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A DISSERTATION APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

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Abstract

I examined avian communities on the shortgrass plains and tested for associations with black-tailed prairie dog (*Cynomys ludovicianus*) towns. The black-tailed prairie dog is one of five members of the genus *Cynomys* (Order Rodentia, Family Sciuridae) and is the only prairie dog species occurring in Oklahoma. Prairie dogs create and maintain a unique habitat by keeping vegetation clipped low to the ground and by construction of extensive, underground tunnel systems. Other species use dog towns as foraging sites, use burrows as dens or refugia from predators or severe weather, or use prairie dogs themselves as prey. Black-tailed prairie dogs have maintained a broad and relatively stable geographic range since the end of the Pleistocene and may have once covered from 40-100 million hectares. Today, they cover less than 5% of this area. The remaining towns are increasingly smaller, fragmented, and more isolated.

I tested the hypothesis that black-tailed prairie dogs influence avian community structure on the shortgrass prairie and essentially function as "islands" in a sea of grass. I surveyed 36 prairie dog towns and 36 paired sites without prairie dogs during summer and fall of 1997, 1998, and 1999 in the Oklahoma Panhandle. Surveys totaled 9,040 individual observations for 73 avian species. Significantly distinct avian communities were present on prairie dog towns when compared to sites within four different macrohabitats of the surrounding landscape: open rangeland, scrub/sandsage (*Artemisia filifolia*) habitats, Conservation Reserve Program (CRP) plots, and fallow crop fields. Relative densities of all bird species combined was higher on prairie dog towns versus paired sites in summer and fall. Mean species richness of birds was significantly higher on prairie dog towns than paired sites during summer, but there were no significant differences in fall. Assemblages of avian communities differed significantly between prairie dog towns and the four macrohabitat types during summer.

Burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferous*), horned larks (*Eremophila alpestris*), and meadowlarks (*Sturnella* spp.) were positively and significantly associated with prairie dog towns during summer, while horned larks and ferruginous hawks (*Buteo regalis*) were significantly associated with prairie dog towns during fall. Richness was not significantly associated with town size or isolation. Richness was however associated with certain local habitat characteristics (percentage of forb coverage) and certain landscape-level variables (area of scrub habitat within 10 km of a focal town). Birds also show a strong geographic trend in richness, increasing significantly from west to east. These results are consistent with the emerging view that communities on relatively small islands are strongly influenced by characteristics of the surrounding landscape, variables other than area and isolation.

It is clear that even in their current remnant state, black-tailed prairie dogs continue to play a significant role in the assembly of ecological communities across the Great Plains. Conservation of prairie dogs goes well beyond a single species, and is an important strategy for the preservation of the prairie ecosystem as a whole.

EVOLUTION AND HISTORICAL BIOGEOGRAPHY OF PRAIRIE DOG ECOSYSTEMS

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Running head: Historical biogeography of prairie dogs

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Abstract. The purpose of this chapter is to place the current ecological role and status of black-tailed prairie dogs within the context of the evolutionary history of the Great Plains ecosystem. Black-tailed prairie dogs (*Cynomys ludovicianus*) have maintained a broad and relatively stable geographic range since the end of the Pleistocene. As such, numerous grassland species have adapted to the availability of this predictable resource. Dramatic declines in coverage of prairie dog towns since the early 1900's stimulated research into all aspects of prairie dog biology. Here we summarize the role of prairie dogs in grassland ecosystems, establishing the importance of this dominant herbivore of the Great Plains. In subsequent chapters, we report that prairie dog towns function as a distinct habitat type, strongly influencing avian distribution and abundance (Chapter 2) and that prairie dog towns can be viewed as "islands" in a sea of grass (Chapter 3). These findings have important insights for those attempting to understand and conserve biological diversity of these native, grassland communities.

Key words: black-tailed prairie dogs; *Cynomys ludovicianus*; Great Plains; Oklahoma; Pleistocene.

THE NORTH AMERICAN GRASSLAND BIOME

Grasslands today are the largest of four major natural vegetation formations covering the earth's land surface (Sims and Risser 2000). They account for approximately 24% of the earth's vegetation and cover more than 4.6 billion ha. In the interior of North America, the Great Plains stretch more than 4000 km from Mexico to central Canada, and are over 640 km wide from the eastern edge of the Rocky Mountains to western Minnesota. Parts of ten states and three Canadian provinces lie within the boundaries of the Great Plains. Originally covering a nearly continuous expanse of almost 370 million ha in the United States, Canada, and Mexico combined, and extending eastward into Indiana, this area has been reduced to approximately 125 million ha since pre-settlement times (Sims and Risser 2000). Still, grasslands remain the largest natural biome in the United States. Grasslands appear in the fossil record almost 20 million years ago (mya), although the interior grasslands of North America did not begin their expansion until the Miocene-Pliocene transition 7-5 mya, and probably did not reach their pre-settlement extent until after the last glacial event 10,000 years ago (Axelrod 1985).

The advance of the Great Plains grasslands was made possible by four major conditions: (1) periods of increased aridity, which favored grasses and forbs at the expense of forested woodlands, (2) an increase in drought, especially west of the 100th meridian, which provided dry grass as a fuel source for fire, (3) an increase in the frequency of fire, both natural and manmade, and (4) grazing by large and small herbivores. Prior to the Pliocene Epoch, the middle Miocene (19-18 mya), was much cooler and moister than today. Fossil beds and palynological data from northwest Nebraska indicate the presence of ferns and monocots but also trees such as hawthorn (*Crataegus* spp.), locust (*Robinia* spp.), and elm (*Ulmus* spp.), which today occur in areas receiving as much as 900 mm of precipitation annually (Axelrod 1985). This area of Nebraska is dry, shortgrass plains today and receives only 400-430 mm of precipitation annually, including snow. By 14-13 mya, the climate of the northern Great Plains was beginning to dry, but was still considerably moister than today. Data from the Nebraska-

South Dakota border from this time period show evidence of predominantly deciduous forest, species such as maple (*Acer* spp.), hickory (*Carya* spp.), and hackberry (*Celtis* spp.) (MacGinitie 1962). The presence of large tortoises and crocodilians indicates a moist, subtropical climate, perhaps receiving as much as 760-890 mm of precipitation annually (Axelrod 1985). *Sabal* palms were also documented from northern New Mexico in this same time period (Axelrod and Bailey 1976). Grass pollen and fossils of grazing mammals are present, which would suggest the presence of grassy clearings within the woodland forest. Climates on the Great Plains were becoming warmer by the late Miocene, although still relatively moist. Tortoises, rhinos, peccaries, and an oreodont (an extinct North American pig-like artiodactyl) were present in fossil beds from Beaver County, Oklahoma 12-10 mya (Hesse 1936). The vegetation in the area was still predominantly floodplain forest, indicating precipitation levels much higher than today. The presence of herd animals, however, suggests at least some open savanna-like areas between the trees.

The onset of the Pliocene Epoch (7-5 mya) saw increasing aridity on the Great Plains. Evidence from fossil flora of Logan County, Kansas, suggests precipitation levels approximating what is found in that area today (Chaney and Elias 1936, Axelrod 1985). Fossils of grasses suggest a surge in speciation rates of during this period (Elias 1942). The much drier climates confined trees and forests to stream borders and valley bottoms allowing grasses to expand into areas previously unavailable to them during the dominance of forest (Axelrod 1985). Much of this drying was presumably due to the chilling of the oceans as the Antarctic ice sheet spread and, perhaps most importantly for the Great Plains, the uplift of the Rocky Mountains which intercepted moisture coming from the Pacific Ocean creating an ever-widening rain shadow as the mountains rose. In summary, the drying trends of the Miocene, and especially the Pliocene corresponded to a shift to increasingly more open ecosystems, with forests confined to valley and riparian sites with large patches of grassland in between (Axelrod 1985). Climates at this time were probably more seasonal than they are today (Hibbard 1970). Climate extremes began to increase during the Pleistocene with the onset of glaciations, but the presence of abundant mammalian browsers and grazers and reptiles continues to suggest a seasonally warm climate.

The cyclic advance and retreat of glaciers during the Pleistocene caused widespread changes globally and within the Great Plains region (see Lomolino et al. 2005). At least four major glacial advances, and the subsequent inter-glacial periods, within the past 600,000 years have shaped the present geographic distribution of the North American interior grasslands and the flora and fauna associated with it. In the early to mid-Pleistocene, oak (Quercus spp.) forest extended farther west onto the plains that it does today, while at least local stands of pine (*Pinus* spp.) and spruce (*Picea* spp.) were present in southwestern Kansas and the Oklahoma Panhandle. Spruce forest also extended into western Nebraska 12,000 years ago, while late Wisconsin boreal forest covered much of present day southern Minnesota, South Dakota, Nebraska, Kansas, and Missouri. The corresponding mammalian fauna, including numerous browsers and grazers, would indicate a mix of woodland and large open grassland patches. By the end of the Pleistocene, spruce forests were retreating north to be replaced by grassland spreading from the southwest. The prairies of southern interior Canada are entirely post-glacial (Axelrod 1985). By roughly 7,000 years ago, however, prairie ecosystems of the Great Plains extended farther north than they do today. By 3,000 years ago, the climate was cooling again and forests were moving south replacing grasslands.

PRAIRIE DOGS

The black-tailed prairie dog (*Cynomys ludovicianus*) is one of five members of the genus *Cynomys* (Order Rodentia, Family Sciuridae) found only in North America. The other members of the genus are the Mexican (*C. mexicanus*), Gunnisoni's (*C. gunnisoni*), white-tailed (*C. leucurus*), and Utah prairie dogs (*C. parvidens*). Differences in morphological, ecological, and behavioral characters as well as non-overlapping ranges allow the five species to be uniquely distinguished (Table 1). Black-tailed prairie dogs have the largest geographic range of any of the prairie dog species (Figure 1) and are believed to be most closely related to Mexican prairie dogs (Hoogland 1996). Black-tailed and Mexican prairie dogs are commonly placed in the subgenus *Cynomys* with Gunnison's, White-tailed, and Utah prairie dogs falling under the subgenus *Leucocrossuromys* (Hoogland 1996; Table 1).

Black-tailed prairie dogs were first identified from a skin obtained by Lewis and Clark on their 1804-1806 expedition (Smith 1967; Table 2). George Ord described the species and called it the Louisiana marmot to which he attributed the Latin name, *Arctomys ludovicianus*. In 1816, Rafinesque proposed the current generic name, *Cynomys*. Prairie dogs are large (400-1,500 g), diurnal, colonial, burrowing ground squirrels. Typical adults are brown or reddish-brown above and whitish below. The distal third of the tail of both sexes is characteristically black. Male pelage is usually redder than female pelage and adult males outweigh adult females by 10-15% (Hoogland 1996). Prairie dogs create large expanses of short surface vegetation, denuded external mounds, and underground tunnel systems. Such areas are called towns or colonies. Burrow entrances are typically 10-30 cm in diameter, 5-10 m long, and 2-3 m deep (Clark 1977). Within a colony, territorial harem-polygynous family groups called coteries are formed (King 1955). Coloniality increases predator detection as well as efficiently reducing tall vegetation. However, there are some costs associated with colonial living. Aggression tends to increase as colonies become denser (King 1955), individual members are more susceptible to contracting disease, and misdirected parental care may result. In fact, infanticide is one of the major causes of juvenile mortality in prairie dog colonies (Hoogland 1995).

Evolution of prairie dogs

The genus *Cynomys* has its first appearance in the fossil record in the late Pliocene, 2.5-1.8 mya (Goodwin 1990). The two subgenera, white-tailed prairie dogs (*C. Leucocrossuromys*) and black-tailed prairie dogs (*C. Cynomys*) are distinctly recognizable by the early Pleistocene, 1.8-0.75 mya (Goodwin 1993; see also Goodwin 1990). Today, white-tailed prairie dogs occupy shrub-steppe in high elevation, cold winter, relatively arid environments with short growing seasons. Black-tailed prairie dogs, on the other hand, inhabit prairie habitats of lower elevation, relatively mesic environments, with milder winters and longer growing seasons. These differences are likely due to thermal tolerances and behavioral differences in the groups that dictate their distributions (Hoogland 1995; Table 1). There is no evidence that these behavioral and physiological characteristics are different today than in the past and therefore, we must assume that the distributions of these groups followed changes in climate and vegetation during the Pleistocene. In fact, the fossil record supports this. As mentioned above, during full glacial climate, the Great Plains exhibited a latitudinal gradient from cold and dry in the north to warm and moist in the south (Barry 1983). Sagebrush-steppe (*Artemisia* spp.) habitat was interspersed with spruce forest on the northern plains (Watts and Wright 1966) and probably extended south onto the central Great Plains (Fredlund and Jaumann 1987). The distribution of prairie dogs followed these vegetation changes. During the late Pleistocene glacials and interglacials, white-tailed prairie dogs (represented by the now extinct *C. niobrarius*) expanded north into the shrub-steppe habitats while black-tailed prairie dogs expanded southward and eastward (Goodwin 1990; Goodwin 1993). Black-tailed prairie dogs at one time extended south to the Gulf of Mexico and east into southeastern Texas and southwestern Iowa, well beyond their current range limits (Goodwin 1990). A southwesterly expansion is also supported by fossil evidence for black-tails (Goodwin 1990). Prairie dogs maintained this distribution throughout the "Ice Ages." There is, however, no indication that black-tailed prairie dogs attained their current northern distribution until the Holocene (Goodwin 1993). Although vegetation zones may have waxed and waned during the cyclic glaciations (Kapp 1965), apparently climatic changes were not enough to displace the white-tailed prairie dogs from their more northern distribution during that time (Goodwin 1993). This would indicate that climatic changes since the last glaciation were more extreme than during the previous interglacials (Graham 1986l; Graham and Mead 1987; King and Saunders 1986), paving the way for replacement of northern white-tailed populations by black-tailed prairie dogs during the Holocene. Throughout much of the Pleistocene, even during the interglacials, prairie dogs maintained a characteristic distribution of white-tails on the northen plains, black-tails in the south, and a zone of overlap on the central plains (Goodwin 1993). This zone of overlap may have shifted north or south with the climatic variations of the Pleistocene, but black-tailed prairie dogs are not found north of Nebraska until the Holocene (Goodwin 1990). Mexican prairie dogs (*C. mexicanus*) are probably a relictual species derived from *C. ludovicianus* during or since the late Pleistocene (McCullough and Chesser 1987).

Breeding Biology

Copulation occurs underground during winter or early spring. Young are born in April and first emerge from their natal burrows in May or June. Males disperse from the natal coterie sometime before sexual maturity, reducing chances for inbreeding (King 1955). Unlike many other rodent species, prairie dogs are not prolific breeders. Females do not reproduce until their second year. Laboratory studies have shown that females give birth to 1-8 young (average 3-5), but under natural conditions, Hoogland (1995) found the mean number of emergent juveniles per year for copulating females is 1.61 ± 1.74 (range 0-6) (Hoogland 1996). Hoogland (1995) found almost all demographic parameters to be highly variable from year to year and somewhat correlated to amount of precipitation the previous year. Larger litters followed wetter years. Further, over their lifetime, females produced an average of just 4.25 ± 3.85 (range 0-18) emergent juveniles (Hoogland 1995). Coupled with fairly short life expectancies (mean of 2-3 years for males, 3-4 years for females in the wild), prairie dogs do not appear capable of recovering quickly from population crashes.

Habitat and Diet

Black-tailed prairie dogs inhabit short and mixed-grass prairies and desert grasslands up to an altitude of 1,700 m above sea level. There they consume numerous grasses and forbs (see Smith 1967 and Hoogland 1995 for exhaustive lists), but several species appear to be preferred. Buffalo grass (*Buchloe dactyloides*), prickly pear cactus (*Opuntia* spp.), and thistle (*Cirsium* spp.) are winter favorites while wheatgrass (*Agropyron* spp.), grama (*Bouteloua* spp.), buffalo grass, scarlet globemallow (*Sphaeralcea coccinea*), and rabbitbrush (*Chrysothamnus* spp.) are preferred in summer (Koford 1958, Summers and Linder 1978). Prairie dog grazing encourages an increase in plant species more tolerant to their grazing. Decreases in grass/forb ratios have been observed in prairie dog colonies providing opportunities for the establishment of more species and leading to greater plant diversity within towns than outside towns (Bonham and Lerwick 1976).

Ecosystem

Prairie dogs produce a homogeneous “lawn” of grasses and forbs within an individual town surrounded by significantly different habitats (Whicker and Detling 1988; Weltzin et al. 1997). Other species may use dog towns for forage, use burrows as dens, for protection from the elements, to escape from predators, or they use prairie dogs themselves as prey. A number of species depend on these prairie dog patches (Sharps and Uresk 1990) and this has led many ecologists to refer to them, we feel justifiably so, as ecosystem engineers and keystone species (Miller et al. 1994; Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000). Ecosystem engineers are, "...organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain, and/or create habitats" (Jones et al. 1994, pg. 376). Our studies indicate that even after being reduced to less than five percent of their historic range, prairie dog towns in western Oklahoma continue to be inhabited by distinct assemblages of vertebrate species and strongly influence community structure, creating a dynamic landscape across short and mixed grass prairie (see Chapters 2 and 3; Lomolino and Smith 2004).

Prairie dog towns are inhabited by a highly distinct assemblage of vertebrate species, including species of conservation priority. Terrestrial vertebrates strongly associated with prairie dog towns include American badgers (*Taxidea taxus*), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), domestic cattle (*Bos taurus*), cottontail rabbits (*Sylvilagus* spp.), coyotes (*Canis latrans*), northern grasshopper mice (*Onychomys leucogaster*), swift fox (*Vulpes velox*), pronghorn (*Antilocapra americana*), burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferous*), horned larks (*Eremophila alpestris*), meadowlarks (*Sturnella* spp.), ferruginous hawks (*Buteo regalis*) and prairie rattlesnakes (*Crotalus viridis*) (Agnew et al. 1986; Barko et al. 1999; Lomolino and Smith 2004; Manzano-Fischer et al. 1999; Winter et al. 1999a; Kretzer and Cully 2001; Chapter 2). Before the turn of the century, this list of town associates likely would have included black-footed ferrets (*Mustela nigripes*), and perhaps bison (*Bison bison*), elk (*Cervus elaphus*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*) (Benedict et al. 1996). Species of special concern that have been listed as town associates include the tiger salamander (*Ambystoma tigrinum*), prairie rattlesnake, ornate box turtle (*Terrapene ornata*), burrowing owl, mountain plover (*Charadrius montanus*), ferruginous hawk, swainson's hawk (*B. swainsoni*), prairie falcon (*Falco mexicanus*), golden eagle (*Aquila chrysaetos*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), long-billed curlew (*Numenius americanus*), black-footed ferret, and swift fox (Tyler 1968; Butts 1976; Knowles et al. 1982; Agnew et al. 1986; Shackford and Tyler 1991; Allison et al. 1995; Desmond et al. 1995; Barko 1996).

Further, Reading et al. (1989) found 164 vertebrate species recorded from prairie dog towns across their entire range (Table 4). Although many of the species on this list are probably only causally dependent on prairie dog towns (e.g. Pied-billed Grebe [*Podilymbus podiceps*]), many others are closely associated with prairie dog towns which, until the previous century, constituted some of the most expansive and predictable resources and refugia for Great Plains species. Note also that most of the species listed as town associates are vertebrates, yet certain invertebrate species such as the black-widow spider (*Latrodectus mactans*) and the harvester ant (*Pogonomyrmex occidentalis*) are attracted to dog towns as well (Hoogland 1996). For other species, higher population densities are often reported on prairie dog towns versus neighboring sites. Agnew et al. (1986) found such a pattern in deer mice (*Peromyscus maniculatus*), grasshopper mice (*Onychomys leucogaster*), and horned larks (*Eremophila alpestris*). Thus, prairie dog towns may be highly influential ecosystems across the Great Plains, providing resources for numerous species during some part of their life histories.

Current Status

Despite the broad and relatively stable range of the black-tailed prairie dog throughout much of the Pleistocene and Holocene (Figure 2), anthropogenic activities have reduced the coverage of this native grassland species and its associated community to approximately 2% of historic numbers (circa 1800). Black-tailed prairie dogs presently occur throughout most of their historic range, but their current distribution within that range is highly fragmented and their numbers have been drastically reduced. Prairie dog colonies are believed to have covered from 40-100 million hectares around the turn of the century, but only cover about 600,000 hectares today (Miller et al. 1994). Our recent surveys of towns in Oklahoma have also documented declines within the past 10-15 years (Lomolino and Smith 2001). In the Oklahoma Panhandle alone, areal coverage of prairie dog towns declined by about 45% between 1989 and 1997 (Lomolino and Smith 2001).

The anthropogenic decline in the geographic range of the black-tailed prairie dog, a species and ecosystem that dominated the Great Plains throughout much of the Pleistocene and early Holocene, has a geographic signature much like that of deforestation and other forms of fragmentation. Concurrent with the decimation of these native ecosystems, remnant patches (while perhaps increasing in number) became both smaller and more isolated. The likely effect of these biogeographic dynamics, whether fragmentation of old-growth forests (see Laurance and Bierregaard 1997; Lomolino and Perault 2000; Perault and Lomolino 2000) or prairie dog towns, is an overall decline in persistence time for the entire metapopulation or metacommunity (see Hanski and Gilpin 1997). A relatively small number of populations, including those in some of the most isolated regions of the species' range, may persist through the 21st century. Given, however, the projected increased isolation of remnant towns, the likelihood of recolonization will be extremely remote. Just as important, because diversity is directly correlated with area for nearly all types of ecosystems (Rosenzweig 1995; Brown and Lomolino 1998), regional and global diversity of native grassland communities will experience substantial declines well before the last prairie dog town becomes extinct in the wild. Such declines in biological diversity are ongoing and evidenced by the documented declines of many town associates (e.g., burrowing owl [*Speotyto cunicularia*], ferruginous hawk [*Buteo regalis*], mountain plover [*Charadrius montanus*], and swift fox [*Vulpes velox]*), and the near extinction of black-footed ferrets (*Mustela nigripes*; Butts 1976; Knowles et al. 1982; Barko 1994; Miller et al. 1994; Desmond et al. 1995). For many of these species, town size may be just as important as town isolation or the total area of towns across the now highly fragmented range of this ecosystem engineer.

The relatively high persistence we observed for the most isolated populations is consistent with patterns in range collapse for endangered species, in general (Lomolino and Channell 1995 and 1998; Channell and Lomolino 2000a and b). It is not that these isolated populations are necessarily more resistant to anthropogenic extinction forces (e.g., land conversion or the spread of commensals and exotic species) or to the plague (an exotic, commensal disease; see Cully 2001), just that the most isolated populations are likely to be the last ones encountered by anthropogenic factors that tend to spread across native landscapes like a contagion. For an overwhelming majority of imperiled species of plants and animals studied, persistent populations are not necessarily the largest or those with highest population densities, but those most isolated from the point of initial contact (Lomolino and Channell 1995 and 1998; Channell and Lomolino 2000a and b). Therefore, areas along the periphery of the black-tailed prairie dog's historic range should not be abandoned as they may in the future provide valuable opportunities to maintain or reestablish populations of this important species. (Note that the last wild population of the black-footed ferret was discovered along the extreme periphery of its historic range.) Where anthropogenic extinction forces can be controlled (i.e., by minimizing poisoning, shooting and land conversion), population persistence of prairie dogs and associated species should be highest for the largest towns, while the likelihood of natural recruitment and recolonization should be highest for the less isolated ones.

Legal Status

On July 30, 1998 the National Wildlife Federation (NWF) petitioned the U.S. Fish and Wildlife Service (Service or USFWS) to emergency list the black-tailed prairie dog as threatened throughout its range. The NWF stated the emergency need was due to unregulated shooting and poisoning of prairie dogs that would occur during the Service's 12-month listing evaluation process. By law, the Service was compelled to respond to the petition within 90 calendar days. In September 1998, the Service responded to the NWF that although it did not believe the threshold had been met for emergency listing the black-tailed prairie dog, listing the species might be warranted and they would further evaluate the petition. On March 23, 1999 a positive 90-day finding for the petition was announced. This action initiated a 9-month review process for the petition. Starting in November 1998, state wildlife agencies and departments of agriculture in Wyoming, Montana, and South Dakota held a series of meetings with the Service and NWF to discuss the petition and the options the states have in regard to the petition. Based on discussions at these meetings, it was determined that involvement by all states, other management agencies, and tribal interest within the historic range of the black-tailed prairie dog was warranted and a meeting should be convened to begin developing an interstate effort to conserve the species.

On March 17, 1999 the Colorado Division of Wildlife (CDOW) invited various state, federal, tribal, and other entities with an interest in black-tailed prairie dogs to a meeting to assess the feasibility of a range wide conservation agreement. Meeting participants agreed that pursuing a conservation agreement was the most reasonable approach for black-tailed prairie dog conservation. They believed that if strong partnerships could be developed under this approach, it would be a significant step forward in bringing local governments, private landowners, and nongovernmental organizations directly into black-tailed prairie dog management. The purpose of the resultant Conservation Agreement is to manage, maintain, and enhance habitat and populations of black-tailed prairie dogs across its historic range and reduce the number of threats impacting their viability through the cooperation of private, tribal, federal, and state landowners. The Conservation Agreement has many elements that provide actions, opportunities, and incentives for interested parties to become involved with conservation.

