Dispersal of black-tailed prairie dogs (*Cynomys ludovicianus*) in Wind Cave National Park, South Dakota

by

Monte George Garrett

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
MASTER OF SCIENCE

Department: Animal Ecology
Major: Wildlife Biology

Iowa State University
Ames, Iowa

1982

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

This 3-year investigation of prairie dogs was supported by a grant from the National Park Service (CX-1200-0-B020). Numerous individuals offered guidance and assistance throughout the study period. They are as follows:

Committee members:

William Franklin, my major advisor, offered advice and was a continuous source of enthusiasm. I am thankful for the encouragement and freedom that he extended me during all phases of this project.

Erwin Klaas, William Clark, and George Thomson provided me with equipment, vehicle, and help with my experimental design. In addition, they offered stimulating coursework during my academic program at ISU.

Park personnel:

Lester McClanahan, Wind Cave National Park Superintendent, was very helpful in providing research facilities and allowing me unrestricted freedom in the park while radiotelemetering prairie dogs. I thank Rich Klukas, park research biologist, for locating my study colony, and providing advice and assistance in data collection. Bruce Freet, Tim Oliverius, Dean Shilts, Joe Allen, Pam Allen, Danny Simms, and Jean Donnell were also very helpful.

Field assistants:

I thank Kurt McAninch and Joan Graden for their dedication and loyalty in the collection of data. These two individuals each logged in excess of 500 hr in the study blind observing prairie dog behavior. In addition, the following persons assisted in field work: Susie Garrett*, Layne Coppock, Terry Johns, Ahmad Abdunabi, Robert Kohlsdorf, Diane Wright, Donna Lewis, Mike Laycock, Doug Shown*, Randy Hayman*, John McDill*, Reed Lewis*, Tim Oliverius*, Steve White*, Ansel Woodenknife*, Jim Dahlberg*, Rich Lasky*, and Deb Buitron* (astericks denote those assisting in the capture of dispersing prairie dogs).

Other acknowledgements:

It is doubtful that this project would have been successful without the constant advice and consultation of John Hoogland. He "showed me the ropes", providing me with technical assistance and interpretation of the behavior of this marvelous study animal. I wish best luck to John and his coterie.

Greg Jones provided technical assistance in the building of my telemetry antennaes. Jewell Popp helped me in the identification of prairie plants so necessary for my vegetation analysis. Steve and Gwen Archer, Deb Buitron, Layne Coppock, Deb Hussey, Preston "Two-lips" Hardison, Reid and Donna Lewis, Doug Shown, Danny Simms, Steve White, and

Ansel and Teri Woodenknife provided me with lively companionship during the study period.

Finally, I thank my son, Shannon, for the capacity to tolerate a part-time papa, and my wife, Susie, who was my sole field assistant during the 1979 field season, and has been my best friend for more than 10 years.

ABSTRACT

An investigation of black-tailed prairie dogs (Cynomys ludovicianus) was conducted to gather baseline information on dispersal activities and to identify factors responsible for dispersal behavior. Study was conducted in Wind Cave National Park from 1979 to 1981. Dispersing prairie dogs were radiotracked to determine distance of movements and survivorship, and a study colony was intensively monitored to determine proximate factors that cause dispersal.

Exchange of individuals between coteries (family groups) within the study colony (intracolony dispersal) occurred during all times of year, while dispersal away from established colonies (intercolony dispersal) occurred only during a predictable period in late spring. Both males and females dispersed, but males were predominantly yearlings while females also included many older individuals. Intercolony dispersers appeared to be in good physical condition, moved an average distance of 2.4 km from the point of capture, and survivors immigrated into existing colonies; no new colonies were established by radiocollared animals. The mortality rate of intercolony dispersers was significantly greater compared with residents of the study colony.

Several proximate factors seem to be related to dispersal. Prairie dogs prefer the new vegetative growth at colony peripheries. An inverse relationship exists between animal density relative to this food resource and the relative change in animal numbers during the dispersal season, although this may not be a linear relationship. There was no relationship between absolute coterie density and change in animal numbers. Other factors include the shortage of unrelated females in the coterie, harassment of females by juveniles, and probably genetic influences.

The initiation of new prairie dog colonies in Wind Cave National Park may be related to factors that disturb the native vegetation. Major differences between newly established colonies and undisturbed prairie seem to be physical characteristics of the site, such as the height of vegetation and the proportion of bare ground. This may be directly influenced by park management practices (e.g., limiting the size of the ungulate herds, controlled burns), and should be an important consideration when implementing management plans.

INTRODUCTION

Dispersal is a natural biological process. The continued occupancy of the same site by both parents and offspring, utilizing a limited resource base, may threaten survival. The effects of dispersal on the species include the maintenance of genetic variability, facilitation of gene flow among populations, and the spread of the species over large geographical areas (Gaines and McClenaghan 1980). Although dispersal may be risky to the individual, benefits accruing to the disperser suggest a strong selective force underlying this behavior. These benefits may include qualitative and quantitative advantages as well as increased long-term survival (Lidicker 1962). Howard (1960) contended that the best measure of dispersal is the distance an individual's genes are transmitted rather than merely the distance the animal moves. But, probably because of the difficulties in recovering marked animals, I find little information on the ultimate fate of dispersers.

Emigration of surplus individuals in sciurids has been reported for thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) (McCarley 1966), Arctic ground squirrels (*S. undulatus*) (Carl 1971), Uinta ground squirrels (*S. armatus*) (Slade and Balph 1974), yellow-bellied marmots (*Marmota flaviventris*) (Armitage and Downhower 1974), Richardson's ground squirrels (S. richardsonii) (Michener and Michener 1977), and California ground squirrels (S. Beecheyi) (Dobson 1979). Dispersal probably functions in population regulation, but there is disagreement among investigators as to the mechanism behind this behavior (Chitty 1967, Christian 1970, Krebs et al. 1973, Lidicker 1975, Krebs 1978).

The purpose of this study was to investigate the dispersal activities of the black-tailed prairie dog (Cynomys ludovicianus). This large colonial ground squirrel is indigenous to the North American shortgrass prairie. Its range was originally bounded by the Rocky Mountains on the west and the tallgrass prairie on the east. Growth of colonies is restricted by tall vegetation and topographic barriers (King 1955, Koford 1958).

Prairie dogs are strictly colonial, and only rarely are individuals reported away from established colonies (Koford 1958:15; Smith 1958:30). A primary benefit of prairie dog coloniality is reduced predation, while costs include increased competition for burrows and mates, and increased ectoparasitism (Hoogland 1979, 1981a). Colonies are subdivided into cooperative family units called coteries (King 1955). Prairie dogs are polygynous; a coterie typically contains 1 adult male, 3-4 adult females, and several yearlings and juveniles of both sexes (Hoogland 1981b). Thus, the sex ratio of most prairie dog populations is skewed in favor of females. Members of a coterie restrict their activities within a well-defined coterie territory, which they defend from members of other coteries. Coterie members generally are amicable toward each other and hostile toward noncoterie members. Prairie dogs frequently suffer cuts and other injuries during fights with conspecifics. Hoogland (1981b) concluded that the coterie system is a mechanism by which the benefits of coloniality are directed primarily toward close genetic relatives.

In northern latitudes, prairie dogs generally do not breed until 2 years old (King 1955, Hoogland 1977, 1982, but see Garrett et al. 1982). Breeding occurs during late February and throughout March. Gestation is about 34 days, infants remain underground for an additional 5-6 weeks, and weaned juveniles emerge from their natal burrows in May and early June. After emergence, litters within the same coterie mix, juveniles using any burrow in the territory and sleeping with any other individual of the coterie. Females usually remain in the natal coterie for their entire lives, whereas males usually spend the first year in their natal coterie and disperse during their second year (Hoogland 1982). Female prairie dogs may live 5-6 years, while their male counterparts usually do not survive longer than 4 years (Hoogland 1981b).

Prairie dogs are almost entirely herbivorous and prefer graminoids over forbs (Kelso 1939, Koford 1958, Smith 1958, Hansen and Gold 1977). Burrowing and grazing by prairie dogs greatly influence the soil and vegetation. Tall plant species are clipped thereby promoting the growth of preferred shortgrasses (bufflaograss, *Buchloe dactyloides*; blue grama, *Bouteloua gracilis*) (Koford 1958, Summers and Linder 1978, Wydeven 1979). King (1955) noted that intensive grazing in the middle of the colony results in depletion of grass; forbs subsequently invade these highly impacted areas and become dominant. Due to these effects, *vegetation zones* in roughly concentric rings may be produced on prairie dog colonies (Osborn and Allan 1949, Bonham and Lerwick 1976, Garrett et al. 1982). As the colony expands into the surrounding prairie, shallow peripheral burrows are excavated in the newly modified vegetation (King 1955). These burrows eventually become well-developed as the animals spend additional time in the area of expansion.

Movement of individuals between coteries of the same colony has been documented (Hoogland 1982), but the mechanism responsible for long-distance dispersal between colonies is not understood. In King's (1955:51) words, if "positive information could be secured about the frequency, cause, and method of...[prairie dog] migration, it would be of biological importance." The objectives of this study were

1) to gather basic information pertaining to prairie dog dispersal including time of dispersal, sex and age of dispersing individuals, distance travelled, and degree of success; and 2) to identify factors contributing to the dispersal of prairie dogs from established colonies.

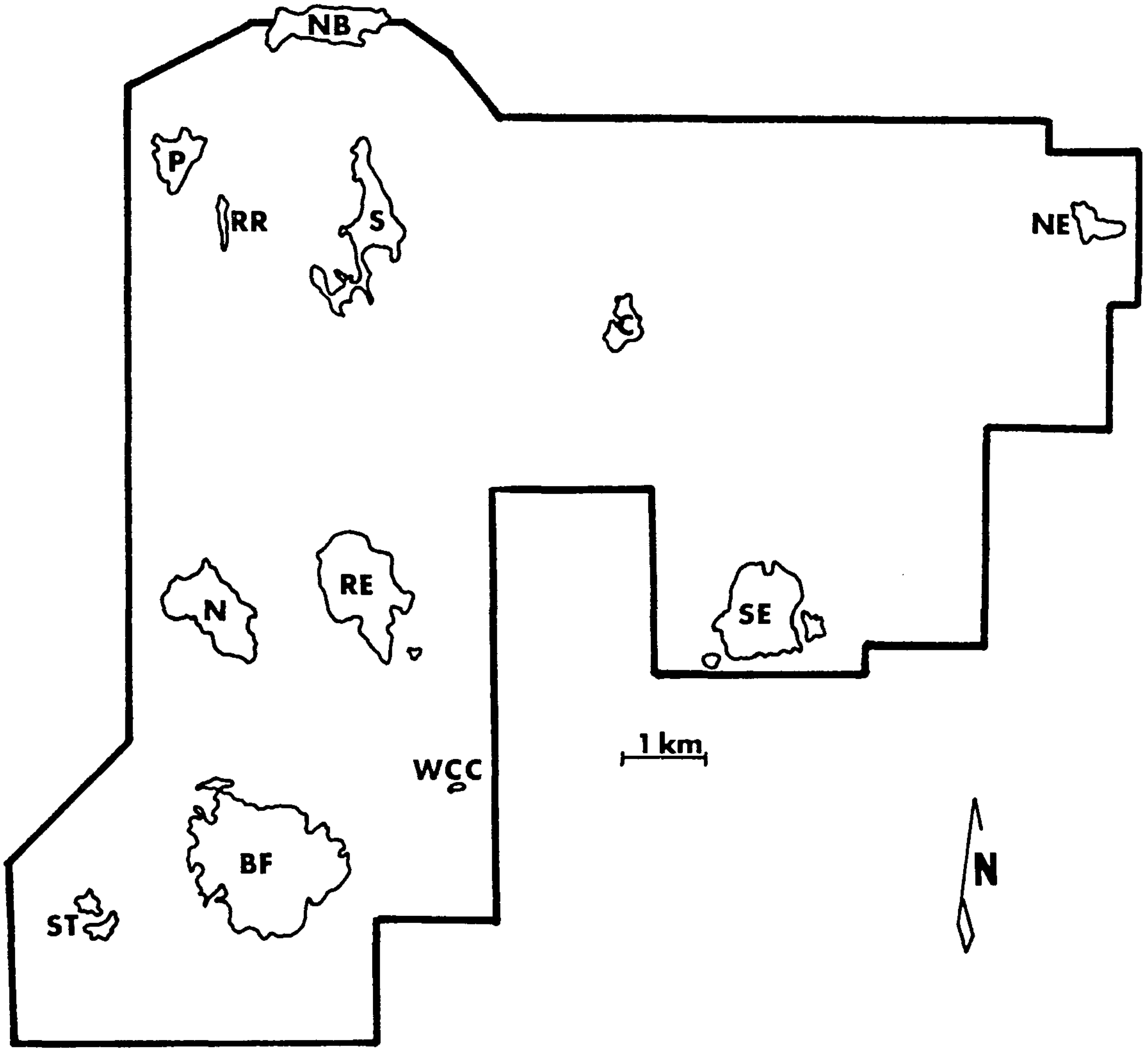
METHODS AND MATERIALS

The Study Area

Wind Cave National Park (WCNP) is located at the southern edge of the Black Hills, South Dakota. The area is rolling mixed-grass prairie with coniferous forest on slopes and ridge tops (see King 1955). The prairie dog is a protected wildlife species in the park, whose numbers have not been officially controlled for at least 15 years. There were 11 large prairie dog colonies in WCNP during the period of study (Dalsted et al. 1981) (Figure 1).

