.5	3
YL♀:YL♀	5.7	10*	2.1	2	1.9	2	2.0	1
	$\chi^2=189.7$ $P<0.001$		$\chi^2=300.0$ $P<0.001$		$\chi^2=16.8$ $P<0.05$		$\chi^2=13.5$ $P<0.065$	

Original harem composition of Ridge, prior to emigration and predation, was six adults (A), two males and four females; six yearlings (YL), two males and four females; and young from five litters. Original harem composition at Penstemon was six adults, two males and four females; four yearlings, one male and three females; and young from two litters. The chi-square test (Altmann and Altmann 1977) analyzes differences among all dyads combined. When observed values for a given dyad contributed a large portion of the chi-square value, they were considered biologically significant and starred (*)

Adult males and females interacted with one another in proportion to their presence in the population (Table 4). Although adult males were more likely to displace than be displaced, behavioral dominance over females was not an apparent feature of male-female interactions. There were no unique behavior patterns that males used to dominate females as occurs in marmots (Armitage 1974). Adult males were interactive in harem-life at least through the end of August, when observations ended.

Adults were neither more amicable nor more agonistic to yearlings of the opposite sex than expected (Table 4). However, the relatively frequent interactions between adult and yearling females were either more amicable (BM) or less agonistic (QC) than expected. At Ridge-QC, there were no agonistic interactions between adult and yearling females. However, although the two reproductive yearling females frequently associated with adult females, 10 of the 11 amicable adult-yearling interactions involved non-reproductive yearlings ($\chi^2 = 9$, $P<0.005$). In contrast, interactions between adult and yearling males were much more agonistic than expected (Table 4), and the interactions were increasingly aggressive as the summer progressed (Rayor 1985a).

Yearlings were relatively interactive. The two interactive male siblings sharing a burrow at QC were both more amicable and more agonistic with one another than expected relative to their number in the harem. Cohesive interactions between yearling male and female burrowmates accounted for the unexpectedly high amicable interactions in this dyad. However at QC where no yearling females shared burrows, frequent amicable interactions occurred between all females, reproductive and non-reproductive.

The prairie dogs were observed to cooperate in territorial defense and defense from predators. For example, on 27 July 1980 at BM, Sage adult female 33 ran 25 m from her burrow, well into Penstemon territory, to chase and attack Penstemon adult female 111, who was near her own burrow. The attack was particularly intense and apparently unprovoked. Yearling male 249, noticing the attack on his mother, 111, charged 18 m toward 33, causing her to break off the attack and retreat to Sage. Similarly, in New Area at QC on 3 July 1981, a long-tailed weasel, entered several burrow entrances in the area and prairie dogs throughout the colony alarm-called. Adult female 891 grabbed one of her recently emerged young in her teeth, dragged him to a burrow entrance and pushed him in. Meanwhile, a yearling male chased the weasel part way through the harem. Then 891 joined him and charged at the weasel until it left the territory.

Behavioral interactions between harems

Many interactions between members of different harems were involved with territory defense, and agonistic behavior toward non-harem members was typically more aggressive than that directed toward harem members (Table 3). All age-classes, including the young, chased members of other harems away from borders. On many occasions young prairie dogs aggressively chased adult or yearling interlopers. Typically, an adult ran some distance toward its own harem domain, then stopped, turned, and threatened the youngster. Ony then did the young stop chasing the intruder. The most dramatic territorial confrontations involved adult males locking incisors at the borderline. But rather than the quick lock and release characteristic of an amicable greeting, each male kept his incisors locked and attempted to turn his head to the vertical, thus forcing the other male's head toward the ground. Then they would leap apart into an aggressive chase. Chases by either of the Penstemon males, 395 or 525, of the Sage male, 347, lasted only into the edge of Sage territory, whereupon the resident male turned around to chase the Penstemon male back into his territory. The males alternately chased and were chased as many as six or seven times in a bout, reversing position each time an animal entered a few meters into the other's territory.