The Conservation Agreement embraces two main components. The first is a Conservation Assessment, which describes the current status of the black-tailed prairie dog in the United States, Mexico, and Canada and identifies the threats limiting its conservation. The second component focuses on reducing or eliminating threats limiting black-tailed prairie dog viability, as defined in the Conservation Assessment. By implementing management actions such as eliminating mandatory control, regulating seasons or possession limits, maintaining and conserving their habitat and ecosystem needs, and establishing core populations on public lands to provide animals for dispersal to uninhabited areas, the cooperators of this conservation agreement contributed toward the conservation of the species. On February 4, 2004, the black-tailed prairie dog was removed from the US Fish and Wildlife Service "Candidate" species list (Table 2)

As mentioned previously and illustrated in Figure 1, the black-tailed prairie dog has the widest distribution of any prairie dog species. Formerly ranging from the Mississippi River in the east to the Rocky Mountains in the west and extending from Mexico to southern Canada, the black-tailed prairie dog occupied parts of eleven states (Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming). Prairie dog colonies today are extirpated from Arizona with documented declines in Colorado (Fitzgerald et al. 1994), Kansas (Vanderhoof et al. 1994, Powell and Robel 1994), North Dakota (Bishop and Culbertson 1976), Oklahoma (Lomolino and Smith 2001), and Wyoming (Campbell and Clark 1981) (Table 3).

The drastic population decline of the black-tailed prairie in less than 100 years can be linked to three major causes: (1) government subsidized eradication campaigns, (2) conversion of optimal habitat to agricultural fields, and (3) extinction of small populations from disease, particularly plague. Since the late 1880's, land owners (particularly ranchers and livestock owners) have been poisoning prairie dogs who they thought competed with their cattle for forage (Table 2). Early on, poisoning was haphazard and uncoordinated. But in 1902, C. Hart Merriam (1902), then Director of the Biological Survey (now the National Biological Service) gave credence to this belief when he estimated that prairie dogs reduced the productivity of grazing lands by 50-75% and authorized government subsidized funding of a prairie dog eradication program. Millions of prairie dogs were poisoned each year. Poisoning programs continue to this day (Roemer and Forrest 1996).

As population sizes decreased due to eradication and conversion of prime habitat to agricultural fields (including land that contained dog towns), prairie dogs became more susceptible to outbreaks of disease, particularly epizootics of sylvatic plague (*Yersinia pestis*) (Cully 1989) which often killed over 99% of individuals in the affected colony. Therefore, even though prairie dogs still occur throughout a significant portion of their historic range, current populations have become exceedingly fragmented and isolated, thus increasing their chances of extirpation by any number of causes, including plague.

Although the impetus for eradication programs was the fear that prairie dogs were competing with cattle for grazing land, several studies have since shown Merriam’s estimate of prairie dog competition with cattle to be an exaggeration (O’Meilia et al. 1982; Collins et al. 1984; Miller et al. 1994). In fact, prairie dogs may improve forage quality within towns by keeping grasses in an early growing, more easily digestible stage, and several studies have documented the preference of cattle for grazing on prairie dog towns (Lomolino and Smith 2004). Further, it may not be economically feasible to control prairie dogs by poisoning when sound grazing practices may be more appropriate (Collins et al. 1984). Unfortunately, because eradication programs began around the turn of the century, before the science of ecology had begun to develop, early research concerning prairie dogs centered on effects of poisoning in an attempt to develop more efficient chemicals. Later, research focused on social behavior and coloniality of these large rodents (King 1955). The importance of prairie dogs as keystone species was not recognized until after most of the damage had been done and negative perceptions of prairie dogs had been ingrained in the minds of ranchers and land owners.

BIODIVERSITY ON THE GREAT PLAINS

There are more vertebrate species on the Great Plains today than at any time in the post-settlement history of the region (Knopf and Samson 1997; Ostlie et al. 1997). Although this might seem promising at first, the influx of more generalist species has come at the expense of endemic grassland vertebrates which tend to be more specialized. This does present a conundrum for conservation biologists and land managers. The Oklahoma Panhandle has 20-40% of its potential natural vegetation remaining (Sieg et al. 1999). These changes in landuse have resulted in a decrease in native species coupled with a dramatic increase in non-endemic species (Samson and Knopf 1994; Sieg et al. 1999) such as forest edge birds, historically only present in midwestern oak and eastern deciduous forests (Knopf 1986). Anthropogenic changes to the landscape have altered the interaction between drought, fire, and grazing such that habitat heterogeneity is decreasing. Such conditions favor generalists, not specialists. Historically, patchiness on the Great Plains was not static, but shifted dynamically in response to unpredictable droughts, irregular fire events, non-random grazing by nomadic large herbivores (Wallace et al. 1995), and correspondingly intense grazing by small herbivores (Vinton and Collins 1997). Black-tailed prairie dogs remain the only feature of this dynamic system still maintaining a broad, albeit sparse and highly fragmented, geographic distribution. Fire is now controlled and limited in its extent, and native large grazing guilds have been replaced by domestic cattle. When properly managed, cattle may be an adequate surrogate for bison (Hartnett et al. 1997), but prairie dogs are currently key to the maintenance of habitat heterogeneity on the plains.

Future conservation planning should take into consideration the need for a diversity of habitats, ranging from high disturbance areas such as prairie dog towns to low disturbance patches such as sandsage scrub. Specialist species and endemic species are often most susceptible to alterations of the landscape, such as fragmentation (Harris1984). Endemics should therefore be the focus of future conservation efforts on the Great Plains (Knopf and Samson 1995; Mulhern and Knowles 1998). To the extent that it is possible, restoration of the processes that shaped the plains should also be a focus of conservation efforts. Recovery of prairie dogs provides the beginning of a solution for both of these tasks. Taken together, it is clear that even in their current remnant state, black-tailed prairie dogs continue to play a significant role in the assembly of ecological communities across the Great Plains. Conservation of prairie dogs goes well beyond a single species, but is in fact an important strategy for the preservation of the prairie ecosystem as a whole.

SUMMARY OF DATA CHAPTERS

Prairie dog towns are distinct features of the Great Plains landscape. Chapter 2 tests the hypothesis that black-tailed prairie dogs influence avian community structure on the shortgrass plains. Bird counts on prairie dog towns paired with non-prairie dog matrix habitats showed that assemblages of avian communities differed significantly between these habitat types. Several species were positively and significantly associated with prairie dog towns, evidence that even in their remnant state, prairie dogs remain an important component of the Great Plains landscape.

Chapter 2 provides evidence that prairie dog towns are an important part of the overall landscape but how do birds respond to characteristics of individual towns? In Chapter 3 we tested patterns of species richness and species composition, treating prairie dog towns as islands in a "sea" of grass. Results suggest that avian communities on prairie dog towns may be more strongly influenced by local and landscape-level habitat characteristics than by island characteristics such as area and isolation of dog towns. These results are indicative of "small island effects." This suggests some important conservation considerations. Namely that preservation of prairie dog towns is not enough. Prairie dog conservation must be approached as part of an ecosystem, not as islands unto their own.

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Table 1. Comparison of five extant prairie dog species (modified from Hoogland 1995).

	Cynomys Cynomys spp.		*Cynomys Leucocrossuromys* spp.		
	Black-tailed	Mexican	Gunnison's	White-tailed	Utah
Length of tail (mm)	60-100	90-110	30-65	30-65	30-65
Number of teats	8	8	10	10	10
Black-tipped tail	Yes	Yes	No	No	No
Black spot above eye	No	No	No	Yes	Yes
Typical colony size	> 1,000	?	< 500	< 500	< 500
# different calls/sounds	12	?	9	7	7?
Hibernation	No	No	Yes	Yes	Yes
2n number	50	50	40	50	50
Gestation (days)	34 or 35	?	29 or 30	?	?
Lactation (days)	37-51	41-50?	35-44	?	?
Age of first copulation	2	1?	1	1	1
Status	Rare	Endangered	Rare	Rare	Threat-ened

Table 2. History of the black-tailed prairie dog in the United States (modified from Barko 1997).

Date	Event
1802-1804	Described and collected by Lewis and Clark.
1815	Taxonomic description by Ord.
late 1880's	Haphazard poisoning, no concerted effort
1902	C.H. Merriam calls for prairie dog eradication
1902 - 1915	Poisoning program controlled by livestock industry
1915	Federally funded poisoning programs began
1920's	Millions of prairie dogs were poisoned each year
1929	Predatory Animal and Rodent Control Division created (Animal Damage Control)
1931	Animal Damage Control Act passed
1939	Fish and Wildlife Service created and Division of Predatory Animal and Rodent Control transferred to its Bureau of Sport Fisheries and Wildlife - responsible for eradicating prairie dogs and protecting species depending on prairie dogs
1971	Nixon bans toxicants causing secondary poisoning - zinc phosphide developed with "prairie dog use only" label
1981	Reagan reverses Nixon's ban, increases ADC programs. Transfers ADC to Department of Agriculture relieving USFWS of contradictory tasks
1990's	Poisoning continues on federal, state, and private lands
July 31, 1998	Petitioned for listing as a Threatened Species by the National Wildlife Federation and Biodiversity Legal Foundation
March 15, 1999	Positive 90-day finding from the US Fish and Wildlife Service.
February 4, 2004	Warranted but Precluded ruling from the US Fish and Wildlife Service.
August 12, 2004	Removed from the "Candidate" species list.

Table 3. Synopsis of vertebrate species sightings on black-tailed prairie dog towns from the literature (Koford 1958; Tyler 1968; Campbell and Clark 1981; Agnew et al. 1986; Reading et al. 1989).

	Number of Times Sighted				
Group	1	2	3	>3	**Total**
Amphibians	9	1	0	0	**10**
Reptiles	8	6	0	1	**15**
Birds	53	16	14	18	**101**
Mammals	15	13	4	6	**38**
Total	**85**	**36**	**18**	**25**	**164**

Table 4. Historic and current extent of prairie dog coverage in all states encompassing their range. Percent 1/4 historic begins calculations assuming only 25% of estimated historic acreage actually existed. Even if historic estimates of prairie dog abundance were off by 25%, dramatic declines are still evident (modified from Van Pelt 1999 and Luce 2002).

State	Historic	¼ Historic	Current	% Historic	% ¼ Historic
Arizona	7,047,137	1,761,784	0	0	0
Colorado	27,352,880	6,838,220	631,102	2.31	9.23
Kansas	35,835,079	8,958,770	130,521	0.36	1.46
Montana	60,442,757	15,110,689	90,000	0.15	0.6
Nebraska	36,035,433	9,008,858	80,000	0.22	0.89
North Dakota	11,045,269	2,761,317	20,500	0.19	0.74
New Mexico	39,021,449	9,755,362	60,000	0.15	0.62
Oklahoma	21,606,120	5,401,530	64,214	0.3	1.19
South Dakota	29,262,553	7,315,638	160,000	0.55	2.19
Texas	78,592,452	19,648,113	177,000	0.23	0.9
Wyoming	22,067,599	5,516,900	125,000	0.57	2.27
Total	**368,308,727**	**92,077,182**	**1,861,436**	**0.51**	**2.02**

Figure Legends:

Figure 1. Geographic distribution of the five prairie dog species in North America (modified from Hoogland 1995).

Figure 2. Until recent centuries, the geographic range of the black-tailed prairie dog remained remarkably stable throughout much of the Pleistocene and Holocene (Graham 1986; Graham et al. 1996; Graham and Lundelius 1994). Symbols represent paleontologic records of the species, whereas the shaded area represents a reconstruction of the historic range at 200 years ago.

Figure 1

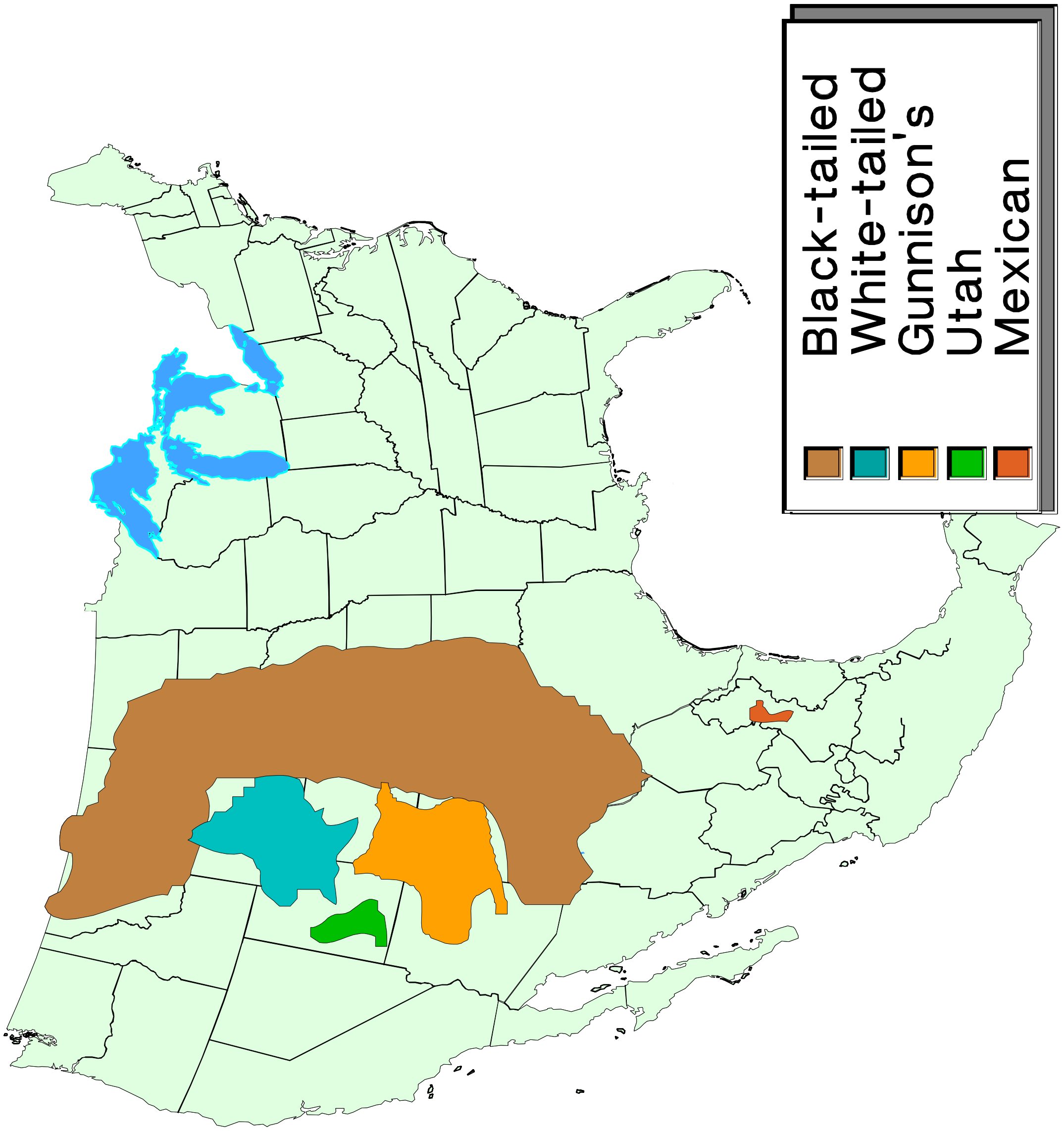
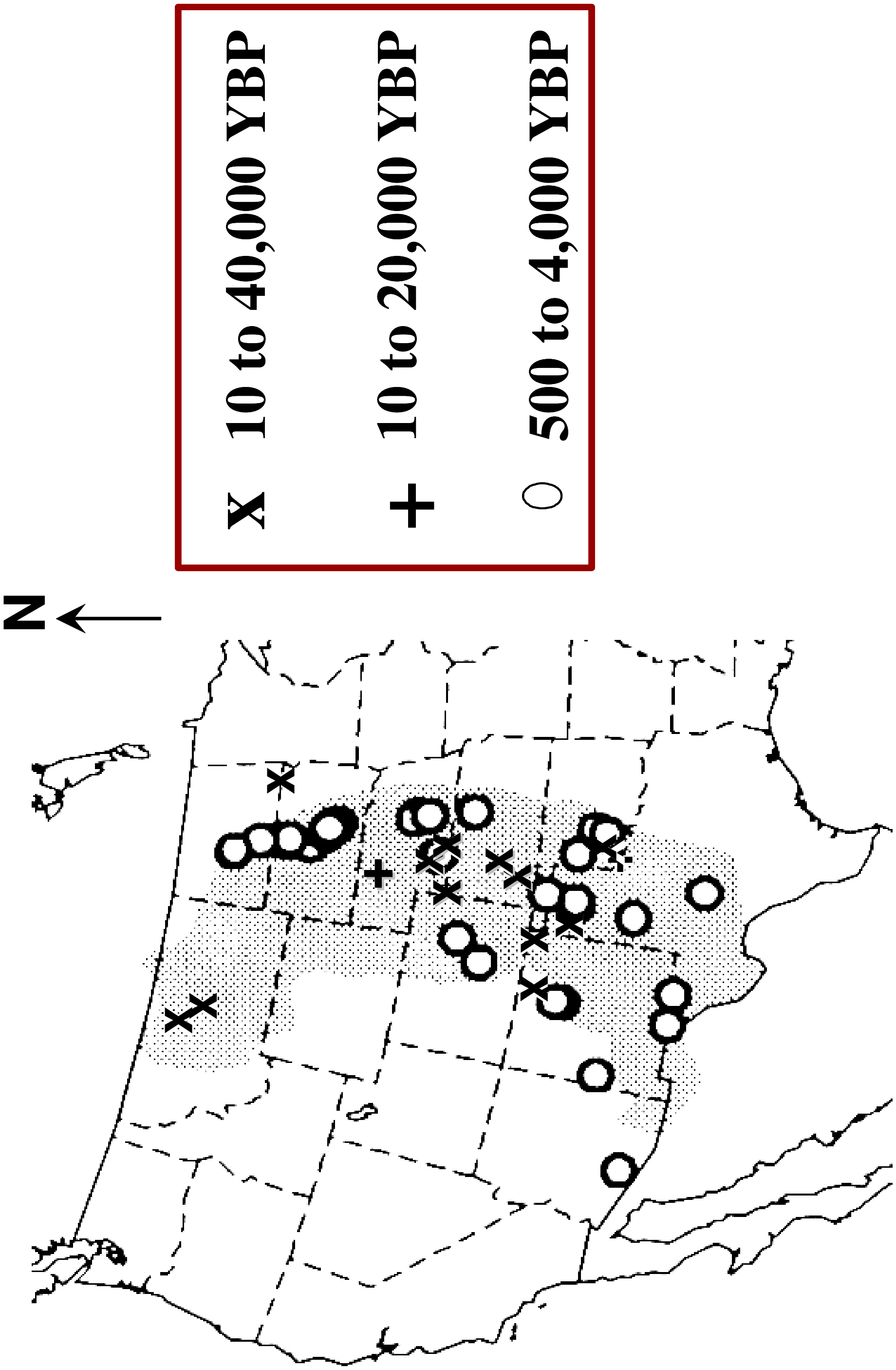


Figure 2



Avian Communities Associated with Black-tailed Prairie Dogs on the Shortgrass Plains

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Running head: Avian communities on prairie dog towns

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Abstract We tested the hypothesis that black-tailed prairie dogs influence avian community structure on the shortgrass prairie. We surveyed 36 prairie dog towns and 36 paired sites without prairie dogs during summer and fall of 1997, 1998, and 1999 in the Oklahoma Panhandle. Our surveys totaled 9,040 individual observations for 73 avian species. Significantly distinct avian communities were present on prairie dog towns when compared to sites within four different macrohabitats of the surrounding landscape: open rangeland, scrub/sandsage (*Artemisia filifolia*) habitats, Conservation Reserve Program (CRP) plots, and fallow crop fields. Relative densities of all bird species combined was higher on prairie dog towns versus paired sites in summer and fall. Mean species richness of birds was significantly higher on prairie dog towns than paired sites during summer, but there were no significant differences in fall. Open rangeland had the highest mean species richness in fall. Assemblages of avian communities differed significantly between prairie dog towns and the four macrohabitat types during summer. Burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferous*), horned larks (*Eremophila alpestris*), and meadowlarks (*Sturnella* spp.) were positively and significantly associated with prairie dog towns during summer, while horned larks and ferruginous hawks (*Buteo regalis*) were significantly associated with prairie dog towns during fall. Even in their current remnant state, black-tailed prairie dogs continue to play a significant role in the assembly of ecological communities across the Great Plains. Conservation of prairie dogs goes well beyond a single species, and is an important strategy for the preservation of the prairie ecosystem as a whole.

Keywords Biological diversity • Conservation • Fragmentation • Grassland birds • Keystone species

Introduction

A small percentage of North American birds are endemic to the Great Plains (Udvardy 1958; Mengel 1970). As a group, grassland birds have shown more significant declines over the past 30 years than any other avian guild (Askins 1993; Knopf 1994, 1996a). Seven of 12 endemic avian species of the Great Plains have steadily declined in recent decades (Table 1; Knopf 1996a; Peterjohn and Sauer 1999). Likewise, 14 of 25 more widespread grassland species have also shown declines (Table 1). One reason for such declines is alteration in the vegetative structure of Great Plains grasslands (Knopf 1994).

Historically, the Great Plains were a "shifting mosaic" of habitat patches shaped by fire and grazing by large and small herbivores. Having evolved in variable fire and grazing regimes, avian grassland endemic birds thus display a range of preferences for disturbance frequency; from mountain plovers (*Charadrius montanus*) nesting on intensively grazed bare ground, to long-billed curlews (*Numenius americanus*) and lark buntings (*Calamospiza melanocorys*) choosing moderately grazed patches, to Cassin's sparrows (*Aimophila cassinii*) breeding in shrubby habitat with little or no grazing (Knopf 1996a and b; Askins 2000). Today, anthropogenic changes to the landscape have homogenized the ecosystem in which these species evolved (Lomolino et al. 2001; see also Lockwood and McKinney 2001). The suppression of fire, conversion of native prairie to agricultural land, and reduction of grazing guilds of the prairie have significantly and permanently altered the landscape on which these birds depend. Fire and grazing by large, native herbivores may, in fact, be functionally extinct processes on the plains (Knopf 1994; McPherson 1995), and the current role of the once dominant, small herbivore – prairie dogs – has recently been brought to the forefront of grassland conservation (Wuerthner 1997; Miller and Cully 2001).

The black-tailed prairie dog (*Cynomys ludovicianus*) is one of five members of the genus *Cynomys* (Order Rodentia, Family Sciuridae) found only in North America (Hoogland 1996). Black-tailed prairie dogs have the widest distribution of any prairie dog species and are the only prairie dog species occurring in Oklahoma (Fig. 1). (Use of the term prairie dog for the remainder of this chapter will refer to black-tailed prairie dogs). Prairie dogs are ecosystem engineers (Lawton and Jones 1995) and appear to be keystone species, strongly influencing community structure and creating a dynamic landscape across short and mixed-grass prairies (Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000; Lomolino and Smith 2004). Prairie dogs create and maintain a unique habitat by keeping vegetation clipped low to the ground and by construction of extensive, underground tunnel systems. Other species use dog towns as foraging sites, use burrows as dens or refugia from predators or severe weather, or use prairie dogs themselves as prey. A number of grassland species may be closely associated with prairie dog towns (Reading et al. 1989; Hoogland 1996) which, until the previous century, constituted some of the most expansive and predictable resources and refugia for Great Plains species (see Goodwin 1995). Many vertebrates generally considered to be town associates are species of special concern, including several members of the grassland bird assemblage:

burrowing owl (*Athene cunicularia*), mountain plover, golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*), Swainson's hawk (*B. swainsoni*), prairie falcon (*Falco mexicanus*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), and long-billed curlew (Butts 1976; Knowles et al. 1982; Allison et al. 1995; Desmond et al. 1995; Barko et al. 1999). In addition, numerous non-volant terrestrial vertebrates of conservation concern are positively associated with prairie dog towns, including tiger salamander (*Ambystoma tigrinum*), prairie rattlesnake (*Crotalus viridis*), ornate box turtle (*Terrapene ornata*), black-footed ferret (*Mustela nigripes*) and swift fox (*Vulpes velox*) (Tyler 1968; Agnew et al. 1986; Shackford and Tyler 1991; Sidle et al. 2001).

Black-tailed prairie dogs are now sparsely distributed across their historic range, and their numbers have been drastically reduced as a result of habitat loss, poisoning campaigns, and outbreaks of sylvatic plague (*Yersinia pestis*) (Miller and Cully 2001). Prairie dog towns are believed to have covered from 40-100 million hectares around the turn of the century, but cover less than 5% of this area today (Miller et al. 1994). Our recent surveys of towns in Oklahoma have also documented declines within the past 10-15 years (Lomolino and Smith 2001). In the Panhandle alone, areal coverage of prairie dog towns during this period has been reduced by almost 45%. The remaining towns are becoming increasingly smaller, fragmented, and more isolated.

Here we test the hypothesis that prairie dogs, even with their presently fragmented distribution, continue to influence local community structure on the shortgrass prairie. In particular, we hypothesize that the species composition, richness, and abundance of bird species differs between prairie dog towns and their adjacent habitat patches. We also discuss the relevance of observed patterns in avian community structure for conserving the character of Great Plains ecosystems.

Materials and methods

Study site

All field work was in the Oklahoma Panhandle, which is a transition zone from mixed grass prairies in the east to shortgrass prairies in the west. The Panhandle is a three county area covering 14,737 km^2 surrounded by the body of the state of Oklahoma, Kansas, Colorado, New Mexico, and Texas. Mean annual precipitation falls from approximately 60 cm in the east to 40 cm in the far west. Elevation rises from approximately 730 m in the east to 1516 m in the west.

