

Response of mountain plovers to plague-driven dynamics of black-tailed prairie dog colonies

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Abstract Sylvatic plague is a major factor influencing the dynamics of black-tailed prairie dog (*Cynomys ludovicianus*) colonies in the western Great Plains. We studied the nesting response of the mountain plover (*Charadrius montanus*), a grassland bird that nests on prairie dog colonies, to plague-driven dynamics of prairie dog colonies at three sites in the western Great Plains. First, we examined plover nest distribution on colonies that were previously affected by plague, but that had been recovering (expanding) for at least 6 years. Plovers consistently nested in both young (colonized in the

past 1–2 years) and old (colonized for 6 or more years) portions of prairie dog colonies in proportion to their availability. Second, we examined changes in plover nest frequency at two sites following plague epizootics, and found that mountain plover nest numbers declined relatively rapidly (≤ 2 years) on plague-affected colonies. Taken together, our findings indicate that available plover nesting habitat associated with prairie dog colonies closely tracks the area actively occupied by prairie dogs each year. Given the presence of plague throughout most of the mountain plover's breeding range in the western Great Plains, important factors affecting plover populations likely include landscape features that determine the scale of plague outbreaks, the distance that plovers move in response to changing breeding habitat conditions, and the availability and quality of alternate breeding habitat within the landscape.

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Introduction

The role that black-tailed prairie dogs (*Cynomys ludovicianus*) play in sustaining the biodiversity of

the western Great Plains has been the subject of considerable controversy and research (Vermiere et al. 2004; Forrest 2005; Hoogland 2006). Prior to European settlement, black-tailed prairie dogs were a widespread and abundant component of the grazing regime in landscapes of central North America. Black-tailed prairie dogs (prairie dogs hereafter) maintained a broad geographic range during the late Pleistocene, and expanded into their current distribution around the onset of the Holocene (Goodwin 1995). Numerous plant and animal species of the western Great Plains exhibit adaptations to the resources and conditions provided by prairie dog colonies (Kotliar et al. 1999; Lomolino and Smith 2003; Smith and Lomolino 2004; Kotliar et al. 2006). In recent decades, declining populations have been documented for some species that rely to varying degrees on prairie dog colonies for habitat (Miller et al. 1996; Desmond et al. 2000; Knopf and Wunder 2006).

Plague caused by the bacterium *Yersinia pestis*, a disease introduced from Asia, is currently a major factor regulating the distribution and abundance of prairie dogs (Cully and Williams 2001; Collinge et al. 2005; Antolin et al. 2006). Prairie dogs have only been exposed to plague for approximately 60 years, and have not evolved resistance to this highly virulent pathogen (Cully et al. 2006). Epizootic plague outbreaks cause rapid and nearly complete mortality within a colony (Cully and Williams 2001; Pauli et al. 2006). In landscapes with a high degree of connectivity among colonies, epizootic plague can decimate colonies distributed over a large geographic area (e.g. >100,000 ha) in a single year (Collinge et al. 2005; Johnson 2005; Augustine et al. 2008). In contrast, in landscapes with greater inter-colony distances and higher densities of roads and water bodies, epizootic plague may only affect colonies distributed across smaller areas within a year (Stapp et al. 2004; Collinge et al. 2005). Epizootic plague outbreaks can induce dramatic fluctuations in the abundance of prairie dogs, and can reoccur within a locality at intervals of 6–15 years (Stapp et al. 2004; Hartley 2006; Cully et al. 2006; Augustine et al. 2008). If prairie dogs are indeed important to sustaining the biodiversity of shortgrass and mixed prairie landscapes, then we need to understand how species that use prairie dog colonies for habitat are influenced by the

spatiotemporal dynamics of prairie dog colonies affected by plague.

In grasslands of the Great Plains, breeding habitat for the mountain plover (*Charadrius montanus*) is associated with prairie dog colonies, heavy grazing by large ungulates, or recent fire (Dinsmore 2003; Knopf and Wunder 2006). In the shortgrass steppe, plovers can nest in grassland without prairie dogs (Knopf and Miller 1994), but occurred at 10 times greater density on prairie dog colonies compared to non-colonized rangeland in 2005 (Tipton 2007). In the more productive northern mixed prairie, plovers nest almost exclusively on prairie dog colonies (Olson and Edge 1985; Dinsmore et al. 2005). Plague occurs throughout most of the breeding range of the mountain plover (Fig. 1), such that plague effects on

