PLAINS POCKET GOPHER SOCIAL BEHAVIOR

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Abstract. Social interactions of plains pocket gophers (*Geomys bursarius*) were studied by monitoring locations of radio-tagged individuals as they moved within their burrow systems. Gophers rarely came within 10 m of each other unless their home ranges abutted. This was determined by matching pairs of fixes obtained by radio-telemetry which were less than 30 minutes apart. However, gophers were aware of changes in surrounding home ranges as they investigated recently vacated home ranges within days of the disappearance of the resident gopher. Use of feces as "signposts" is suspected as one mechanism for sensing presence and reproductive status of a neighbor. Seismic vibrations from gopher digging and from their clicking vocalization are proposed as other mechanisms for detecting activities of neighboring gophers. Agonistic behavior was recorded by the tracking system more often than affiliative behavior. By the time juveniles were large enough to carry a transmitter, they had already dispersed. Seven intrusions into an occupied home range resulted in four displacements, one death, and two withdrawals. Den sites were defended from intruders. Agonistic behavior appears to be the mechanism which insures that each gopher has an adequate food supply.

INTRODUCTION

Pocket gophers have been characterized as solitary and highly territorial (Vaughan 1962). Caged gophers were fiercely intolerant of each other, with larger gophers killing or starving smaller animals (Howard and Childs 1959). Lack of sufficient detailed observations on behavior in the wild has led to the belief that pocket gophers defend their territories through combat (Hansen and Reid 1973). If death does not result from actual combat, the loser would probably withdraw to seclusion in its burrow system. Physical antagonism might also be a factor operating in the geographical separation of different species of gophers (Best 1973).

The burrow systems of pocket gophers have been described as being vigorously defended against intruders throughout most of the year, except during breeding season where plural occupancy of burrows was associated with a brief mating period (Miller and Bond 1960). Hansen and Miller (1959) reported 63 plural captures of 133 individual northern pocket gophers *(Thomomys talpoides)* in a total sample of 881 captures during breeding season. Adult females were together with young in 36.5 percent of those captures. Males with young were taken together 18.9 percent of the time and males together with females occurred in 13.5 percent of the captures (Hansen and Miller 1959). In three plural occupancies involving valley pocket gophers *(Thomomys bottae)*, males burrowed into the tunnel system of adjacent females (Bandoli 1981). Howard and Childs (1959) conducted a study in which they removed trapped gophers during breeding season. Other gophers subsequently trapped in the same burrow system were always neighbors. Valley pocket gophers appeared to be polygamous in that male home ranges overlapped female home ranges, but males did not overlap other male home ranges and females did not overlap other female home ranges (Howard and Childs 1959).

Gophers live in a stable group in the sense they consistently encounter the same individuals as neighbors and they compete with these individuals for the same resources. Individual recognition is one of the basic components required for complex social behavior and implies prior experience with neighboring gophers. Howard and Childs (1959) conducted homing experiments and concluded gophers seem to be acquainted with neighboring burrow systems. The existence of relatively permanent deeper, larger tunnels may permit easy exploration of neighboring burrow systems. Howard and Childs (1959) found gophers utilizing existing burrow systems to return in homing experiments. They also found that opposite sex gophers had a limited penetration of tunnels across the outermost boundaries of their home ranges, but rarely found overlap in boundaries between gophers of the same sex. Thus, our working hypothesis was that there would be differences in frequency of encounter between same sex and opposite sex gophers.

METHODS

A population of free-ranging gophers on the Cedar Creek Natural History Area in east-central Minnesota was studied to determine whether there was contact between conspecifics. Radio transmitters were implanted (Zinnel and Tester 1991) in the body cavities of 37 individuals from October 1983 through September 1985. During this two year study, as many as six individuals were on the 50 x 50 m tracking grid at the same time. A micro-processor controlled monitoring system was able to locate one gopher every minute with a precision of 0.25 m (Zinnel 1992). Telemetry data for 22 pairs of gophers were sorted by date and time, and observations less than 30 minutes apart were matched.

Gopher interactions were summarized by examining the telemetry records for pairs of gophers and determining how

Table 1. Frequency of interactions between gophers. Telemetry fixes less than 30 minutes apart for opposite sex (A) and same sex (B) pairs of gophers were used to calculate statistics with respect to the Euclidean distance separating each pair.