Historically, much of the Panhandle was shortgrass plains dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) (Blair and Hubbell 1938; Sims and Risser 2000) along with dense concentrations of sand sage (*Artemisia* spp.) in the east. Over the past two centuries, agricultural development and cattle ranching have expanded westward (see Ramankutty and Foley 1999) across the region leaving some remnants of native prairie, fragmented prairie dog towns, and riparian corridors sparsely distributed amongst large parcels of cropland. Rocky mesas are a prominent feature of the extreme western portion of the panhandle. Today, approximately 20-40% of potential natural vegetation remains in this region (Sieg et al. 1999).

Survey methods

Paired community studies were conducted in summer and fall of 1997, 1998, and 1999 (Fig. 1). Summer surveys were done between mid-May and early August, while fall surveys were conducted from mid-November to mid-December. Prairie dog towns were located from previous roadside surveys conducted across the panhandle region of Oklahoma (Lomolino and Smith 2001) as well as from information from land owners and Game Wardens. Permission was obtained for every site used. Once a prairie dog town was located, we searched for a paired habitat site (without prairie dogs) within the surrounding habitat matrix, between 0.6 and 8.0 km of the town, and obtained permission to use the site. Paired sites were located using roadside surveys extending out from the focal prairie dog town and were classified using habitat measurements (see below) and visual observations as open rangeland (shortgrass prairie in the absence of prairie dogs), scrub/sandsage, CRP grasses (Conservation Reserve Program, primarily *Bothriochloa ischaemum*), or fallow crop field. Including prairie dog towns we identified five macrohabitat types. During each summer we conducted avian surveys at 12 prairie dog towns and 12 paired sites resulting in 36 total dog towns and 36 total paired sites (19 open rangeland, 8 scrub/sandsage, 6 fallow crop field, and 3 CRP) over three years combined. During each fall, we repeated surveys at half of these sites for a total of 6 prairie dog towns and 6 paired sites per fall, and 18 towns and 18 paired sites (10 open rangeland, 6 scrub/sandsage, and 2 CRP) total during all fall surveys. Therefore, we conducted 108 survey sessions (72 summer, 36 fall) combining all sites, years, and seasons. Prairie dog towns ranged in size from 9.0 to 211.0 ha and paired sites were habitat patches at least as large as the dog town it was paired with.

Avian surveys were conducted as variable distance line transects, using modifications of Emlen's (1971; 1977) methods (Bibby et al. 1992). A transect 300 to 700 m long was established on each prairie dog town based on the size of that town. Birds were recorded within band widths of 10 m, 25 m, 50 m, 100 m, 150 m, and 150+ m from the center line. Survey protocol and transect dimensions were exactly duplicated on paired sites. Each transect was walked twice in the morning within 2-3 hours of sunrise and twice in the evening within 2-3 hours of sunset (432 total bird counts were performed in > 220 hours of surveys). Counts were conducted on a prairie dog town and its paired site on two consecutive mornings and evenings. Count order was reversed so that if a prairie dog town was counted first one morning, the paired site would be counted first the second morning. Count order in the evening was also reversed. All counts were conducted by a single observer (GAS) using 10x25 binoculars, a 15x-60x spotting scope, data sheets, and a field guide. Transects were walked slowly with occasional stops such that each count lasted 30-45 min. Individual birds were recorded by sight and call to species within a specific band width from the center line. The observer was allowed to move away from the center line, but the position of the individual bird was always recorded as distance from the center line and not distance from the observer. Avian densities were calculated using the program DISTANCE with the half-normal cosine detection function and all data truncated to include only observations within 150 m of the center line (Thomas et al. 1998). For these analyses, all observations from the four counts were combined and transect length was multiplied by four. This was done in order to reduce problems of duplicating counts of individuals, but renders our results as relative densities of individuals.

Habitat measurements were taken as point counts along each transect. Regardless of transect length, 20 stops were established along the transect. Counting the initial starting point, each transect had 21 stops. At each stop, a 10 m rope with a knot at 1 m intervals was laid perpendicular to the transect to the left and to the right. Therefore, habitat measurements were taken across a 20 m line perpendicular to the center line of the transect. The center point was only counted once so at each stop there were 21 measurement points giving 441 points (21 stops x 21 points at each stop) per transect. At each point, vegetation height was recorded as <10 cm, 11-25 cm, 26-50 cm, 51-75 cm, 76-100 cm, and >100 cm. Vegetation type was also recorded at each point as grass, forb, soil, litter, cacti, yucca, cow patty, shrub/woody, rock, and other. For each site, vegetation was recorded as the percentage of 441 total points within each category listed above.

Statistical analyses

Paired t-tests were used to compare mean species richness of avian species on prairie dog towns vs. paired sites. Analyses were also run on a subset of species which are of conservation priority (threatened or endangered, rare, or species of special concern). Repeated measures ANOVA tested for differences between years and between seasons for those species that occurred across years and seasons. To compare relative densities of each species on prairie dog towns vs. paired sites, a resampling program was written using Resampling Stats, version 4.1b4 (Resampling Stats., Inc. 1997; Appendix A). This program tested the hypothesis that relative densities of individual bird species differ significantly between prairie dog towns and paired sites. The program first calculates the observed differences and sum of differences in population densities between each pairing of the actual data and then calculates the observed number of times the relative density of that species was higher on the prairie dog town vs. its paired site. The data are then pooled and shuffled. Half of the observations are selected (regardless of identity as a prairie dog town or a paired site) and paired with the remaining half. Differences and sums of differences are calculated for this random data set, and the program calculates the number of times values in the first set of shuffled observations ("prairie dog towns") exceed those of the second set ("paired sites"). These values are compared to those for the observed data where treatment effects (prairie dog town vs. non-town site) were preserved. The program repeats these routines 10,000 times and calculates the number of iterations in which the sum of differences were higher, the same, or lower than the observed sum of differences. P-values were calculated as the proportion of randomized iterations greater than or equal to the observed (unshuffled) data.

To test the hypothesis that prairie dog towns harbor distinct assemblages of birds, we used discriminant function analysis. In order to eliminate problems associated with zero data (i.e., very rare species), we used only species that were recorded on at least 5 pairings of the summer or fall sites. We counted an occurrence as presence on either the dog town or paired site of a particular pairing. The species did not have to occur on both sites of a pair. The analysis was run twice using relative density measures and presence/absence data. First, we treated all paired sites as one macrohabitat and compared prairie dog towns versus paired sites. Second, paired sites were split into separate macrohabitat categories (see above) and all macrohabitats were compared against prairie dog towns as well as against each other. Finally, we used correspondence analysis to investigate differences in environmental characteristics and species composition among macrohabitats. SYSTAT, version 10 (SPSS, Inc. 2000), was used for all statistical analyses except resampling routines.

Results

Local habitat variables differed significantly between prairie dog towns and paired sites during summer (discriminant function analysis, between groups $F\text{-}vaule_{14,57}=14.678$, $p<0.001$) and fall ($F_{13,22}=7.863$; $p<0.001$). Likewise, for each season there were significant differences in habitat between the five macrohabitats: CRP, fallow crop fields, prairie dog towns, rangeland, and scrub (summer, $F_{13,55}=17.415$, $p<0.001$; fall, $F_{8,25}=7.348$, $p<0.001$; Fig. 2). Thus, the macrohabitats can be considered distinct landscape level treatments in subsequent analyses. Based on the jackknifed classification matrix of the DFA, fallow crop fields, prairie dog towns, and scrub habitats were the most distinct (% classification success=100, 97, and 88, respectively). During fall, prairie dog towns and scrub habitats remained distinct (100% and 83%, respectively).

Seventy-three species of birds were detected during our surveys. Across all seasons, there were 9,040 individual observations. After removing observations >150 m, 7,928 observations remained in the analyses: 5,044 during summer and 2,884 during fall.

Prairie dog towns accounted for 2,817 observations (55.8%) during summer, and 2,175 observations (75.4%) during fall. Typical of these grassland communities, horned larks (*Eremophila alpestris*) and meadowlarks (eastern and western combined, *Sturnella* spp.) accounted for 54.5% of all summer detections (66.2% on prairie dog towns), while horned larks alone accounted for 55.8% of fall detections (68.0% on prairie dog towns) (Kantrud and Kologiski 1982; Knopf 1996a). Although not as abundant as horned larks, grasshopper sparrows (*Ammodramus savannarum*) and meadowlarks accounted for 48.3% of observations on paired sites during summer, while meadowlarks and longspurs (*Calcarius* spp.) dominated paired sites during fall (62.5%).

None of the species used in our analyses exhibited significant differences in relative density across years (repeated measures ANOVA model), thus we combined data within a season across years. Relative densities of all birds, combined, was highest on prairie dog towns, in comparison to all other habitats, during summer and fall (Fig. 2). The high relative density of species in fall was due to very large flocks (mostly horned larks) that gathered at this time of year. Such large flocks, often hundreds of birds, were not observed in summer. When comparing birds across macrohabitats, fallow crop fields and prairie dog towns had the highest relative density of birds in summer, while prairie dog towns and CRP had high abundance levels during fall (Fig. 2). Again, horned larks and meadowlarks were dominant species on prairie dog towns during summer, while grasshopper sparrows were relatively common at paired sites. Horned larks and longspurs were the most abundant fall species.

Avian species richness in summer was significantly higher on prairie dog towns than at paired sites (data from all summers combined: $\bar{x}$=9.5 for prairie dog towns and 8.2 for paired sites; t=2.714, p=0.010; Fig. 3). There were no significant differences in species richness for fall surveys ($\bar{x}$=5.7 for prairie dog towns and 5.6 for paired sites; t=0.251, p=0.805; Fig. 3). Overall, prairie dog towns and fallow crop fields were the most species-rich summer macrohabitats while rangeland and prairie dog towns had the highest mean richness in fall (Fig. 3).

Similar results were obtained when analyses were limited to species of conservation concern; significant differences in species richness were evident between prairie dog towns and paired sites in summer and fall (summer: $\bar{x}$=1.7 for prairie dog towns and 0.4 for paired sites, t=6.489, p<0.001; fall $\bar{x}$=1.5 for prairie dog towns and 0.8 for paired sites, t=2.608, p=0.018; Fig. 3). With burrowing owls removed from the summer analyses, marginally significant differences between prairie dog towns and paired sites relative to richness of species of conservation priority were still observed ($\bar{x}$=0.7 for prairie dog towns and 0.4 for paired sites, t=1.919, p=0.063).

Individual species often appeared to prefer or avoid prairie dog towns. Thirteen species detected during summer surveys met the requirements for analysis with the resampling routine. Of these species, burrowing owls (p<0.001), killdeer (p=0.042), horned lark (p=0.003), and meadowlarks (p=0.014) exhibited significant, positive associations with prairie dog towns, while northern bobwhites (*Colinus virginianus*) (p=0.027), Cassin's sparrows (p<0.001), and grasshopper sparrows (p<0.001) were significantly associated with paired sites (all summer data combined). Although not significant, scissor-tailed flycatcher (*Tyrannus forficatus*), brown-headed cowbird

(*Molothrus ater*), and lark sparrow (*Chondestes grammacus*) were more common on prairie dog towns than at paired sites, while Mourning doves (*Zenaida macroura*) were more common on paired sites.

At the community level, discriminant function analysis showed a highly significant difference in species composition of avian assemblages between summer prairie dog towns and paired sites (all paired sites combined as one treatment: using relative density measures, between groups F-value$_{13,58}$=6.328, $p < 0.001$; using presence/absence data, $F_{30,41}$=11.965, p<0.001). During fall, avian assemblages were also significantly different based on relative density measures ($F_{6,29}$=2.739, p=0.031), but were only marginally significant using presence/absence data ($F_{12,23}$=1.885, p=0.092). When paired sites were split into their respective macrohabitats, we detected highly significant differences in summer avian assemblages across the five macrohabitats: prairie dog towns, open rangeland, scrub/sandsage, CRP, and fallow crop fields (overall differences for summer data using relative density data, $F_{13,55}$=3.127, p<0.001, Fig. 4; using presence/absence data, $F_{30,38}$=3.718, p<0.001, Table 2). All five macrohabitats were identifiable by distinct assemblages of summer species, with jackknifed classification successes for avian communities of 94% for prairie dog towns, 84% rangeland, 75% scrub, 67% CRP, and 50% fallow crop fields. Differences among avian communities across macrohabitats during fall were much less distinct than those for summer surveys (using relative density data, $F_{6,27}$=1.047, p=0.421; using presence/absence data, $F_{12,21}$=1.361, p=0.142). However, species assemblages at prairie dog towns were significantly different from those inhabiting scrub/sandsage habitat (based on presence/absence data, $F_{12,21}$=3.335, 0.01>p>0.005, Table 3). In addition, prairie dog towns had the highest jackknifed classification success (50%) based on species incidence data during fall. Classification success for avian communities at scrub followed that for prairie dog towns at 33%, and values for range and CRP were 10% and 0%, respectively.

Ordinations of summer avian communities based on correspondence analysis indicated that burrowing owl, scaled quail (*Callipepla squamata*), killdeer, red-tailed hawk *(Buteo jamaicensis*), and to lesser degrees horned lark, long-billed curlew, and loggerhead shrike (*Lanius ludovicianus*) were positively associated with prairie dog towns (Figs. 5 and 6). Seasonal turnover in the regional species pool is evident, as summer sites (whether prairie dog town or paired site) ordinate together while fall sites plot together (Fig. 5). When summer sites are split into their respective macrohabitats, the association between prairie dog towns and fallow crop fields is clear (Fig. 6). Avian assemblages in fallow crop fields plot near prairie dog towns while range sites, scrub/sandsage, and CRP plot farther away and closer to each other than any are to prairie dog towns or fallow crop fields (Fig. 6). Thus, summer avian assemblages in fallow crop fields appear to most closely resemble prairie dog towns in vegetation structure and the avian species attracted to this habitat type. During fall, ferruginous hawk, golden eagle, American kestrel (*Falco sparverius*), horned lark, and longspurs were strongly associated with prairie dog towns (Figs. 5 and 7). The raptor complex, with the exception of rough-legged hawk (*Buteo lagopus*) and to a lesser degree northern harrier (*Circus cyaneus*), plotted near prairie dog towns (Fig. 7), a possible indication of the importance of this habitat type as a winter resource for these species.

Discussion

Birds are particularly sensitive to landscape patchiness (Rotenberry and Wiens 1980; McIntyre 1995). The historic factors shaping the structure of the Great Plains produced a grassland ecosystem characterized by local homogeneity and regional heterogeneity (Collins 1992). Biological diversity of the Great Plains was derived from this heterogeneity, and black-tailed prairie dogs were a major factor shaping the landscape (Miller et al. 1994). Prairie dogs produce a homogeneous "lawn" of grasses and forbs within an individual town surrounded by significantly different habitats (Whicker and Detling 1988; Weltzin et al. 1997). A number of species depend on these homogeneous patches (Sharps and Uresk 1990) and this has led many ecologists to refer to them, we feel justifiably so, as ecosystem engineers and keystone species (Miller et al. 1994; Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000). Our studies indicate that even after being reduced to less than five percent of their historic range, prairie dog towns in western Oklahoma continue to be inhabited by distinct assemblages of avian species.

Patterns reported here are consistent with those obtained during similar studies of vertebrate species and prairie dog towns (Agnew et al. 1986; Barko et al. 1999; Manzano-Fischer et al. 1999; Winter et al. 1999a; Kretzer and Cully 2001). Our results for avian communities are also consistent with our concurrent studies of mammal, reptile, and amphibian communities at these sites (Lomolino and Smith 2004). That is, prairie dog towns were inhabited by a highly distinct assemblage of these vertebrate species (including species of conservation priority). Non-volant, terrestrial vertebrates strongly associated with prairie dog towns included American badgers (*Taxidea taxus*), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), domestic cattle (*Bos taurus*), cottontail rabbits (*Sylvilagus* spp.), coyotes (*Canis latrans*), northern grasshopper mice (*Onychomys leucogaster*), swift fox, pronghorn (*Antilocapra americana*), and prairie rattlesnakes (Lomolino and Smith 2004). We found these differences despite, not just the decimation of prairie dog towns, but also the homogenization of species pools across the Great Plains. Before the turn of the century, this list of town associates likely would have included black-footed ferrets, and perhaps bison (*Bison bison*), elk (*Cervus elaphus*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*) (Benedict et al. 1996). Further, the particular species of vertebrates associated with prairie dog towns and their relative use of dog towns versus paired sites, appear to be variable across regions and their species pools, and also across seasons and multi-annual variation in climate. Previous studies have suggested that the influence of prairie dog towns on habitat choice of grassland birds may be related to precipitation (Barko et al. 1999; Winter et al. 1999a and 1999b). Particularly in mixed-grass prairie, during dry years, vegetation characteristics within paired habitats may not differ much from prairie dog towns. However, during wet years when grasses are taller, prairie dog towns and their associated communities become more distinctive.

We found that seasonal differences in bird communities were more apparent than yearly differences. Prairie dog towns were distinct from all other macrohabitat types during summer (Table 2). This strong distinction was driven not only by species that were positively associated with prairie dog towns (e.g. burrowing owls, horned larks, killdeer, and long-billed curlews), but also by species associated with paired habitats (e.g.

Cassin's sparrows, grasshopper sparrows, lark buntings, northern bobwhites, and western kingbirds (*Tyrannus verticalis*)). Avian communities at prairie dog towns were less distinct from paired sites during fall, however. Meadowlarks, for example, were associated with prairie dogs during summer, but not fall. Loggerhead shrikes showed a similar pattern. We also observed a significant reduction of the regional species pool from summer to fall. That is, species lost due to migration out of the region are not replaced at an equal rate by species moving into the region from farther north. Mean richness during summer was 9.5 and 8.3 for prairie dog towns and paired sites, respectively (Fig. 3). During fall, mean richness dropped to 5.7 for prairie dog towns and 5.6 for paired sites (Fig. 3).

Despite the lack of overall patterns in richness for fall species, species of conservation priority continued to show higher diversity on prairie dog towns than paired sites. Therefore, the role of prairie dogs in winter communities should not be underestimated. For species that depend on prairie dog burrows for winter roosting (e.g. burrowing owls; Butts 1976) or depend on prairie dogs as a prey item (e.g. ferruginous hawks; Allison et al. 1995; Bak et al. 2001), prairie dog towns may be an important overwintering resource. As such, these species were highly associated with prairie dog towns across seasons (Fig. 5). These species continue to depend on prairie dogs and, therefore, our conservation focus should not be limited to breeding communities. Unlike neotropical migrants that winter into South America, grassland birds winter mostly within the Great Plains (Knopf and Samson 1995). Winter ecology of these species has not been well studied (Knopf 1994). Seasonal changes in species pools, population dynamics, and ecological interactions among species dependent on prairie dog towns or paired sites are important topics for future research. Abundance, richness, and species composition of grassland birds likely varies across the vast, Great Plains region. Therefore, a comparative study using standardized ecological surveys across the historic range of black-tailed prairie dogs will likely provide some key insights into the ecological role, both past and present, of this native community.

Historically, patchiness on the Great Plains was not static, but shifted dynamically in response to unpredictable droughts, irregular fire events, non-random grazing by nomadic large herbivores (Wallace et al. 1995), and correspondingly intense grazing by small herbivores (Vinton and Collins 1997). Fire is now controlled and limited in its extent, and native large grazing guilds have been replaced by domestic cattle. The Great Plains are becoming a more simplified ecological system (Ostlie et al. 1997), one perhaps less capable of renewing itself and adapting to environmental change (Tilman et al. 1996). We believe it is clear that even in their current remnant state, black-tailed prairie dogs play a significant role in the assembly of ecological communities across the Great Plains. Prairie dogs increase diversity on the plains and as a result, increase the complexity of interactions between plant and animal species found there. Prairie dog towns themselves may function as biodiversity islands for certain species groups and as seasonal refugia for other groups. As such, conservation of prairie dogs goes well beyond a single species, but is an important strategy for the preservation of the prairie ecosystem as a whole.

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Table 1. North American grassland avifauna of the Great Plains (modified from Mengel 1970 and Knopf 1996). Bold species have shown overall declining trends on Breeding Bird Survey routes from 1966-1993 (Knopf 1996) or 1966-1996 (Peterjohn and Sauer 1999).

Nonpasserines	*Passerines*
Primary Species (Endemics)	
Ferruginous Hawk (*Buteo regalis*)	**Sprague's Pipit (*Anthus spragueii*)**
Mountain Plover (*Charadrius montanus*)	**Cassin's Sparrow (*Aimophila cassinii*)**
Long-billed Curlew (*Numenius americanus*)	**Baird's Sparrow (*Ammodramus bairdii*)**
*Marbled Godwit (*Limosa fedoa*)	**Lark Bunting (*Calamospiza melanocorys*)**
*Wilson's Phalarope (*Phalaropus tricolor*)	**Chestnut-collard Longspur (*Calcarius ornatus*)**
*Franklin's Gull (*Larus pipixcan*)	McCown's Longspur (*Calcarius mcccownii*)
Secondary Species (More Widespread)	
Mississippi Kite (*Ictinia mississippiensis*)	**Horned Lark (*Eremophila alpestris*)**
Northern Harrier (*Circus cyaneus*)	*Sage Thrasher (*Oreoscoptes montanus*)
Swainson's Hawk (*Buteo swainsoni*)	*Green-tailed Towhee (*Pipilo chlorurus*)
Prairie Falcon (*Falco mexicanus*)	**Clay-colored Sparrow (*Spizella pallida*)**
Greater Prairie-Chicken (*Tympanuchus cupido*)	*Brewer's Sparrow (*Spizella breweri*)
Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*)	**Lark Sparrow (*Chondestes grammacus*)**
Sharp-tailed Grouse (*Tympanuchus phasianellus*)	*Sage Sparrow (*Amphispiza belli*)
*Sage Grouse (*Centrocercus* spp.)	**Grasshopper Sparrow (*Ammodramus savannarum*)**
Upland Sandpiper (*Bartramia longicauda*)	**Henslow's Sparrow (*Ammodramus henslowii*)**
Short-eared Owl (*Asio flammeus*)	**Savannah Sparrow (*Passerculus sandwichensis*)**
Burrowing Owl (*Athene cunicularia*)	**Vesper Sparrow (*Pooecetes gramineus*)**
	Dickcissel (*Spiza americana*)
	Eastern Meadowlark (*Sturnella magna*)
	Western Meadowlark (*Sturnella neglecta*)

**Species generally associated with wetlands and sagebrush (Artemisia spp.) habitat of the Great Plains and Great Basin.*

Table 2. Between-groups F-matrix based on discriminant function analysis for five macrohabitats in the Oklahoma Panhandle. Data are for avian communities during summers, 1997 to 1999, and were either relative abundance measures or presence/absence data. Bold values are significant to at least the 0.05 level.

Relative Abundance Data (df = 13,55)

	CRP	Fallow Crop	P-dog	Range	Scrub
CRP	---				
Fallow Crop	1.611	---			
P-dog	1.646	1.844	---		
Range	0.322	**3.016**	**5.961**	---	
Scrub	1.765	**5.486**	**8.849**	**3.354**	---

Presence/Absence Data (df = 30,38)

	CRP	Fallow Crop	P-dog	Range	Scrub
CRP	---				
Fallow Crop	1.654	---			
P-dog	**4.700**	**2.961**	---		
Range	1.452	**2.244**	**14.013**	---	
Scrub	**2.500**	**2.269**	**6.183**	**4.199**	---

Table 3. Between-groups F-matrix based on discriminant function analysis for five macrohabitats in the Oklahoma Panhandle. Data are for avian communities during falls, 1997 to 1999, and were either relative abundance measures or presence/absence data. Bold values are significant to atleast the 0.05 level.

Relative Abundance Data (df = 6,27)

	CRP	P-dog	Range	Scrub
CRP	---			
P-dog	1.418	---		
Range	0.550	1.334	---	
Scrub	0.380	1.936	0.343	---

Presence/Absence Data (df = 12,21)

	CRP	P-dog	Range	Scrub
CRP	---			
P-dog	1.228	---		
Range	0.815	0.841	---	
Scrub	1.027	**3.335**	1.609	---

Figure Legends

Fig. 1 (**A**) Locations of survey sites in the Oklahoma Panhandle and location of the Panhandle relative to surrounding states. Dark circles represent prairie dog towns, light circles are paired sites. Years (1997, 1998, and 1999) and seasons (summer and fall) are combined. (**B**) Geographic distribution of the five extant prairie dog species (modified from Hoogland 1995).

Fig. 2 Plot of discriminant function factor scores for habitat variables at A) 72 summer sites and B) 36 fall sites in the Oklahoma Panhandle during 1997, 1998, and 1999 . Habitat differed significantly between five macrohabitat types (prairie dog towns, open range, scrub/sandsage, CRP grasses, and fallow crop field) in summer ($F_{13,55} = 17.415$, $p < 0.001$) and between four macrohabitat types (prairie dog towns, open range, scrub/sandsage, and CRP grasses) in fall ($F_{8,25} = 7.348$, $p < 0.001$). Explanation of symbols: • prairie dog towns; • open rangeland; ▲ scrub/sandsage; ■ CRP grasses; ♦ fallow crop fields.

Fig. 3 Relative density of all observations combined, calculated with DISTANCE from variable distance line transect counts (see Methods), of grassland bird species during summer and fall (1997, 1998, and 1999 combined) on A) prairie dog towns and paired sites (n = 36 sites for each treatment in summer, 18 sites for each treatment in fall) and B) five macrohabitats of the Oklahoma Panhandle (prairie dog towns: n = 36 summer sites, 18 fall sites; open rangeland: n = 19 summer sites , 10 fall sites; scrub/sandsage: n = 8 summer sites, 6 fall sites; fallow crop fields: n = 6 summer sites, 0 fall sites; CRP grasses: n = 3 summer sites, 2 fall sites).

