# Attributes of Black-tailed Prairie Dog Colonies in Northcentral Montana, with Management Recommendations for the Conservation of Biodiversity

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*Abstract.*—Black-tailed prairie dog (BTPD; *Cynomys ludovicianus*) colony dynamics and associated vertebrate species were studied in Phillips County, Montana in 1981, 1984, and 1988. Average colony size increased, whereas mean expansion rate decreased. Colony size was related to colony expansion rate. Smaller colonies expanded at faster rates than larger colonies, but this difference was greater from 1981-1984 than from 1984-1988. Expansion rate was not related to nearest colony distance, nor to the number or area of surrounding colonies. Burrow opening density was not related to colony size, but was related to the distance to the nearest colony and to the number and area of surrounding colonies. These findings are discussed in relation to a logistic model of colony growth, physical barriers, recreational prairie dog hunting, and human disturbances. In 1988 70 bird species, 12 mammal species, and 1 reptile species were found associated with prairie dog colonies. Of these, 30 birds and 1 mammal were previously unreported in association with BTPDs. Colony size and number of colonies within 4 mi (6.4 km) of a colony accounted for 47.6 of the variation in bird species richness associated with each colony. These findings were consistent with island biogeographic theory. Management of BTPD colonies for the conservation of biodiversity is discussed in relation to our findings and theories of insular biology.

Black-tailed prairie dog (BTPD; *Cynomys ludovicianus*) colonies are distinct and important biotic communities in the mid- to short-grass prairies and desert grasslands of North America (Whicker and Detling 1988). These communities and their physical environment comprise what has been referred to as the prairie dog ecosystem (Montana Black-footed Ferret Working Group 1988). The relationships between community members are complex and largely unexamined (Clark 1986). One of the primary goals in the management of prairie dog ecosystems should be the maintenance of biological diversity. To further that objective, we examined BTPD colony attributes and associated species richness.

The value of both ecological and genetic diversity is increasingly emphasized for a variety of reasons (Fisher et al. 1969, Myers 1979, Terborgh 1979, Wilson 1986). Ecological diversity has been associated with ecosystem stability and, while the loss of a single species may not produce obvious detrimental effects, grave consequences including ecosystem collapse are possible especially with the loss of "keystone" species (Slobodkin and Sanders 1969, Pimm 1986). Genetic diversity provides the source of innumerable agricultural, medicinal, and industrial products and enables species to adapt and evolve in the face of environmental changes (Ehrlich et al. 1977, Wilson 1986).

BTPDs create a habitat mosaic relative to adjacent communities that can be beneficial to other species. Colony boundaries are characterized by abrupt vegetation change (Koford 1958, Knowles 1982). Prairie dogs burrow extensively, clip tall vegetation, and forage on perferred plant species (Osborn 1942, Koford 1958, Archer et al. 1987). The result is a habitat characterized by decreased vegetative height and cover, and increased bare ground, soil movement, and vegetative diversity compared with surrounding areas. Grasses and shrubs are usually reduced, while forbs generally increase (Koford 1958, Knowles 1982, Knowles et al. 1982, Olson 1985). Population and burrow-opening densities are usually correlated (Houston et al. 1986). Both vary considerably, the former reportedly ranging from as few as 1-2/ac (2-4/ha) to as many as 33.4/ac (82.6/ha) for a young, rapidly expanding colony (King 1955, Koford 1958, Smith 1958, Tileston and Lechleitner 1966, Sheets et al. 1971, Garret 1982, Knowles 1982, Archer et al. 1987, Clark et al.1987). For a further review of prairie dog literature see Clark (1986).

This paper characterizes BTPD colony dynamics and vertebrate species associations in Phillips County, Montana over an eight year period (1981-1988). The factors influencing colony expansion and numbers of avian species associated with prairie dog colonies are analyzed.

## STUDY AREA

This study was conducted in the Bureau of Land Management's (BLM) Phillips Resource Area (Phillips RA),



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located in northcentral Montana (Figure 1). It encompasses 2.9 million acres (1.17 million ha), 1.3 million acres (0.52 million ha) of which are under Federal ownership. The topography varies from flat upland plains and rolling hills to badlands, rough breaks, and mountains. Elevation varies from 2,500-5,500 ft (750-1650 m). Soils are derived from glacial till, sedimentary bedrock, and alluvium from mixed rock sources, resulting in complex and diverse soil patterns (U.S.D.I., BLM 1982). Climate is continental with mean annual precipitation of 11-13 in (28-33 cm) and temperature of -40 to 100 °F (-40 to 38 °C; Clark et al. 1987). Grasslands typical of the Northern Great Plains dominate the area, but sagebrush (*Artemisia* spp.) and greasewood (*Sarcobatus vermiculatus*) are common. Major grasses include needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), Sandberg bluegrass (*Poa sandbergii*), and green needlegrass (*Stipa viridula*). Human population density is about 1 person per $mi^2$ (0.4 persons per $km^2$). Cattle ranching and grain farming represent the major land uses. For a more complete description see U.S.D.I., BLM (1982).

Prairie dog management in Phillips RA includes both poisoning and recreational shooting. A prairie dog management plan was prepared in 1982 which emphasized poisoning (U.S.D.I., BLM 1982); however, personnel and money constraints forced plan modification. The plan currently aims at encouraging recreational prairie dog shooting by providing hunters with information letters and maps of prairie dog colonies and posting (marked with signs to guide recreationalists) larger colonies. Large scale shooting began in 1984. Although all colonies on public lands are open to hunting, only colonies over 50 ac (22 ha) are posted.