A: Opposite Sex Pairs

First Gopher ID#	Second Gopher ID#	# ofObs <30 min Apart	Separation (Meters) Avg.	S.D.	Min	Median	Max	# of Obs <10 m Apart
17	25	636	10.8	3.4	3	9	27	325
11	28	344	15.9	0.4	15	16	17	0
17	28	365	18.0	2.0	14	17	38	0
01	06	558	20.6	4.4	0	22	25	39
22	25	756	21.5	5.0	12	19	42	0
24	25	549	25.3	6.4	1	27	51	15
11	25	91	28.2	1.7	24	27	33	0
06	08	261	32.6	4.1	19	31	41	0
24	28	218	36.2	4.0	8	36	37	2
01	04	179	37.3	4.0	17	38	48	0
06	07	138	49.6	3.1	28	49	54	0

B: Same Sex Pairs

First Gopher ID#	Second Gopher ID#	# ofObs <30 min Apart	Separation (Meters) Avg.	S.D.	Min	Median	Max	# of Obs <10 m Apart
25	28	156	13.1	1.8	9	12	27	4
01	02	330	17.2	13.3	0	19	50	102
07	08	95	22.6	5.3	15	22	52	0
22	24	409	24.0	5.0	10	23	36	0
17	24	529	28.0	4.9	6	28	39	10
11	17	361	28.6	0.9	22	28	31	0
17	22	997	29.9	4.9	6	27	47	1
01	08	634	37.0	5.8	15	34	47	0
01	07	238	40.9	11.1	11	46	49	0
11	22	20	41.4	3.1	37	40	46	0
11	24	150	52.1	0.3	51	52	53	0

often they were less than 10 m apart when the observations were less than 30 minutes apart. Using SPSS-X (Norusis 1988), the Euclidean distance in meters was calculated between each matched pair of fixes separated by the shortest time interval. Frequency histograms of separation distances and elapsed time were used to summarize interactions between pairs of gophers.

RESULTS

Neighboring gophers seemed to recognize when a den site and corresponding home range became vacant. Data from telemetry revealed six instances where a den site was investigated by another radio-tagged gopher within a few days of becoming vacant. In three of these cases, the investigating gopher took up residence. Gophers rarely were recorded as "close" to one another (Table 1). This may imply a mechanism for gophers to detect other gophers without physical contact. On seven occasions a gopher suddenly took up residence at a den site previously known to be vacant for at least two months. The transitions were usually abrupt, as determined by telemetry fixes, mound surveys, and trapping.

Within a home range, gophers vigorously defended den sites. Data from telemetry revealed seven instances where a radio-tagged gopher invaded an already occupied home range. In four of these situations, the resident gopher was displaced and in one case, killed. In the other two incidents, the gopher tracking system recorded what appeared to be conflict over a den site lasting several days. In these two cases, the resident