Fig. 4 Mean richness of avian species during summer and fall (1997, 1998, and 1999 combined) on A) prairie dog towns and paired sites (for all species and only those of conservation concern; n = 36 sites for each treatment in summer, 18 sites for each treatment in fall) and B) five macrohabitats of the Oklahoma Panhandle (prairie dog towns: n = 36 summer sites, 18 fall sites; open rangeland: n = 19 summer sites , 10 fall sites; scrub/sandsage: n = 8 summer sites, 6 fall sites; fallow crop fields: n = 6 summer sites, 0 fall sites; CRP grasses: n = 3 summer sites, 2 fall sites). Bars represent mean + 1 SE (* $p < 0.05$, based on paired t-tests; bars with different letters are significantly different at the 0.05 level based on two-sample t-tests).

Fig. 5 Plot of discriminant function factor scores for avian communities at 72 sites in the Oklahoma Panhandle during summers of 1997, 1998, and 1999. Sites are subdivided into five macrohabitat types (prairie dog towns, open range, scrub/sandsage, CRP, and fallow crop field) and scores reflect relative density of avian species at each site (between groups F-value$_{13,58}$ = 6.328, $p < 0.001$; see Table 2). Explanation of symbols: • prairie dog towns; • open rangeland; ▲ scrub/sandsage; ■ CRP grasses; ♦ fallow crop fields. Species codes: Buow, Burrowing Owl; Grsp, Grasshopper Sparrow; Hola, Horned Lark; Labu, Lark Bunting; Lasp, Lark Sparrow; Modo, Mourning Dove; Nobo, Northern Bobwhite; Weki, Western Kingbird.

Fig. 6 Differences in assemblages of avian communities on 36 prairie dog towns and 36 paired sites in the Oklahoma Panhandle during summer and fall of 1997, 1998, and 1999, combined. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least 5 sites. Summer paired sites are a combination of 4 paired habitat types (open rangeland, scrub/sandsage, fallow crop field, and CRP grasses). Fall paired sites do not include fallow crop fields. Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Seasonal turnover in the regional species pool is reflected by the positioning of summer and fall sites on opposite sides of the plot. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name.

Fig. 7 Differences in assemblages of avian communities on 5 macrohabitats in the Oklahoma Panhandle during summers of 1997, 1998, and 1999, combined. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least 5 sites. Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Prairie dog towns were most similar to fallow crop fields relative to their avian communities while open rangeland, scrub/sandsage, and CRP grasses were more similar to each other than any were to prairie dog towns or fallow crop fields. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name.

Fig. 8 Differences in assemblages of avian species on 4 macrohabitats in the Oklahoma Panhandle during falls of 1997, 1998, and 1999. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least 5 sites. Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Note the raptor complex clustered around prairie dog towns. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name.

Figure 1

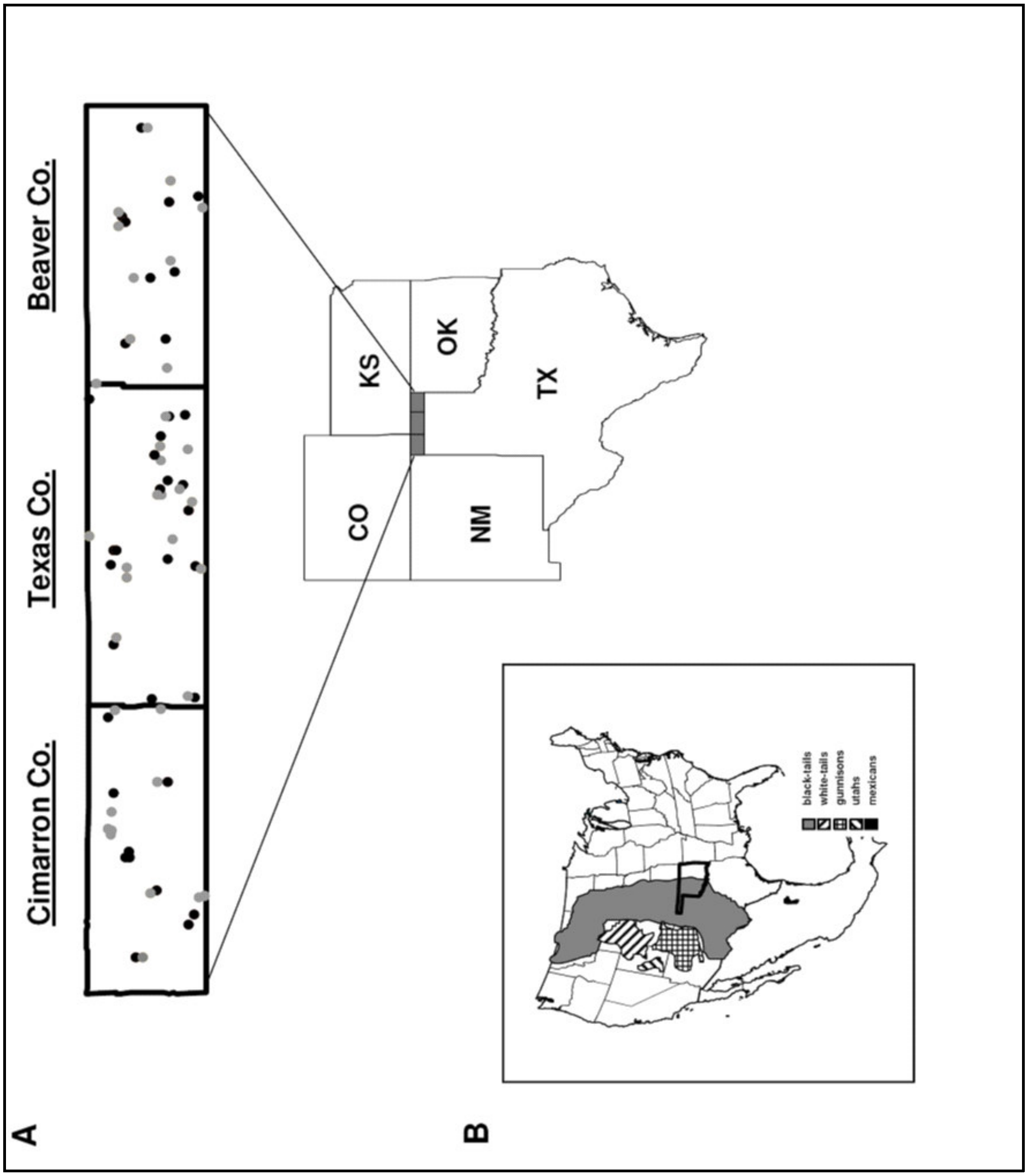

A
Cimarron Co.
Texas Co.
Beaver Co.
KS
OK
TX
CO
NM
B
black-tails
white-tails
gunnisons
utahs
mexicans

Figure 2

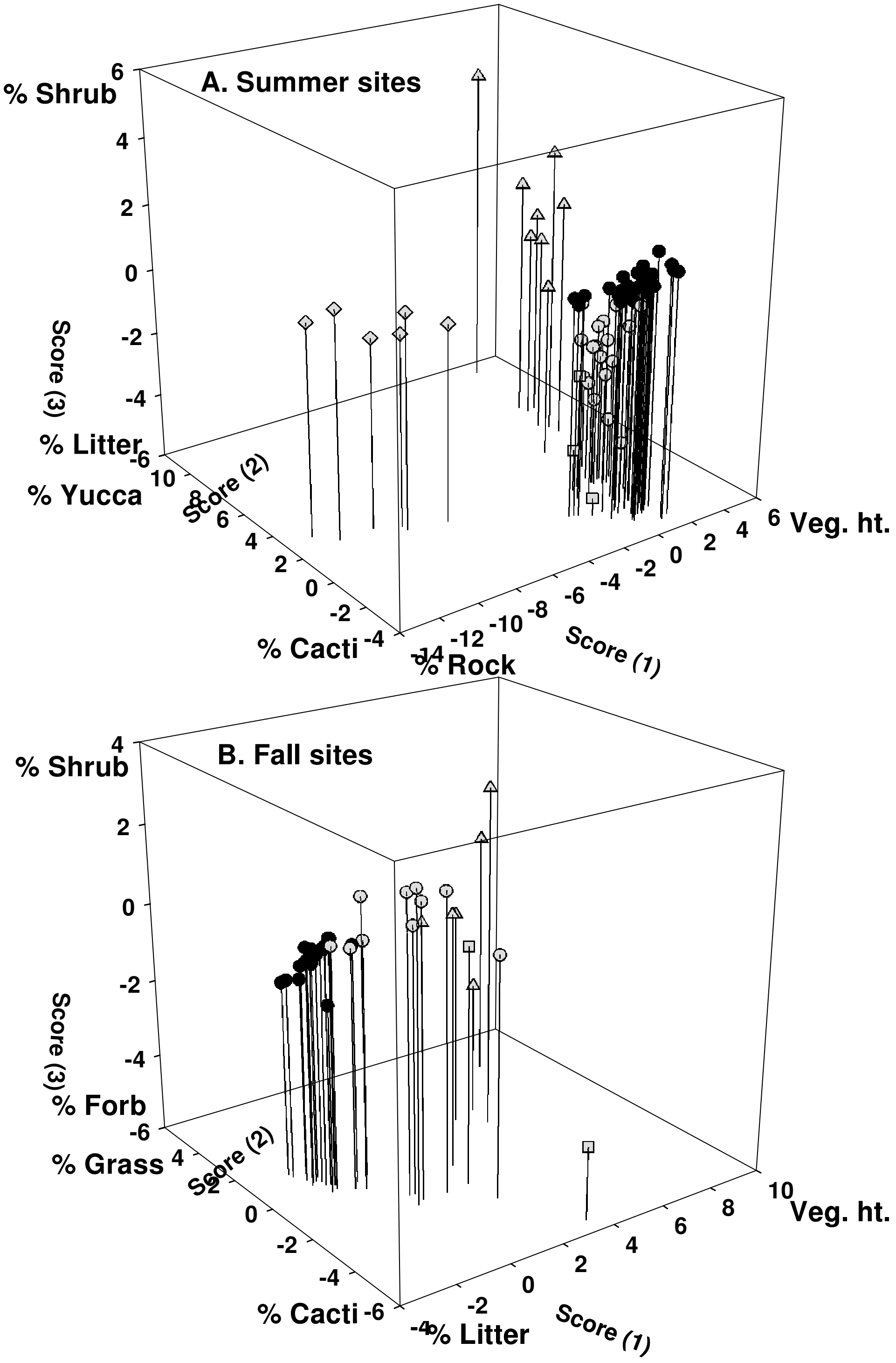

A. Summer sites
% Shrub
6
4
2
0
-2
-4
-6
Score (3)
% Litter
% Yucca
10
8
6
4
2
0
-2
-4
Score (2)
% Cacti
-14
-12
-10
-8
-6
-4
-2
0
2
4
6
Score (1)
% Rock
Veg. ht.
B. Fall sites
% Shrub
4
2
0
-2
-4
-6
Score (3)
% Forb
% Grass
4
2
0
-2
-4
-6
Score (2)
% Cacti
-4
-2
0
2
4
6
8
10
Score (1)
% Litter
Veg. ht.

Figure 3

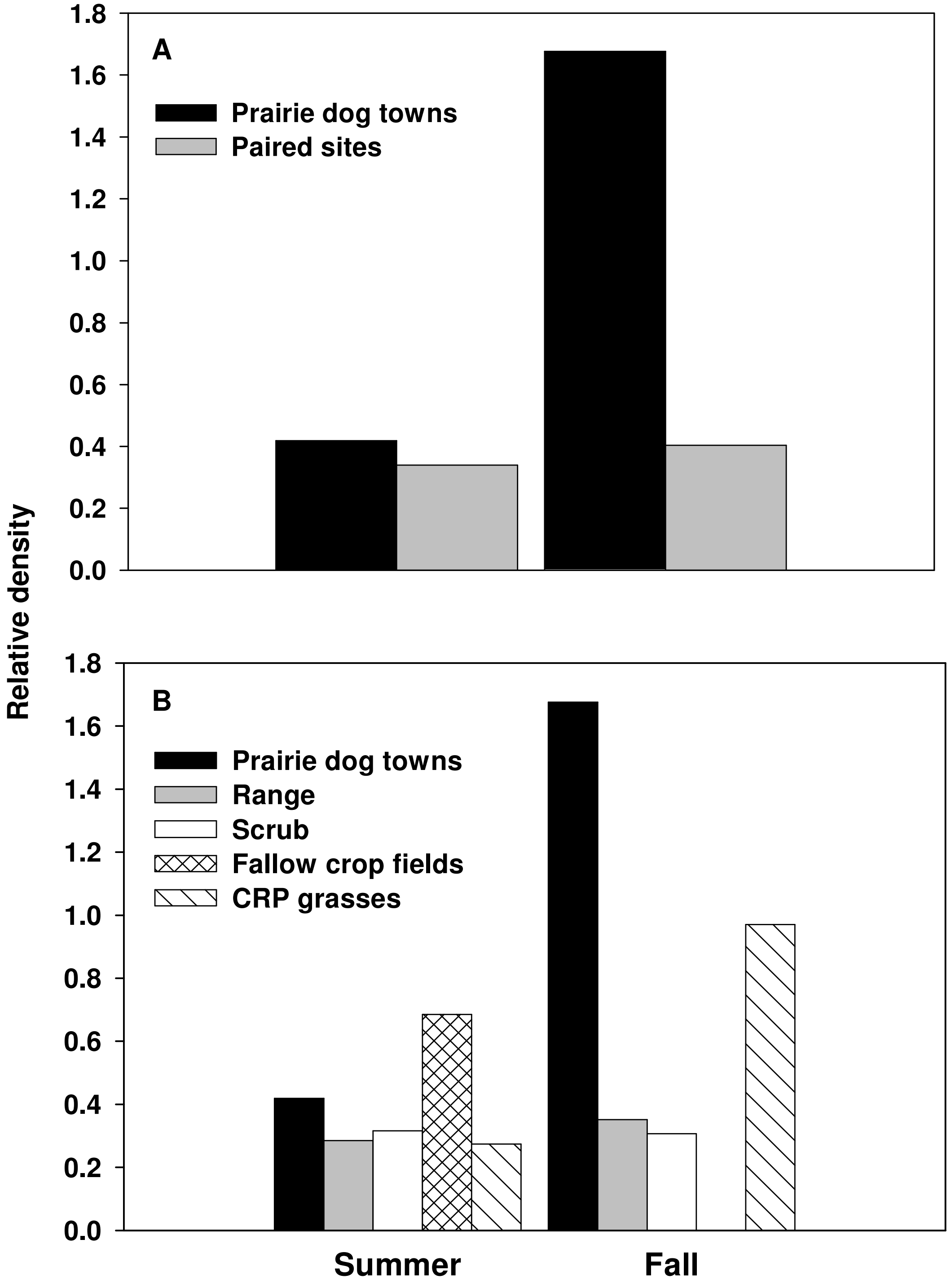
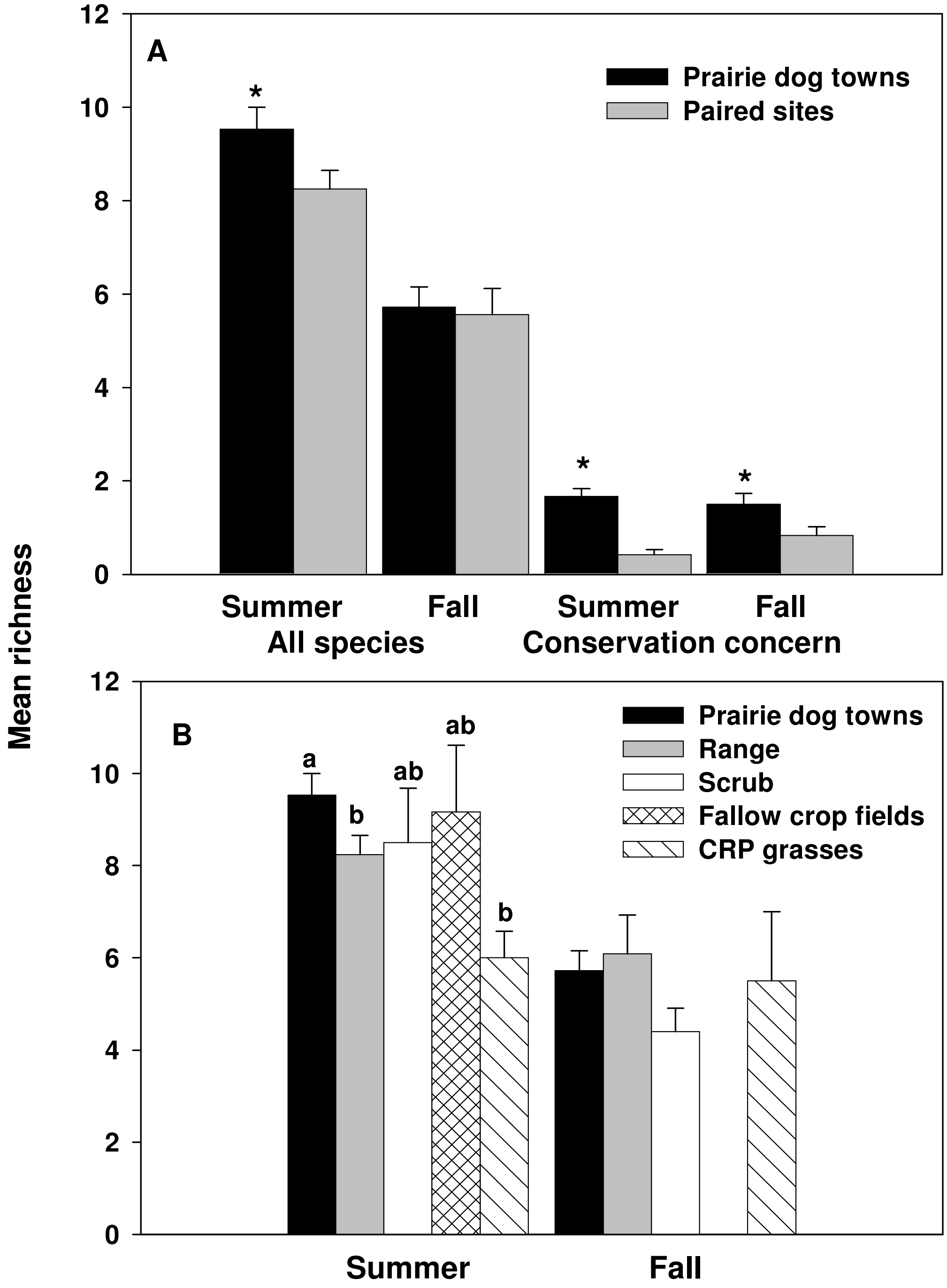

A
Prairie dog towns
Paired sites
B
Prairie dog towns
Range
Scrub
Fallow crop fields
CRP grasses
Relative density
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
Summer
Fall

Figure 4



Mean richness
A
12
10
8
6
4
2
0
Prairie dog towns
Paired sites
*
*
*
Summer
Fall
Summer
Fall
All species
Conservation concern
B
Prairie dog towns
Range
Scrub
Fallow crop fields
CRP grasses
a
b
ab
ab
b
Summer
Fall

Figure 5

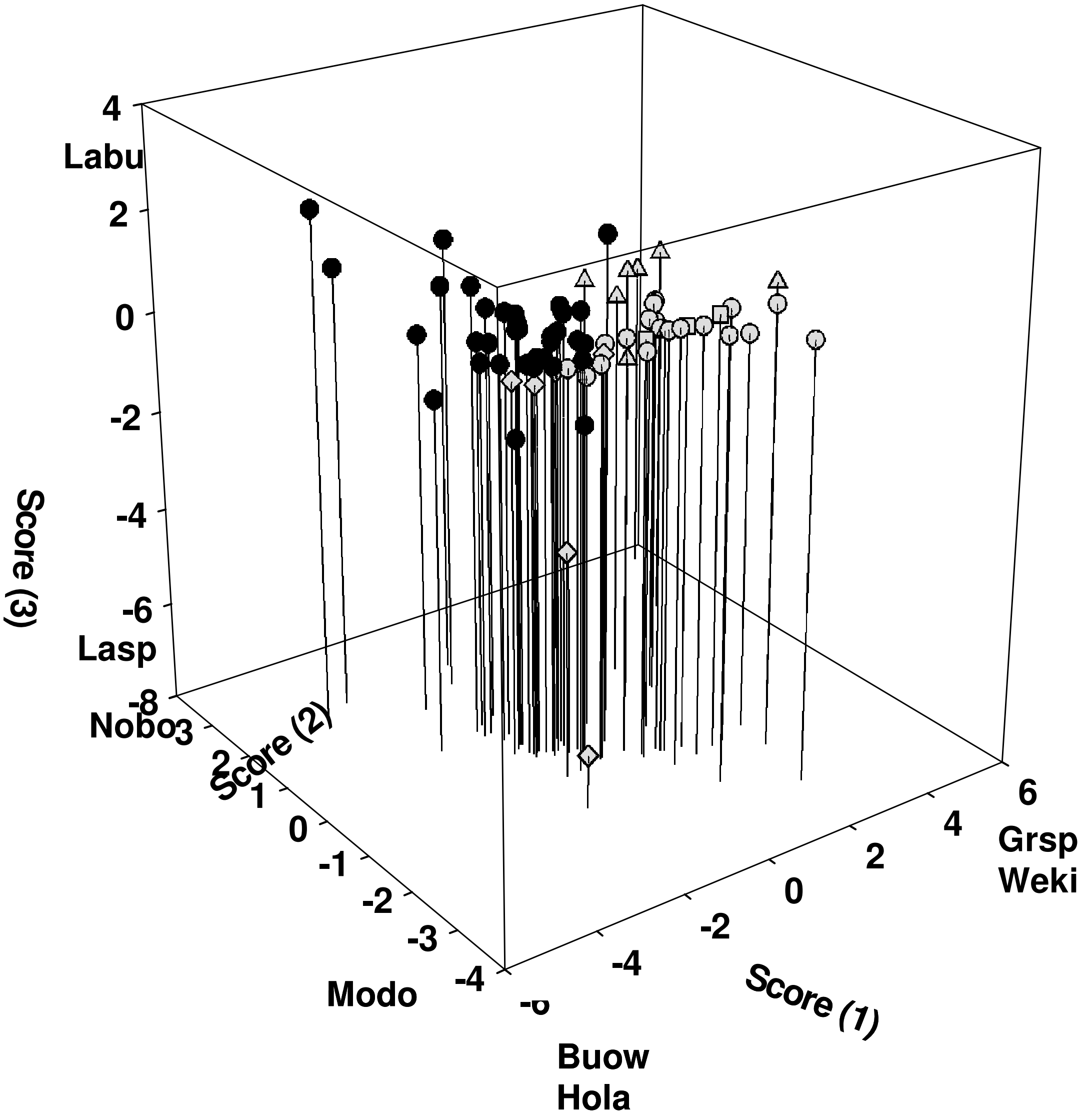
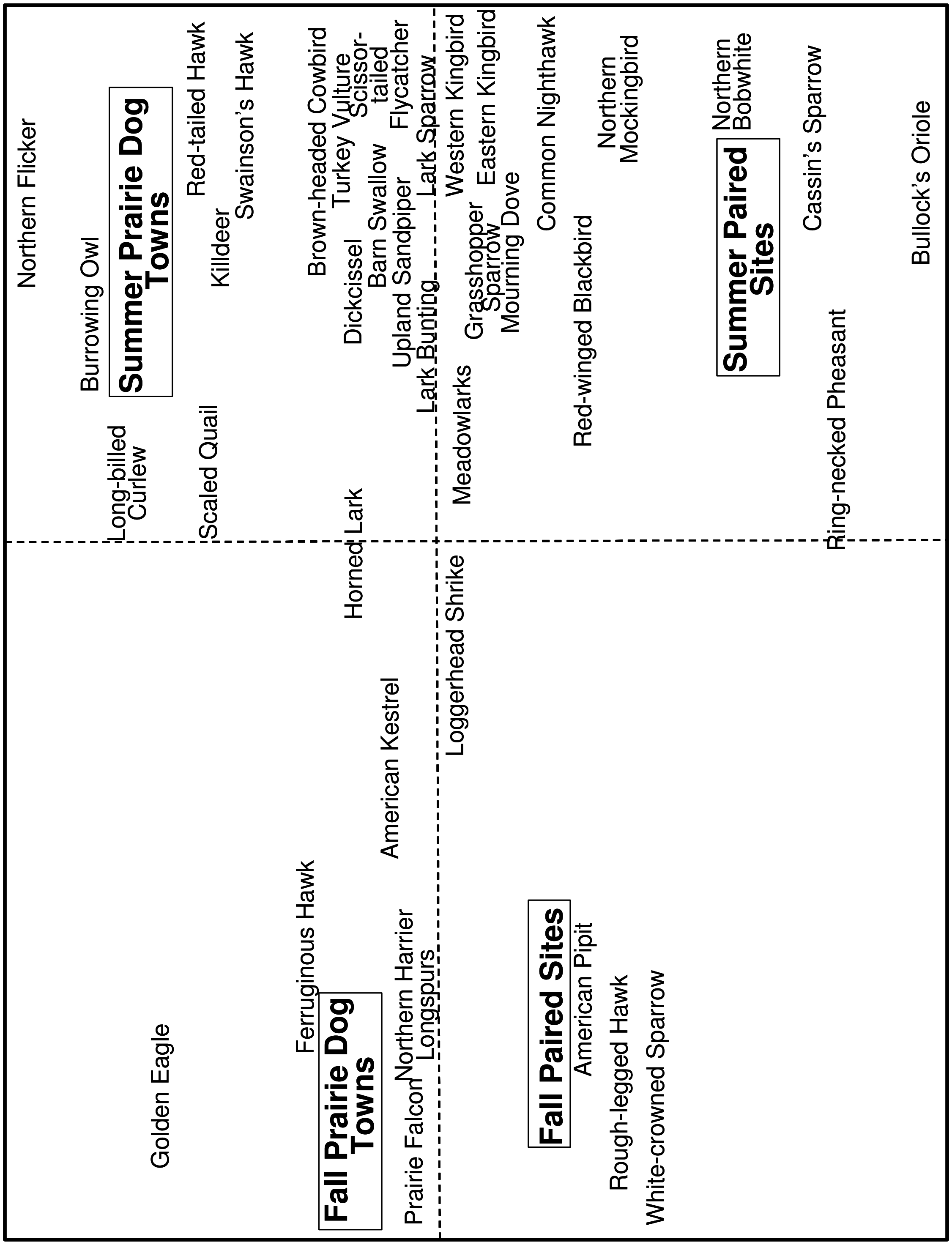