Field work was conducted from June to September 1979, March to October 1980, and May to November 1981. The study colony was located in Wind Cave Canyon, section 6, T. 6 S., R. 6 E., at an elevation of approximately 1300 m. The colony was located on a 3.6 ha floodplain of an ephemeral watercourse. The soil is a deep dark silt loam. The site was a horse pasture until 1973, and was burned as part of a research project in the spring of 1976. Prairie dogs were first discovered at the site in the fall of 1976 and were shot by a park ranger (Dean Shilts, WCNP ranger, personal communication). Survivors or immigrants repopulated the site. When research began in May 1979, the colony covered a 0.47 ha section of the floodplain. By November 1981, the colony had expanded 295% to include 1.86 ha, and 380 new

Figure 1. Locations of prairie dog colonies in Wind Cave National Park 1980. NB = Northboundary, P = Pringle, RR = Rankin, S = Sanctuary, C = Central, NE = Northeast, SE = Southeast, N = Norbeck, RE = Research Reserve, ST = Shirttail, BF = Bison Flats, WCC = Wind Cave Canyon (study colony)


NB
P
RR
S
NE
C
N
RE
SE
WCC
1 km
BF
ST
N

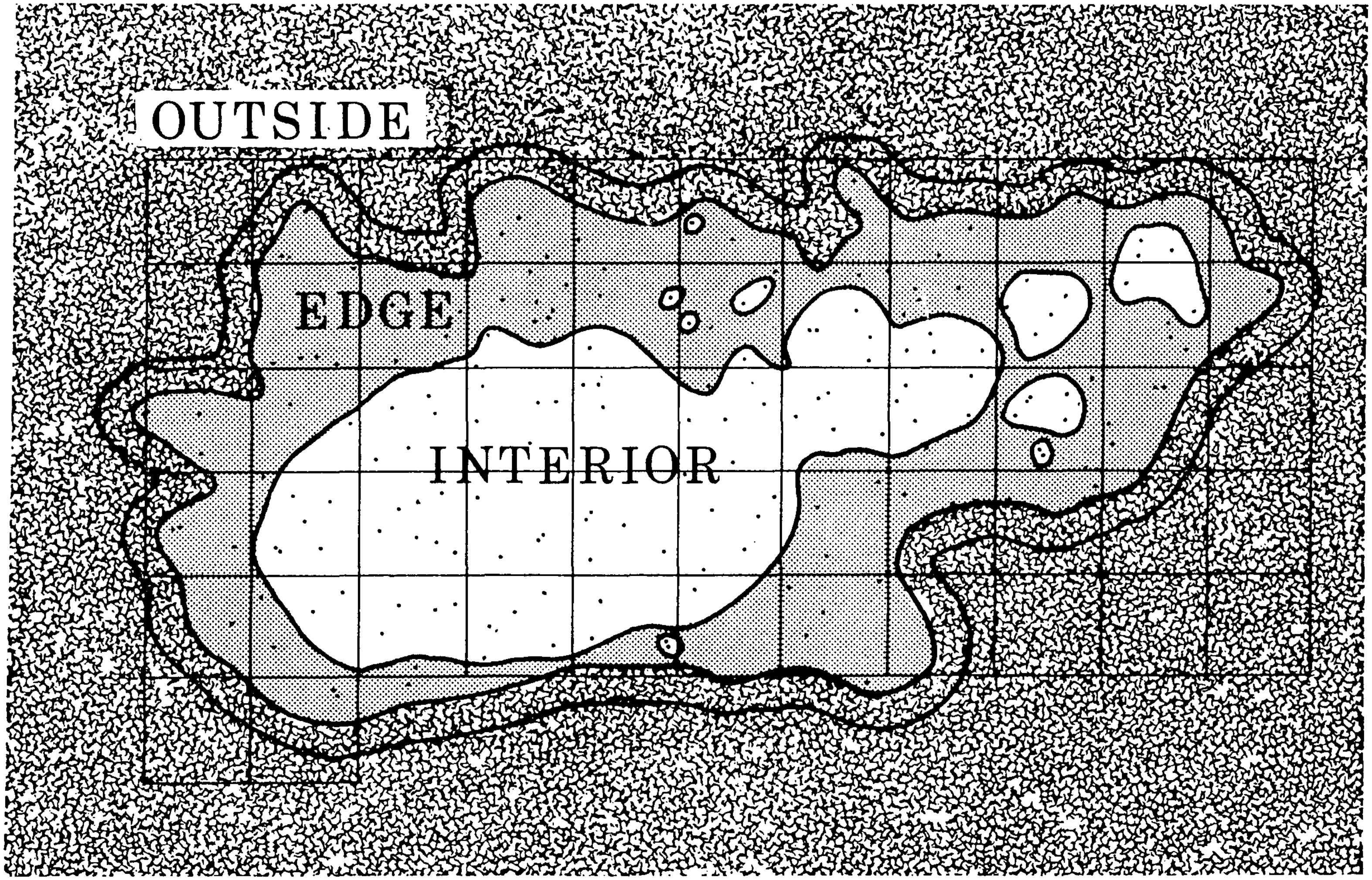
burrow entrances were excavated (189% increase) (cf. Garrett et al. 1982). Rapid colony expansion resulted in rapid modification of the vegetation; thus, vegetation zones were particularly visible on this colony (Figure 2).

The population of the study colony increased from 32 individuals in May 1979 to 80 individuals in November 1981 (150% increase). However, numbers actually decreased from a high of 85 in October 1980, a probable result of treatment with diethystilbestrol to the prairie dogs during the breeding season of 1981 (Garrett and Franklin 1982).

Definition of Terms

A colony was defined as the physical area inhabited by prairie dogs, which is characterized by burrow mounds and modified vegetation. The population refers to the prairie dogs inhabiting the colony area. A disperser was considered to be any prairie dog found away from a colony, and individuals that immigrated into the study colony. A successful disperser was defined as a disperser that was integrated into a population (interacting amicably with the other animals). I defined infant prairie dogs as individuals in the natal burrow prior to first emergence. Subsequent age classes were determined relative to the prairie dog breeding season (February): juveniles from first emergence to 7 months postemergence, yearlings from 8 to 20 months, 2-year-olds from 21 to 32 months, and so on.

Figure 2. Vegetation zones of the study colony present May 1980. These zones are described in detail by Garrett et al. (1982). The heavy line in the outside zone denotes a 5-m area surrounding the edge zone in which prairie dogs were occasionally observed feeding. A 15-m grid system is superimposed on the colony. Dots indicate burrows


OUTSIDE
EDGE
INTERIOR

Procedures

Trapping and observation of prairie dogs

All prairie dogs of the study colony during 1979-1981 were captured and marked to make behavioral observations, distinguish between residents and immigrants, determine coterie membership, and identify genetic relationships among individuals. Trapping occurred following each molting period: June and September for adults; June, July and September for juveniles. Adults were captured with National 15cm x 15cm x 60cm doubledoor live traps; juveniles usually required the use of National 13cm x 13cm x 40cm single-door live traps. Trap treadles were smeared with vegetable oil to prevent blowing away of the oat bait. Adults were captured by randomly placing traps near active burrow entrances (those with loose dirt, fresh scats). Young prairie dogs were captured immediately after first emergence from natal burrows to determine maternal and sibling relationships. The nest burrow was encircled with traps as soon as young were first seen emerging, and nearby burrow entrances (that might be connected to the nest burrow) were blocked. In this manner, all litters within a coterie were captured and marked before litter-mixing occurred.

Each captured prairie dog was transferred to a conical bag for handling, number and size of head scars counted, and molars checked for wear. Dispersers usually were fitted with a radiocollar. Fur dye (Nyanzol D) provided excellent temporary identification (King 1955, Tileston and Lechleitner 1966, Hoogland 1977). Each prairie dog was marked with a unique combination of stripes, rings, circles, and other gross patterns. Permanent identification was insured by placing a National #1 eartag in each ear. After the dye pattern was lost through molting, the animals were retrapped, identified by eartag numbers, and remarked with dye.

Observations at the study colony were made from a blind constructed on an uphill edge of the colony. Because prairie dogs do not colonize rocky slopes (Koford 1958), this location probably had little influence on colony expansion activities. In 1979, habituation by the prairie dogs near the blind required nearly a month. Habituation to a new blind constructed in 1981 required only a week, perhaps because animal density directly in front of the new blind was lower and the prairie dogs had become more accustomed to my presence.

The locations of territorial disputes were regularly recorded on a map of the colony. Determining exact locations was made possible by a 15-m grid system (Figure 2) and large plastic markers at well-used burrow mounds. In this manner, territorial boundaries were delineated and coterie compositions identified. Thus, any change in coterie composition due to immigration or emigration was easily observed. Vegetation zones were remapped every 2-3 months to quantify changes in colony size and types of vegetation available in each coterie territory.

Aging prairie dogs by tooth wear

Tooth wear on the molars was determined by holding the mouth open with a large pair of ring pliers. Wear on the molars was classified as 1) high cusps, 2) cusps slightly worn, 3) cusps rounded with dentin visible, 4) molars completely flattened at or near the gum line. By 1981, tooth wear data from known-age residents of the study colony indicated the first 2 categories to be yearlings and 2-year-olds, respectively. Adult sized individuals with high cusps in 1979 fit into the third class in 1981, indicating that they were probably 3-year-olds. The fourth category was classified as ≥ 4-year-olds. Dispersers and immigrants captured in 1980 and 1981 were aged according to these tooth-wear classes.

Radiotelemetering of dispersing prairie dogs

Radiotelemetry has been used by several investigators to monitor movements of rodent species (Banks et al. 1974, Cranford 1977, Mineau and Madison 1977), but not for the semifossorial prairie dog. Radiocollars were designed especially for this study by Cedar Creek Bioelectronics Lab, 2660 Fawn Lake Drive N.E., Bethel, Minnesota. Each collar weighed about 30 g (approximately 3% of the body weight of an adult prairie dog), and transmitted at frequencies of 164.1-164.9 Mhz. The effect of the radiocollars on the behavior of 5 residents of the study colony was investigated in 1979 (Table 1). The behavior of the experimental animals was not significantly different from that of uncollared colony residents ($X^2 = 7.53$, df = 9, $P > .50$). Because prairie dogs commonly groom each other, the collars were made of a polyester/fiberglass cord that proved to be impervious to gnawing. Prairie dogs have large heads, and it is improbable that the radiocollars could slip off. Three residents of the study colony wore collars for 5 months during 1980.

Dispersers found away from colonies were captured with nets and burlap bags. These individuals were radiocollared and immediately released at the capture location. The dispersers were tracked with a hand-held yagi antenna and portable AVM receiver. To avoid chasing the disperser or otherwise affecting its movement, the tracker maintained a distance of approximately 0.5 km behind the prairie dog. Tracking continued until the the disperser died, stopped moving at dusk, or entered a colony. Locations of dispersers were checked daily, and eventually weekly, until the transmitters failed (approximately 3 months). A mortality was counted if the disperser's body was found or its collar

Table 1. A comparison of the behavior of radiocollared and uncollared prairie dogs of the study colony, July 1979. The colony was scanned at hourly intervals. Activities of both radiocollared and uncollared individuals were recorded simultaneously. Percentages of total are within parentheses

	FREQUENCY OF OBSERVATIONS	
ACTIVITY	RADIOCOLLARED PRAIRIE DOGS	UNCOLLARED PRAIRIE DOGS
SITTING	16 (5)	49 (5)
STAND ALERT	12 (4)	44 (5)
WALKING	36 (11)	85 (9)
RUNNING	6 (2)	16 (2)
ALLOGROOMING	2 (1)	10 (1)
AUTOGROOMING	2 (1)	12 (1)
HEAD OUT	2 (1)	13 (1)
SUNNING	2 (1)	12 (1)
AGONISTIC	4 (1)	14 (2)
FEEDING	251 (75)	691 (73)
TOTAL	333	946

was found. In case of the latter, a predation was counted only if the collar was severely chewed and accompanied by blood or body parts. If a disperser was lost during tracking, data on dispersal distance for that individual were disregarded.