## METHODS

Data collection was initiated in the absence of hypotheses and procedures were not established to conform to research design. Any *post hoc* hypotheses would consequently be artificial, therefore none were attempted. Since hypotheses were not being tested, statistical descriptions are intended to illustrate trends, not statistical inference. We do not report inferential test statistics (e.g., $F$ values) because such values might infer a precision which was not present in this study.

BTPD colonies were studied during the summers of 1981, 1984 , and 1988. Field work for 1981 and 1984 was completed prior to the onset of large scale prairie dog shooting. In 1981, colonies were mapped from aerial photographs, whereas in 1984 and 1988, colonies were mapped on 7.5 minute USGS topographic maps. We (JG and RR) mapped 92 colonies in 1981, an additional 57 colonies (149 colonies total) in 1984, and an additional 21 colonies (170 colonies total) in 1988. Most of the additional 78 (57 + 21) colonies examined were not new colonies, but ones which expanded from private or state land onto federal property. Colony area was determined to the nearest 0.1 ac (0.04 ha) using an electronic planimeter. Expansion rates were calculated to compound size increases yearly using the formula:

$$\left( \sqrt[x-y]{(size_x/size_y)} \right)^{-1}$$

where x = the most recent year sampled and y = the previous year sampled.

Additional data were collected on the 170 colonies mapped in 1988: (1)burrow density, calculated from counts obtained by walking perpendicular transects across the widest portion of each colony and counting all burrow-openings falling within armspan; (2) distance to a colony's nearest neighbor; (3) the number of colonies within 4 mi (6.4 km) of its perimeter; and (4) the area of colonies within 4 mi (6.4 km). A distance of 4 mi (6.4 km) was selected because it approximates the common daily movement distances of black-footed ferrets (*Mustela nigripes*), an important member of the prairie dog ecosystem (Forrest et al. 1985, Richardson et al. 1987, Biggins et al. 1985, 1988).

Colonies examined in 1988 were also surveyed for associated vertebrate species. Each colony was surveyed once by one to three observers. Surveys were conducted during daylight hours, beginning shortly after sunrise and continuing until early evening, but not all colonies were surveyed during the same time of day. Surveys were not performed in temperatures over 95 °F (35 °C) or in rainy weather. The length of time spent on each colony varied with colony size and the number of animals observed, but was generally 1 - 4 hours.

Associated species surveys were conducted by driving across each colony at approximately 75 ft (23 m) intervals. All vertebrates sighted on or foraging over colonies were recorded. If a bird appeared to be nesting further observations were made. Species sighted while walking transects and mapping colonies were also recorded. Although recorded, waterbirds (e.g., Anseriformes, Podicipediformes, Pelecaniformes) were considered to be associated with reservoirs rather than with prairie dog colonies and were therefore not included in the analyses.

Data were analyzed using a SYSTAT statistical package (Wilkinson 1988). Variables were examined for kurtosis and skewness to check for normality. Three variables; colony size, distance to nearest neighbor, and avian species richness, warranted natural log transformations. Parametric statistical analyses were used to compare variables over time, to examine correlations between variables, and to test the significance of linear and multiple regressions. Statistical significance was considered as $P \leq 0.05$.

## RESULTS

Results cover two major areas: BTPD colony dynamics and vertebrate species associations. The former addresses colony size, expansion, and population, whereas the latter focuses on colony attributes relating to the number of associated vertebrate species present.

### *Prairie Dog Colony Dynamics*

The average size of 92 BTPD colonies increased significantly from 93.4 ac (37.8 ha) in 1981 to 135.4 ac (54.8 ha) in 1984 (Wilcoxon rank sum = 6.8, $P<0.001$) and from 135.4 ac (54.8 ha) in 1984 to 153.4 ac (62.1 ha) in 1988 (Wilcoxon rank sum = 3.0, $P<0.01$; Figure 2). Mean colony expansion rate decreased significantly between the 1981-1984 and the 1984-1988 intervals (Wilcoxon rank sum = -5.5, $P< 0.001$; Figure 2).