4
Labu
2
0
-2
-4
-6
Lasp
-8
Score (3)
Nobo
3
2
1
0
-1
-2
-3
-4
Score (2)
Modo
-6
-4
-2
0
2
4
6
Score (1)
Grsp
Weki
Buow
Hola

Figure 6



Summer Prairie Dog Towns
Summer Paired Sites
Fall Prairie Dog Towns
Fall Paired Sites
Northern Flicker
Burrowing Owl
Long-billed Curlew
Red-tailed Hawk
Killdeer
Scaled Quail
Swainson's Hawk
Brown-headed Cowbird
Turkey Vulture
Dickcissel
Horned Lark
Scissor-tailed Flycatcher
Barn Swallow
Upland Sandpiper
Lark Sparrow
Lark Bunting
Western Kingbird
Grasshopper Sparrow
Meadowlarks
Eastern Kingbird
Mourning Dove
Common Nighthawk
Red-winged Blackbird
Northern Mockingbird
Northern Bobwhite
Cassin's Sparrow
Ring-necked Pheasant
Bullock's Oriole
Loggerhead Shrike
American Kestrel
Golden Eagle
Ferruginous Hawk
Northern Harrier
Longspurs
Prairie Falcon
American Pipit
Rough-legged Hawk
White-crowned Sparrow

Figure 7

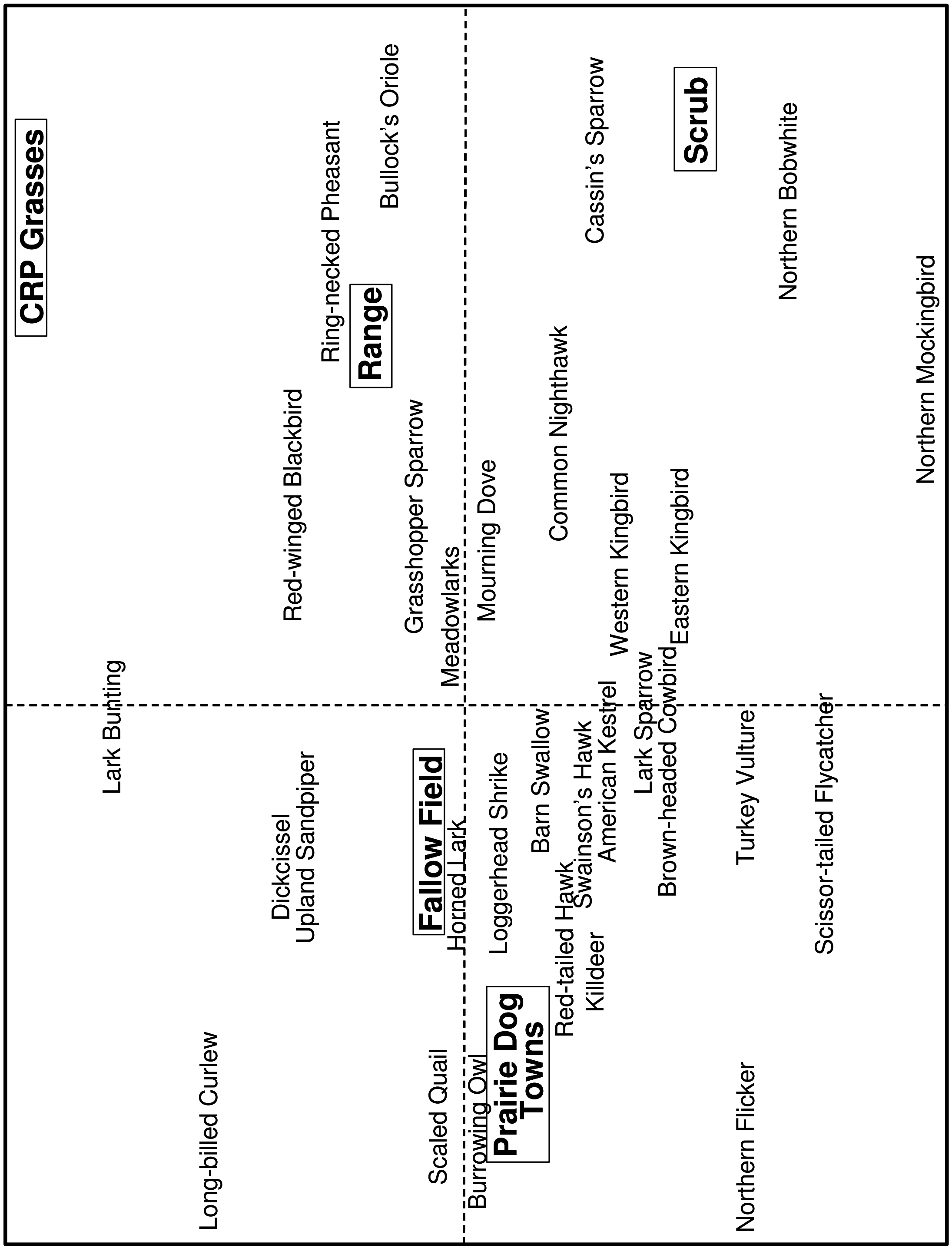
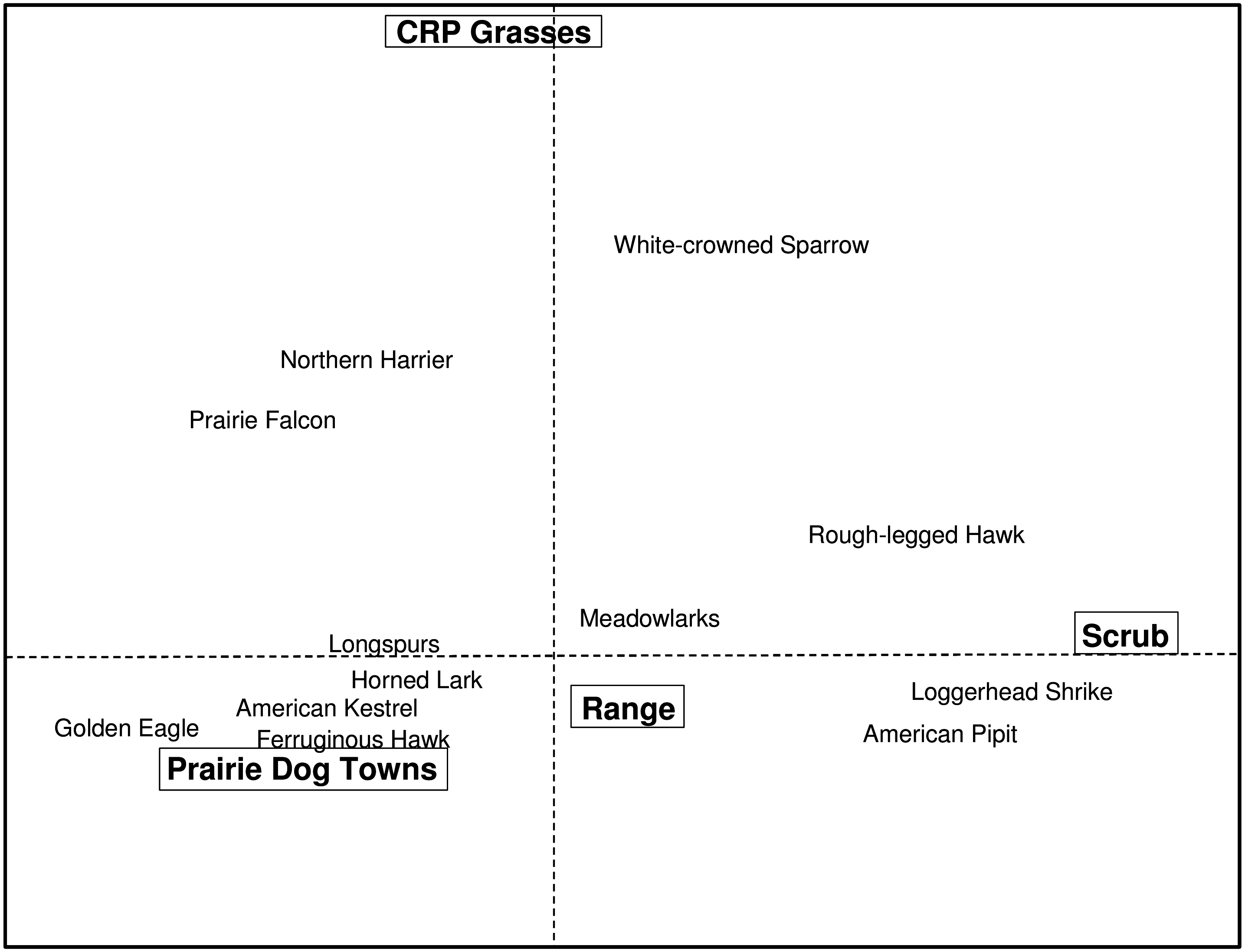

CRP Grasses
Range
Scrub
Fallow Field
Prairie Dog Towns
Lark Bunting
Ring-necked Pheasant
Bullock's Oriole
Red-winged Blackbird
Grasshopper Sparrow
Meadowlarks
Mourning Dove
Common Nighthawk
Cassin's Sparrow
Western Kingbird
Eastern Kingbird
Northern Bobwhite
Northern Mockingbird
Dickcissel
Upland Sandpiper
Horned Lark
Loggerhead Shrike
Barn Swallow
Swainson's Hawk
American Kestrel
Lark Sparrow
Brown-headed Cowbird
Turkey Vulture
Scissor-tailed Flycatcher
Red-tailed Hawk
Killdeer
Long-billed Curlew
Scaled Quail
Burrowing Owl
Northern Flicker

Figure 8


CRP Grasses
White-crowned Sparrow
Northern Harrier
Prairie Falcon
Rough-legged Hawk
Meadowlarks
Scrub
Longspurs
Horned Lark
American Kestrel
Golden Eagle
Ferruginous Hawk
Prairie Dog Towns
Range
Loggerhead Shrike
American Pipit

Appendix 1. Code written in *Resampling Stats* (Resampling Stats., Inc., 1997) for comparison of relative densities of individual species on and off prairie dog towns. Bold statements are program code, non-bold statements are comments.

```
'RESAMPLING STATISTICAL ANALYSES FOR PAIRED OBSERVATIONS
********************************************************

'PROGRAM WRITTEN IN RESAMPLING STATS BY M. V. LOMOLINO AND G. A.
SMITH

'THIS PROGRAM TESTS THE HYPOTHESIS THAT OBSERVATIONS AT ONE SET
        OF SITES, THAT IS FOR ONE TREATMENT (PDTs)
'DIFFERS SIGNIFCANTLY FROM OBSERVATIONS AT SITES PAIRED WITH
        EACH OF THE TREATMENT SITES (PAIRs)

'DATA IS PASTED BETWEEN THE BRACKETS BELOW FOR THE TREATMENT
        (PDT) SITES, AND THEN FOR THE PAIRED SITES

'THE PROGRAM FIRST CALCULATES THE OBSERVED DIFFERENCES AND
        SUM OF DIFFERENCES BETWEEN EACH PAIRING AND THEN
        CALCULATES THE OBSERVED NUMBER OF TIMES OBSERVATIONS
        WERE HIGHER ON A PDT SITE VERSUS ITS PAIRED SITE

'THE PROGRAM THEN POOLS THE DATA INTO ONE LARGE VECTOR,
        SHUFFLES THE OBSERVATION SO THAT OBSERVATIONS AT
        TREATMENT SITES ARE MIXED WITH THOSE AT PAIRED SITES, AND
        THEN SELECTS ONE HALF OF THESE ELEMENTS AND PAIRS THEM UP
        WITH THE REMAINING HALF OF THE ELEMENTS

'THE PROGRAM THEN CALCULATES THE SAME PARAMETERS
        (DIFFERENCES, SUM OF DIFFERENCES AND NUMBER TIMES VALUES
        IN THE FIRST SET OF SHUFFLED OBSERVATIONS EXCEED THOSE OF
        THE RANDOM PAIRS) AND COMPARES THESE PARAMETERS FOR THE
        RANDOMIZED (SHUFFLED) DATA TO THOSE FOR THE OBSERVED
        DATA WHERE TREATMENT EFFECTS WERE PRESERVED.

'THE PROGRAM REPEATS THESE ROUTINES AND CALCULATES THE
        NUMBER OF ITERATIONS WHERE THE SUM OF DIFFERENCES WERE
        HIGHER, THE SAME OR LOWER THAN THE OBSERVED SUM OF
        DIFFERENCES

'THE PROGRAM ALSO COUNTS THE NUMBER OF ITERATIONS WHERE THE
        FREQUENCY OF RANDOM PAIRINGS WITH HIGHER LEVELS ON
```

```
        PAIRED VERSUS TREATMENT SITES EXCEED THE OBSERVED
        FREQUENCY OF PAIRINGS WITH HIGHER LEVELS ON THE PAIRED
        VERSUS TREATMENT (PDT) SITES

'P-VALUES CAN THEN BE CALCULATED AS THE PROPORTION OF
        ITERATIONS WITH RESULTS MORE EXTREME THAN THOSE FOR THE
        OBSERVED (UNSHUFFLED) DATA

'PASTE DATA BETWEEN BRACKETS BELOW

NUMBERS () PDT
NUMBERS () PAIR

CONCAT PDT PAIR OPOOL

DATA 0 LESSPOS
DATA 0 MOREPOS
DATA 0 SAMEPOS
DATA 0 GTINRAND
DATA 0 LTINRAND
DATA 0 EQINRAND
DATA 0 MOREPDTS
DATA 0 SAMEPDTS
DATA 0 LESSPDTS

' RUN ANALYSES ON ACTUAL, UNSHUFFLED DATA, THEN SCORE THE
        RESULTS TO BE USED IN COMPARISONS

        COUNT PDT >=0 NUMPAIRS
        ADD NUMPAIRS 1 NUMPLUS1
        MULTIPLY NUMPAIRS 2 NUMELEMS

        TAKE OPOOL 1,NUMPAIRS D
        TAKE OPOOL NUMPLUS1,NUMELEMS E

        SUBTRACT D E F

                SUM F OSUMDIFF
                SCORE OSUMDIFF OBSDIFF

                COUNT F < 0 PDTLESS
                SCORE PDTLESS OPDTLESS
```

```
                COUNT F = 0 PDTSAME
                SCORE PDTSAME OPDTSAME

                COUNT F > 0 PDTMORE
                SCORE PDTMORE OPDTMORE

' NOW PRINT THE RESULTS FOR THE UNSHUFFLED DATA, INCLUDING THE
        NUMBER OF TIMES OR PAIRS WITH HIGHER VALUES ON THE
        TREATMENT (PDT) SITES = OPDTMORE, LOWER VALUES ON THE
        TREATMENT SITES = OPDTLESS OR THE SAME VALUE ON THE TWO
        TYPES OF SITES = OPDTSAME

'ALSO PRINT THE SUM OF THE DIFFERENCES BETWEEN TREATMENT AND
        PAIRED SITES FOR THE OBSERVED DATA = OBSDIFF

PRINT OPDTMORE OPDTLESS OPDTSAME OBSDIFF

' HERE IS WHERE YOU CAN CHANGE THE NUMBER OF ITERATIONS

REPEAT 10000

' NOW LET US POOL THE OBSERVATIONS INTO ONE VECTOR AND SHUFFLE
        IT SO THAT LATER PAIRINGS WILL BE AT RANDOM WITH RESPECT
        TO THE ORIGINAL TREATMENT (PDTS VERSUS PAIRS)

        CONCAT PDT PAIR POOL
        SHUFFLE POOL RANDPOOL

        CLEAR PDTLESS
        CLEAR PDTMORE
        CLEAR PDTSAME
        CLEAR SUMDIFF
        CLEAR D
        CLEAR E
        CLEAR F

' NOW LET US TAKE THE FIRST HALF OF THIS RANDOM VECTOR AND PAIR
        THOSE ELEMENTS WITH THE SECOND HALF

        TAKE RANDPOOL 1,NUMPAIRS D
        TAKE RANDPOOL NUMPLUS1,NUMELEMS E

' FIND THE DIFFERENCE BETWEEN VALUES FOR EACH OF THE RANDOM
```

```
        PAIRINGS AND STORE THEM IN F

        SUBTRACT D E F

' CALCULATE THE SUM OF THE DIFFERENCES

        SUM F SUMMDIFF

' COUNT THE NUMBER OF TIMES VALUES FROM THE FIRST RANDOMIZED
        VECTOR WERE > OR < OR = THOSE FROM THE SECOND

                IF SUMMDIFF > OBSDIFF
                ADD GTINRAND 1 GTINRAND
                END

                IF SUMMDIFF < OBSDIFF
                ADD LTINRAND 1 LTINRAND
                END

                IF SUMMDIFF = OBSDIFF
                ADD EQINRAND 1 EQINRAND
                END

' NOW COUNT NUMBER OF TIMES DENSITY HIGHER FOR ELEMENTS IN THE
        FIRST VECTOR (PDTS)

        COUNT F > 0 PDTMORE

' NOW COUNT THE NUMBER OF TIMES RANDOM ROUTINES HAD MORE, =,
        FEWER POSITIVES THAN OBSERVED PAIRINGS

                IF PDTMORE > OPDTMORE
                ADD MOREPOS 1 MOREPOS
                END


                IF PDTMORE = OPDTMORE
                ADD SAMEPOS 1 SAMEPOS
                END

                IF PDTMORE < OPDTMORE
                ADD LESSPOS 1 LESSPOS
                END
```

```
' END THE REPEAT STATEMENT, LOOP

END

' PRINT THE RELEVANT RESULTS,

'NUMBER OF TIMES SUM DIFFERENCE GREATER IN RANDOM VERSUS
        OBSERVED VECTORS

'NUMBER OF TIMES SUM DIFFERENCE IN RANDOMIZED DATA EQUALED
        THAT OF OBSERVED DATA

'NUMBER OF TIMES SUM DIFFERENCE LESS IN RANDOM VERSUS
        OBSERVED VECTORS

PRINT GTINRAND LTINRAND EQINRAND

'PRINT THE REMAINING RESULTS BASED ON HOW MANY PAIRINGS HAD
        HIGHER VALUES IN THE FIRST VERSUS 2ND VECTOR HERE WILL
        PRINT NUMBER OF ITERATIONS WHERE RANDOM RUNS PRODUCED
        MORE PAIRINGS WITH HIGH VALUES IN THE FIRST RANDOMIZED
        VECTOR = MOREPOS, WITH THE SAME NUMBER OF PAIRINGS WITH
        HIGH ... = SAMEPOS AND WITH FEWER PAIRINGS WITH HIGH VALUES
        IN THE FIRST VERSUS SECOND VECTOR = LESSPOS

PRINT MOREPOS LESSPOS SAMEPOS

'CALCULATE P-VALUES AS THE PROPORTION OF ITERATIONS WITH
        RESULTS MORE EXTREME THAN THOSE FOR THE OBSERVED
        (UNSHUFFLED) DATA

'PRINT THE PROPORTIONS

DIVIDE GTINRAND 10000 PROPGT
DIVIDE LTINRAND 10000 PROPLT
DIVIDE EQINRAND 10000 PROPEQ
DIVIDE MOREPOS 10000 PROPMORE
DIVIDE LESSPOS 10000 PROPLESS
DIVIDE SAMEPOS 10000 PROPSAME

PRINT PROPGT PROPLT PROPEQ PROPMORE PROPLESS PROPSAME

ADD GTINRAND EQINRAND GTEQRAND
```

```
DIVIDE GTEQRAND 10000 PROPGTEQ
ADD LTINRAND EQINRAND LTEQRAND
DIVIDE LTEQRAND 10000 PROPLTEQ
ADD MOREPOS SAMEPOS MORESAME
DIVIDE MORESAME 10000 PMORESAM
ADD LESSPOS SAMEPOS LESSSAME
DIVIDE LESSSAME 10000 PLESSSAM

PRINT PROPGTEQ PROPLTEQ PMORESAM PLESSSAM
```

Appendix 2. Avian species detected in the Oklahoma Panhandle during summer and fall 1997, 1998, and 1999. Species given a relative density measure were recorded during line transect counts at the site. Species with an "X" were recorded at the site incidental to the formal counts. A dashed line indicates the species was not recorded at the site. Site code, county, and macrohabitat to which each site was assigned is also given.

Season / Year	Site	County	Macrohabitat	American Avocet	American Crow	American Goldfinch	American Kestrel	American Pipit	American Tree Sparrow	Bald Eagle
Summer 1997	S97-01	Beaver	P-dog	---	---	---	---	---	---	---
	S97-02	Beaver	Range	---	---	---	---	---	---	---
	S97-03	Beaver	P-dog	---	---	---	---	---	---	---
	S97-04	Beaver	Range	---	---	---	---	---	---	---
	S97-05	Beaver	P-dog	---	---	---	---	---	---	---
	S97-06	Beaver	Range	---	---	---	---	---	---	---
	S97-07	Texas	P-dog	---	---	---	---	---	---	---
	S97-08	Texas	Range	---	---	---	X	---	---	---
	S97-09	Texas	P-dog	---	---	---	---	---	---	---
	S97-10	Texas	Range	---	---	---	---	---	---	---
	S97-11	Texas	P-dog	X	---	---	---	---	---	---
	S97-12	Texas	Scrub	---	---	---	---	---	---	---

Barn Swallow	Black-billed Magpie	Blue Grosbeak	Blue-winged Teal	Brown-headed Cowbird	Bullock's Oriole	Burrowing Owl	Cassin's Sparrow	Chihuahuan Raven	Cliff Swallow	Common Grackle	Common Nighthawk
X	---	---	---	---	---	X	---	---	---	---	---
X	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	X	---	---	---	---	X
X	---	---	---	---	---	---	0.056	---	---	---	X
X	---	---	0.017	0.017	---	0.069	---	---	---	---	X
X	---	---	---	---	---	---	---	---	---	---	0.017
---	---	---	---	---	---	0.056	---	---	---	---	X
---	---	---	---	---	---	---	---	---	---	---	X
---	---	---	---	---	---	0.398	0.083	---	---	---	X
---	---	---	---	---	---	---	---	---	---	---	X
X	X	---	---	---	---	0.190	---	---	---	---	---
---	X	---	---	---	---	---	---	---	---	---	---

Curve-billed Thrasher	Dark-eyed Junco	Dickcissel	Eastern Kingbird	Eastern Wood-Pewee	European Starling	Evening Grosbeak	Ferruginous Hawk	Field Sparrow	Golden Eagle	Grasshopper Sparrow	Great Blue Heron
---	---	---	---	---	---	---	---	---	---	0.082	---
---	---	---	X	---	---	---	---	---	---	1.336	---
---	---	---	X	---	---	---	---	---	---	0.234	---
---	---	---	---	---	---	---	---	---	---	1.175	---
---	---	X	---	---	---	---	---	---	---	0.091	---
---	---	X	---	---	---	---	---	---	---	0.715	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	0.169	---
---	---	---	---	---	---	---	---	---	---	0.194	---
---	---	---	---	---	---	---	---	---	---	2.406	---
---	---	X	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	0.957	---

Great-tailed Grackle	Harris's Sparrow	Horned Lark	House Sparrow	Killdeer	Lark Bunting	Lark Sparrow	Lesser Prairie-Chicken	Loggerhead Shrike	Long-billed Curlew	Longspur	Meadowlark
---	---	2.027	---	0.232	---	1.059	---	---	---	---	0.543
---	---	0.020	---	---	---	---	---	---	---	---	0.396
---	---	0.144	---	---	---	0.014	---	---	---	---	0.800
---	---	---	---	---	---	0.217	---	---	---	---	1.381
---	---	0.486	---	0.555	---	0.358	---	---	---	---	0.189
---	---	0.086	---	0.017	---	0.224	---	---	---	---	0.453
---	---	1.617	---	0.028	---	0.014	---	---	---	---	0.451
---	---	1.209	---	---	---	0.168	---	---	---	---	0.348
---	---	1.337	---	---	---	0.659	---	---	---	---	0.528
---	---	0.908	---	---	---	---	---	---	---	---	0.417
---	---	0.416	---	0.138	---	---	---	---	---	---	0.033
---	---	---	---	---	---	---	---	---	---	---	0.205