Immigrants to the study colony were radiocollared to facilitate the collection of survival data, and to monitor any additional movement. Because it was not possible to simultaneously track numerous animals, not all dispersers and immigrants were radiocollared.

Vegetation analyses

In 1979, 5 newly established colonies were located that were no more than 3 months old. Because of the young age of these colonies, I assumed that the condition of the vegetation was not due to prairie dog modification. Vegetation species groups and characteristics were analyzed by sampling 30 plots at regular intervals along a transect across the greatest length of the colony (Daubenmire 1959). Vegetation height was measured to the nearest cm. These new colonies were compared with disturbed, but uncolonized, sites: 1 recently burned, 1 surrounding a buffalo watering hole, and 3 cattle pastures randomly located on private land outside the park boundary. In addition, undisturbed prairie sites were randomly located inside the park in 1979 and 1980, and compared with the above areas.

A small controlled burn was conducted by WCNP staff in the fall of 1979 beside a large colony. In March and October 1980, active burrows were counted on burned and unburned 1 ha plots. The sample plots were situated in colony expansion areas with similar soil, topography, and vegetation.

Statistical procedures

Data were analyzed by parametric chi-square tests, t-tests, F tests, Fisher's Exact Tests, and analysis of variance. For the latter, significant differences between means were determined using Duncan's New Multiple-range Test. Because data for the vegetation analysis were recorded as percentages, an arcsine transformation was used to correct for non-normal distribution. Exact probability for multiple-cell chi-square analysis followed Baker (1977) but modified by Ken Koehler, Statistics Department, Iowa State University.

All significance levels are reported from one-tailed statistical analyses. Means are expressed ± one standard deviation and sample sizes are indicated by parentheses.

RESULTS AND DISCUSSION

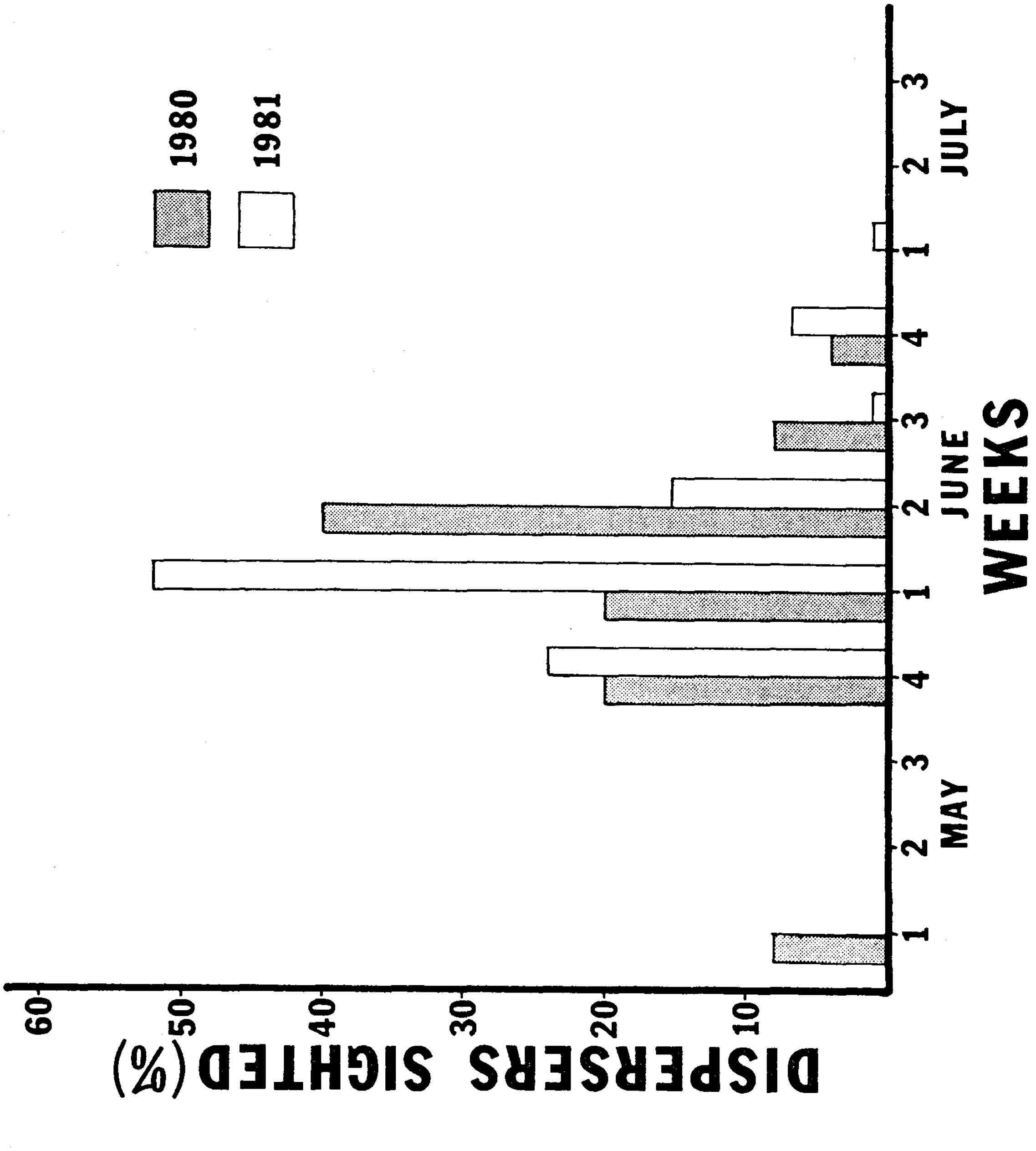
Attributes of Dispersers

Two distinct types of prairie dog dispersal occurred. _Intracolony_ dispersal was movement away from the natal coterie into another coterie of the same colony. This usually resulted in colony expansion due to plant modification and burrow excavation on the colony periphery (King 1955). _Intercolony_ dispersal was movement away from the natal colony and generally involved long-distance movements. Intercolony dispersal may result in either colony expansion or the initiation of new colonies.

Dispersal season

Intercolony dispersal occurred only during an annual 5-week period, the peak occurring in early June (Figure 3). Dispersal seasons coincided with spring precipitation and the emergence of litters. Thus, dispersing individuals probably had good food and cover for travel, and emigrated at a time when animal density was highest on prairie dog colonies (King 1955, Koford 1958). Prairie dogs have never been reported away from established colonies in WCNP at other times of the year (Rich Klukas, WCNP Research Biologist, personal communication).

Figure 3. Dispersing prairie dogs sighted away from established colonies during 1980 (N = 25) and 1981 (N = 75). Proportions were calculated independently for each year. No dispersers were sighted at any other times


DISPERSERS SIGHTED(%)
60
50
40
30
20
10
WEEKS
MAY
1
2
3
4
JUNE
1
2
3
4
JULY
1
2
3
1980
1981

Intracolony dispersal at the study colony was observed throughout the year. However, most intracolony dispersal and unexplained disappearances of animals occurred during winter and spring ($X^2 = 24.5$, df = 4, $P < .005$) (Figure 4). The spring period coincided with sightings of intercolony dispersers, and was the only time that immigrants arrived at the study colony. Many of the unexplained disappearances during spring were probably due to emigration. Because these animals do not hibernate, winter may be a critical time of year (Koford 1958). Thus, most disappearances in winter were believed to be *in situ* mortality.

Sex and age of dispersers

There was a significant sexual difference in the age of intercolony dispersers captured in WCNP during 1980 and 1981; males tended to be yearlings, while females included both yearlings and older individuals ($X^2 = 16.9$, df = 2, $P < .005$) (Table 2). If dispersers represented a random subset of the population, then a female-skewed ratio should result because females generally outnumber males in prairie dog populations (Koford 1958, Hoogland 1977). However, there was no statistical difference between the sexes of dispersers captured during this study ($X^2 = 0.58$, df = 1, $P > .25$). Moreover, the sex ratio of yearlings (prereproductives) was unexpectedly skewed in favor of *males* (2.6:1).

Figure 4. Intracolony dispersal and unexplained disappearances at the study colony during 5 time periods in 1980 and 1981. Winter included the 4-month period from November through February; other time periods were 2 months each. Proportions were calculated based on 75 movements-disappearances over the 2-year period

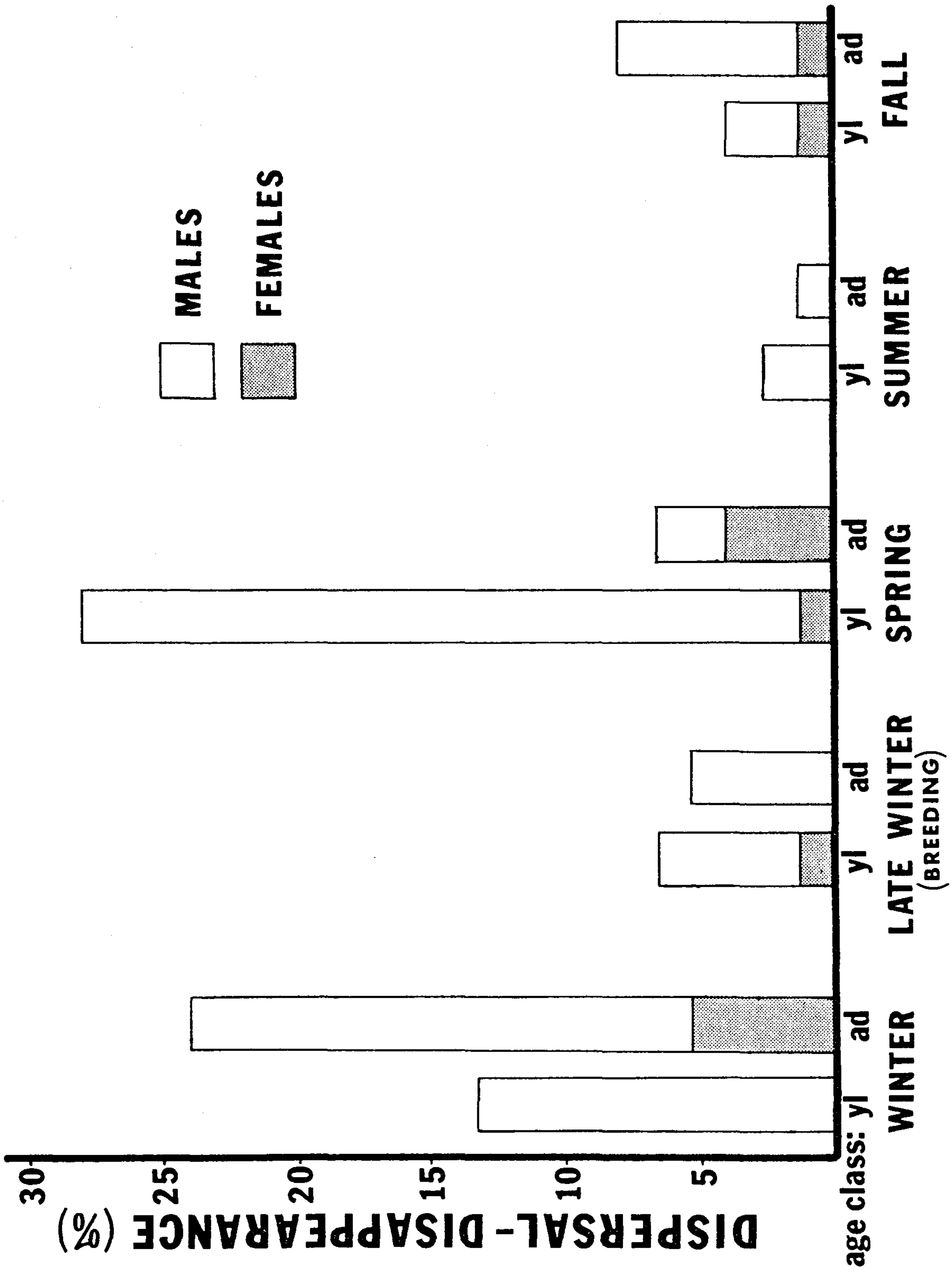

DISPERSAL-DISAPPEARANCE (%)
30
25
20
15
10
5
age class: yl
ad
WINTER
yl
ad
LATE WINTER
(BREEDING)
yl
ad
SPRING
yl
ad
SUMMER
yl
ad
FALL
MALES
FEMALES

Table 2. Sex and age of intercolony dispersers (including 3 roadkills) during 1980 and 1981. Relative frequencies are within parentheses

	FREQUENCY	
AGE	MALE	FEMALE
YEARLING	31 (91)	12 (42)
2 YEARS	2 (6)	8 (29)
>2 YEARS	1 (3)	8 (29)
TOTAL	34	28

During the dispersal seasons at the study colony, disappearance and intracolony dispersal was also more likely for yearling males than yearling females (P < .001, Fisher's Exact Test), and for yearling males than adult males (P = .001, Fisher's Exact Test) (Figure 4). Dispersal of predominantly prereproductive individuals is common in sciurids (McCarley 1966, Armitage 1973, Barash 1973, Michener 1982) and occasional in cricetids (Gaines and McClenaghan 1980). A male-skewed sex ratio of dispersers prior to first breeding may reduce inbreeding (Howard 1960, Lidicker 1962) and allow females to remain and breed in a familiar area, enhancing reproductive success (Michener 1982).