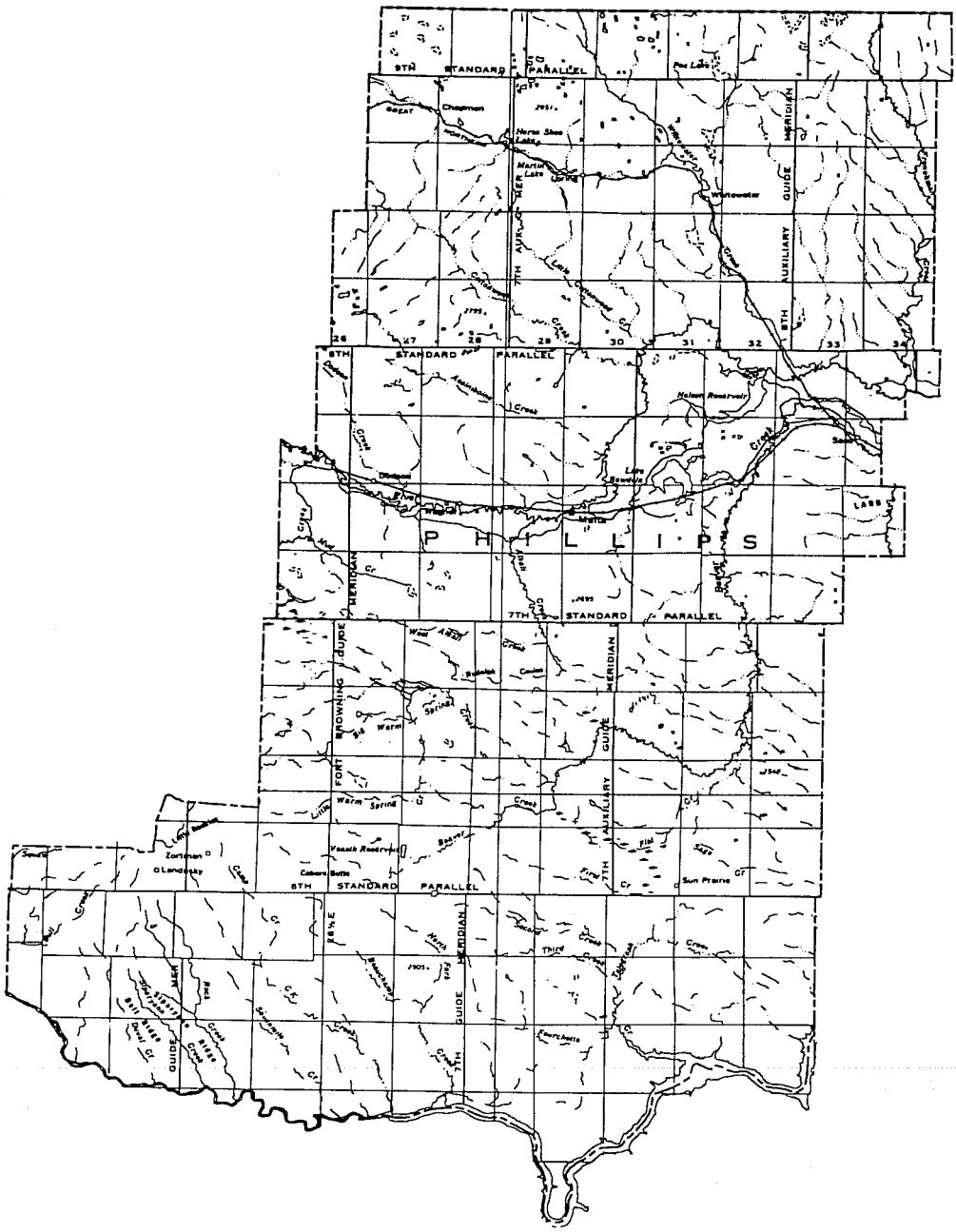
Colonies generally expanded over the entire 8 years. Of 92 colonies, 77 (84 percent) showed increases during both the 1981-1984 and the 1984-1988 intervals, three (3 percent) remained unchanged, two (2 percent) decreased during both intervals, and the remaining 10 (11 percent) colonies decreased from 1981-1984, but then remained constant until 1988. No colony increased during one time interval and decreased during the other.



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Figure 1.—Map of Phillips Resource Area in northcentral Montana.

# Bureau of Land Management
## Phillips Resource Area, Montana

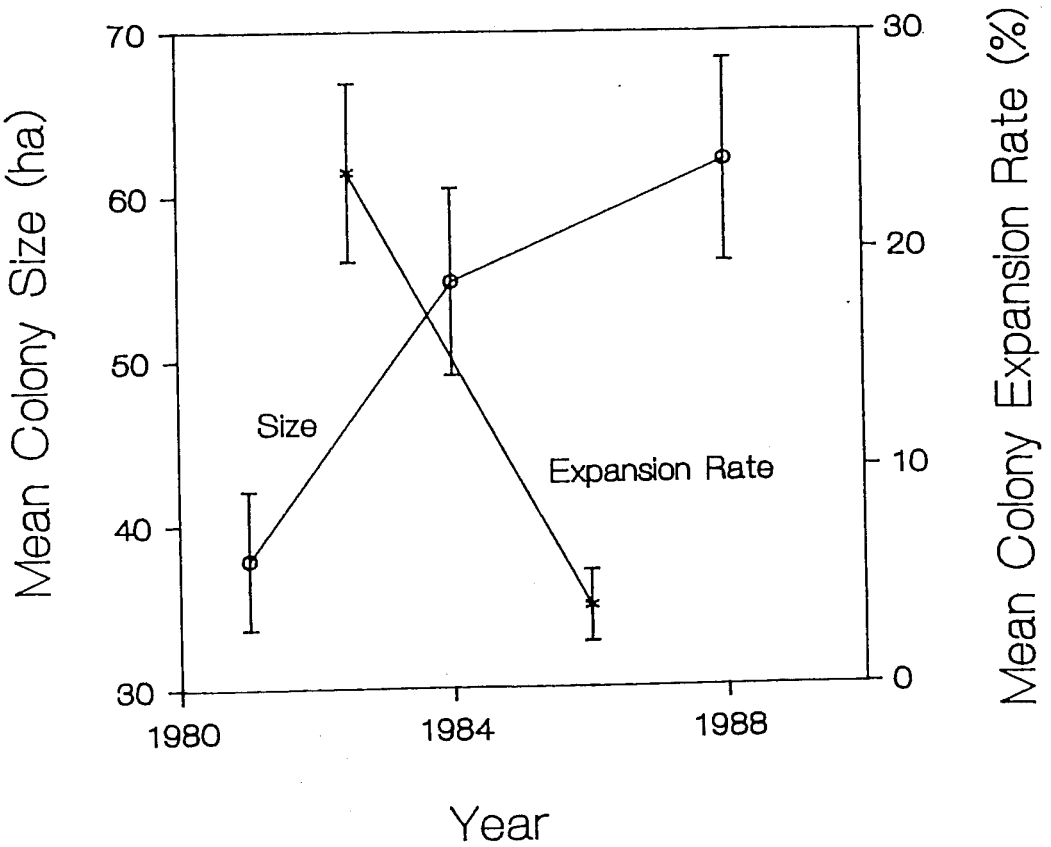





1989

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Figure 2.—Colony size and expansion rate trends for 92 BTPD colonies in Phillips County, MT. Expansion data represent the 1981-1984 and 1985-1988 intervals. Bars represent standard errors.