Defense of harem domain was similar at QC. Intrusions of animals passing to the irrigated meadow were the source of most interharem spatial overlap and behavioral confrontations. In an extreme example, a 3-legged adult female, 891, from New Area regularly passed through East en route to the meadow during August 1981. A resident adult female, 924, was particularly aggressive towards 891 and doggedly defended East's territory. Over a period of several weeks 891 and 924 engaged in prolonged chases, tooth chattering, barking, and active grappling when 891 persisted in entering East. Eventually 891 died of wounds inflicted by 924.

Discussion

Gunnison's prairie dogs, *Cynomys gunnisoni*, live in complex, interactive societies fitting current definitions of highly social ground squirrel societies (Armitage 1981; Michener 1983). Gunnison's prairie dog displays all of the traits characteristic of the highly social ground squirrels, at least during the period after the emergence of young: 1) the social unit is a harem; 2) harem territories are used and defended cooperatively; 3) behavioral interactions are predominantly amicable and cohesive among harem members but agonistic toward non-harem members; 4) adult males remain territorial and interactive through the active season and do not dominate females; 5) litters readily mingle soon after emergence; 6) offspring remain in the natal territory, at least into the yearling summer; and 7) adults and young are simultaneously active through most of their annual cycle (Armitage 1981; Michener 1983, 1984). Thus, the predictive value of Armitage's (1981) model linking certain life-history traits to various levels of sociality is substantiated. Gunnison's prairie dogs are best categorized as members of the most social Class 5 which Michener (1983) termed an 'egalitarian polygynous harem'.

Black-tailed prairie dogs (*Cynomys ludovicianus*) have been studied longer and for a larger portion of the animals' life-cycle; however, at this time, it appears that the Gunnison's and black-tailed prairie dogs share most life-history and behavioral traits (King 1955; Hoogland 1979, 1981a, b, 1986). This similarity is of particular interest because Gunnison's prairie dog shares with the white-tailed prairie dog (*C. leucurus*: subgenus *Leucocrossuromys*) the trait of hibernation (Bakko and Nahorniak 1986; Rayor et al. 1987), and they are taxonomically most closely related (Pizzimenti 1976a, b). Yet, *C. leucurus* is only moderately social, with a social organization apparently resembling that of ground squirrel species like *Spermophilus richardsonii* (Tileston and Lechleitner 1966; Clark 1977; Michener's 1983 Class 2). Further, hibernation patterns differ with *C. leucurus* adults immerging for hibernation by mid to late summer (Tileston and Lechleitner 1966; L. Cooke pers. comm.), whereas *C. gunnisoni* adults immerge in autumn (Rayor et al. 1987). The source of differences in annual cycles is unknown.

Although Gunnison's and black-tailed prairie dog societies are similar, there are several major differences. The behavioral repertoire of *C. gunnisoni* is more limited and, overall, its social, communicative, and cohesive behaviors are not as well-developed as those of *C. ludovicianus*. The characteristic 'jump-yip' ('wee-oo' of Waring 1970) and anal gland displays of *C. ludovicianus* (King 1955; Z. Halpin personal comm.) were not seen in *C. gunnisoni*. During agonistic interactions *C. gunnisoni* may raise their tails, but the anal glands are not flared outward nor are there displays that emphasize the glands. Allogrooming is rarely observed in *C. gunnisoni*. Unlike *C. ludovicianus, C. gunnisoni* rarely modify vegetation around burrows or elsewhere in their territory (Koford 1958). In 1980 at BM, tumble mustard, *Sisymbrium altissimum*, spread to a dense cover on the previously open area occupied by two harem groups. Mustard grew over 0.5 m high, blocking the prairie dogs' view of the horizon. The prairie dogs appeared not to remove vegetation to improve visibility in this area or elsewhere. Nor did they seem to avoid the tall, dense vegetation.