Given the risks involved in intercolony dispersal (see p. 41-42), it is difficult to understand why older females dispersed. Though seemingly healthy (body weight, general appearance), several were extremely old (molars worn to the gum line). There was little movement or disappearance of female residents of the study colony. The typical pattern was for yearling males to disperse and females of all ages to remain in their natal coteries.

Hoogland (1982) reported that males disperse within their natal colony as yearlings. After about 2 years, these adult males again move to different coteries within that colony leaving their mates and female offspring. In this study, there was a conspicuous absence of adult males in the sample of intercolony dispersers (Table 2). The difference in lifespan between males and females may account for this. By their third or fourth year, males appeared to be in poorer condition compared with females of the study colony. The longer-lived females probably were capable of long-distance movement at older ages.

Distance of dispersal

During 1980 and 1981, 16 dispersing prairie dogs were radiocollared and tracked to their destination (Table 3). Destination refers to their death or to their establishment within a previously existing colony. Note that the distance travelled was measured from the point of capture while *en route*. Therefore, these values should be considered minimum. The dispersal routes were generally meandering; the straightline distance ($\overline{X} = 2.4 \pm 1.7$ km) was somewhat less than the actual distance travelled ($\overline{X} = 3.0 \pm 2.1$ km). The mean distance travelled by males was significantly greater than that of females (males: $\overline{X} = 3.9 \pm 2.4$ km, $N = 8$; females: $\overline{X} = 2.1 \pm 1.5$ km, $N = 8$; $t = 1.79$, $P < .05$). The adaptive value of distance-differential dispersal between the sexes is the reduced chance of inadvertently mating with a close genetic relative (Howard 1960). Difference in dispersal distances between the sexes has been reported for thirteen-lined ground squirrels (Rongstad 1965), woodchucks (*Marmota monax*) (Snyder 1976), meadow voles (*Microtus*

Table 3. Characteristics of intercolony dispersers radiocollared during 1980 and 1981. Included are individuals captured on roadsides away from colonies and immigrants captured at, and subsequently dispersed away from, the study colony. Rate of travel was calculated using actual dispersal distance/hours

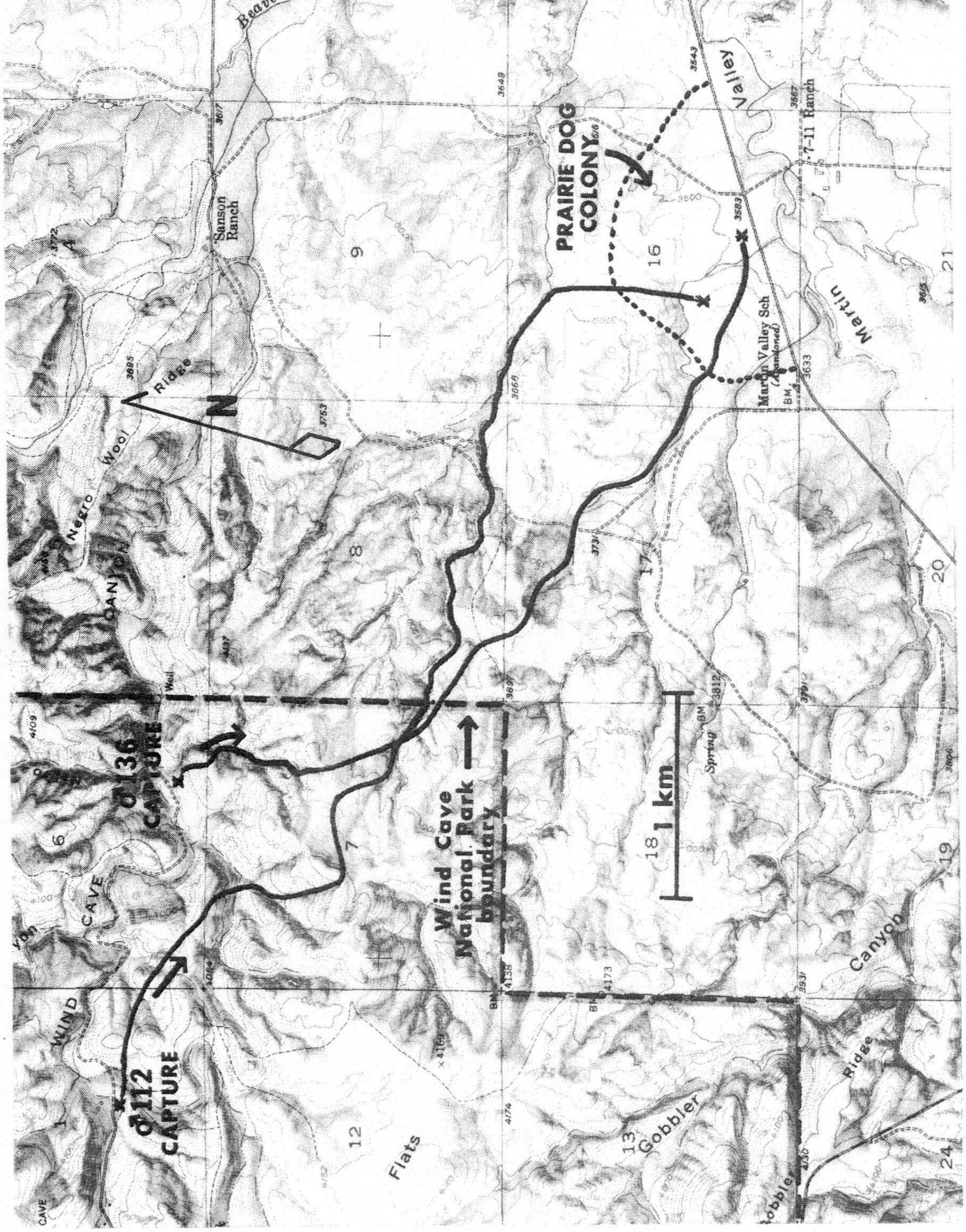
	TIME		DISTANCE (KM)		RATE OF
DISPERSER	DAYS	HOURS	STRAIGHTLINE	ACTUAL	TRAVEL
F 103	1	0.8	1.9	2.2	2.8
F 109	1	3.0	0.5	0.8	0.3
M 111	2	4.8	1.8	2.6	0.5
M 112	2	5.8	5.5	6.7	1.2
F 114	1	1.0	1.7	2.6	2.6
M 136	1	1.5	4.3	4.9	3.3
M 138	1	4.5	4.5	6.4	1.4
F 140	1	1.5	2.6	3.4	2.3
F 142	1	0.5	0.9	1.0	2.0
F 200	1	2.5	3.9	4.8	1.9
M 201	2	5.0	2.9	3.3	0.7
F 213	1	0.3	0.5	0.5	1.7
F 221	1	2.5	1.3	1.5	0.6
M 222	1	5.5	4.2	5.6	1.0
M 223	1	0.2	0.5	0.5	2.5
M 224	2	0.8	0.7	0.8	1.0
MEANS (N = 16)		2.5±2.0	2.4±1.7	3.0±2.1	1.6±0.9

pennsylvanicus) (Tamarin 1977), Richardson's ground squirrels (Michener and Michener 1977), and California ground squirrels (Dobson 1979).

Dispersers not captured as immigrants into the study colony were captured on the sides of park roads. Aside from the fact that animals were most likely seen here, the weedy vegetation along roadsides also offered good cover for movement (Koford 1958). Routes taken by 2 dispersers are illustrated in Figure 5. Except for occasional dashes across open prairie, dispersers usually followed ravines, drainage areas, canyons, and other protected areas that provided some concealment from predators. Dispersers frequently travelled through extremely rough terrain (dense forests, mountainous areas) uncharacteristic of normal prairie dog habitat. The meandering routes usually resulted in slow rates of travel ($\overline{X} = 1.6 \pm 0.9$ km/hr) (Table 3). Most dispersers seemed to have no destination in mind, the movement being almost investigatory in nature. They generally moved from one point of cover to the next, frequently changing directions. However, if their route brought them near a prairie dog colony, a straightline dash for the colony sometimes resulted (for example, male 112; Figure 5).

It appeared that some movements were merely short-term exploratory journeys. For example, female 114 was a lactating female captured as an immigrant at the study

Figure 5. Routes of 2 radiocollared dispersers tracked during 1980 (male 112) and 1981 (male 136)


♂112 CAPTURE
♂136 CAPTURE
PRAIRIE DOG COLONY
Wind Cave National Park boundary
1 km
N
WIND CAVE CANYON
Negro Wool Ridge
Sanson Ranch
Beaver
Martin Valley
Martin Valley Sch (Abandoned)
7-11 Ranch
Gobbler Ridge
Gobbler Canyon
Flats
Spring
Well

colony. Upon her release, she left the colony, travelled 2.6 km in 1 hr to another colony, and was immediately seen "ID kissing" (King 1955) with an adult and 6 young prairie dogs. This was so uncharacteristic of both the rate of travel and the reception usually afforded an immigrant that it is likely she returned to her home coterie. Another example was male 67, a resident of the study colony. He reappeared in a different coterie after an absence of nearly a week during the dispersal season of 1981. But such cases were atypical. Most dispersers moved slowly and if they found a colony, their dispersal ended.

Condition of dispersers

Slade and Balph (1974) surmised that dispersing Uinta ground squirrels were as healthy as resident squirrels. Likewise, there were no obvious physical differences between dispersing and resident prairie dogs. Using scarring data as an index of social conflict prior to dispersal, I compared intercolony dispersers with study colony residents. I found that, in most cases, dispersers were less scarred than residents (Table 4). However, the average age of adult ($\geq$ 2 years) dispersers in 1981 was younger than the average adult resident of the study colony; therefore, scarring data for this cohort may not be comparable. But yearling male dispersers for both years were significantly less scarred than yearling male residents (1980: $t = 2.93$, $N = 16$,

Table 4. A comparison of the mean number of head scars per animal between residents of the study colony and intercolony dispersers during 1980 and 1981

	MALES			FEMALES	
	YEARLINGS	ADULTS		YEARLINGS	ADULTS
			1980		
RESIDENT	1.5 ± 0.8 (8)	3.6 ± 1.6 (7)		1.5 ± 1.6 (8)	2.4 ± 1.2 (10)
DISPERSER	0.4 ± 0.7 (8)	——		1.0 ± 1.2 (4)	1.8 ± 1.5 (4)
			1981		
RESIDENT	1.2 ± 1.3 (25)	4.1 ± 0.7 (7)		0.6 ± 1.2 (14)	1.9 ± 1.7 (16)
DISPERSER	0.3 ± 0.6 (21)	1.5 ± 2.1 (2)		0.4 ± 0.8 (7)	0.2 ± 0.4 (11)

$P < .01$; 1981: $t = 2.92$, $N = 46$, $P < .01$).