Colony size was inversely correlated with colony expansion rates (Figure 3). Smaller colonies expanded at significantly faster rates than larger colonies. From 1981-1984, however, colonies expanded significantly faster than from 1984-1988. The slope of the expansion rate-colony size regression (Figure 3) was significantly greater for 1981-1984 compared with 1984-1988 ($P<0.001$, by ANCOVA). Initial colony size showed a significant negative correlation with expansion rate for both 1981-1984 and 1984-1988, and a positive correlation with area expanded/year for 1981-1984 (Figure 3, Table 1). By the end of the expansion interval, however, colony size was positively correlated with expansion rate for 1984-1988 and with area expanded/year for both 1981-1984 and 1984-1988 (Table 1). Burrow density was not significantly related to colony size (Table 2, Figure 4), and averaged 44.0 ± 1.3 S.E. burrows/ac (108.8 ± 3.3 S.E. burrows/ha) for 170 colonies in 1988 (range=5.5-99.7 burrows/ac, 13.6-246.9 burrows/ha).

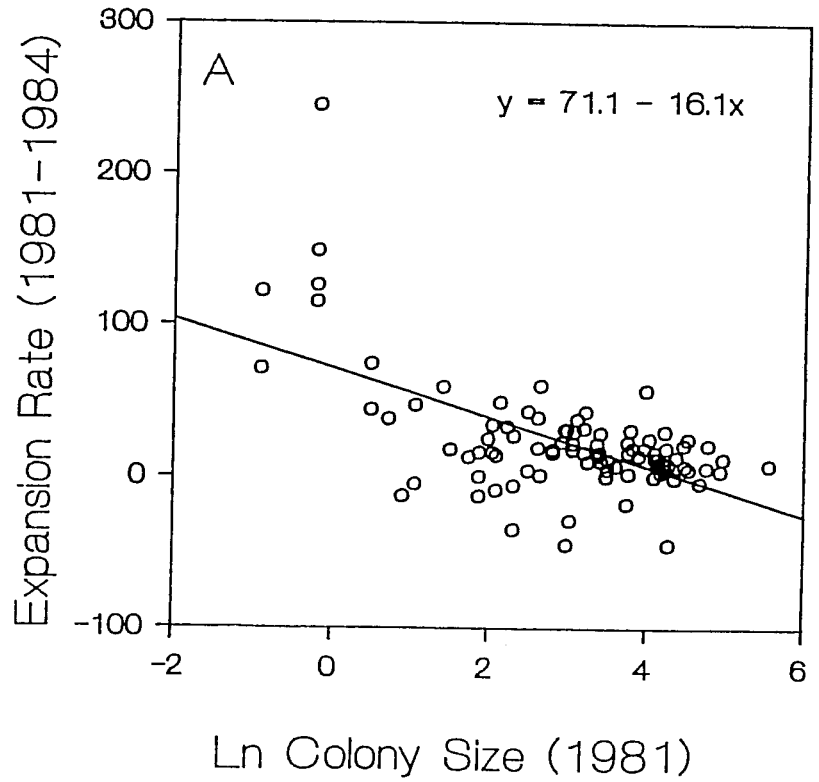
Three characteristics of surrounding BTPD colonies were measured; distance to nearest neighbor, and number and area of colonies within 4 mi (6.4 km). We found no significant relationship between these variables and colony expansion rate or area expanded/year for the 149 colonies measured in 1984 and 1988 (Table 2). However, burrow density was significantly correlated with all three variables: positively with distance to a colony's nearest neighbor, negatively with the number of colonies, and negatively with area of colonies within 4 mi (6.4 km) of the colony (Table 2).

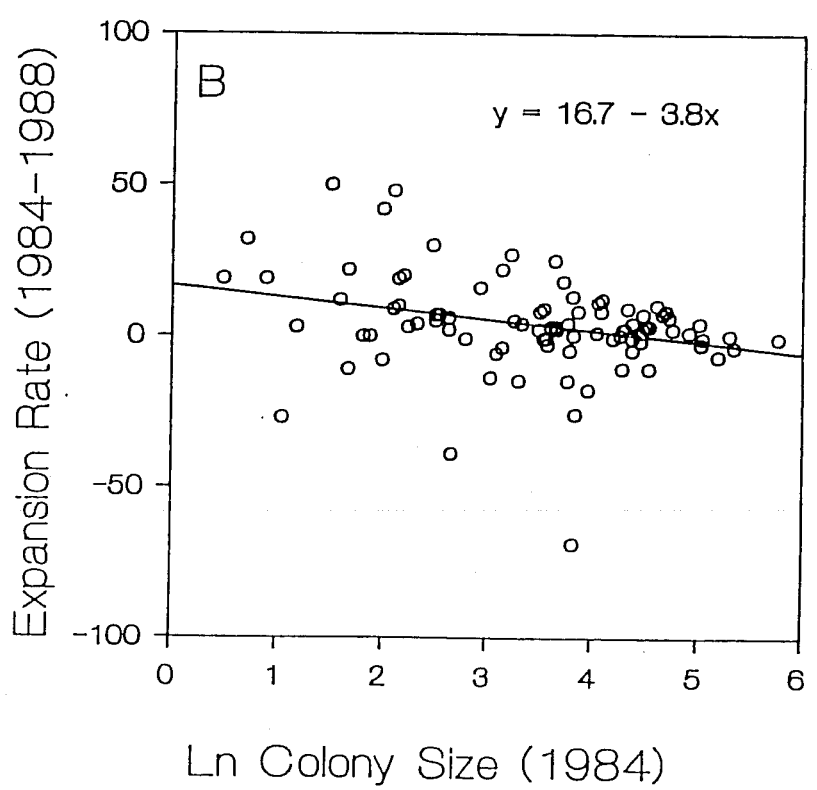
Table 1.—Pearson's Correlation Coefficients for 1981-1988 size and expansion characteristics for 92 black-tailed prairie dog colonies