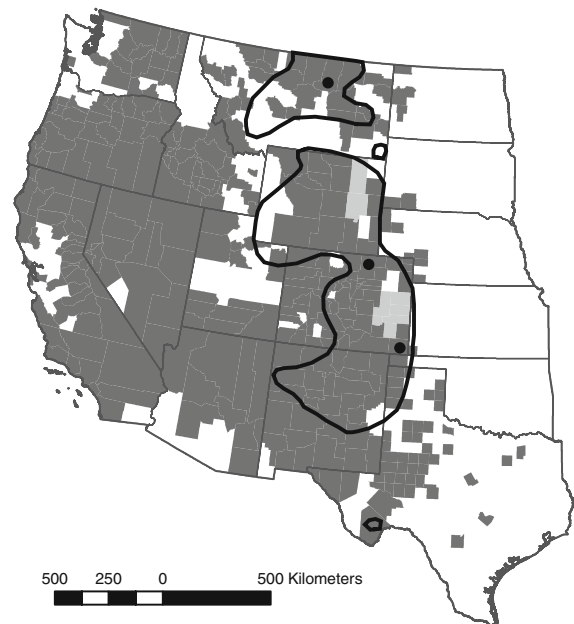


Fig. 1 Map showing the U.S. portion of the breeding distribution of mountain plovers (solid black outline, from Knopf and Wunder (2006)) and U.S. counties where evidence of plague has been documented in the western United States. The distribution of counties with plague is based on records from the Center for Disease Control and Prevention, Fort Collins, CO (dark grey shading) and observations of large-scale prairie dog mortality due to apparent plague in eastern Colorado (light grey shading; V. Dreitz, *personal observation*) and eastern Wyoming (light grey shading; Johnson 2005). The white background shows counties with no documented evidence of plague. Black dots show the Phillips County study area in north central Montana, the Pawnee study area in northern Colorado, and the Comanche study area in southeast Colorado

prairie dog colony dynamics, and the potential consequences for vegetative conditions, may have significant implications for mountain plovers.

Increasing length of prairie dog occupancy at a site can lead to progressive reductions in tall-structure grasses, and increased abundance of forbs and subshrubs (Coppock et al. 1983; Archer et al. 1987). In shortgrass steppe, plague can alter prairie dog effects on the plant community by reducing differences in vegetative cover, biomass and species composition between colonized and uncolonized sites (Hartley 2006). Observations of plover nesting activity on a plague-affected prairie dog colony in the same area studied by Hartley (2006) documented a rapid decline in the number of plover nests 1–2 years after a plague outbreak, and only a small increase in the number of plover nests after the colony had returned to its pre-plague size (Fig. 2). This suggested that after a plague event, nesting habitat for plovers may not return as quickly as the prairie dogs. Observations in mixed prairie also suggested that soon after an epizootic plague outbreak, vegetative conditions on colonies may become unsuitable for mountain plovers (Dinsmore et al. 2005). Here, we examine responses of nesting mountain plovers to plague-driven dynamics of prairie dog colonies in the shortgrass steppe of Colorado and mixed prairie of Montana. Our first objective was to evaluate the time frame in which prairie dog colonies become suitable for plover nesting as colonies recover after epizootic plague outbreaks. Our second objective was to examine the response of plover nesting activity to recent epizootic

plague outbreaks in shortgrass steppe and mixed prairie.

Study areas

Study areas and prairie dog colony surveys

Study areas consisted of (1) the Carrizo Unit of the Comanche National Grassland in Baca County, CO (Augustine et al. 2008), (2) the Pawnee National Grassland and adjacent Central Plains Experimental Range in Weld County, CO (Stapp et al. 2004), and (3) Bureau of Land Management and private lands in southern Phillips County, Montana (Dinsmore et al. 2005; Augustine et al. 2008; Table 1). On the Comanche study area, surveys of prairie dog colony boundary locations using handheld global position system (GPS) units were conducted in 1995, 1999, 2001, 2002, 2003 and 2004 (Augustine et al. 2008). Observations in 1994 and 1995 indicated that all colonies were affected by a plague epizootic that started in 1994 and continued after 1995. All colonies in the Comanche study area were expanding (i.e. boundaries of each colony encompassed a larger area in each successive year) during 1999–2004, and did not exhibit any signs of plague activity. Prairie dog colony boundaries were surveyed annually using GPS units during 1993–2006 on the Pawnee National Grassland and during 1999–2006 on the adjacent Central Plains Experimental Range. Epizootic plague affected a small proportion of colonies in this area in most years since 1981, with more extensive plague epizootics occurring in 1992 and 1999 (Stapp et al. 2004). Prairie dog colony boundaries in the Phillips County study area were surveyed using GPS units in 1993, 1995–1997, 1998, 2000, 2002 and 2004 (Augustine et al. 2008). During 1995–1997, a non-overlapping third of the colonies in the area were surveyed each year; results from these surveys were combined and are referred to hereafter as the 1996 survey. A plague epizootic was first recorded in Phillips County in 1992, when the area occupied by prairie dogs was reduced by approximately 50% (Collinge et al. 2005; M. R. Matchett, unpublished data), and declines continued through 1996. Most colonies in the study area were expanding during 1996–2002, and a portion of the colonies were affected by a plague epizootic during 2002–2004.