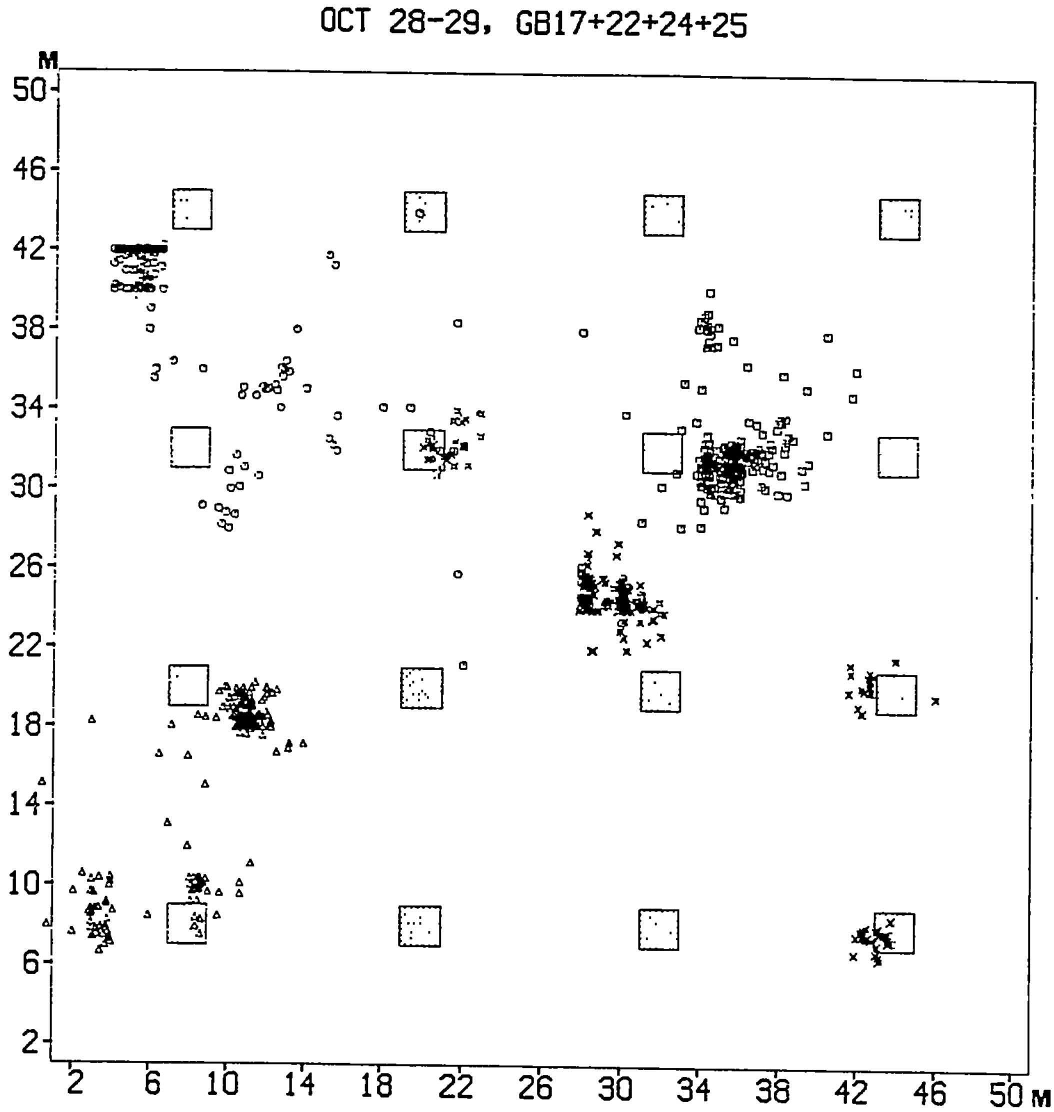

Figure 1. Gopher interactions on October 28 & 29, 1984. The 0.25 ha gopher tracking grid is indicated as a square outline. Tracking system coordinate labels are indicated in meters; the "interface zone" is approximately at X=22, Y=32 in this plot. There are 16 4 m^2 fertilized patches indicated as shaded squares. A square is the symbol for gopher 17, an x for gopher 25, a triangle for gopher 22, and an octagon for gopher 24.

gopher remained in possession of the den site. Details of one of these conflicts involve interactions of four gophers monitored by the gopher tracking system during October, 1984 (Figure 1). The principals were a large female (#24, 200g) and a small male (#25, 145g). The neighboring gophers were another large female (#22, 180g) and a small female (#17, 125g).

Data from telemetry revealed a discrete site centered around coordinates (24, 32) where fixes for different gophers appear in close proximity (Figure 1). This area will be referred to as an "interface zone" in the following discussion. We believe the burrow systems were interconnected in this region. Gophers 24 and 25 maintained a presence in this area, except for the last period, which was after their conflict. During the period from October 12 through 29, gopher 24 was recorded as being in this zone 48 times and gopher 25 was recorded 181 times. Gopher 17 also visited this area on two separate occasions. From October 12 through 23, gophers 24 and 25 were "close" to each other on only six occasions (Table 2) despite many individual fixes in this area. Generally, gopher 24 would visit the interface zone about three hours after 25 left. From October 24 through 28, gopher 25 intruded into the home range of 24 but they were never closer than 9 m, and were this close on only two occasions. When 25 started

Table 2. Interactions of Gopher 24 and Gopher 25. For 549 paired observations when the gopher tracking system recorded locations for gophers 24 and 25 separated by less than 30 minutes, there were only 15 instances where gophers 24 and 25 were less than 10 m apart.