| Period | Colony Characteristics | Ln Colony Size 1981 | 1984 | 1988 |
|---|---|---|---|---|
| 1981-1984 | Expansion Rate | -0.586** | -0.062 | 0.030 |
| | Area Expanded/ Year | 0.368** | 0.672** | 0.595** |
| 1984-1988 | Expansion Rate | -0.301** | -0.283** | 0.308** |
| | Area Expanded/ Year | -0.003 | -0.029 | 0.342** |

**$P<0.001$

Figure 3.—The relationship expansion rate (%) and colony size (acres)— for 92 BTPD colonies in Phillips County, MT from 1981-1984 (A) and 1984-1988 (B). The linear regressions are significant: (A) $R$=0.59, $P$<0.001, (B) $R$=0.28, $P$<0.01.





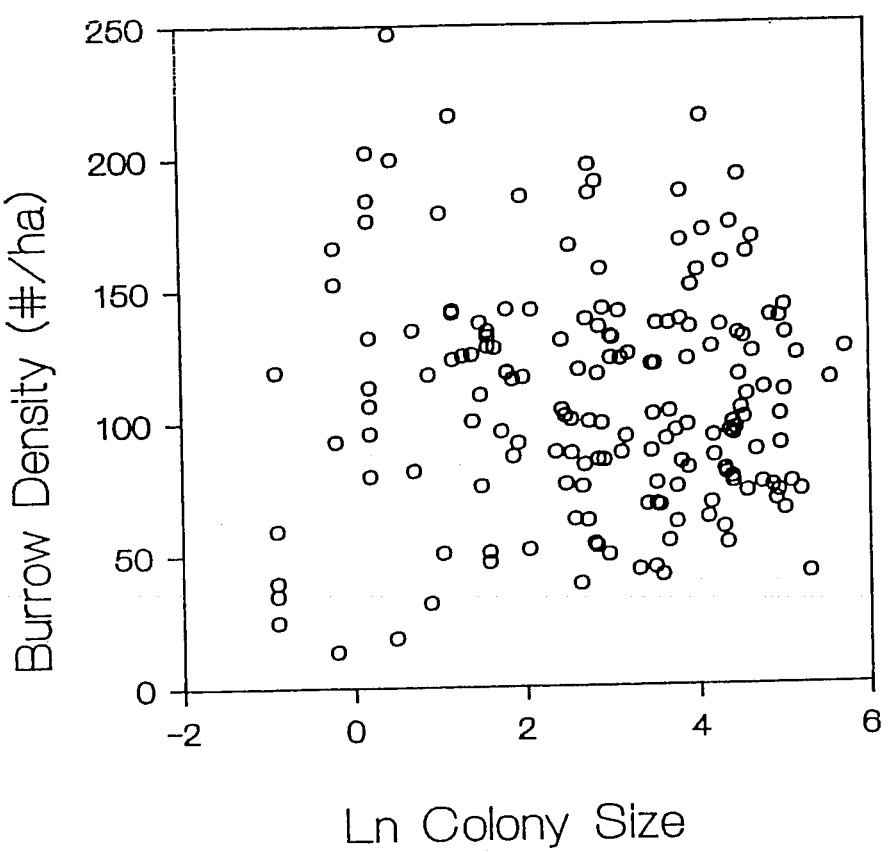

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Table 2.—Descriptive statistics and Pearson's Correlation Coefficient for prairie dog colony characteristics in 1988

| Colony Characteristics | *N* | Mean (±S.E.) | Colony Characteristics | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1. Ln Size | 170 | 44.6 (±4.1) | | | | | | | |
| 2. Burrow Density | 170 | 108.8 (±3.3) | -0.029 | | | | | | |
| 3. Expansion Rate | 149 | 3.6 (±1.4) | 0.268** | 0.049 | | | | | |
| 4. Area Expanded/Year | 149 | 5.5 (±2.1) | 0.331** | 0.076 | 0.502** | | | | |
| 5. Ln Dist. to Nearest Neighbor | 170 | 1.7 (±0.1) | -0.109 | 0.154* | -0.056 | 0.030 | | | |
| 6. No. Colonies Within 6.4 km | 170 | 9.1 (±0.4) | 0.167* | -0.346** | 0.127 | 0.151 | -0.325** | | |
| 7. Area Colonies Within 6.4 km | 170 | 417.5 (±25.5) | 0.139 | -0.339** | 0.069 | 0.085 | -0.296** | 0.874** | |
| 8. Ln Avian Species Richness | 170 | 6.7 (±0.3) | 0.660** | -0.029 | 0.231** | 0.242** | -0.093 | 0.285** | 0.274** |

*$P<0.05$
**$P<0.01$

Figure 4.—Burrow density vs. colony size (ha) relationship for 170 BTPD colonies in Phillips County, MT. No linear relationship exists ($P$=0.71).