Merlin	Mississippi Kite	Mountain Plover	Mourning Dove	Northern Bobwhite	Northern Flicker	Northern Harrier	Northern Mockingbird	Northern Rough-winged Swallo	Orchard Oriole	Pine Siskin	Prairie Falcon
---	---	---	0.041	---	0.020	---	---	---	---	---	---
---	---	---	0.186	0.133	---	---	---	---	---	---	---
---	---	---	X	---	0.356	---	---	---	---	---	---
---	---	---	0.123	---	---	---	---	---	---	---	---
---	X	---	---	---	X	---	---	---	---	---	---
---	---	---	0.086	---	---	---	---	---	---	---	---
---	---	---	0.069	---	---	---	---	---	---	---	---
---	---	---	0.014	---	---	---	---	---	---	---	---
---	---	---	0.028	---	---	---	---	---	---	---	---
---	---	---	0.083	---	---	---	---	X	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.033	---	---	---	---	---	---	---	---

Song Sparrow	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Short-eared Owl	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Scissor-tailed Flycatcher	¦	¦	0.089	¦	0.017	¦	¦	¦	¦	¦	¦	¦
Scaled Quail	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Say's Phoebe	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Rufous-crowned Sparrow	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Rough-legged Hawk	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Rock Dove	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Ring-necked Pheasant	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦	¦
Red-winged Blackbird	¦	¦	¦	¦	¦	0.017	¦	¦	¦	¦	¦	X
Red-tailed Hawk	¦	X	¦	¦	¦	¦	¦	¦	X	¦	¦	¦
Red-headed Woodpecker	¦	¦	X	¦	¦	¦	¦	¦	¦	¦	¦	¦

White-crowned Sparrow	---	---	---	---	---	---	---	---	---	---	---	---
Western Kingbird	X	---	0.126	X	X	0.017	---	---	---	---	---	---
Upland Sandpiper	---	---	---	---	---	---	---	---	---	---	---	---
Turkey Vulture	---	X	X	---	---	---	---	---	---	---	---	---
Swainson's Hawk	---	---	X	---	---	---	---	X	---	---	---	---
Spotted Towhee	---	---	---	---	---	---	---	---	---	---	---	---

	S97-13	Texas	P-dog	---	---	---	X	---	---	---
	S97-14	Texas	CRP	---	---	---	---	---	---	---
	S97-15	Texas	P-dog	---	---	---	---	---	---	---
	S97-16	Texas	Range	---	---	---	---	---	---	---
	S97-17	Cimarron	P-dog	---	---	---	---	---	---	---
	S97-18	Cimarron	Range	---	---	---	---	---	---	---
	S97-19	Cimarron	P-dog	---	---	---	---	---	---	---
	S97-20	Cimarron	Range	---	---	---	---	---	---	---
	S97-21	Cimarron	P-dog	---	---	---	---	---	---	---
	S97-22	Cimarron	Range	---	---	---	---	---	---	---
	S97-23	Cimarron	P-dog	---	---	---	X	---	---	---
	S97-24	Cimarron	Range	---	---	---	---	---	---	---
Summer 1998	S98-01	Cimarron	P-dog	---	---	---	---	---	---	---
	S98-02	Cimarron	Range	---	---	---	---	---	---	---
	S98-03	Cimarron	P-dog	---	---	---	---	---	---	---
	S98-04	Cimarron	CRP	---	---	---	---	---	---	---
	S98-05	Cimarron	P-dog	---	X	---	---	---	---	---
	S98-06	Cimarron	Range	---	---	---	0.014	---	---	---
	S98-07	Texas	P-dog	---	---	---	---	---	---	---
	S98-08	Texas	Scrub	---	---	---	---	---	---	---
	S98-09	Texas	P-dog	---	---	---	---	---	---	---
	S98-10	Texas	Range	---	---	---	---	---	---	---
	S98-11	Texas	P-dog	---	---	---	---	---	---	---
	S98-12	Texas	Ag	---	---	---	---	---	---	---
	S98-13	Texas	P-dog	---	---	---	---	---	---	---
	S98-14	Texas	Range	---	---	---	---	---	---	---
	S98-15	Texas	P-dog	---	---	---	---	---	---	---

---	---	---	---	---	---	0.619	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	0.262	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	0.012
---	---	---	---	---	---	1.330	---	---	---	---	---
---	---	---	---	---	---	---	0.033	---	---	---	---
---	---	---	---	X	---	0.024	---	---	---	---	---
X	---	---	---	---	X	---	---	---	---	---	---
---	---	---	---	0.278	---	0.014	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	X
---	---	---	---	1.669	---	0.038	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	0.051	---	---	---	---	---
---	---	X	---	---	X	---	0.038	---	---	---	---
X	---	---	---	---	---	0.273	---	---	---	---	---
---	---	---	---	---	---	---	0.015	---	---	---	---
X	---	---	---	---	---	0.069	---	---	---	---	---
---	---	---	---	---	---	---	0.376	---	---	---	X
---	---	---	---	---	---	0.317	---	---	---	---	---
---	---	---	---	0.106	---	---	0.673	---	---	---	---
---	0.103	---	---	---	---	---	0.013	---	---	---	X
---	---	---	---	---	---	---	0.300	---	---	---	X
---	---	---	---	---	---	0.438	---	---	---	---	---
---	---	---	---	---	---	X	---	---	---	---	---
---	---	---	---	---	---	0.482	---	---	---	---	---
---	---	---	---	---	X	---	0.111	---	---	---	0.019
---	---	---	---	---	---	0.143	---	---	---	---	X

---	---	---	---	---	---	---	---	---	---	0.042	---
---	---	0.021	---	---	---	---	---	---	---	0.617	---
---	---	---	---	---	---	---	---	---	---	0.095	---
---	---	---	---	---	---	---	---	---	---	1.130	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	1.899	---
---	---	---	---	---	---	---	X	---	X	0.077	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	X	---	---	---	---
---	---	---	---	---	---	---	---	---	---	0.688	---
X	---	---	---	---	---	---	---	---	---	---	---
0.181	---	---	---	---	---	---	---	---	---	0.013	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	0.013	---	0.679	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	1.244	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	0.015	---
---	---	---	---	---	---	---	---	---	---	0.282	---
---	---	---	---	---	0.013	---	---	---	---	0.149	---
---	---	---	---	---	---	---	---	---	---	0.509	---
---	---	---	---	---	---	---	---	---	---	0.351	---
---	---	---	---	---	---	---	---	---	---	0.154	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.019	---	---	---	---	---	---	0.074	---
---	---	---	---	---	---	---	---	---	---	0.238	---

---	---	0.585	---	---	---	0.042	---	---	---	---	0.421
---	---	---	---	---	---	---	---	---	---	---	0.021
---	---	1.297	---	---	---	---	---	---	0.012	---	0.512
---	---	0.183	---	---	0.254	---	---	---	---	---	0.095
---	---	2.125	---	0.083	---	0.083	---	---	---	---	0.501
---	---	0.580	---	---	0.535	---	---	---	---	---	0.200
---	---	5.684	---	---	X	---	---	X	X	---	0.194
---	---	0.342	---	---	0.024	---	---	---	X	---	0.012
---	---	3.240	---	0.014	---	---	---	---	---	---	---
---	---	0.555	---	---	---	---	---	---	---	---	0.303
---	---	4.042	---	X	---	---	---	---	---	---	---
---	---	0.410	---	---	1.040	---	---	---	---	---	0.239
---	---	2.136	---	0.119	---	---	---	---	0.068	---	0.058
---	---	---	---	---	---	---	---	---	---	---	0.256
---	---	1.043	---	---	---	---	---	---	X	---	0.320
---	---	---	---	---	---	---	---	---	---	---	0.181
---	---	2.125	---	---	---	0.014	---	---	X	---	0.111
---	---	0.056	---	---	---	0.028	---	---	---	---	---
---	---	0.982	---	0.015	---	---	---	---	---	---	0.106
---	---	---	---	X	---	X	---	---	---	---	0.167
---	---	0.482	---	0.580	---	0.922	---	---	---	---	0.149
---	---	0.035	---	---	---	0.013	---	---	---	---	0.269
---	---	1.143	---	---	---	0.017	---	---	---	---	0.895
---	---	3.472	---	---	---	---	---	---	---	---	0.067
---	---	0.590	---	X	---	0.815	---	---	---	---	0.333
---	---	---	---	---	---	0.694	---	---	---	---	0.663
---	---	1.054	---	0.024	---	0.048	---	---	---	---	0.429

---	---	---	0.136	---	---	X	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.131	---	---	X	---	---	---	---	---
---	---	---	0.024	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.068	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.156	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.013	---	---	---	---	---	---	---	---
---	---	---	0.051	---	---	---	---	---	---	---	---

---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.091	---	---	---	---	---	---	---	---
---	---	---	0.091	---	---	---	---	---	---	---	---
---	---	X	---	---	---	---	---	---	---	---	---
---	---	---	0.328	---	---	---	X	---	---	---	---
---	---	---	0.015	---	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	---	---
---	---	---	0.231	X	---	---	---	---	---	---	---
---	---	---	0.103	---	---	---	---	---	---	---	---
---	---	---	0.430	---	---	---	---	---	---	---	---
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	S98-16	Texas	Scrub	---	---	---	---	---	---	---
	S98-17	Texas	P-dog	---	---	---	---	---	---	---
	S98-18	Texas	Ag	---	X	---	---	---	---	---
	S98-19	Beaver	P-dog	---	X	---	---	---	---	---
	S98-20	Beaver	Range	---	---	---	---	---	---	---
	S98-21	Beaver	P-dog	---	X	---	---	---	---	---
	S98-22	Beaver	Scrub	---	---	---	---	---	---	---
	S98-23	Beaver	P-dog	---	---	---	---	---	---	---
	S98-24	Beaver	Ag	---	---	---	---	---	---	---
Summer 1999	S99-01	Texas	P-dog	---	---	---	X	---	---	---
	S99-02	Texas	Ag	---	---	---	---	---	---	---
	S99-03	Texas	P-dog	---	---	---	---	---	---	---
	S99-04	Texas	Range	---	---	---	---	---	---	---
	S99-05	Texas	P-dog	---	---	---	---	---	---	---
	S99-06	Beaver	Scrub	---	---	---	---	---	---	---
	S99-07	Cimarron	P-dog	---	---	---	---	---	---	---
	S99-08	Cimarron	Range	---	---	---	---	---	---	---
	S99-09	Cimarron	P-dog	---	---	---	---	---	---	---
	S99-10	Cimarron	Range	---	---	---	---	---	---	---
	S99-11	Texas	P-dog	---	---	---	---	---	---	---
	S99-12	Cimarron	Ag	---	---	---	---	---	---	---
	S99-13	Beaver	P-dog	---	---	---	---	---	---	---
	S99-14	Beaver	Scrub	---	---	---	---	---	---	---
	S99-15	Beaver	P-dog	---	---	---	---	---	---	---
	S99-16	Beaver	Scrub	---	---	---	---	---	---	---
	S99-17	Beaver	P-dog	---	---	---	---	---	---	---
	S99-18	Beaver	Scrub	---	---	---	---	---	---	---

---	---	0.024	---	---	---	---	---	---	---	---	X
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X	---	---	---	---	---	X	---	---	X	---	X
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---	---	---	---	X	---	0.048	---	---	---	---	---
0.119	---	---	---	X	---	---	---	---	---	---	---
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---	---	---	---	---	---	0.093	---	---	---	---	---
---	---	---	---	---	0.373	---	0.274	---	---	---	0.019
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---	0.661	---	---	---	---	---	0.476	---	---	---	---
---	---	---	---	---	---	0.014	---	---	---	---	---
X	---	---	---	0.118	0.014	---	0.374	---	---	---	---
---	---	---	---	0.133	---	0.480	X	---	---	---	---
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X	---	---	---	0.015	---	---	0.091	---	---	---	X
X	---	---	---	---	---	0.815	---	---	---	---	---
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---	---	0.962	---	0.050	---	0.153	---	---	---	---	0.241
---	---	X	---	0.019	---	---	---	---	---	---	0.111
---	---	0.021	---	0.541	---	---	---	---	---	---	0.811
---	---	0.203	---	---	---	---	---	---	---	---	0.415
---	---	0.977	---	0.874	---	X	---	---	---	---	1.039
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---	---	2.189	---	X	---	---	---	X	---	---	0.238
---	---	---	---	X	---	0.071	---	---	---	---	0.024
---	---	X	---	6.649	---	0.970	---	---	---	---	0.750
---	---	6.604	---	0.198	0.264	0.682	---	---	---	---	0.021
---	---	1.270	---	0.019	---	0.074	---	---	---	---	0.259
---	---	---	---	---	---	0.730	---	---	---	---	0.516
0.021	---	0.021	0.021	---	---	0.136	---	---	---	---	0.559
---	---	---	---	---	---	0.302	---	---	---	---	0.417
---	---	1.547	---	X	---	0.014	---	---	0.014	---	0.161
---	---	0.014	---	---	---	0.244	---	---	---	---	0.153
---	---	1.082	---	0.335	---	0.017	---	---	---	---	0.250
---	---	0.293	---	X	---	X	---	---	---	---	0.483
---	---	0.253	---	---	0.037	---	---	---	---	---	0.481
---	---	2.519	---	0.019	---	---	---	---	---	---	0.130
---	---	2.333	---	7.254	---	1.216	---	---	---	---	6.613
---	---	0.069	---	---	---	0.514	---	---	---	---	0.519
---	---	0.176	---	0.205	---	0.205	---	0.051	---	---	1.802
---	---	---	---	---	---	0.026	---	---	---	---	0.410
---	---	0.607	---	0.061	---	0.227	---	---	---	---	0.470
---	---	0.099	---	---	---	0.535	---	---	---	---	0.703

---	---	---	0.387	0.426	---	---	0.655	---	---	---	---
---	X	---	0.369	---	---	---	---	---	---	---	---
---	---	---	0.074	---	---	---	---	---	---	---	---
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---	---	---	0.057	---	---	---	---	---	---	---	---
---	---	---	0.136	---	---	---	---	---	---	---	---
---	---	---	0.112	---	---	---	---	---	---	---	---
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---	---	---	0.228	---	---	---	0.024	---	---	---	---
---	---	---	0.164	---	---	---	X	---	---	---	---
---	---	---	5.552	---	---	---	---	---	---	---	---
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---	---	---	0.204	---	---	---	---	---	---	---	---
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---	---	---	0.362	0.061	---	---	---	---	---	---	---
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---	---	---	0.159	0.051	---	---	---	---	---	---	---
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	S99-19	Cimarron	P-dog	---	---	---	---	---	---	---
	S99-20	Cimarron	CRP	---	---	---	---	---	---	---
	S99-21	Texas	P-dog	---	---	---	---	---	---	---
	S99-22	Texas	Ag	---	---	---	---	---	---	---
	S99-23	Texas	P-dog	---	---	---	0.017	---	---	---
	S99-24	Texas	Range	---	---	---	---	---	---	---
Fall 1997	F97-01	Texas	P-dog	---	---	---	X	---	---	---
	F97-02	Texas	Range	---	---	---	X	---	---	---
	F97-03	Texas	P-dog	---	---	---	---	0.028	---	---
	F97-04	Texas	Range	---	---	---	---	0.076	---	---
	F97-05	Texas	P-dog	---	---	---	X	---	---	X
	F97-06	Texas	Scrub	---	---	---	---	0.646	---	---
	F97-07	Cimarron	P-dog	---	---	---	---	---	---	---
	F97-08	Cimarron	Range	---	---	---	---	0.012	0.243	---
	F97-09	Cimarron	P-dog	---	---	---	---	11.082	---	---
	F97-10	Cimarron	Range	---	---	---	---	0.076	---	---
	F97-11	Cimarron	P-dog	---	---	---	X	---	---	---
	F97-12	Cimarron	Range	---	---	---	---	---	---	---
Fall 1998	F98-01	Cimarron	P-dog	---	---	---	---	---	---	---
	F98-02	Cimarron	Range	---	---	X	X	X	---	---
	F98-03	Cimarron	P-dog	---	---	---	---	---	---	---
	F98-04	Cimarron	CRP	---	---	---	---	---	---	---
	F98-05	Cimarron	P-dog	---	---	---	X	---	---	---
	F98-06	Cimarron	Range	---	---	---	0.090	---	0.196	---
	F98-07	Texas	P-dog	---	---	---	---	---	---	---
	F98-08	Texas	Scrub	---	---	---	---	---	---	---

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---	---	---	0.028	---	---	---	---	---	---	1.890	---
---	---	---	0.083	---	---	---	---	---	---	0.083	---
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0.012	---	---	---	---	---	---	---	---	---	---	---
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---	---	0.934	0.264	1.606	---	2.646	---	---	---	---	0.167
---	---	1.339	---	---	0.333	0.108	---	0.033	---	---	2.569
---	---	0.017	---	---	---	---	---	---	---	---	0.133
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---	---	1.749	---	---	---	---	---	---	---	---	0.118
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---	---	0.833	---	---	---	---	---	---	---	---	0.139
---	---	3.842	---	---	---	---	---	---	---	0.815	0.326
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---	---	1.124	---	X	---	---	---	---	---	0.374	0.013
---	---	0.532	---	---	---	---	---	---	---	2.972	0.115
---	---	6.590	---	---	---	---	---	---	---	0.866	3.147
---	---	0.143	---	---	---	---	---	---	---	0.223	0.184
---	---	2.490	---	---	---	---	---	---	---	0.580	0.014
---	---	0.118	---	---	---	---	---	0.014	---	0.132	1.345
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---	---	---	0.050	0.083	---
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	F98-09	Texas	P-dog	---	---	---	---	---	0.087	---
	F98-10	Texas	Range	---	---	---	---	---	---	---
	F98-11	Beaver	P-dog	---	---	---	---	---	---	---
	F98-12	Beaver	Scrub	---	---	---	---	---	---	---
Fall 1999	F99-01	Beaver	P-dog	---	X	---	---	---	---	---
	F99-02	Beaver	Scrub	---	---	---	---	0.099	---	---
	F99-03	Beaver	P-dog	---	---	---	---	---	---	---
	F99-04	Beaver	Scrub	---	---	---	---	---	---	---
	F99-05	Beaver	P-dog	---	---	---	---	---	---	X
	F99-06	Beaver	Scrub	---	---	---	---	0.026	---	---
	F99-07	Texas	P-dog	---	---	---	---	---	---	---
	F99-08	Texas	Range	---	---	---	X	---	---	---
	F99-09	Texas	P-dog	---	---	---	0.019	---	---	---
	F99-10	Texas	Range	---	---	---	---	---	---	---
	F99-11	Cimarron	P-dog	---	---	---	---	0.014	---	---
	F99-12	Cimarron	CRP	---	---	---	---	---	---	---

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---	---	0.318	---	---	---	---	---	0.015	---	X	0.076
---	---	0.246	---	---	---	---	0.062	X	---	---	0.350
---	---	1.722	---	---	---	---	---	---	---	0.270	0.170
---	---	0.015	---	---	---	---	---	---	---	0.045	0.106
---	---	4.101	---	---	---	---	---	---	---	0.377	0.308
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---	---	1.967	---	---	---	---	---	---	---	0.100	0.152
---	---	0.017	---	---	---	---	---	---	---	0.473	0.387
---	---	0.759	---	---	---	---	---	---	---	0.181	---
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BIOGEOGRAPHY AND LANDSCAPE ECOLOGY OF AVIAN SPECIES ON BLACK-TAILED PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*) TOWNS

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Running head: Biogeography and landscape ecology of prairie dog towns

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ABSTRACT

In this study, we considered black-trailed prairie dog towns as islands and tested traditional biogeographic predictions for avian richness on “islands” of varying size and isolation. We also evaluated local habitat characteristics of prairie dog towns and characteristics of the habitat matrix surrounding prairie dog towns for their influence on avian richness and abundance. We conducted variable distance line transect counts for birds on 36 prairie dog towns during summer and fall of 1997, 1998, and 1999 in the Oklahoma Panhandle. We quantified local habitat characteristics of each focal town. To assess landscape variables, we used a Geographic Information System (GIS) to characterize the landscape within 10 km of each town. Pairwise correlations were used to compare richness to local and landscape variables, while Canonical Correspondence Analysis was used to investigate and visualize how distributions of birds varied along geographic gradients, and with local and landscape-level environmental variables.

Our surveys totaled 4,992 individual observations for 36 avian species on prairie dog towns ranging from 9.0 to 211.0 ha. Species richness was not correlated with area or isolation of prairie dog towns. Richness, however, was significantly correlated with percent cover of forbs on prairie dog towns and with area of scrub habitat surrounding a prairie dog town during summer. During fall, richness was significantly correlated with area of non-native grass habitat surrounding a focal dog town. Finally, there was a strong geographic gradient of richness, with the number of bird species on prairie dog towns increasing significantly from west to east.

These results are contrary to traditional island biogeography theory. However, they are consistent with recent reevaluations suggesting that small islands are strongly influenced by characteristics of the local habitat and adjacent landscape. Networks of reserves for prairie dogs and their associated species should include complexes of towns of various sizes and of varying distances from one another. Management should also include optimizing the local and intervening habitats for avian diversity and for particular species of conservation concern.

Keywords

Birds, black-tailed prairie dog, conservation, *Cynomys ludovicianus*, fragmentation, island biogeography, landscape ecology, Oklahoma.

INTRODUCTION

Habitat reduction and fragmentation of native ecosystems remains one of the greatest threats to biological diversity. A broad variety of ecosystems suffer from downsizing and fragmentation (World Conservation Monitoring Centre, 1992; Meffee & Carroll, 1997) and the Great Plains are no exception. Tallgrass prairie now occupies less than 5% of its historic extent (Steinauer & Collins, 1996), and in the mixed and shortgrass plains, black-tailed prairie dog *(Cynomys ludovicianus*) towns have been reduced to less than 3% of their historic coverage (Knowles, 1998; Miller & Cully, 2001).

Prairie dog towns have been prominent features of the Great Plains landscape since the late Pleistocene (Goodwin, 1995). Over time, numerous native species of plants and animals became associated with the expansive and predictable resources afforded by prairie dog towns. The result is that prairie dog towns were, and still continue to be inhabited by distinct assemblages of plants and animals, and that prairie dogs may well represent ecosystem engineers and keystone species (Miller et al., 1994; Stapp, 1998; Barko et al., 1999; Kotliar, 2000; Kretzer & Cully, 2001; see Chapter 2). However, the prairie dog ecosystem persists today only as downsized and scattered towns within a matrix of anthropogenic habitats (Graber et al., 1998; Knowles, 1998; Miller et al., 2000; Lomolino et al. 2001; Lomolino & Smith, 2001).

Predicting the effects of habitat fragmentation and homogenization, or the effects of mitigation of such impacts, is important for conservation and management efforts and attempts to do so have relied on the tenets of the equilibrium theory of island biogeography and its various corollaries (MacArthur & Wilson, 1963, 1967; Brown, 1971; Diamond, 1975; Wilson & Willis, 1975; Brown & Kodric-Brown, 1977; Harris, 1984; Shafer, 1990). The relevance of the island paradigm for anthropogenically fragmented ecosystems depends heavily on three assumptions: (1) the characteristics of insular habitats do not vary significantly among islands, (2) the intervening habitat is inhospitable and homogeneous across the regional landscape, and (3) the islands are large enough to support populations of the focal species and to render differences among islands and stochastic extinction forces irrelevant. In other words, as islands become smaller and more fragmented, diversity of native communities is less likely to be driven by extinction/immigration dynamics and more likely to be driven by extrinsic factors such as local and landscape-level characteristics (Rosenberg & Raphael, 1990; Murcia, 1995; Hawrot & Niemi, 1996; Lawrence & Bierregaard, 1997; Woodroffe & Ginsberg, 1998; Lomolino & Perault, 2000; Lomolino & Weiser, 2001). MacArthur & Wilson (1967) referred to the lack of significant species-area relationships on small islands, as “small island effects.”

Previous studies of vertebrates inhabiting true islands, or archipelagoes of naturally and anthropogenically fragmented forests revealed that species richness and composition of these communities may be strongly influenced by, not just area and isolation, but by local habitat characteristics of the fragments, and by differences in the intervening waters or habitats separating the focal ecosystems (Lomolino, 1994; Songer et al., 1997; Davis et al., 1988; Lomolino et al., 1989; Lomolino & Perault, 2000; Perault & Lomolino, 2000; Lomolino et al., 2001; see also Rosenberg & Raphael, 1990; Donovan et al., 1997; Aberg et al., 1995; Murcia, 1995; Hawrot & Niemi, 1996; Lawrence & Bierregaard, 1997; Woodroffe & Ginsberg, 1998; Fox & Fox, 2000).

The purpose of this study is to test the hypothesis that archipelagoes of prairie dog towns function as traditional insular communities. Specifically, we test the following predictions for birds inhabiting black-tailed prairie dog towns in the Oklahoma Panhandle: (1) species richness of birds should increase with town area, but decrease with town isolation; (2) species richness of birds should not be significantly correlated with local habitat characteristics or with characteristics of the adjacent landscape. Given this size of towns in our system, “small island effects” might be apparent. If so, the predictions given above would be reversed and we would not expect species richness to be correlated with area and isolation, but would expect correlations with local and landscape-level variables. Analyses of these patterns in community structure should provide some key insights for conserving native avian species associated with prairie dog towns.