These observations suggest that the evolution of complex sociality may have been relatively recent in *Cynomys gunnisoni*. Alternatively, the ecology and habitats of black-tailed and Gunnison's prairie dogs may differ sufficiently that similar behaviors did not develop in both species. Complex, harem-based sociality appears to have evolved independently in both prairie dog subgenera (*Leucocrossuromys*, the white-tailed branch; *Cynomys*, the black-tailed branch) in response to the presence of suitable life-history traits that promote sociality.

Further study on the social organization and ecology of the remaining prairie dog species (*Cynomys: C. mexicanus; Leucocrossuromys: C. parvidens*) and comparisons with an outgroup such as *Spermophilus columbianus* will be needed to elucidate the evolution of sociality in the prairie dogs.

There were few apparent differences in social structure or behavior between *Cynomys gunnisoni* at the Blue Mesa and Quartz Creek sites, although other life-history traits differed (Rayor 1985a). The primary difference was that at QC, where some yearling females were sexually mature, there was less spatial overlap between adult and yearling females within a harem, although the frequency of amicable behavioral interactions between these age-sex classes was similar at both sites. However, this study may have been too brief to discern intraspecific differences in sociality.

The length of time over which intraspecific alterations in life-history traits could cause changes in sociality is unresolved. Any changes in sociality should be the result of a balance between the opposing factors of cooperation and competition within the social group that allows its members to maximize their life-time reproductive success (Wrangham and Rubenstein 1986). Animals attempt to maximize their fitness by increasing the probability that their offspring survive to reproductive age. Sociality, which permits juveniles to remain in the relative safety of the natal area until they are reproductively mature, increases the probability of survival, regardless of the sources of mortality (e.g. predation, Hoogland 1981a). Armitage (1981) proposed that sociality is a means of prolonging reproductive investment beyond weaning in those large-bodied ground squirrels where the active season is too short or the nutrition too poor for offspring to become reproductively mature as yearlings. Differences in the levels of sociality may ultimately reflect differences in the timing of first reproduction, which in turn affects competition with adults.

Because an earlier initiation of reproduction dramatically increases an individual's reproductive success, there is strong selection pressure to reach sexual maturity at as early an age as possible (Cole 1954; Stearns and Koella 1986), especially for animals, such as ground squirrels, that breed only once a year (Armitage 1981). Phenotypic plasticity in life-history traits will substantially increase the individual fitness of those animals, such as yearling prairie dogs, facultatively capable of breeding at an earlier age. A characteristic of increasing sociality in ground squirrels is for adult daughters to settle near their mother's home range, and, in the most social species, for the daughters to be recruited into the mother's matriline and communally use the area (Michener 1983). By retaining daughters in their natal area, adult females increase the probability that their daughters will leave descendents, increasing life-time reproductive success for both individuals (Armitage 1986, 1987). The fitness benefits to both parents and offspring from cooperating to retain and tolerate offspring in the natal area suggests that complex ground squirrel societies should remain socially cohesive.

However at the same time, it is better for an individual's life-time reproductive success to invest in its own offspring rather than those of kin-including grandchildren (Rubenstein and Wrangham 1980). Offspring remaining in the natal area, and their offspring, compete with the parents for space and forage. Evidence of competition is emerging from studies of social ground squirrel societies. Mother-daughter competition in yellow-bellied marmots, *Marmota flaviventris*, reduces the fecundity of daughters living with their mothers, although presumably their lifetime reproductive output is enhanced through greater survivorship (Armitage 1986). Infanticide among relatives occurs at a startlingly high frequency in black-tailed prairie dogs (Hoogland 1985). The breeding grandmother may kill her own grandchildren and thus reduce competition with her new generation of offspring. Clearly, mutual tolerance is not necessarily the best option in all circumstances. If long-term environmental conditions improved, such that highly social ground squirrels could acquire sufficient weight to reduce the typical age of maturity, the costs of competition could exceed the benefits of cooperation and selection should drive the ground squirrel society toward decreased sociality.

The effect of a change in life-history traits on the sociality of a species should depend on the specific environmental circumstances and the balance between resulting cooperative and competitive forces on the social organization.

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