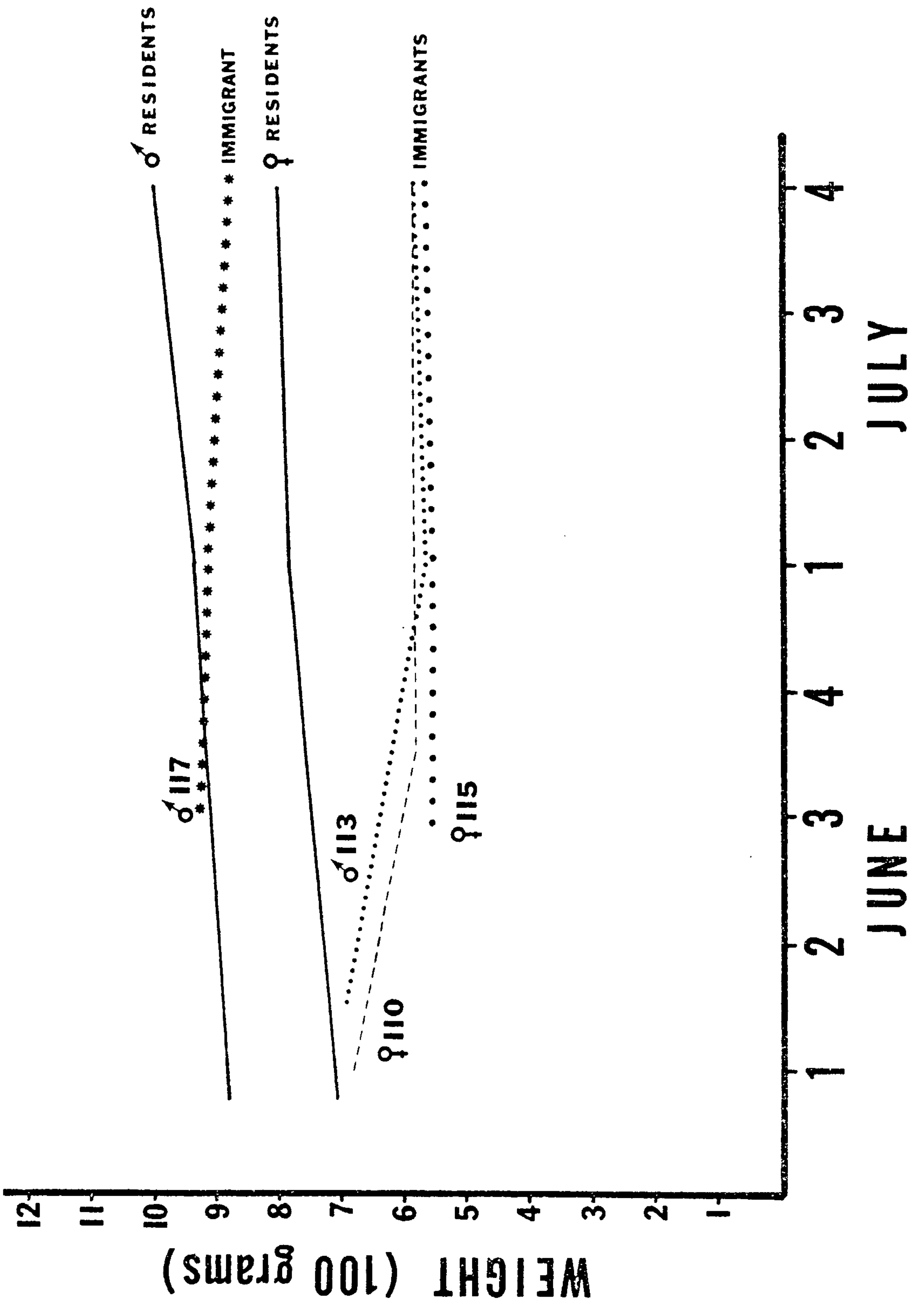
Body weight may be an indicator of physical condition. Weights of dispersers were significantly less than those of residents of the study colony (males: $t = 3.11$, $N = 60$, $P < .01$; females: $t = 3.66$, $N = 58$, $P < .01$) (Table 5). However, when compared with residents of another colony (Rankin Ridge) in WCNP, there was no difference between female mean weight ($t = 0.57$, $N = 105$, $P > .50$), and male dispersers were insignificantly heavier than male residents ($t = 1.45$, $N = 81$, $.05 < P < .10$). Therefore, I cannot conclude that dispersers were in poorer physical condition than residents.

There is some evidence that good physical condition may be necessary for successful immigration. Immigrants were probably subjected to considerable stress when attempting to enter a new colony. During the 1980 dispersal season, the 4 surviving immigrants into the study colony lost or maintained body weight while the residents were gaining weight (Figure 6). This placed the immigrants at a distinct disadvantage during the subsequent winter. Reduced weight at the onset of winter can result in poorer survivorship (Koford 1958, Michener 1974, Slade and Balph 1974). Of the 4 immigrants, only the heaviest survived to participate in the 1981 breeding season.

Table 5. A comparison of body weights between dispersers and 2 colonies of prairie dogs during the dispersal seasons of 1980 and 1981

	LIVE WEIGHT (G)		
	DISPERSERS	STUDY COLONY	RR COLONY
MALES	780.4 ± 92.5 (29)	848.6 ± 76.9 (31)	743.9 ± 116.2 (52)
FEMALES	686.6 ± 109.7 (28)	786.5 ± 98.4 (30)	674.5 ± 89.3 (77)

Figure 6. A comparison of body weight changes between residents and immigrants to the study colony during 1980

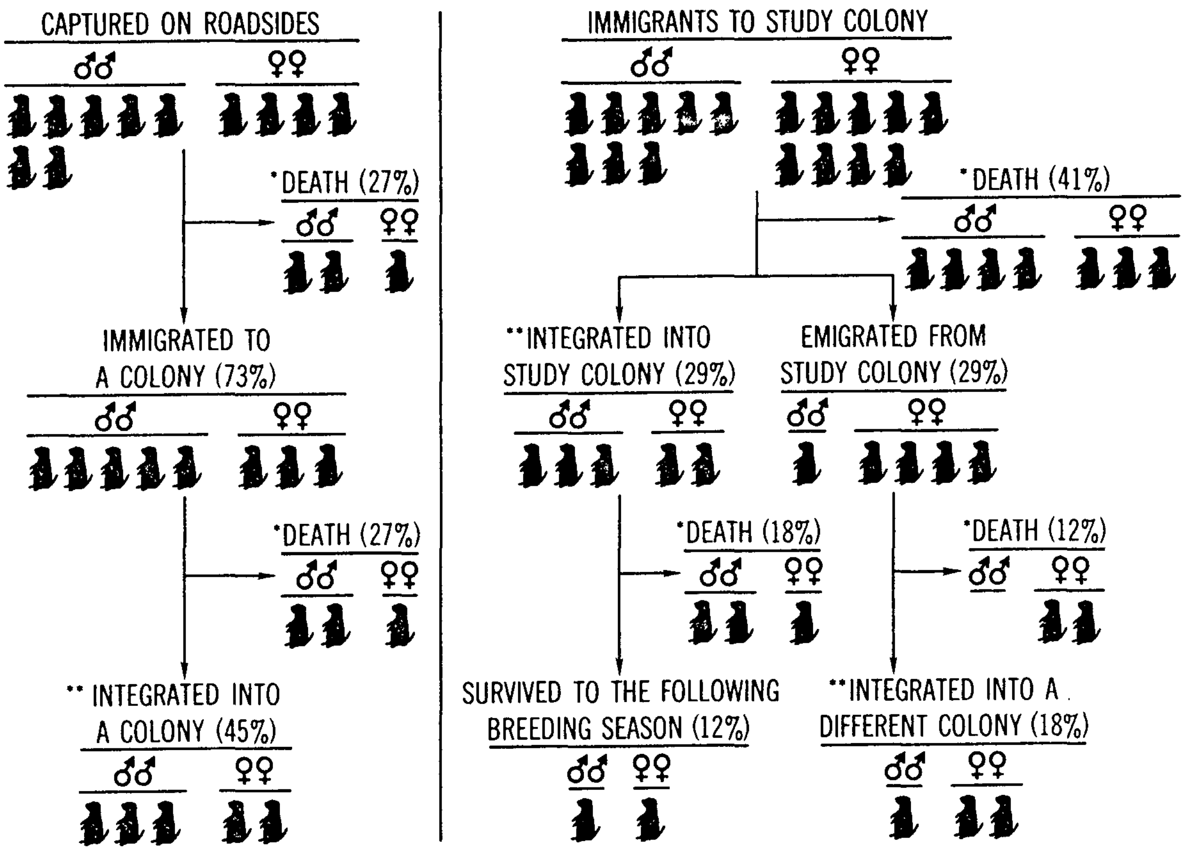

♂ RESIDENTS
IMMIGRANT
♀ RESIDENTS
IMMIGRANTS
♂117
♂113
♀110
♀115
WEIGHT (100 grams)
12
11
10
9
8
7
6
5
4
3
2
1
1
2
3
4
1
2
3
4
JUNE
JULY

Success of dispersers

A primary benefit of coloniality in prairie dogs is reduced predation (Hoogland 1981b). This may be due to increased "selfish herd" effects (Hamilton 1971) and increased awareness of predators via visual and vocal signals (Hoogland 1981a). Further, the collective result of vegetation clipping by colony members is a clear field of vision and, consequently, early detection of predators (King 1955, Koford 1958). In other words, prairie dogs effect changes in the environment of the colony that contribute to their survival. Observed predations of prairie dogs in colonies are rare (Garrett et al. 1982). Chances of survival for an individual that leaves favorable habitat and travels into unfamiliar habitat are poor (Errington 1946, Metzgar 1967, Ambrose 1972).

Figure 7 illustrates the ultimate fate of 28 radiocollared dispersers captured during 1980 and 1981. Of these, 17 were immigrants to the study colony, and 11 were captured on roadsides in WCNP. No individual initiated a new colony. Because dispersers were always observed moving alone, they had no opportunity to take advantage of social behavior that promotes survival in a colonial situation. To initiate a new colony, an individual must avoid predation until a suitable site is found, excavate a secure burrow system, await the chance arrival of another disperser of the

Figure 7. The fate of radiocollared dispersers captured during 1980 and 1981. Percentages indicate the proportion of the original total in each category. * = death due to predation, accidents, or aggression from conspecifics. ** = observed interacting amicably with colony residents and defending a territory within the colony


RADIOCOLLARED DISPERSERS

opposite sex, and survive for months until the onset of breeding. Thus, the probability of development of a new colony must be extremely small (Koford 1958:16).

Rather than start a new colony, immigration into a previously existing colony may increase the probability of survival. However, immigrants to the study colony were met with a great deal of hostility from residents. Although prairie dogs are territorial and repel any individual not of their coterie, they seemed particularly agitated by the presence of a newcomer to the colony (see Wilson 1975: 273-274). Immigrants were prevented from entering the colony proper; consequently, they wandered throughout the tall unmodified grass that surrounded the colony, and occupied shallow peripheral burrows that were excavated by the immigrants themselves or by residents during the normal course of colony expansion. Five of the 17 (29%) immigrants were eventually tolerated by the residents and filled a vacancy in a coterie territory, but only 2 (12%) survived to participate in the following breeding season. If the same rate of success applied to road-captured dispersers integrated into other colonies (Figure 7), then possibly 2 others (18%) succeeded in making a genetic contribution to a different population. Poor survivorship of immigrants was probably due to 1) increased predation because of their peripheral position in the colony relative to residents, and

2) a decline in their physical condition after arrival. The latter may have been promoted by aggression from residents, and by their peripheral location resulting in less time feeding and more time watching for predators (Hoogland 1981a).

Overall, dispersing prairie dogs were significantly less likely to survive compared with those individuals that enjoyed the benefits of colonial life [dispersers: 15 of 28 (64%) died; residents: 18 of 193 (10%); $X^2 = 40.1$, df = 1, $P < .001$]. Predation was not the only cause of death; 3 died in burrows from wounds inflicted by residents, and 1 died after apparently falling from a cliff. Disperser success did not vary according to sex ($X^2 = 0.08$, df = 1, $P > .75$) or age ($X^2 = 2.52$, df = 2, $P > .25$).