### *Species Associated With Prairie Dog Colonies*

We sighted 83 vertebrate species on or foraging over BTPD colonies, including 70 birds, 12 mammals, and one reptile (Appendix I). We found 30 avian and one mammalian species previously unreported in association with BTPD colonies.

Relatively few mammal species were found on prairie dog colonies (Mean=0.64 ± 0.06 S.E. species/colony), so bird and mammal analyses were performed separately. The log-log species area curve for mammals was linear with a slope of 0.10 ($P<0.001$).

Figure 5A shows the effect of colony size on avian species richness. As expected, avian species richness increased significantly with increasing colony size. Species richness also increased significantly with increasing area of colonies within 4 mi (6.4 km; Figure 5B). There was no significant relationship between species richness and burrow density of each colony (Figure 5C). Avian species richness was also significantly related to prairie dog colony expansion rate, area expanded/year, and number of colonies within 4 mi (6.4 km; Table 2).

To examine further the factors affecting BTPD colony/avian species richness, we performed a stepwise linear regression using all measured variables. Colony size and area of colonies within 4 mi (6.4 km) entered into the stepwise regression. Colony size entered the model first ($R^2$=0.439). Area of colonies within 4 mi (6.4 km) entered second and, together with colony size, accounted for 47.6 percent of the variance in avian species richness. All other variables were eliminated from the model. Correlations between the expansion rate, area expanded/year, number of colonies within 4 mi (6.4 km) of a colony and its avian species richness are probably explained by direct relationships between a colony's expansion rate, the area it expanded/year, and its size and between number of colonies and area of colonies within 4 mi (6.4 km) (Table 2).

## DISCUSSION

The study results are discussed below with respect to the various aspects and relationships of the BTPD ecosystem. Recommendations are made for future research and management.

### *Prairie Dog Colony Dynamics*

Average BTPD colony size increased from 1981 to 1988, while average colony expansion rate decreased (Figure 2). Analysis of the relationship between colony size and expansion rate explains this. From 1981-1984 smaller colonies expanded at higher rates than larger colonies, but larger colonies added more area per colony. From 1984-1988 smaller colonies still expanded at greater rates than larger colonies, but larger colonies no longer added significantly more area per colony than did smaller colonies. In addition, colonies with greater expansion rates became larger than colonies with lower expansion rates by the end of the study.

These findings, and those by Knowles (1982), agree with Garret et al.'s (1982) suggestion that colony populations exhibit logistic growth. As a colony's population grows, it expands in size. Initially, colonies expand rapidly in the presence of abundant resources and low competition. As colonies grow competition increases and resource abundance decreases. Garret and Franklin (1988) suggested that one primary driving force behind BTPD dispersal was a reduction in preferred colony edge vegetation. However, at least two other factors probably forced a reduction in colony growth rates encouraging extracolonial dispersal in our study.

First, physical barriers (e.g., steep slopes or tall, dense vegetation) can slow larger colony expansion. In small colonies, dispersal to the colony's periphery permits rapid expansion into the surrounding prairie and greater access to edge vegetation. But as colonies grow, physical barriers may limit the amount of available, uncolonized prairie. Dispersal in these larger colonies might occur extracolonially, because intracolonial dispersal might result in reduced access to edge vegetation. Future studies should examine how low vegetation height and density, poor soil productivity, and physical barriers affect BTPD dispersal and colony expansion rates.

Second, the BLM prairie dog shooting program might have affected BTPD colony expansion. Shooting, starting in 1984, might have caused some of the decline in colony expansion rates. Unfortunately there are no data on BTPD numbers shot, but prairie dog shooting might effectively control prairie dogs if there are a sufficient number of hunters (Knowles 1988). Research should examine the impact of recreational hunting on BTPD colonies.

Colony expansion and new colony establishment are often associated with human disturbances (Osborn and Allan 1949, Knowles 1982). In this study we found a large, though unquantified, number of colonies associated with cattle salting grounds, reservoirs, and other regions affected by humans. Such areas are characterized by decreased vegetative height and density, often a result of intense cattle traffic (Knowles 1986). Grazing practices offer a potentially important prairie dog management tool. Research should compare effects of livestock grazing with effects of increased livestock traffic on colony establishment and expansion.

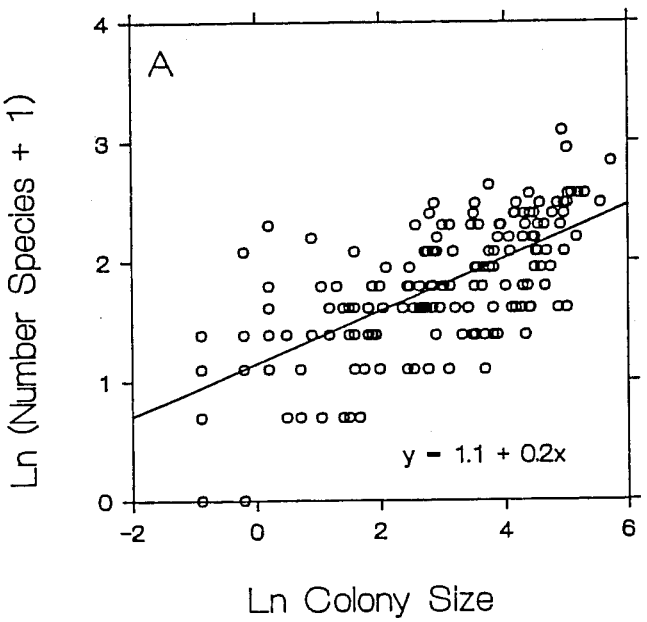
The range of burrow-opening densities in this study (13.6-246.9 burrows/ha, 5.5-99.7 burrows/ac) is within the range of densities reported elsewhere (6-116 burrows/ac, 15-287 burrows/ha; Koford 1958, Archer et al. 1987). Koford (1958) suggested that most BTPD colonies have 20-40 burrows/ac (50-100 burrows/ha). Various studies showed BTPD densities as: 25 burrows/ac (62 burrows/ha; Cottom and Caroline 1965), 34-64 burrows/ac (85-158 burrows/ha; Merriam 1902), 41-42 burrows/ac (101-104 burrows/ha; Knowles 1982), 42 burrows/ac (104 burrows/ha; Tileston and Lechleitner 1966), 51 burrows/ac (125 burrows/ha; King 1955), 55 burrows/ac (136 burrows/ha;Smith 1958) and 69 burrows/ac (169 burrow/ha; O'Meilia et al. 1982).