		G # 24		G # 25		Minutes	Meters
Mo.	Day	X	Y	X	Y	Elapsed	Separation
10	13	20.02	32.79	24.44	33.84	21	4.54
10	14	22.00	38.62	23.72	32.19	16	6.66
10	14	22.01	38.00	24.57	32.32	10	6.23
10	17	21.82	39.15	24.42	33.92	10	5.84
10	17	22.79	38.95	24.17	32.01	18	7.08
10	21	15.39	33.05	21.80	32.38	23	6.44
10	24	5.58	40.32	14.30	37.03	15	9.32
10	28	12.82	35.98	21.75	31.82	23	9.85
10	30	29.74	24.47	28.51	23.76	22	1.42
10	30	27.90	28.25	24.41	23.92	22	5.56
10	30	30.01	24.02	27.41	23.90	23	2.60
10	30	30.16	24.66	27.82	24.12	25	2.40
10	31	32.10	22.00	24.54	25.78	24	8.45
10	31	33.57	22.27	25.96	25.81	23	8.39
11	01	21.51	32.06	25.81	23.88	23	9.24

intruding into 24's home range, 24 would visit exactly the same area where 25 had been recorded, but 3 to 7 hours later. We interpret these patterns as exploratory behavior on the part of gopher 25. Because his home range was very close to gopher 17, he was probably seeking another direction in which to extend his activities.

At 1430 hours on October 29, gopher 25 traveled 15 m in the opposite direction from 24, apparently exploring the vacant den site previously used by gophers 04 and 07, and subsequently by 11 (Figure 2). As recorded by the tracking system, only 22 minutes elapsed from the time 25 left his den site until the time 24 arrived. It could have been less time because 22 minutes was the minimum time separating those two frequencies in the programming schedule. From October 29 through November 1, gopher 24 went to the den site belonging to gopher 25 several times while 25 was absent. Gopher 24 may have raided 25's food cache which was located 3 m away from the den. Gopher 24 made six trips back and forth between its den site and 25's cache in 17 hours, always taking the same path and traveling through the interface zone.

Around 0800 hours on October 30, gopher 25 returned to its den site. Telemetry fixes 22 minutes apart show 25 within 1.42 m of 24, who was at 25's food cache. We believe a fight may have occurred, maybe even on the surface, because the signal strengths doubled and the antenna pattern fluctuated wildly. This interaction lasted less than one hour because 25 was located back at its den site around 0900 hours. For approximately another hour, signal levels for 24's transmitter were very low. Then 24 was recorded as being back at its own den site. We suspect 24 used a deep permanent tunnel to make its escape. The route 24 had been using to return to its den site before the combat had always registered clearly with the tracking system. In 549 observations, less than 30 minutes apart for both gophers, they were recorded as separated by less than 10 m on only 15 occasions (Table 2). Since gophers seem to avoid each other (Table 1), it appears that a high cost might be incurred with agonistic behavior.

Affiliative interactions were inferred from manual telemetry fixes and trapping records. No interactions of this type took place in range of the tracking system. During breeding season, male gophers would stay close to, within 2 or 3 m, but not under the same tussock as the females. This was observed for three male-female pairs, one case with a male and two females, and one case with a male and three females. There were three instances where a male gopher relocated to be closer to females during the spring and summer, and then moved back to his previous home range for fall and winter. From manual observations on radio-tagged gophers, we believe males dug into adjoining female burrow systems to initiate reproductive behavior. On one occasion, we monitored a radio-tagged female away from her den site. We dug into the tussock to set a trap because her transmitter battery was almost dead. When we scooped out a shovel full of dirt, a male gopher was in the soil on the shovel.