Factors Affecting Dispersal

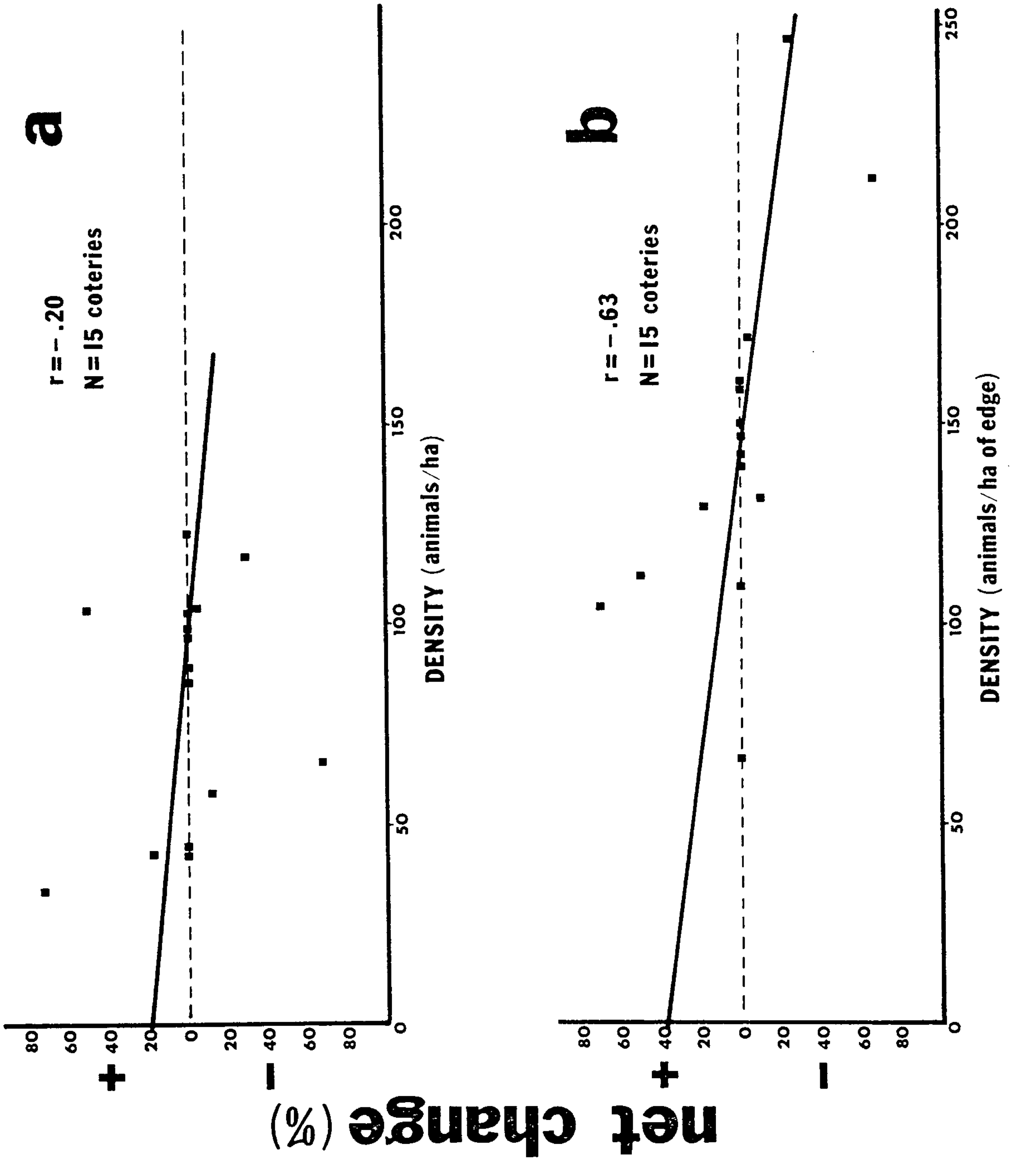
A number of proximate factors responsible for dispersal have been suggested by several investigators. However, many of these studies were not specifically directed toward dispersal activity and little evidence was produced in support of the theories. In the present study, I examined 5 possible factors: 1) animal density in relation to food supply, 2) shortage of available mates, 3) eviction of residents by invading prairie dogs, 4) harassment of adults by juvenile prairie dogs, and 5) genetic factors.

Density in relation to food supply

Dispersal as a density-dependent response has been suggested by several investigators (Errington 1957, Davis et al. 1964, Carl 1971). The fact that intercolony dispersal of prairie dogs occurred during the time of peak colony density (i.e., period of juvenile emergence) implied such a relationship. To examine this possibility, I compared peak animal density in coteries of the study colony to the relative change in animal numbers in those coteries during the dispersal seasons of 1980 and 1981 (Figure 8a); there was no significant relationship ($F = 0.52$, $N = 15$ coteries, $P > .10$; $r = -.20$). Further, intracolony dispersal occurred at any time of year, not just during periods of peak animal density.

As mentioned above, discrete vegetation zones may be produced on colonies due to time-differential effects of prairie dog grazing. Garrett et al. (1982) noted a pronounced feeding preference for the grass-dominated edge zone (Figure 2). The well-developed burrows in the middle of the colony (interior zone) were used almost exclusively for sleeping nests and nurseries, but most feeding activity occurred at the periphery. A significant inverse relationship existed between animal density relative to the preferred edge zone (animals/ha of edge) and the relative change in animal numbers during the dispersal seasons

Figure 8. Relationship between relative change in animal numbers and (a) the peak animal density (total area) and (b) the peak animal density per ha of preferred vegetation type for coteries of the study colony


a
r = −.20
N = 15 coteries
b
r = −.63
N = 15 coteries
net change (%)
+
−
80
60
40
20
0
20
40
60
80
0
50
100
150
200
250
DENSITY (animals/ha)
DENSITY (animals/ha of edge)

(F = 8.66, N = 15, P < .025; r = .-63) (Figure 8b). But this may not be a linear relationship. If the 2 data points in Figure 8b representing high-density coteries are excluded, no significant relationship exists (F = 1.97, P > .25). Because I have little data for high-density coteries, no definitive conclusion can be reached. However, a curvilinear relationship is possible; that is, a response to high density-low food supply is elicited only after a certain critical point is attained.

Eberhardt (1970) pointed out a problem with the type of analysis presented above. Because population size is used in the calculation of both the dependent and independent variables, some correlation would be expected even in the absence of a true relationship. However, 2 lines of evidence suggest the importance to prairie dogs of the preferred grazing area, and imply that dispersal may result from a shortage of this resource.

First, coterie territories of the small (1.9 ha) study colony were almost always situated so that coterie members had access to the edge. In the few cases where individuals were confined to areas in the interior zone, they did not fare well. For example, in March 1980, 3 prairie dogs were restricted to the interior zone due to development of "split coteries" (Hoogland 1981b). During the following 3-month period, the physical condition of these individuals deteriorated rapidly: 1 eventually died in a burrow, another disappeared, the third survived after he abandoned his interior territory and was accepted by his brother in a coterie adjacent to the colony periphery. During this time period, only 3 of the other 39 residents that had access to the edge died or disappeared ($P = .033$, Fisher's Exact Test). Two other prairie dogs were similarly confined in May of 1981. However, unlike the previous year, this occurred when vegetation was growing in the middle of the colony. These 2 individuals survived, but they were prevented from grazing in the preferred edge zone. By October, they both weighed significantly less than their cohort average ($t = 3.13$, $N = 17$, $P < .01$). Reduced body weight during fall may lessen chances of winter survival. Because prairie dog colonies frequently cover 50 ha or more (Cheatheam 1977, Koford 1958), the presence of interior territories probably is common. Food shortages must be at least periodic occurrences during the time of juvenile emergence, as well as during periods of drought. This kind of crisis would affect all individuals regardless of sex or age. This may account, at least in part, for dispersing females of all age classes (Table 2). Adult males probably were less capable of long-distance movements than adult females.

Second, even though females of the study colony rarely moved, an exception occurred in 1 coterie during the dispersal season of 1981. In this case, the coterie density was high and the territory was severely lacking in the preferred edge zone. Within a 3-week period, 3 (2 adults, 1 yearling) of 6 females moved or disappeared from this coterie while no changes occurred in other coteries (N = 26 females) (P = .004, Fisher's Exact Test). These observations are consistent with Dobson's (1979) conclusion that female California ground squirrels disperse in response to shortages of food.

Bailey (1926, 1931), King (1955), Koford (1958), and Coppock (1981) reported prairie dog populations concentrated near the borders of colonies. If a territory is located adjacent to the colony periphery, increased demand for food at the time of juvenile emergence would cause the coterie to expand into the prairie surrounding the colony. However, if restricted to a territory in the center of the colony, dispersal may be the only alternative for individuals facing a food shortage.

Shortage of available mates

The coterie is the reproductive unit for black-tailed prairie dogs (Foltz and Hoogland 1981, Hoogland 1981b). Inasmuch as most coterie members are close genetic relatives, it follows that inbreeding degeneration may result. However, Hoogland (1982) reported that prairie dogs avoid inbreeding through behavioral mechanisms; specifically, dispersal of males prior to first breeding or absence of breeding behavior if such dispersal does not occur.

In this study, males of the study colony almost always dispersed from their natal coteries as yearlings. Of 33 yearling males, 30 moved away from close genetic relatives ($X^2 = 22.1$, df = 1, $P < .001$). Of the 3 that remained in their natal coteries, 2 divided their natal territories after an unrelated female immigrated, and defended the area and the female newcomer against their relatives. In the third case, all female relatives had died or disappeared prior to the breeding season of his yearling year; thus, breeding opportunities were not inhibited by relatives. Because older males typically move to different coteries before their daughters attain breeding age, incestuous mating between father and daughters is unlikely (Hoogland 1982, this study). In only 4 of 9 cases (44%) in the present study was a father still present at the time of his daughter's first breeding season. Two of these females did not copulate; the other 2 were part of a "split" coterie and copulated only with an unrelated male. These data suggest that relatedness of individuals affects the likelihood of breeding, and that dispersal (for males) may be the only alternative for reproduction.

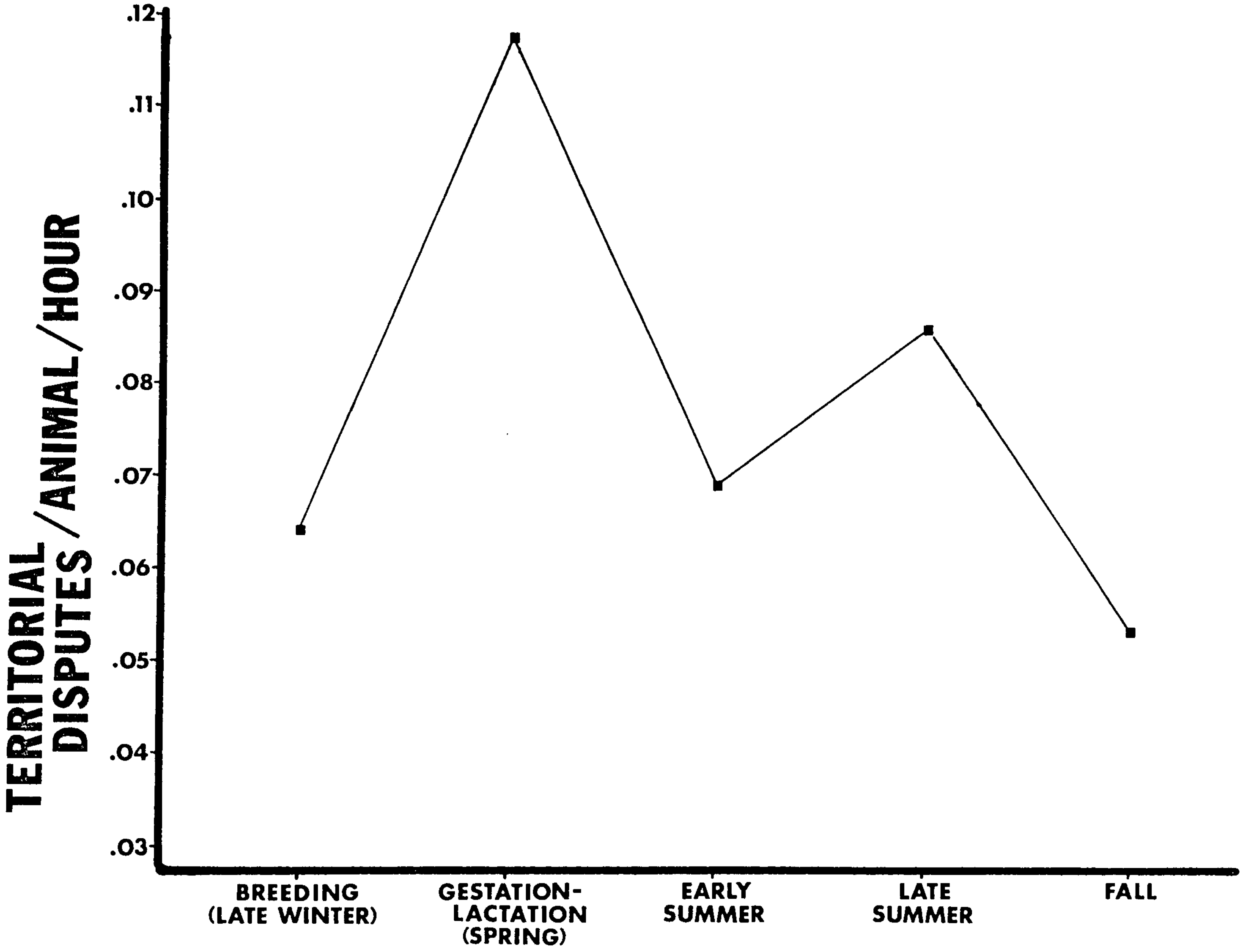
Eviction from the coterie territory

Christian (1970) suggested that dominant individuals force subordinates into suboptimal habitat when density reaches high levels. However, for canids, Bekoff (1977) believed that social interactions during juvenile ontogeny was a more important determinant of dispersal than aggression. King (1955) reported little overt display of dominance among prairie dogs. But the older male of the coterie holds a specialized dominance position in that his primary responsibility is defending the group from territorial interlopers. I frequently observed females and yearling males respond submissively to the approach of their dominant male. It follows that this dominant animal might respond to high density by forcibly evicting some coterie members. I have no data to support this possibility. As mentioned above, intercolony dispersers generally were less scarred than residents of the study colony. Although common in other highly social animals (e.g., vicuna, Franklin 1974; marmots, Barash 1973, Armitage and Downhower 1974), prairie dogs in this study were never expelled by their fellow coterie members.