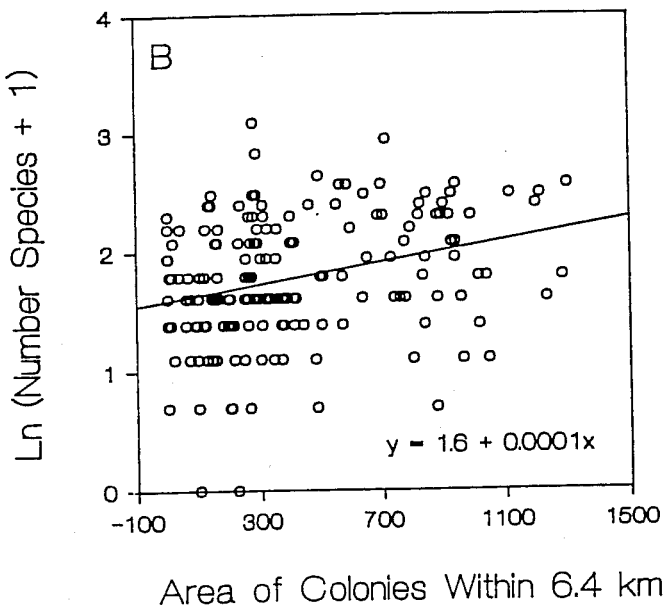
Burrow density may be positively correlated with prairie dog population density (Forrest et al. 1985, Houston et al. 1986). In this study, burrow density was not significantly related to colony size. This finding is consistent with King's (1955) suggestion that population densities are probably not related to colony size. Houston et al. (1986) noted that burrow density is not always an accurate indicator of population density. Burrow density reflects historical and recent past colony conditions. Also, BTPDs clean out more burrows in the spring than they use (Koford 1958). Burrow density can remain relatively constant even though population density decreases (Knowles 1982). Both population density and burrow density are probably more closely associated with habitat quality than with colony size. Potentially important factors affecting habitat quality include soil type, slope, vegetative cover type, and rainfall. Biggins et al. (1988) suggest using the ratio of active to inactive burrow-openings as a measure of population density.

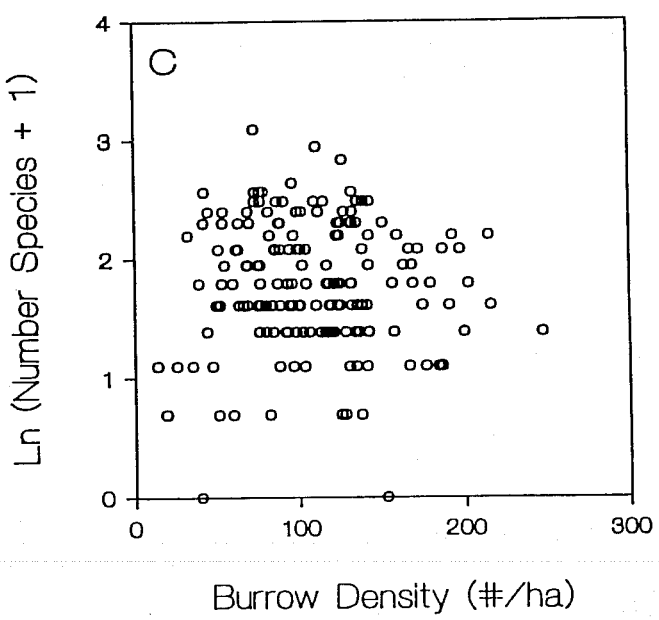


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Figure 5.—The effect of colony size (A), area of colonies within 4 mi. (6.4 km) (B), and burrow density (C) on avian species richness in 1988 for 170 BTPD colonies in Phillips County, MT. We added "1.0" to the number of avian species for computational purposes. Avian species richness-colony relationships: (A) $R$=0.66, $P$<0.001, (B) $R$=0.28, $P$<0.001, (C) No linear relationship exists ($P$=0.59).




Colonies are dynamic, responding to a number of interacting biotic and abiotic factors. Future research should examine the effectiveness of the censusing technique suggested by Biggins et al. (1988) for white-tailed prairie dogs (*C. leucurus*) on BTPDs and investigate the influence of physical and biological factors (e.g. slope, topography, soils, and vegetative cover) on BTPD colony attributes.