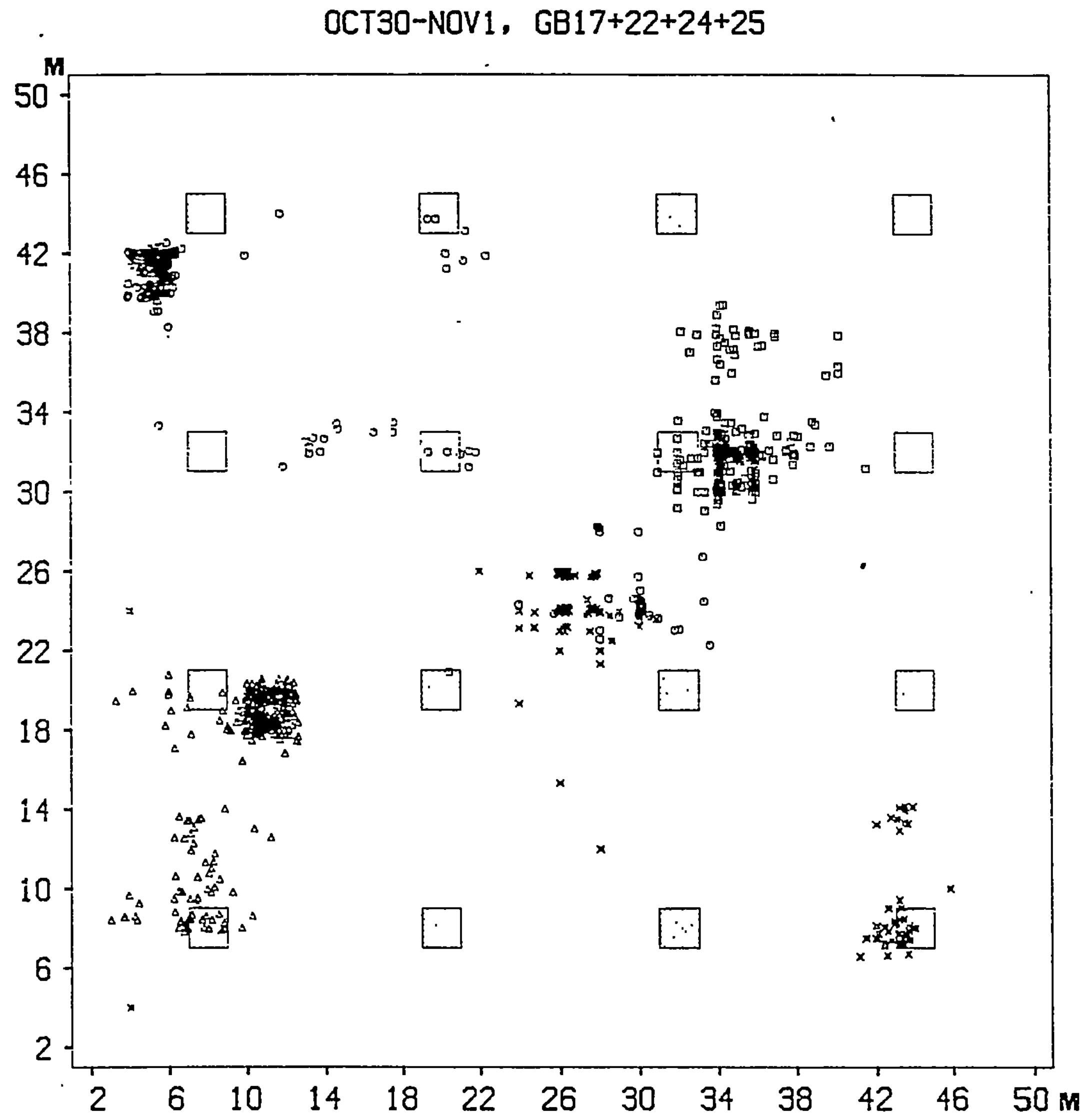

Figure 2. Gopher interactions from October 30 to November 1, 1984. The 0.25 ha gopher tracking grid is indicated as a square outline. Tracking system coordinate labels are indicated in meters; the "interface zone" is approximately at X=22, Y=32 in this plot. There are 16 4 m^2 fertilized patches indicated as shaded squares. A square is the symbol for gopher 17, an x for gopher 25, a triangle for gopher 22, and an octagon for gopher 24.

Juvenile gophers were determined to be the offspring of particular females on the basis of where the young gophers were initially trapped. The closest female which had been trapped while pregnant or lactating was assumed to be the parent. In nine of 16 cases, females relocated leaving female juveniles in possession of the natal burrow (Zinnel 1992). In the other seven instances, juveniles dispersed into nearby vacant home ranges. All three male juveniles dispersed.