Agonistic behavior between coterie members was pronounced only during the time when females defended their unweaned infants against any intruder, from within or outside the coterie. The rate of territorial encounters was compared during 5 time periods in 1980, including female defense of nest burrows (Figure 9). Note that the peak in aggression occurred just prior to the dispersal season (early summer). The peculiarity of this was that much of the aggression was directed toward yearling males within their own coterie. I rarely observed the dominant male trespassing near the nest burrow, but yearling males (and other females) were frequently chased by the mother as they attempted to enter her burrow. It is logical that, after a certain level of intracoterie aggression is reached, some coterie members might emigrate during the following dispersal season (King 1955).

Most territorial disputes were settled between adult males of adjacent coteries. Because dominant males occasionally move to other coteries, the remaining coterie members may be threatened with aggression from invaders after his departure. Forcible expulsion by invaders was observed by Hoogland (assistant professor, Princeton University, personal communication), but I have never observed this at the study colony. After a new male immigrated into a coterie, the residents typically avoided contact with him until accustomed to his presence. Yearling males frequently emigrated soon after but were never chased out by the newcomer. Nevertheless, the mere presence of a new dominant male may represent an intolerable change to some resident

Figure 9. Comparison of rates of territorial disputes for prairie dogs of the study colony during 5 time periods in 1980


TERRITORIAL DISPUTES/ANIMAL/HOUR
.12
.11
.10
.09
.08
.07
.06
.05
.04
.03
BREEDING (LATE WINTER)
GESTATION-LACTATION (SPRING)
EARLY SUMMER
LATE SUMMER
FALL

yearling males, and the possibility of passive displacement may be an important factor pertaining to dispersal.

Harassment of adults by juvenile prairie dogs

During the first few months following emergence, juveniles constantly followed and interacted with adults (King 1955, Tileston and Lechleitner 1966). This interaction may take the form of jumping on the adult's backs, biting their tails, crawling under their chins as they attempted to feed, or other antics that generally interfered with normal activities. King (1955) suggested that some adults may emigrate to avoid this incessant harassment. Juveniles may also effect dispersal of adults in other species (Harper 1970). In the present study, lactating females were particularly irritated by this juvenile behavior, frequently drubbing the young with their forepaws and running from their approach. Males seemed less bothered and spent more time than females in playing with and grooming the young. Considering the physiological strain of gestation and lactation, females especially needed uninterrupted time for feeding [females molted later and weighed less when lactating (lactating: 705.0 ± 47.5 g, $N = 13$; nonlactating: 851.3 ± 58.1 g, $N = 13$; $t = 7.03$, $P < .001$)].

Two lines of evidence suggest that harassment by juveniles may cause dispersal of females. First, when males occasionally "split" a coterie, resident females used the entire original territory but the new male defended his newly acquired subterritory from other males and juveniles. Therefore, although females rarely dispersed at the study colony, they could occasionally escape the attention of their young by spending their time in such a subterritory. During the first 3 months following juvenile emergence in 1980 and 1981, 11 females moved into subterritories away from their young. No female remained near her offspring if presented with an opportunity to do otherwise (i.e., development of a "split" coterie). For the same time periods, only 3 of 9 males dispersed to coteries with less young (P = .002, Fisher's Exact Test). In other words, male movement was independent of the number of juveniles present; if females had the opportunity to escape harassment by juveniles, they did.

Second, 2 intercolony dispersers that immigrated to the study colony were lactating females (7% of female dispersers). Therefore, females occasionally may disperse long distances away from their young. One of these immigrants remained and became part of an established coterie. The other apparently returned to her original coterie in a colony 2.6 km away where she was observed with 6 juveniles. This is an unusually large litter size for prairie dogs (Hoogland 1979, this study). This is weak evidence but may indicate that the presence of juveniles affects dispersal behavior. To this point, I have no data to show that the absence of young resulted in more time for feeding and other activities, but the implication is possible.

Genetic factors

Genetic differences among individuals have been recognized as a possible influence on dispersal. Blair (1953) thought that some individuals in rodent populations possess an inherent tendency to disperse. Howard (1949) found nonrandom dispersal distances and speculated that an innate mechanism was responsible. Lidicker (1962, 1975) referred to an "emigratory drive", some individuals being genetically predisposed to respond to increasing density before environmental pressure is exerted on the population. Krebs (1978) took Chitty's (1967) analysis of population fluctuation in rodents and espoused the view that dispersal is a genetic response to increasing animal density.

Several investigators have found genetic differences (electrophoretic loci) between residents and dispersers (ref. in Gaines and McClenaghan 1980). Results of these studies are unclear because single locus studies may not be meaningful for a likely polygenic trait such as dispersal. However, if there is a genetic basis for dispersal, heritability is likely in offspring of dispersers. Hilborn (1975) found that the tendency to disperse was nonrandomly distributed among litters of 4 species of Microtus. Moreover, Beacham (1979) found that littermates tended to disperse at the same age.

I examined the above relationship among male offspring of females of the study colony. Because females rarely dispersed, daughters were not included. Although males were not found to disperse before their first breeding season in other investigations, this was a common occurrence in the colony I studied (Garrett et al. 1982). The dispersal behavior of direct male descendents of 11 females is compared in Table 6. Sons and grandsons were separated into 2 categories: 1) those that dispersed prior to their first breeding season and 2) those that remained in their natal coterie during their first breeding season. Overall, there was a significant difference in the likelihood of early dispersal ($X^2 = 23.58$, df = 10, $P = .01$). Note that all male descendents of female 52 dispersed. If this female is excluded, the difference is not significant ($X^2 = 12.16$, df = 9, $P = .22$). Therefore, although it may be difficult to predict the tendency for early dispersal by maternity, there may be situations in which all male offspring of a particular blood line follow a predictable dispersal pattern for no obvious environmental reason. There was no relationship between the mother's weight at parturition and subsequent early dispersal of her sons ($N = 13$ females, $r = .07$,

Table 6. Comparison of the number of males born in 1979 and 1980 that dispersed prior to their first breeding season and those that remained in their natal coterie during their first breeding season

	NUMBER OF MALE DESCENDENTS	
FEMALE	DISPERSED	DID NOT DISPERSE
52	6	0
15	1	6
48	1	3
5	0	1
16	0	3
24	1	5
27	0	1
19	1	1
3	0	2
54	2	0
18	0	3

P > .50). There also was no relationship between early dispersal and total area per animal (N = 8 coteries, r = -.08, P = .50) or preferred feeding area per animal (N = 8 coteries, r = .11, P = .50). Further, I found no relationship between litter size and proportion of males that dispersed prior to their first breeding season (N = 12 litters, r = .11, P = .50). These results suggest the presence of an innate mechanism but are difficult to interpret because of the various social factors that may influence early dispersal (e.g., maternal effects, behavioral differences among littermates) (Bekoff 1977), and because of subtle environmental factors that are difficult to measure. Clearly, a more lengthy study relating this information to an electrophoretic analysis is necessary.

Conclusions

Dispersal of prairie dogs is likely the result of a variety of factors. It is probable that different individuals respond to different pressures depending on conditions particular to that animal. This study found that environmental factors include shortages of food and mates, as well as social factors within the coterie. But because of benefits that the species derives from dispersal, this behavior would be selected for even in the absence of environmental stimuli (Howard 1960, Lidicker 1962).

Intracolony dispersal is a low risk venture. Although it may be difficult to enter a different coterie, the prairie dog remains in a familiar setting thereby still benefiting from a colonial situation (i.e., reduced predation). Dispersal within the study colony was limited almost entirely to males. These individuals were prereproductive yearlings and adults moving away from closely related females, and suggests that males were moving for reproductive purposes. Data are limited on intracolony dispersal of females, but food shortages and harassment by juveniles may be proximate causal factors. This is consistent with Dobson's (1979) conclusion that male California ground squirrels disperse to avoid inbreeding, while females move in response to food shortages.

Intercolony dispersal is a high-risk venture. The disperser is unprotected in unfamiliar surroundings, and survivorship is poor. Because of the risks involved, it is logical that this kind of movement should occur only during the time of year when food and cover are abundant. These long-distance dispersers fall into 2 distinct categories (cf. King 1955): 1) yearling males and 2) females of all ages. The stimulus for yearling male emigration may be primarily innate; yearling males moved farther than females, movements were made without prior experience or an instructor to imitate, travel frequently was across unfavorable habitat bypassing favorable habitat, and the stimulus was of short duration when the animal reached reproductive maturity (Howard 1960). The male-skewed sex ratio of yearling dispersers may also indicate an innate mechanism. However, lack of unrelated females in the coterie may also stimulate dispersal of yearling males. The all-age female dispersers most likely were reacting to both environmental and innate stimuli. The shorter dispersal distances of females may indicate that they were moving just far enough to secure an adequate food supply, a factor affecting all individuals regardless of age. Data from the study colony suggest that such pressure does result in female movement. But, if environmental conditions were optimal, the development of new colonies could not occur without the evolution of a dispersal tendency in both sexes.

It is difficult to determine if intercolony dispersal is a more extreme response to the same factors that cause intracolony dispersal. It seems likely that a prairie dog could lessen some dispersal pressure in its coterie by simply moving to a different territory within the same colony. However, because the exchange of genetic material between colonies obviously benefits the species, long-distance dispersal should be selected for. It is tempting to speculate that most all intercolony dispersal is innate. Additional study of prairie dog life requisites and behavior may answer this question, as well as illuminate the relative importance of factors presented in this report.

MANAGEMENT OF PRAIRIE DOG DISPERSAL

The increase in the size and number of prairie dog colonies in WCNP has been a chronic problem since control programs were discontinued in the mid-1960s. In 1967, there were an estimated 254 ha of prairie dog colonies in the park (Lovaas 1972). Aerial photographs in 1978 indicated an excess of 500 ha (Dalsted et al. 1981). This worsening situation is a concern of park managers because 1) the native prairie component of the park is shrinking every year due to encroachment of forest and modification by prairie dogs, 2) prairie dogs are believed to be competing for forage with other grazing wildlife, e.g., buffalo (*Bison bison*) and elk (*Cervus canadensis*), and 3) park managers are being accused by local landowners of maintaining a reservoir of prairie dogs infesting adjacent rangeland.

The prairie dog historically was an integral component in the prairie ecosystem. However, records indicate that numbers of colonies increased since the time of Lewis and Clark, peaking during the early 1900s before massive extermination campaigns eliminated prairie dogs from much of their range (Koford 1958). Increased tillage and the introduction of domestic livestock in the late 1800s may have significantly contributed to the spread of prairie dogs. Generally limited by tall vegetation and other visual barriers, colony growth probably was encouraged by the heavy grazing that occurred throughout western United States during the period (see Bentley 1898). Without exception, all the large colonies in WCNP have a history of plant community disturbance prior to colonization. For example, Bison Flats started around a water hole that was regularly trampled by bison, Pringle after long-term cultivation, and Norbeck and Sanctuary were heavily grazed areas in which bison and elk were pastured (Cole 1958).

Plant groups and physical characteristics of newly colonized sites in 1979 were compared with undisturbed prairie in 1979 and 1980, and with disturbed sites in 1980 (Table 7). Although there were significant differences in abundance of plant groups among the different areas, highly significant differences occurred only in physical characteristics: bare ground ($F = 75.9$, $P < .001$) and vegetation height ($F = 225.5$, $P < .001$). Thus, colony initiation may be a response to those characteristics that result from the disturbance of native vegetation.

Mead (1899) observed that "the foot of the buffalo was necessary for their [prairie dog] existence." Coppock et al. (1980) reported that bison may actively seek prairie dog colonies during certain times of year for the more palatable and nutritious grasses growing on colony edges compared with unmodified prairie. The associated trampling of colony

Table 7. Vegetation analysis of 5 recently colonized sites, 5 disturbed (but uncolonized) sites, and 10 undisturbed sites during 1979 and 1980 within and surrounding WCNP. N = 150 sample plots for each category. Supercripts indicate significance ranking according to Duncan's New Multiple Range Test. * $P < .05$ ** $P < .001$

PLANT GROUP-CHARACTERISTICS	% CANOPY COVERAGE			
	1979 PRAIRIE	1980 PRAIRIE	DISTURBED SITES	NEW COLONIES
SEDGE SPECIES*	5.3	2.2	2.2	0.5
WESTERN WHEATGRASS*	6.4	10.8	2.4	2.1
OTHER COOL-SEASON GRASSES*	22.7	18.7	4.7	20.7
BUFFALOGRASS AND BLUE GRAMA*	37.5	37.9	34.1	24.4
OTHER WARM-SEASON GRASSES*	2.7	5.5	4.3	7.1
FORB SPECIES*	3.2	2.9	4.7	7.4
BARE GROUND**	22.1^{A}	22.3^{A}	45.8^{B}	38.1^{B}
VEGETATION HEIGHT**	16.3^{A}	26.9^{B}	5.5^{C}	4.4^{C}

peripheries probably promotes the expansion of colonies into the surrounding tall grasses. Implied in this symbiotic relationship is a direct correlation between the size of the bison herd (and possibly elk) and the increase in colony surface area in the park. But records of total colony acreage are limited due to infrequent mapping of prairie dog colonies. There are only 3 years with data since 1964, yet a strong correlation exists between the size of the combined bison and elk herds and total acreage of colonies ($r = .99$). Regular monitoring of prairie dog colonies is necessary to validate the relationship, but this possibility must be considered when determining numbers to be periodically culled from the herds of large ungulates in the park.