METHODS

Study area

All field work was conducted in the Oklahoma Panhandle, which constitutes a transition zone from mixed grass prairies in the east to shortgrass prairies in the west. The Panhandle is a three county area covering 14,737 km^2 surrounded by the body of the state of Oklahoma, Kansas, Colorado, New Mexico, and Texas. Historically, much of this area was shortgrass plains dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) (Blair and Hubbell, 1938; Sims and Risser, 2000) along with dense concentrations of sand sage (*Artemisia filifolia*) in the east. Over the past two centuries, agricultural development and cattle ranching have expanded westward (see Ramankutty and Foley, 1999) across the region leaving some remnants of native prairie, fragmented prairie dog towns, and riparian corridors sparsely distributed amongst large parcels of cropland. Rocky mesas are a prominent feature of the extreme western portion of the panhandle. Precipitation and elevation gradients are noticeable as one moves from east to west in the Panhandle. Mean annual precipitation falls from approximately 60 cm in the east to 40 cm in the far west. Elevation rises from approximately 730 m in the east to 1440 m in the west. The highest point in the state of Oklahoma is found in the northwestern corner of the Panhandle on top of Black Mesa, standing 1515.8 m.

Local survey methods

Avian surveys were conducted during summer and fall of 1997, 1998, and 1999. Summer surveys were done between mid-May and early August, while fall surveys were conducted from mid-November to mid-December. Prairie dog towns were located from previous roadside surveys conducted across the panhandle region of Oklahoma (Lomolino and Smith, 2001) as well as from information from land owners and Game Wardens. Permission was obtained for every site used. During each summer we conducted avian surveys at 12 prairie dog towns resulting in 36 total dog towns over the three years combined. During each fall, we repeated surveys at half of these sites giving six prairie dog towns per fall, and 18 towns total during fall surveys. Therefore, we conducted 54 survey sessions on prairie dog towns (36 summer, 18 fall) combining all sites, years, and seasons. Prairie dog towns ranged in sized from 9.0 to 211.0 ha.

Avian surveys were conducted as variable distance line transects, using modifications of Emlen's (1971, 1977) methods (Bibby *et al.*, 1992). A transect was established on each prairie dog town with a minimum length of 300 m and a maximum length of 700 m. Birds were recorded within band widths of 10 m, 25 m, 50 m, 100 m, 150 m, and 150+ m from the center line. Each transect was walked four times, twice in the morning within 2-3 hours of sunrise and twice in the evening within 2-3 hours of sunset (216 total bird counts were performed, amassing over 110 hours of surveys). All counts were conducted by a single observer (GAS) using 10x25 binoculars, a 15x-60x spotting scope, data sheets, and a field guide. Transects were walked slowly with occasional stops such that each count lasted 30-45 min. Individual birds were recorded by sight and call to species within a specific band width from the center line. The observer was allowed to move away from the center line but the position of the individual bird was always recorded as distance from the center line and not distance from the observer. Avian densities were calculated using the program DISTANCE with the half-normal cosine detection function and all data truncated to include only observations within 150 m of the center line (Thomas *et al.*, 1998). For these analyses all observations from the four counts were combined and transect length was multiplied by four. This was done in order to reduce problems of duplicating counts of individuals, but renders our results as relative densities instead of absolute densities.

Habitat measurements were taken as point counts along each transect. Regardless of transect length, 20 stops were established along the transect. Counting the initial starting point, each transect had 21 stops. At each stop, a 10 m rope with a knot at 1 m intervals was laid perpendicular to the transect to the left and the right. Therefore, habitat measurements were taken across a 20 m line perpendicular to the center line of the transect. The center point was only counted once so at each stop there were 21 measurement points giving 441 points (21 stops x 21 points at each stop) per transect. At each point, vegetation height was recorded as <10 cm, 11-25 cm, 26-50 cm, 51-75 cm, 76-100 cm, and >100 cm. Vegetation type was also recorded at each point as grass, forb, soil, litter, cacti, yucca, cow, shrub/woody, rock, and other. For each site, vegetation was recorded as the percentage of the 441 total points within each category listed above. Along the vegetation transect, we also counted the number of burrows and noted whether they were active (currently being used by prairie dogs).

GIS and Statistical Analyses

To characterize the landscape adjacent to each town, we first used a Geographic

Information System (ArcView 3.3; ESRI, 2000) to create a 10-km buffer around each of the 36 towns we studied (this buffer approximates the maximum dispersal distance reported for this species; see Knowles, 1985). We then measured the coverage of seven dominant landcover types based on a modification of 1990 GAP imagery (Scott *et al.*, 1993). Landcover variables included deciduous forest, young agricultural crops, active agricultural crops, native grasses (warm season, C4), scrub (including some native grasses), non-native grasses (cool season, C3), and prairie dog towns (excluding the focal town). These landcover types are distinctly visible on Landsat Thematic Mapper images (Price et al., 1999). We calculated relative coverage of each landcover type as a percentage of the entire 10-km buffer that it occupied. We also recorded geographical coordinates (as meters easting and northing) of each of the 36 focal towns from the GIS imagery.

We used SYSTAT (version 11) and SigmaStat (version 3.1) (Systat Software, Inc. 2004) for all non-ordination analyses as well as XLSTAT-Pro (version 2007) for ordinations (Addinsoft, 2007). Correlations between avian richness and abundance and local and landscape variables were performed with simple, pairwise Pearson Product Moment Correlation analysis or Spearman Rank Order Correlation, depending on the normality of the variables (tested with Kolmogorov-Smirnov normality tests).

We used canonical correspondence analysis (CCA) to investigate and visualize how distributions of birds varied along geographic gradients, and with local and landscape-level environmental variables. CCA is a unimodal, direct gradients ordination method used to visualize and evaluate the relationships between species and environmental data. It constructs linear combinations of environmental variables along which species distributions are maximally separated. For summer birds, we restricted our CCA to only those species that occurred in at least four of the 36 prairie dog towns studied, leaving 12 species in the analyses (Table 1). Because fall diversity was lower, in order to increase the number of species used in the CCA, we included some species that were recorded incidental to the standardized point counts. To do this, we added 0.01 to the density values for all birds that were sighted on a prairie dog town. This increased the number of birds available for fall analyses from three to eight (Table 1).

RESULTS

General results

Thirty-six prairie dog towns were surveyed across the three county Panhandle area. Town size ranged from 9.0 to 211.0 ha and increased significantly east to west ($R_p = 0.487$, $P = 0.002$; Fig. 1) but not south to north ($R_p = 0.244$, $P = 0.151$). Thirty-six species of birds were detected on prairie dog towns during our surveys (29 during summer and 13 during fall). Mean richness of dog towns during summer was 9.5 bird species per town (range = 5 to 16). This number fell to 5.7 birds per town during fall (range = 2 to 9). Across all seasons, there were 4,992 individual observations (2,817 observations during summer and 2,175 observations during fall). Typical of these grassland communities, horned larks (*Eremophila alpestris*) and meadowlarks (eastern and western combined, *Sturnella* spp.) accounted for 66.1% of all summer detections, while horned larks alone accounted for 68.0% of fall detections (Kantrud and Kologiski, 1982; Knopf, 1996). None of the species used in our analyses exhibited significant differences in relative density across years (see Chapter 2), thus we combined seasonal data across years. We conducted separate analyses of summer and fall surveys.

Richness as a function of biogeographic variables

During summer, species richness of birds was not significantly correlated with town area (R_p = -0.064, P = 0.709; Fig. 2) or isolation (R_s = -0.252, P = 0.139; Fig. 3). Species-area regression using the power model (log(S) vs. log(A)) also produced non-significant results (F = 0.598, P = 0.445). There was, however, a significant geographic trend in avian species richness across the Panhandle. Richness increased significantly from west to east (R_p = -0.473, P = 0.004; Fig. 4). There was no significant northing trend (R_p = -0.124, P = 0.470; Fig. 4). Results from fall surveys were similar, yielding no significant correlations between richness and town area (R_p = -0.059, P = 0.817; Fig. 5) or isolation (R_s = 0.417, P = 0.085; Fig. 6). During fall, there were also no significant correlations with geographic variables: easting (R_p = -0.124, P = 0.623), northing (R_p = 0.061, P = 0.809).

Richness as a function of local and landscape level variables

During summer, avian richness on prairie dog towns was significantly correlated with only one local environmental variable. Richness increased significantly with % forb coverage on towns (R_p = 0.371, P = 0.026; Fig. 7). None of the remaining local environmental variables (vegetation height, vegetation type, or number or activity of prairie dog burrows) were significantly correlated with richness. Likewise, of all of the geographic and landscape variables tested, only one was significantly correlated with avian richness. Richness increased significantly with area of scrub habitat within 10 km of the focal town ($R_s = 0.367$, $P = 0.028$; Fig. 7). During fall, none of the local characteristics we recorded at each town was significantly correlated with species richness. However, one landscape variable was negatively correlated with richness. Richness decreased significantly as the area covered by non-native grasses increased ($R_p = -0.473$, $P = 0.046$; Fig. 8).

Geographic gradients in local habitat, land cover, and species distributions

Analyses of variation in species composition and environmental variables (local and landscape variation) among prairie dog towns are reported here only for summer surveys. Fall data showed no significant relationships among or between these variables. Canonical correspondence analyses indicated that 64.84% of the species-environmental variance was explained by the first two canonical axes (McCune & Grace, 2002). Permutation tests (1000 iterations) of species and environmental matrices yield a Pseudo-F of 1.658 ($P = 0.002$). The resulting ordination plot (Fig. 9) illustrates geographical gradients in landscape level variables, local habitat conditions, and species distributions across our study area. Several gradients emerge from this ordination. Along a strong north-westward gradient, size of prairie dog towns increased, the relative cover of grass on our sites increased, but relative cover of forbs decreased. Along this gradient, percent cover of non-native grasses surrounding the study sites increased while percent cover of native grasses and scrub decreased. Incidence of horned lark and brown-headed cowbird increased along this gradient while grasshopper sparrow, meadowlark, and mourning dove showed an opposite trend. There was no distinct gradient north to south. This makes sense given that the panhandle is much longer (267.1 km) than it is wide (56.3 km).

In order to investigate relationships among habitat characteristics, landscape variables, and species without the influence of the strong geographic gradient, we partialled out the easting and northing variables and ran the analysis again. Without the geographic gradient, 56.70% of the species-environmental variance was explained by the first 2 canonical axes. Permutation tests (1000 iterations) of species and environmental matrices yield a Pseudo-F of 1.056 ($P < 0.0001$). The resulting ordination plot (Fig. 10) illustrates relationships between landscape level variables, local habitat conditions, and species distributions on our study sites. Here we can see two major gradients in the data. The first is a local habitat gradient, along a grass-forb axis. As grass cover increases on prairie dog towns, forb cover decreases. Horned larks once again show a strong trend toward sites with increased grass cover (and therefore decreased forb cover). Meadowlark and grasshopper sparrow show higher incidence with increasing forbs. The second gradient is at the landscape level. This is an axis of increasing grass (native and non-native) and crops surrounding prairie dog towns on one end to increasing scrub and area of additional prairie dog towns on the other. Killdeer, brown-headed cowbird, and lark sparrow show higher abundance at prairie dog towns surrounded by increasing scrub and other towns, while scissor-tailed flycatcher, mourning dove, and burrowing owl show an affinity to towns surrounded by increasing amounts of grass and crop.

DISCUSSION

The results of this study are not consistent with predictions based on traditional island biogeography theory. Avian richness was not significantly correlated with area (summer, Fig. 2; fall, Fig. 5) or isolation (summer, Fig. 3; fall, Fig. 6) of prairie dog towns. However, these observations were consistent with “small island effects” (Losos & Schluter, 2000; Crawley & Harral, 2001; Lomolino & Weiser, 2001). The general form of the species-area relationship may be sigmoidal, with richness remaining relatively low and varying independently of area on smaller islands (Lomolino, 2000a, b, c; Lomolino & Weiser, 2001; Lomolino, 2003). Therefore, the structure of native communities on small islands may be more strongly influenced by differences among local or landscape level factors than by simple measures of area and isolation. This was, in fact, true for our data. Avian richness was significantly correlated with a local habitat variable (percent coverage by forbs) and a landscape variable (area within 10 km of the focal town occupied by scrub habitat) for summer surveys (Fig. 7). Although local variables did not influence fall birds, one landscape variable was significantly correlated with richness (area within 10 km of the focal town occupied by non-native grass habitat) (Fig. 8). Further, the distribution of birds across the Panhandle was significantly linked to gradients of both local habitat characteristics and landscape variables (Fig. 9 and Fig. 10). These results are similar to our studies of nonvolant terrestrial vertebrates (Lomolino & Smith, 2003). This is interesting given that the increased vagility of birds can alter the way birds use the landscape compared to vertebrates that are less mobile (Schoener, 1976). This was not the case. In fact, birds responded more strongly to local and landscape variables than did mammals, reptiles, or amphibians.

The results presented here provide some important insights for conservation of avian communities associated with prairie dog towns. As towns continue to become smaller and more isolated, "small-island effects" are likely to become much more prevalent and focusing simply on the towns themselves will not be an effective strategy for conservation of associated species. Effective conservation of avian communities on towns as small as those we studied will, therefore, require effective management of entire landscapes, and not just the limited archipelago of pristine systems. Yet, even the relatively small towns we studied should continue to serve as key habitats within the landscape, providing important resources for many species dependent on the resources of a prairie dog town.

Area and isolation of prairie dog towns should not be ignored in conservation strategies, however. Even though richness of birds was not significantly correlated with area or isolation for the towns we studied, other studies in this region have shown that, over time, large towns and more isolated towns were most likely to persist (Lomolino & Smith, 2001). While town size and isolation may be a poor predictor of current levels of richness for a range of relatively small towns, they are not irrelevant measures for conservation of these ecosystems and their associated communities. Large towns are more likely to buffer populations of prairie dogs and town associates against the vagaries of small population sizes, while more isolated towns can protect prairie dogs in the face of a plague (*Yersinia pestis*) (see Cully & Williams, 2001). Therefore, biogeographic characteristics of the towns themselves may be more important for prairie dogs, while local “island” habitat and landscape-level characteristics of the surrounding habitat matrix might be more relevant for other grassland species. As such, a mixed, adaptive, strategy for conserving prairie dog ecosystems should be the best approach. We recommend a network of native prairie reserves strategically located across the historic range of this species. The networks should be comprised of complexes of large towns, as well as large, but isolated towns. Large size and increased isolation are good predictors of town persistence in this area (Lomolino and Smith, 2001). Finally, significant geographic trends in avian richness (Fig. 4) can help prioritize complex building. The eastern portion of the Panhandle region is being rapidly altered for agricultural purposes. The prairie dog towns in this area are small and isolated (Fig. 1) but still maintain high avian diversity. Taken together, these results indicate that conservation of these native grassland ecosystems and their imperiled biota may rely heavily on our abilities to conserve and encourage the restoration of large complexes of towns, and to manage effectively the intervening matrix of natural and anthropogenic habitats.

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Table 1. Avian species included in canonical correspondence analyses. We provide the bird's four-letter identification code, common and Latin name, and indicate if the bird was included in the summer analyses, fall analyses, or both. All surveys were conducted on 36 different black-tailed prairie dog towns in the Oklahoma Panhandle during 1997, 1998, and 1999.

Identification Code	Species	Summer	Fall
Amke	American Kestrel (*Falco sparverius*)		X
Bhco	Brown-headed Cowbird (*Molothrus ater*)	X	
Buow	Burrowing Owl (*Athene cunicularia*)	X	
Cclo	Chestnut-collared Longspur (*Calcarius ornatus*)		X
Feha	Ferruginous Hawk (*Buteo regalis*)		X
Goea	Golden Eagle (*Aquila chrysaetos*)		X
Grsp	Grasshopper Sparrow (*Ammodramus savannarum*)	X	
Hola	Horned Lark (*Eremophila alpestris*)	X	X
Kill	Killdeer (*Charadrius vociferus*)	X	
Lalo	Lapland Longspur (*Calcarius lapponicus*)		X
Lasp	Lark Sparrow (*Chondestes grammacus*)	X	
Mead	Meadowlarks (*Sturnella sp.*)	X	X
Modo	Mourning Dove (*Zenaida macroura*)	X	
Nofl	Northern Flicker (*Colaptes auratus*)	X	
Noha	Northern Harrier (*Circus cyaneus*)		X
Stfl	Scissor-tailed Flycatcher (*Tyrannus forficatus*)	X	
Upsa	Upland Sandpiper (*Bartramia longicauda*)	X	
Weki	Western Kingbird (*Tyrannus verticalis*)	X	

Figure Legends:

Figure 1. Area of prairie dog towns surveyed as a function of easting. Town area decreases significantly from west to east (R_p=0.487, P=0.002).

Figure 2. Species richness of birds during summer surveys as a function of size of black-tailed prairie dog towns in the Oklahoma Panhandle. This relationship is not significant (R_p=-0.064, P=0.709).

Figure 3. Species richness of birds during summer surveys as a function of cover of other black-tailed prairie dog towns (an inverse measure of isolation) within 10 km of the focal town. This relationship is not significant (R_s=-0.252, P=0.139).

Figure 4. Geographic trend in species richness for birds at black-tailed prairie dog towns in the Oklahoma Panhandle. Locations of each point approximates the location of that prairie dog town in real space. Richness increases significantly from west to east across the panhandle (R_p=-0.473, P=0.004). There was no significant northing trend (R_p=-0.124, P=0.470).

Figure 5. Species richness of birds during fall surveys as a function of size of black-tailed prairie dog towns in the Oklahoma Panhandle. This relationship is not significant (R_p=-0.059, P=0.817).

Figure 6. Species richness of birds during fall surveys as a function of cover of other black-tailed prairie dog towns (an inverse measure of isolation) within 10 km of the focal town. This relationship is not significant (R_s=0.417, P=0.085).

Figure 7. Species richness of birds during summer surveys as a function of a local environmental variable on prairie dog towns and a landscape variable around

prairie dog towns. Richness increases significantly with forb coverage on prairie dog towns (Rp=0.371, p=0.0263). Richness also increases significantly with area of scrub habitat within 10 km of the focal town (R_s=0.367, P=0.028).

Figure 8. Species richness of birds during fall surveys at prairie dog towns as a function of cover of pasture grasses within 10 km of the focal town. Richness decreases significantly as the area covered by pasture grasses around prairie dog towns increases (R_p=-0.473, P=0.046).

Figure 9. Ordination of local habitat characteristics (red arrows), percent cover by dominant vegetation types within 10 km of a focal prairie dog town (green arrows), and geographic gradients (blue arrows) for summer bird surveys in the Oklahoma Panhandle. See Table 1 for a description of species codes.

Figure 10. Ordination of local habitat characteristics (red arrows) and percent cover by dominant vegetation types within 10 km of a focal prairie dog town (green arrows), with geographic gradients partialled out, for summer bird surveys in the Oklahoma Panhandle. See Table 1 for a description of species codes.