### *Species Associated With Prairie Dog Colonies*

A total of 163 vertebrate species have been sighted on BTPD colonies in this and in five other studies (Koford 1958, Tyler 1968, Campbell and Clark 1981, Clark et al. 1982, Agnew 1983; Appendix I). This includes 10 amphibians, 15 reptiles, 101 birds, and 37 mammals. Most of the previously unreported avian species (19 of 30) seen in this study are probably associated with reservoirs rather than with the colonies (i.e., Anseriformes, Pelecaniformes, Podicipediformes).

BTPD activities increase plant and vertebrate diversity on colonies (Hansen and Gold 1977). Agnew et al. (1986) found significantly higher densities of birds and mammals, and greater avian species richness on prairie dog colonies than on adjacent prairie. Several species prey on prairie dogs (e.g., black-footed ferrets; and golden eagles, *Aquila chrysaetos*), some inhabit unused burrows (e.g., burrowing owls, *Athene cunicularia*; and cottontails, *Sylvilagus* spp.), and still others benefit from the environmental alterations of prairie dogs (e.g., mountain plovers, *Charadrius montanus*; and McCown's longspur, *Calcarius mccownii*). Several authors report preferential ungulate grazing on colonies, especially by bison (*Bison bison*), cattle (*Bos tarsus*), and pronghorn (*Antilocapra americana*; Smith 1958, Coppock et al. 1983, Wydeven and Dahlgren 1985, Krueger 1986, Detling and Whicker 1988). For



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arthropods, however, the biomass on pastures grazed by cattle alone was three times greater than on pastures grazed by cattle and prairie dogs (O'Meilia et al. 1982). These studies demonstrate the importance of BTPD colonies to other species and highlight the significance of managing colonies favorable to biodiversity. Future studies should examine the dependency of associated species to BTPD colonies, especially threatened or endangered species or organisms listed as species of special concern by state agencies.

BTPD colonies represent distinct, "island-like" habitat patches (Whicker and Detling 1988). Although the prairie between colonies may not present a formidable barrier to dispersal for some vertebrates associated with BTPD colonies, for other vertebrate species it may. An area with a large number of habitat patches may increase dispersal rates into that area and maintain a larger number of immigrants capable of repopulating individual patches (Askins et al. 1987). Our results support predictions from island biogeographic theory that isolated patches of habitat maintain larger numbers of species with increasing patch size and proximity to sources of immigration (MacArthur and Wilson 1967). The number of bird species sighted on prairie dog colonies was significantly related to colony size and area of colonies within 4 mi (6.4 km), the former being the more important variable (Table 2; Figure 5A, B). Other researchers have obtained similar results for birds species distributions in forest habitat patches (e.g., Howe 1984, Askins et al. 1987).

In this study the relationship between colony size and avian species richness was linear, with a slope of 0.220 (Figure 4A), well within the predicted range for insular habitat patches and true islands. Preston (1962), MacArthur and Wilson (1967), and May (1975) predicted that species richness on islands should increase with island area such that the log-log plot is linear with a slope between 0.15 and 0.35. Similar patterns are suggested for habitat islands (MacArthur and Wilson 1967, Diamond 1984). Alternatively, sample plots and continental habitats are theoretically characterized by linear relationships of 0.12-0.17 (MacArthur and Wilson 1967, Diamond and Mayr 1976).

Unfortunately, we were unable to distinguish between avian species strongly associated with, or dependent on colonies and more casually associated or facultative species. Increased sampling effort with increased colony size could, therefore, account for some or all of the relationship. Blake and Karr (1984), however, obtained a slope of 0.223 for all avian species in Illinois forest patches. Future studies should sample on and off colonies to determine which species are strong or dependent associates.

Eight of the mammal species (80 percent) sighted in this study were sighted on fewer than 9 percent of the BTPD colonies examined. These species are probably not associated with prairie dog colonies, but with colonies as a part of the surrounding mid- to short-grass prairies. The relationship between colony size and mammalian species richness supports this suggestion, being linear with a slope (0.10) more similar to that of sample plots and continental habitats than islands or insular habitats.

Insular biology has important implications for the conservation of biodiversity, especially with respect to the size and shape of reserves (review in Simberloff 1988). Early applications of island biogeography theory to reserve design prescriptions aimed at maximizing species richness led researchers to recommend several reserve design principles (e.g., single large reserves are superior to several small ones, minimization of reserve boundaries relative to reserve area; Diamond 1975, Wilson and Willis 1975). Most of these design principles (other than a single large reserve is superior to a single small one) were subsequently challenged (Simberloff 1988). Using empirical evidence, further analysis of island biogeography theory, and metapopulation (groups of subpopulations characterized by greater movement within groups than between them; Andrewartha and Birth 1954) concepts, several researchers recommended establishing several small reserves characterized by at least minimal migration over one large reserve (Higgs and Usher 1980, Gilpin and Diamond 1980, Goodman 1987). An increase in the number of reserves might also decrease the probability of species extinction due to environmental stochasticity via risk-spreading (Simberloff and Abele 1976, Quinn and Hastings 1987). Although the debate continues, insular biological theory can play a useful role in the conservation of biodiversity on prairie dog colonies.

Conservation management of prairie dogs and their associated species should occur at the ecosystem level. BTPD ecosystems are comprised of colony complexes (clusters of colonies; Minta and Clark 1989) which can be thought of as metapopulations of prairie dogs and their associated fauna (Clark et al. 1987). Results of this study suggest that richness of associated vertebrate species on BTPD colonies increases with colony size and regional colony density. Managers should therefore maintain complexes of relatively large colonies linked by "stepping-stone" colonies for species dispersal. Reserve design and future BTPD management should concentrate on the maintenance of biodiversity on prairie dog complexes. Additional research and management knowledge is needed to achieve this goal.

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