DISCUSSION

Most of the detailed examples of gopher interactions recorded by telemetry were agonistic. Gophers were rarely recorded as being close to each other. Even during breeding season, males were never found in the same nest chamber with females, although males relocated closer to females. After raising a litter, more than 50 percent of adult females relocated, leaving female offspring in possession of the natal den site. All of these factors support the idea that gopher agonistic behavior has evolved to ensure an adequate food supply. However, we cannot rule out the possibility that agonistic behavior of males is related to defense or guarding of females.

When one gopher actually displaced another through combat, the larger gopher displaced the smaller 71 percent of the time. Data from this study support the findings by Williams and Cameron (1990) that gopher population density may be regulated at or near the ecological carrying capacity by intraspecific aggression. Gopher agonistic behavior appears to space individuals so as to insure a year-long food supply for both sexes and to protect immature females by leaving them in possession of the natal burrow system.

Gophers appear to be aware of burrow systems other than their own because gophers were recorded at newly-vacant den sites within days, and in one case, within hours, of the sites being vacated. Howard and Childs (1959) asserted that some tunnels were more or less common property and allowed gophers to find their way through other burrows without getting into lethal fights. Perhaps the many recorded occurrences of plural occupancy of burrow systems (Howard and Childs 1959, Hansen and Miller 1959, Miller and Bond 1960, Vaughan 1962, Bandoli 1981) represent rapid reinvasion. Gophers were probably aware of their neighbors. One possible mechanism for detecting presence or absence of neighboring gophers is "signposts" of feces left where tunnels come in contact with other burrow systems. During our trapping efforts, we frequently observed fresh gopher feces left in tunnels. As the microclimate of gopher burrows is very humid (Kennerly 1964), scent would remain longer and be more pervasive than with aboveground scats. A male gopher digging into a female burrow during breeding may have been able to detect a female's reproductive status from fecal hormones. Maternal pheromones present in the soft feces, caecotrophe, of rats have been found to mark mother and nest (Albone 1984). Similar processes might operate in equally coprophagous gophers.

Another possible mechanism for detecting presence is substrate vibrations which could be sensed by the long stiff hairs on the face and wrists, or by the long guard hairs and naked tail which help the gopher navigate when moving backwards through tunnels (Chase et al. 1982). Gophers make a loud clicking sound, easily transmitted by the packed soil because the intensity of low frequency sounds (<200 Hz) falls off more slowly in a burrow than in open air (D. R. Griffin pers. comm. 1985).

Based on measurements made on a variety of moist soils, Lewis and Narins (1985) found frog thump signals typically merged with the seismic background at distances of 3 to 6 m from the origin of the thumping. Vibrations from gopher digging or clicking vocalization probably would be detectable at distances of 6 m, the maximum distance for the propagation of Rayleigh waves (Lewis and Narins 1985), because gophers are able to make louder sounds than frogs. The minimum separation distance recorded for gopher 17 versus 24 and for gopher 22 versus 17 was 6 m (Table 1B). Table 2 clearly shows the threshold separation distance for gophers 24 and 25 to be just over 6 m. Geophones were able to detect both the clicking vocalization and "shushing" sound of digging better than microphones placed in a burrow (D.R. Griffin personal communication 1985). Telemetry data reveal that gophers do not have to come into physical contact to be aware of activities of neighboring gophers.

We have offered two hypotheses for the observed behavior of gophers sensing the presence or absence of other gophers without approaching closer than 6 m. These suggestions need to be verified by further experimentation. The function of substrate-born seismic signals in gopher communication can be tested by burying remotely controlled playback equipment and monitoring gopher movements in response to seismic stimuli with telemetry. The informational content of gopher feces could be verified by placing fecal signposts in a vacant home range during August/September dispersal to determine if feces presence deters occupancy.

Our interpretations of underground movement patterns of plains pocket gophers, as revealed by telemetry, support concepts of strong territoriality, but also indicate use of burrows by several individuals. Social interactions suggested by movement patterns provide further insight into population dynamics and the relationship between pocket gophers and their prairie environment.

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