The control of rank growth of graminoids and invasion of woody species by controlled burning also may influence colony expansion. Following a fire in 1977, Northtown (Figure 1) rapidly expanded into the area affected by the burn (Rich Klukas, personal communication). A small burn was conducted adjacent to the Pringle colony in the fall of 1979. Burrow excavation during the following year was significantly greater in the burned area compared with an unburned but similar area on the opposite side of the colony (burned: 67 new burrows; unburned: 4) ($X^2 = 60.5$, $df = 1$, $P < .001$). Fire initially reduces vegetation height and stimulates succulent new growth, conditions that are likely favorable to prairie dog invasion.

The management needs of a national park are different than those of the rancher whose land is devoted exclusively to production of crops and livestock. The preservation of wildlife populations requires control of animal numbers, not complete eradication. Yet, park managers have a responsibility in regard to the rights of their neighbors. The inability to control numbers of prairie dogs within the park may threaten the livelihood of adjacent landowners. Because WCNP is a relatively small area, prairie dogs probably are capable of dispersing onto adjacent land from any location in the park [5 of 16 (31%) radiocollared individuals dispersed out of the park]. However, most dispersal activity could be controlled by directing management efforts toward populations located within 2 km of the boundary ($\overline{X}$ dispersal distance = 2.4 ± 1.7 km). Further, because animal density is likely to be greatest near colony peripheries, intensive efforts should be directed toward specific areas. The use of visual barriers to control colony expansion and diethystilbestrol to control reproduction has been tested by Garrett and Franklin (1982), but further research is needed.

The ranching community in the vicinity of the park must play an active role in avoiding conditions that encourage prairie dog invasion. Dispersing animals may find less trouble immigrating into a colony on private land compared with colonies in a protected area. Poisoning programs and varmint shooting result in lower animal densities on colonies immediately outside the park. Presuming that animal populations in the park are regulated by natural means, dispersing prairie dogs may find the vacant burrows, sparse vegetation, and fewer predators on private rangeland more attractive. There is some evidence that they initially may survive better. Of the 3 prairie dogs that were radiotracked onto private land, all successfully immigrated into a colony; only 40% (10 of 25) of the dispersers that remained in the park survived the summer following the dispersal season (P = .034, Fisher's Exact Test). However, survival in the longterm probably is lower on private land due to private extermination attempts.

It follows that the movement of prairie dogs from the park onto surrounding rangeland will continue unless a concerted effort is made between park manager and private landowner. Heavy grazing by livestock may be the single greatest controllable factor influencing the spread of prairie dogs (Koford 1958, Smith 1958, U.S. Forest Service 1978). Wise management of grazing animals both within and outside of the park will produce healthy range, promote the welfare of the livestock industry, and insure the fair preservation of this native wildlife species.

LITERATURE CITED

Ambrose, H. W. 1972. Effect of habitat familiarity and toe-clipping on rate of owl predation in Microtus pennsylvanicus. J. Mammal. 53:909-912.

Armitage, K. B. 1973. Population changes and social behavior following colonization by the yellow-bellied marmot. J. Mammal. 54:842-854.

Armitage, K. B., and J. F. Downhower. 1974. Demography of the yellow-bellied marmot populations. Ecology 55:1233-1245.

Bailey, V. 1926. A biological survey of North Dakota. U.S. Dept. Agric., N. Am. Fauna 49. 226 pp.

Bailey, V. 1931. Mammals of New Mexico. U.S. Dept. Agric., N. Am. Fauna 53. 412 pp.

Baker, R. J. 1977. Exact distributions derived from two-way tables. Appl. Stat. 26(2):199-206.

Banks, E., R. Brooks, and J. Schnell. 1974. A radiotracking study of home range and activity of the brown lemming (Lemmus trimucronatus). J. Mammal. 56:888-901.

Barash, D. P. 1973. The social biology of the Olympic marmot. Anim. Behav. Monogr. 6:173-245.

Beacham, T. D. 1979. Dispersal tendency and duration of littermates during population fluctuations of the vole Microtus townsendii. Oecologia 42:11-22.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. Am. Nat. 3:715-732.

Bentley, H. L. 1898. Cattle ranges of the southwest: a history of the exhaustion of the pasturage and suggestions for its restoration. U.S. Dept. Agric., Farm Bull. 72. 31pp.

Blair, W. F. 1953. Population dynamics of rodents and other small mammals. Adv. Genetics 5:1-41.

Bonham, C. D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. J. Range Manage. 29(3):221-225.

Carl, E. A. 1971. Population control in Arctic ground squirrels. Ecology 52:395-413.

Cheatheam, L. K. 1977. Density and distribution of the black-tailed prairie dog in Texas. Tex. J. Sci. 29:33-40.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Aust. 2:51-78.

Christian, J. J. 1970. Social subordination, population density, and mammalian evolution. Science 168:84-90.

Cole, J. E. 1958. Ten-year summary prairiedog [sic] report: Wind Cave National Park. Memorandum to Superintendent of Wind Cave National Park. (WCNP files) Wind Cave National Park, Hot Springs, South Dakota. 27 pp.

Coppock, D. L. 1981. Impacts of black-tailed prairie dogs on vegetation in Wind Cave National Park. M.S. thesis, Colorado State Univ., Fort Collins. 86 pp.

Coppock, D. L., J. K. Detling, and M. I. Dyer. 1980. Interactions among bison, prairie dogs, and vegetation in Wind Cave National Park. Unpublished report to the National Park Service, Wind Cave National Park, South Dakota. 195 pp.

Cranford, J. A. 1977. Home range and habitat utilization by Neotoma fuscipes as determined by radiotelemetry. J. Mammal. 58:165-172.

Dalsted, K. J., S. Sather-Blair, B. K. Worcester, and R. Klukas. 1981. Application of remote sensing to prairie dog management. J. Range Manage. 34(3):218-223.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest. Sci. 33:43-64.

Davis, D. E., J. J. Christian, and F. Bronson. 1964. Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J. Wildl. Manage. 28:1-9.

Dobson, F. S. 1979. An experimental study of dispersal in the California ground squirrel. Ecology 60(6):1103-1109.

Eberhardt, L. L. 1970. Correlation, regression, and density dependence. Ecology 51(2):306-310.

Errington, P. L. 1946. Predation and vertebrate populations. Q. Rev. Biol. 21:144-177, 221-245.

Errington, P. L. 1957. Of population cycles and unknowns. Cold Spring Harbor Sym. Quant. Biol. 22:287-300.

Foltz, D. W., and J. L. Hoogland. 1981. Analysis of the mating system in the black-tailed prairie dog (Cynomys ludovicianus) by likelihood of paternity. J. Mammal. 62(4):706-712.

Franklin, W. L. 1974. The Social behavior of the vicuna. Pages 477-487 in G. Geist and F. Walther, eds. The behaviour of ungulates and its relation to management. IUCN (Intermnational Union for Conservation of Nature and Natural Resources), Morges, Switz.

Gaines, M. S., and L. R. McClenaghan, Jr. 1980. Dispersal in small mammals. Ann. Rev. Ecol. Syst. 11:163-196.

Garrett, M. G., and W. L. Franklin. 1982. Prairie dog dispersal in Wind Cave National Park: Possibilities for control. Pages 185-198 in R. M. Timm and R. J. Johnson, eds. Proc. Fifth Great Plains Wildl. Dam. Cont. Workshop. Univ. Nebraska, Lincoln.

Garrett, M. G., J. L. Hoogland, and W. L. Franklin. 1982. Demographic differences between an old and a new colony of black-tailed prairie dogs (Cynomys ludovicianus). Am. Midl. Nat. 108(1):51-59.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hansen, R. M., and I. K. Gold. 1977. Blacktail [sic] prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. J. Range Manage. 30(3):210-214.

Harper, L. V. 1970. Ontogenetic and phylogenetic functions of the parent-offspring relationship in mammals. Adv. Stud. Behav. 3:75-117.

Hilborn, R. 1975. Similarities in dispersal tendency among siblings in four species of voles (Microtus). Ecology 56:1221-1225.

Hoogland, J. L. 1977. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: Cynomys leucurus and C. ludovicianus). Ph.D. dissertation. Univ. of Michigan. 292 pp.

Hoogland, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: Cynomys spp.) coloniality. Behaviour 69:1-35.

Hoogland, J. L. 1981a. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: Cynomys leucurus and C. ludovicianus). Ecology 62(1):252-272.

Hoogland, J. L. 1981b. Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: Cynomys ludovicianus). Pages 283-310 in R. D. Alexander and D. W. Twinkle, eds. Natural selection and social behavior. Chiron Press, New York. 532 pp.

Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. Science 215:1639-1641.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of deer mice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. 43. Univ of Michigan, Ann Arbor. 50 pp.

Howard, W. E. 1960. Innate and environmental dispersal in individual vertebrates. Am. Midl. Nat. 63:152-161.

Kelso, L. H. 1939. Food habits of prairie dogs. U.S. Dept. Agric. Circ. 529. 15pp.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog [sic] town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol. 67. Univ. of Michigan, Ann Arbor. 126 pp.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildl. Monogr. 3:1-78.

Krebs, C. J. 1978. A review of the Chitty hypothesis of population regulation. Can. J. Zool. 56:2463-2480.

Krebs, C. J., M. S. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. Science 179:35-41.

Lidicker, W. Z., Jr. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Am. Nat. 96:23-29.

Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammal populations. Pages 103-134 in F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds. Small mammals: Their productivity and population dynamics. Cambridge Univ. Press, Great Britain.

Lovaas, A. L. 1972. Report on the prairie dogs of Wind Cave National Park. Memorandum to Superintendent of Wind Cave National Park. (WCNP files) Wind Cave National Park, Hot Springs, South Dakota. 19 pp.

McCarley, H. 1966. Annual cycle, population dynamics and adaptive behavior of Citellus tridecemlineatus. J. Mammal. 47:294-316.

Mead, J. R. 1899. Some natural history notes of 1859. Trans. Kans. Acad. Sci. 16:280-281.

Metzgar, L. H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (Peromyscus leucopus). J. Mammal. 48:387-391.

Michener, G. R. 1974. Development of adult-young identification in Richardson's ground squirrels. Develop. Psychobiol. 7:375-384.

Michener, G. R. 1982. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In J. F. Eisenberg and K. G. Kleiman, eds. Recent advances in the study of mammalian behavior. Am. Soc. Mammal Spec. Publ. 7. (in press)

Michener, G. R., and D. R. Michener. 1977. Population structure and dispersal in Richardson's ground squirrels. Ecology 58:359-368.

Mineau, P., and D. Madison. 1977. Radiotracking of peromyscus leucopus. Can. J. Zool. 55:465-468.

Osborn, B., and P. F. Allan. 1949. Vegetation of an abandoned prairie-dog town in tall grass prairie. Ecology 30:322-332.

Rongstad, O. J. 1965. A life history study of thirteen-lined ground squirrels in southern Wisconsin. J. Mammal. 46:76-87.

Slade, N. A., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology 55:989-1003.

Smith, R. E. 1958. Natural history of the prairie dog in Kansas. Mus. Nat. Hist. State Biol. Surv. Kans., Misc. Publ. 16. 36 pp.

Snyder, R. L. 1976. The biology of population growth. Croom Helm, London. 227 pp.

Summers, C. A., and R. L. Linder. 1978. Food habits of the black-tailed prairie dog in western South Dakota. J. Range Manage. 37:363-366.

Tamarin, R. H. 1977. Dispersal in island and mainland voles. Ecology 58:1044-1054.

Tileston, J. V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. Am. Midl. Nat. 75:292-316.

U.S. Forest Service. 1978. Management of prairie dogs on lands administered by the supervisor of the Nebraska National Forest. Final Environmental Statement. USDA, Washington, D.C. 187 pp.

Wilson, E. O. 1975. Sociobiology: The new synthesis. Harvard Univ. Press, Cambridge, Mass. 697 pp.

Wydeven, P. R. 1979. A comparison of prairie dog stomach and fecal material with a microhistological technique. M.S. thesis. Iowa State Univ., Ames. 50 pp.