Figure 1

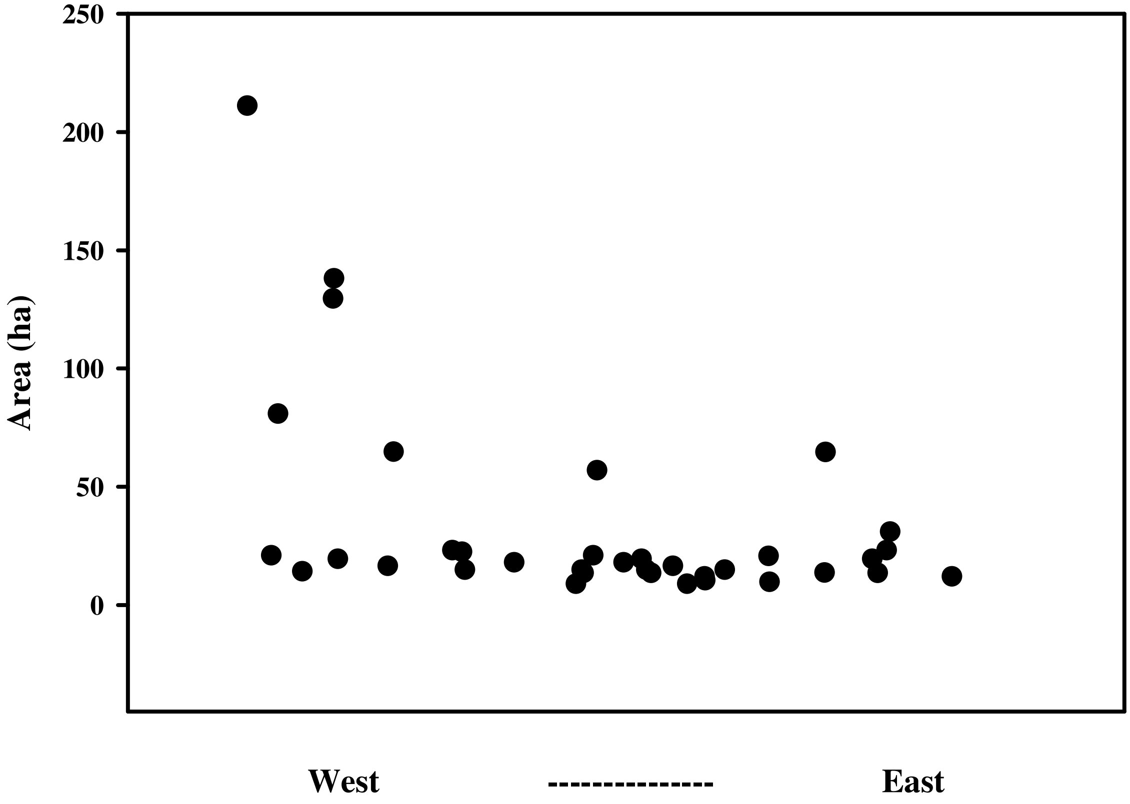


Figure 2

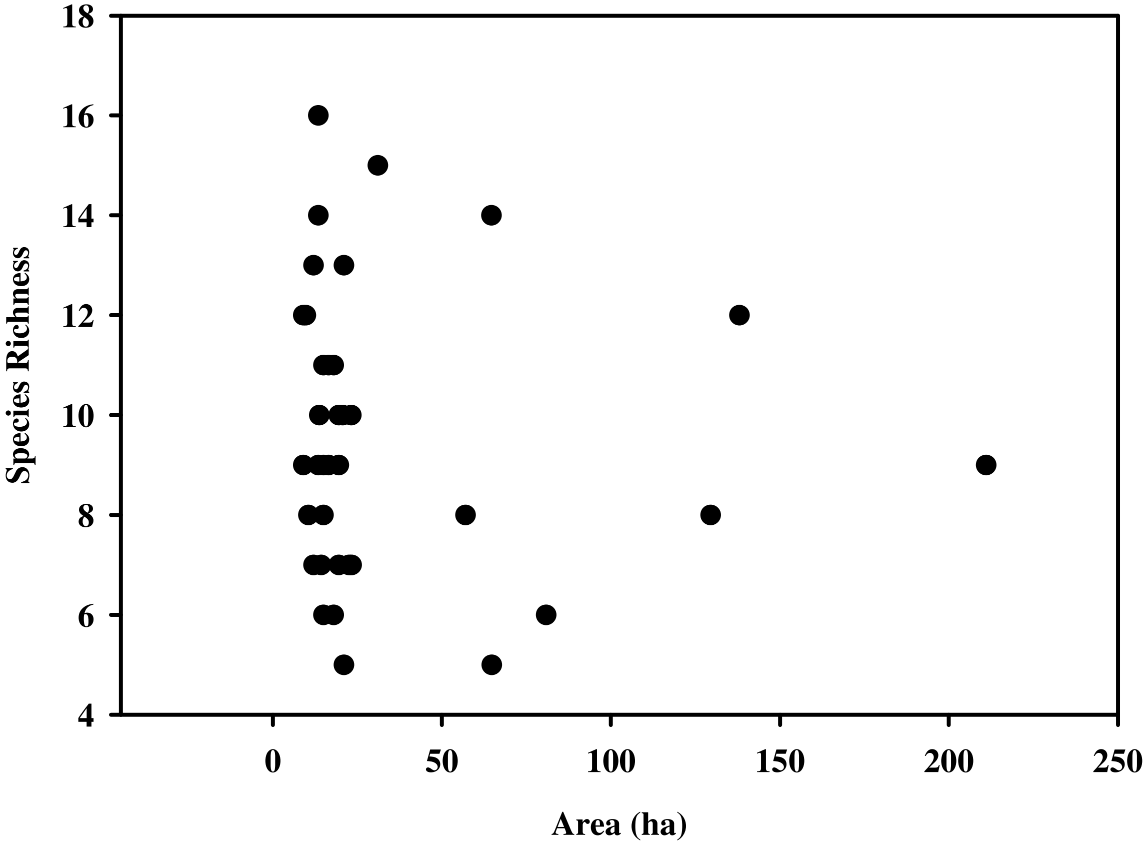
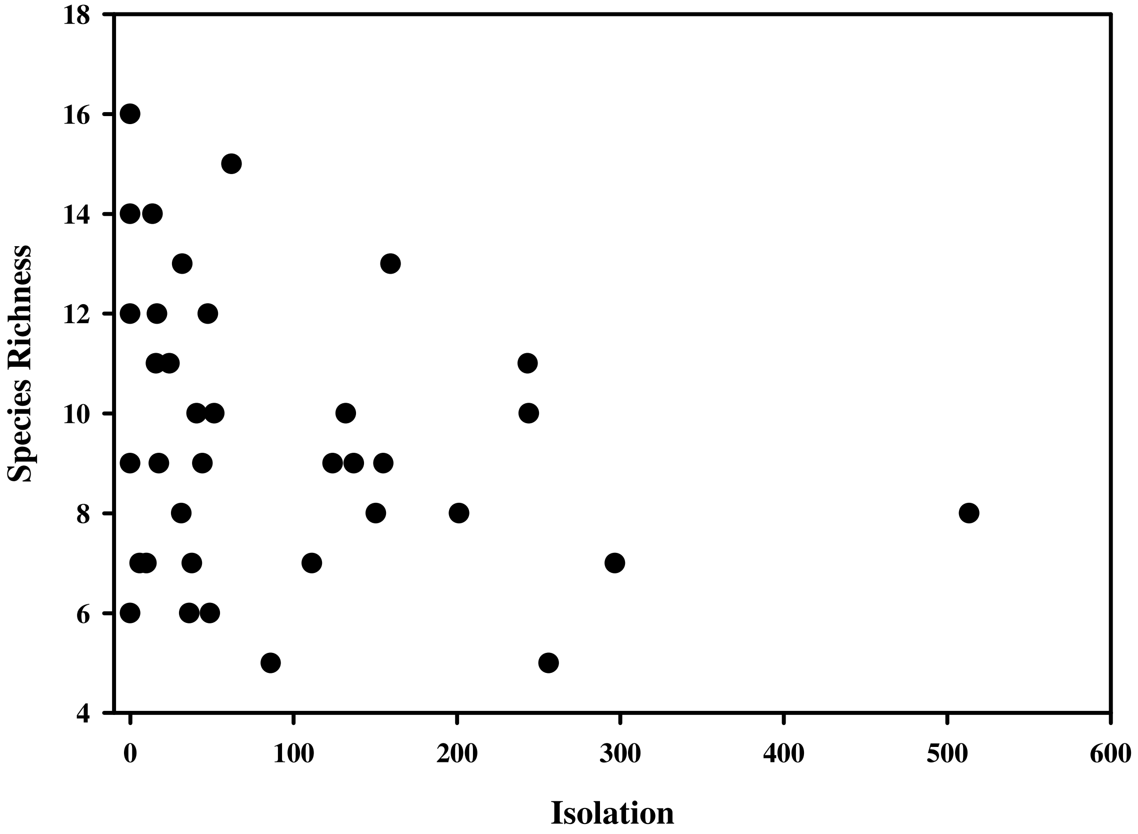
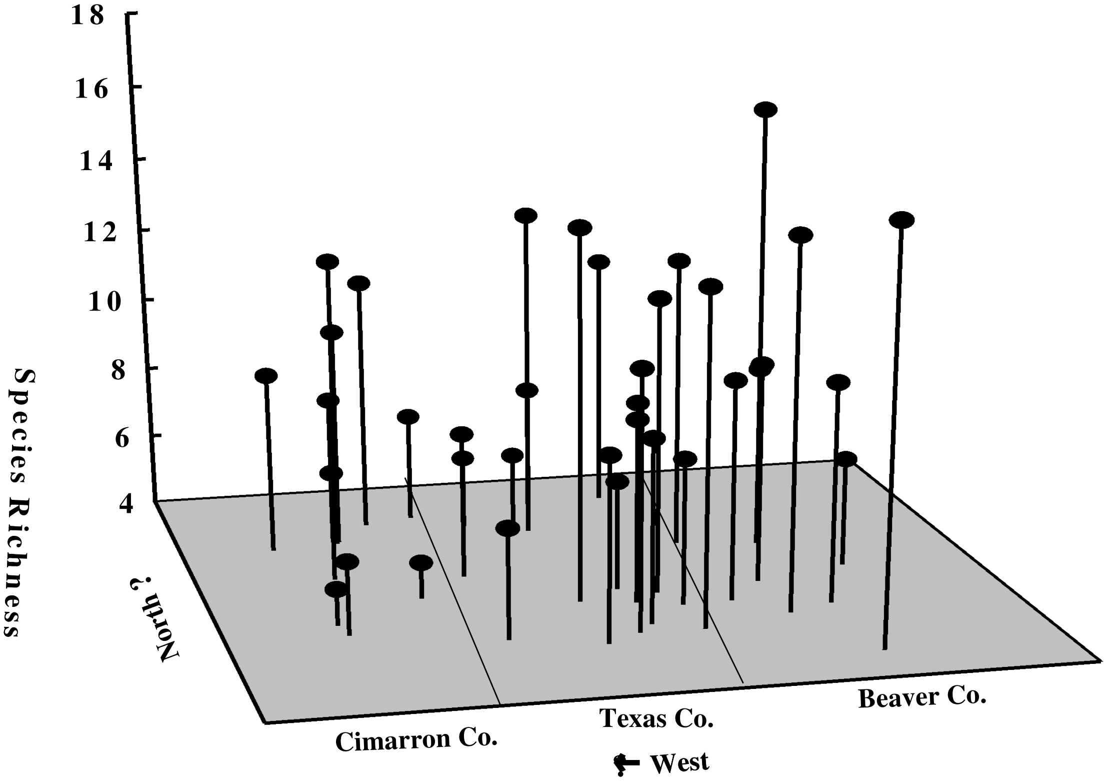


Figure 3



Species Richness
18
16
14
12
10
8
6
4
0
100
200
300
400
500
600
Isolation

Figure 4



Species Richness
18
16
14
12
10
8
6
4
North ?
Cimarron Co.
Texas Co.
Beaver Co.
← West

Figure 5

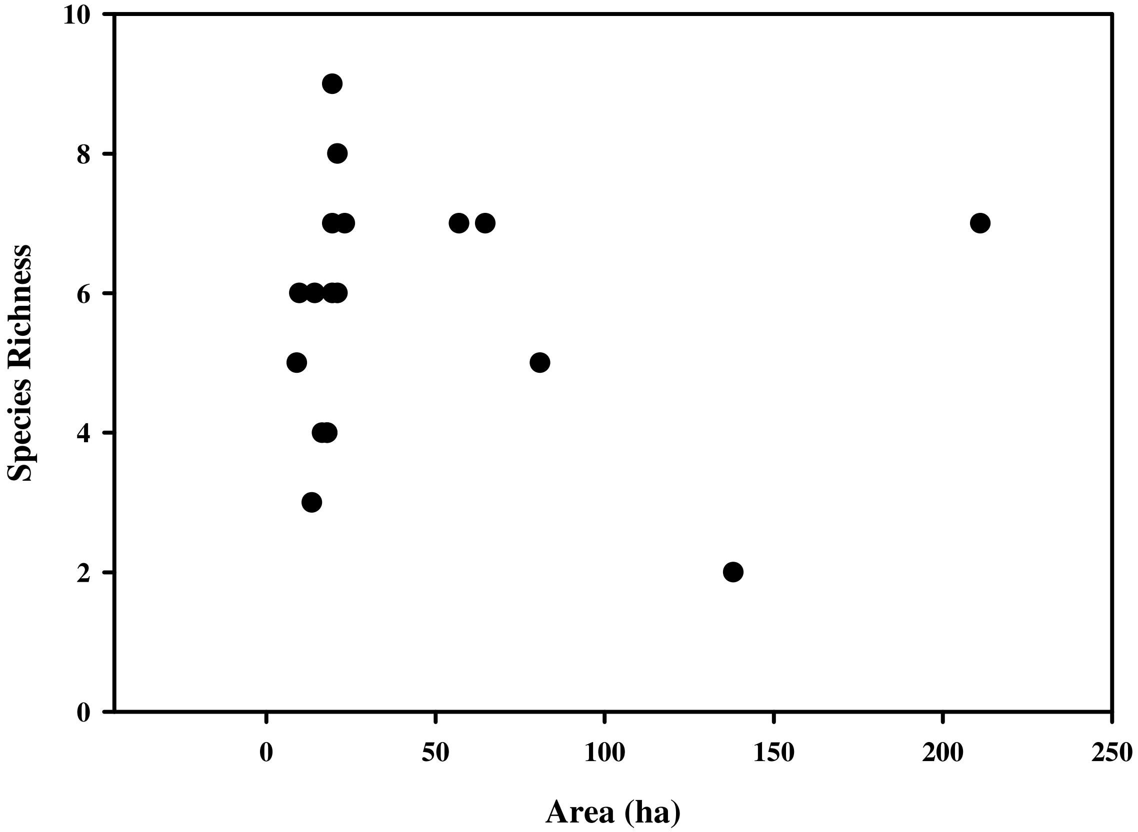


Figure 6

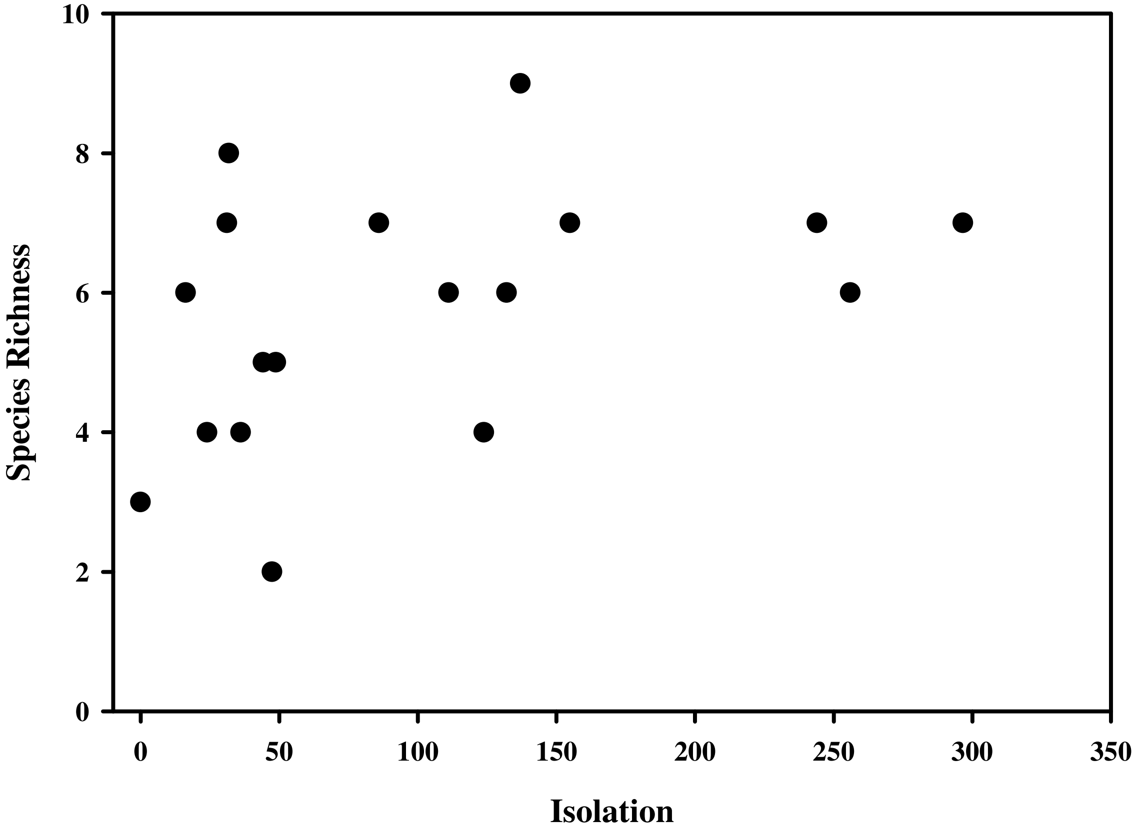

10
8
6
4
2
0
Species Richness
0
50
100
150
200
250
300
350
Isolation

Figure 7

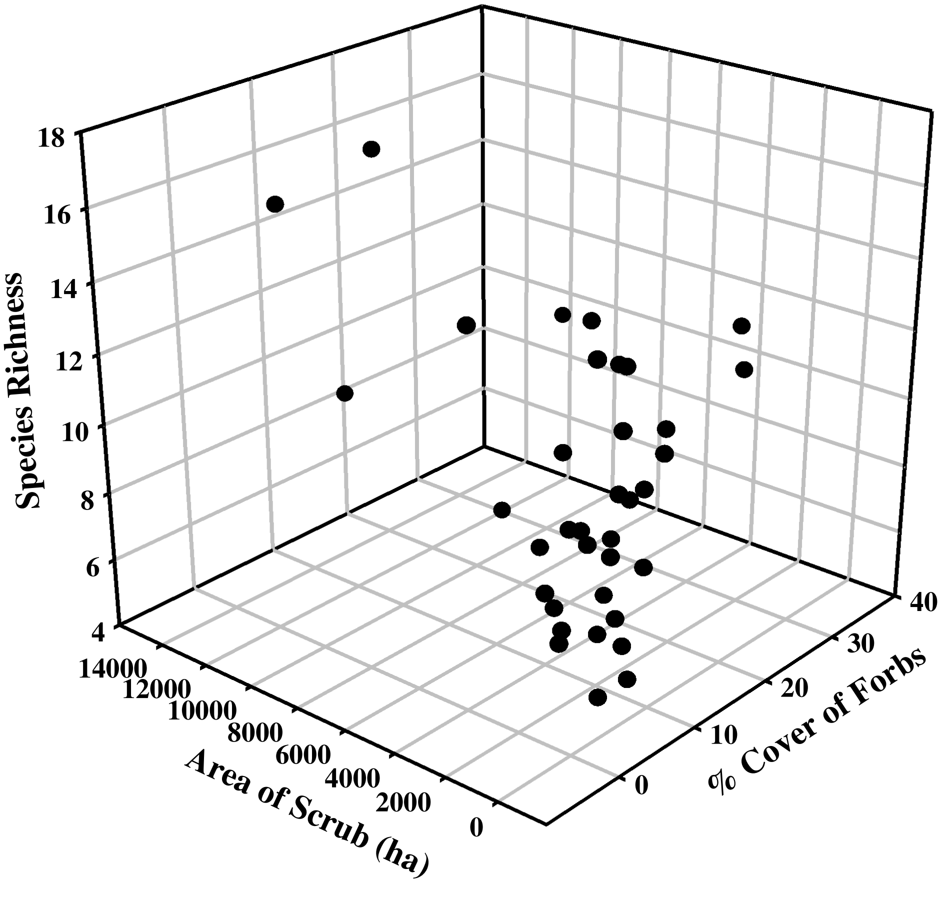

Species Richness
18
16
14
12
10
8
6
4
Area of Scrub (ha)
14000
12000
10000
8000
6000
4000
2000
0
% Cover of Forbs
0
10
20
30
40

Figure 8

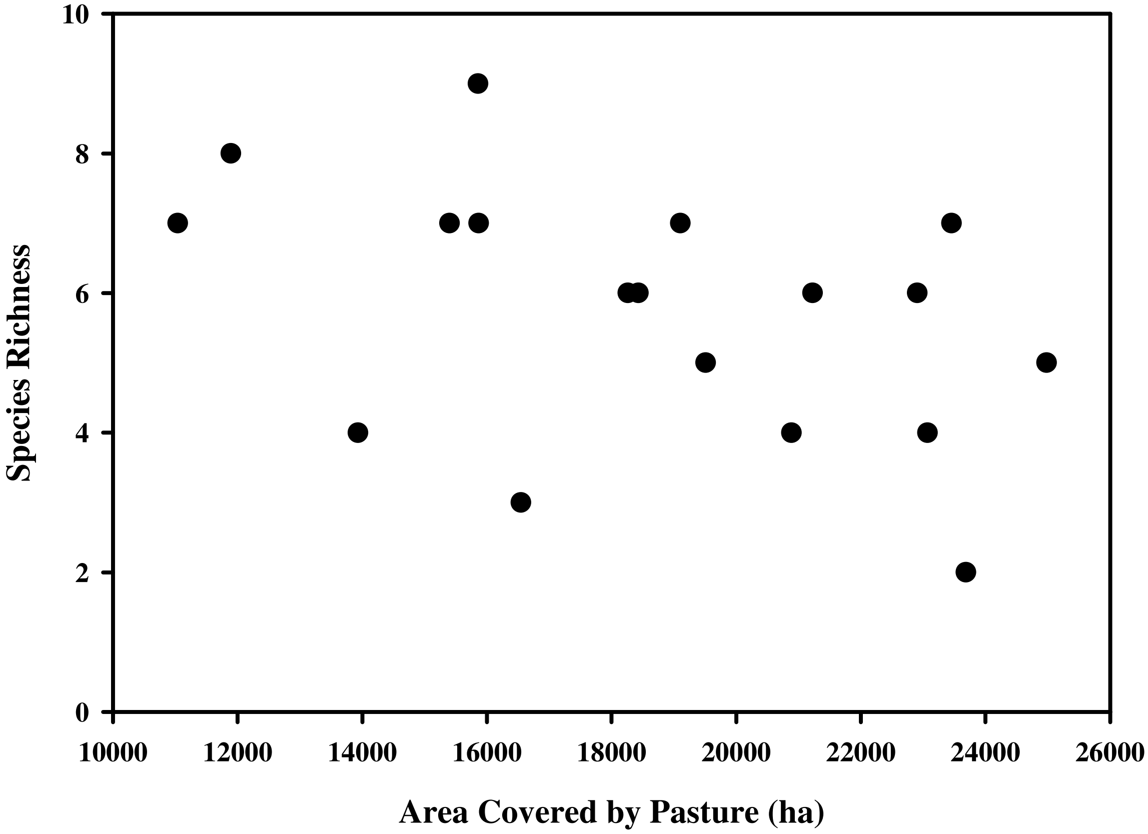

Species Richness
0
2
4
6
8
10
10000
12000
14000
16000
18000
20000
22000
24000
26000
Area Covered by Pasture (ha)

Figure 9

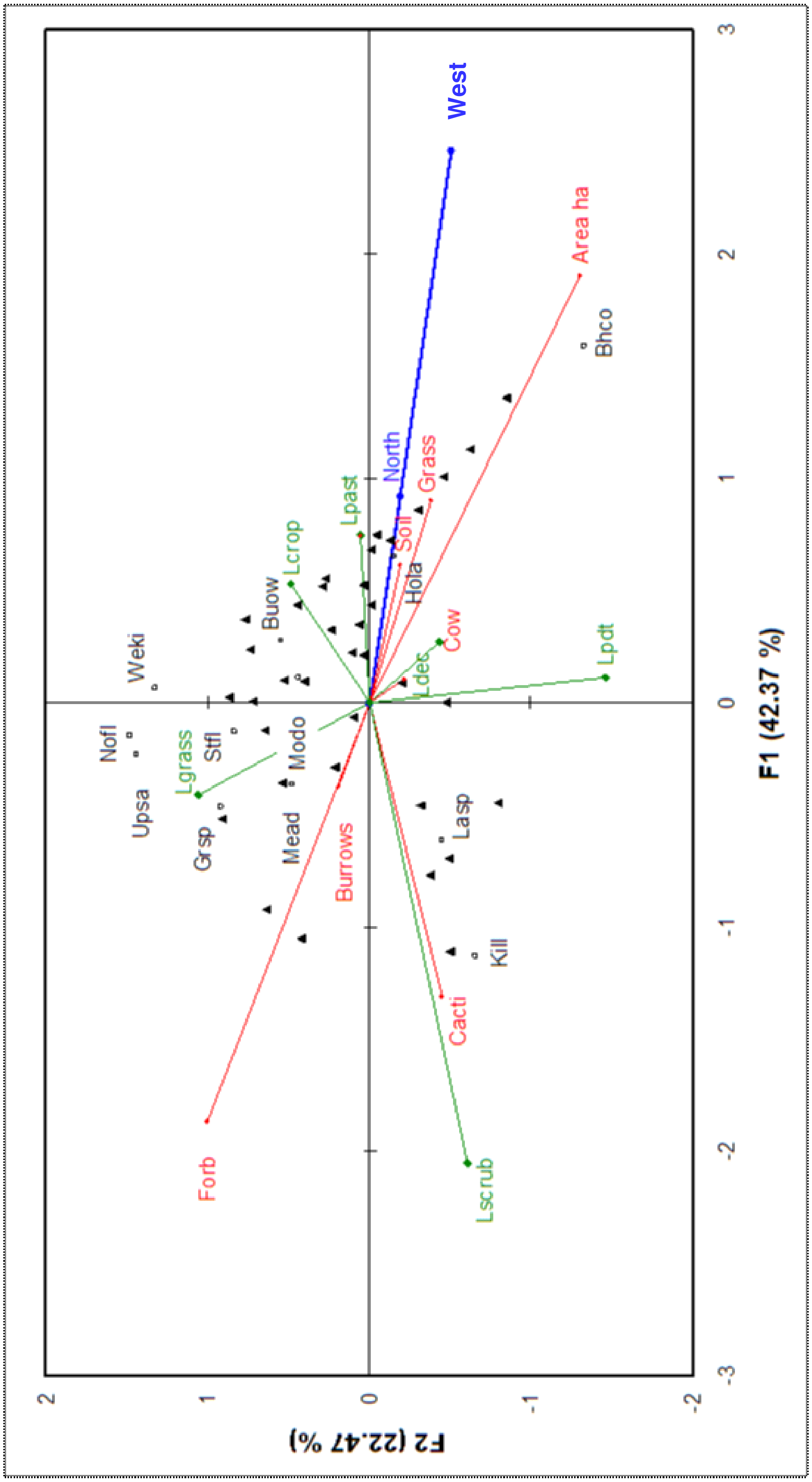
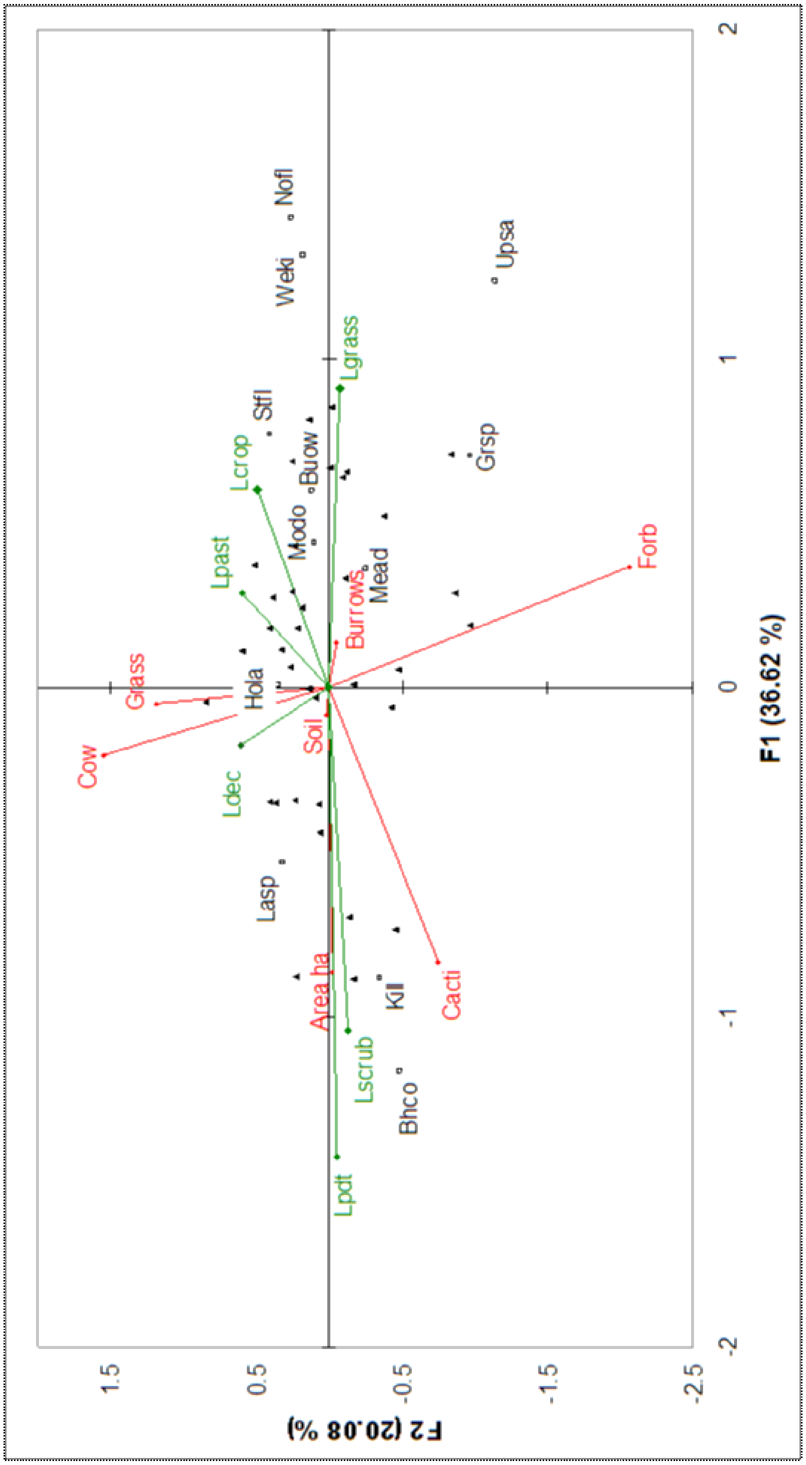

West
Area ha
Bhco
North
Grass
Soil
Lpast
Hola
Lcrop
Buow
Cow
Weki
Ldec
Lpdt
Nofl
Stfl
Lgrass
Modo
Upsa
Mead
Grsp
Burrows
Lasp
Kill
Cacti
Forb
Lscrub
F1 (42.37 %)
F2 (22.47 %)
3
2
1
0
-1
-2
-3
2
1
0
-1
-2

Figure 10


F1 (36.62 %)
F2 (20.08 %)
2
1
0
-1
-2
1.5
0.5
-0.5
-1.5
-2.5
Nofl
Weki
Upsa
Lgrass
Stfl
Lcrop
Buow
Grsp
Modo
Lpast
Mead
Burrows
Forb
Grass
Hola
Cow
Soil
Ldec
Lasp
Area ha
Kil
Cacti
Lscrub
Bhco
Lpdt