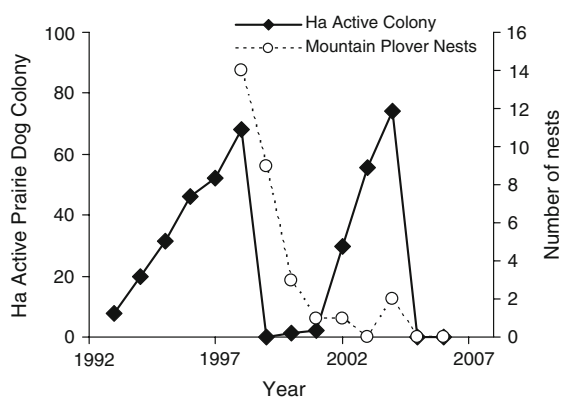


Fig. 2 Changes in number of mountain plover nests located on a plague-affected prairie dog colony during 1998–2006 on the Pawnee National Grassland, Colorado

Table 1 Summary of study sites in the western Great Plains where we examined the distribution of mountain plover nests in relation to the history of black-tailed prairie dog distribution

Ecosystem	Mean annual precipitation (mm)	Dominant vegetation ^a		Site	Year of nest survey	Number of mountain plover nests	Number of prairie dog colonies
		On colonies	Off colonies				
Shortgrass steppe	403	<i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i> , <i>Aristida purpurea</i>	<i>Bouteloua curtipendula</i> , <i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i>	Comanche National Grassland, CO	2005	24	10
Shortgrass steppe	322	<i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i> , <i>Sphaeralcea coccinea</i>	<i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i> , <i>Carex eleocharis</i>	Pawnee National Grassland, CO	2003–2007	20	6
Mixed prairie	320	<i>Artemisia frigida</i> , <i>Bouteloua gracilis</i> , <i>Pascopyrum smithii</i>	<i>Artemisia tridentata</i> , <i>Bouteloua gracilis</i> , <i>Pascopyrum smithii</i>	Phillips County, MT Phillips County, MT	2003 2005	114 76	22 15

^a From Winter et al. (2002), Johnson-Nistler et al. (2004), and Hartley (2006)

Mountain plover surveys

We surveyed mountain plovers on prairie dog colonies by systematically driving a vehicle slowly across each colony and periodically stopping to scan for plovers. We watched individual adult birds from a distance until they returned to a nest, and recorded the geographic coordinates of the nest. In the Comanche study area, we surveyed mountain plovers on 10 prairie dog colonies ≥ 2 times during May of 2005. A plague epizootic during 2006 affected all of this study area. In late April of 2007, we conducted a single systematic survey at four colonies that had the highest nest densities in 2005. In the Pawnee study area, we surveyed prairie dog colonies for mountain plovers during 2003–2007, as part of long-term studies on plover ecology (Wunder 2007; Dreitz and Knopf 2007). Colonies were surveyed ≥ 2 times during May–June of each year. In the Phillips County study area, we systematically searched active prairie dog colonies ≥ 3 times during May–July in 2003 and 2005.

Data analysis

We imported prairie dog colony boundary coordinates into a geographic information system (GIS). For the Comanche study area, we used the GIS to determine that all 10 colonies we surveyed for mountain plovers in 2005 had been expanding during 1999–2004. For the Pawnee and Phillips County study areas, we used the GIS to identify all colonies that were expanding for at least 6 years preceding a mountain plover survey.

For the analysis of plover nest distribution on expanding colonies, we calculated the area of each colony in each of three age classes: young, mid, and old. For all study areas, we define “young” portions of colonies as those areas colonized by prairie dogs only within the past 1–2 years prior to the mountain plover survey. Due to differences among sites in the timing of prairie dog colony surveys (every other year in Phillips County, no survey in 2000 for the Comanche study area), we define “mid”-aged portions of colonies as areas occupied by prairie dogs for the past 3–5 years at Comanche and Pawnee, and as areas occupied by prairie dogs for the past 3–6 years in Phillips County. Finally, we define “old” portions of colonies as areas occupied by prairie dogs for

6+ years at Comanche and Pawnee, and areas occupied by prairie dogs for 7+ years in Phillips County. The 1 year difference in colony age used to define age classes was necessary to ensure a balanced sample of age classes for each of the three sites. Because mountain plovers arrive on the breeding range in March–April of each year, which was at least several months prior to when prairie dog colonies were mapped, we used boundaries of prairie dog colonies mapped in the year prior to mountain plover nest surveys as the best measure of available plover habitat.

For each mountain plover nest, we used the GIS to determine the history of prairie dog occupancy at the nest location. We calculated the expected distribution of nests in the different occupancy classes for each individual prairie dog colony based on the total number of nests found on that colony and the area of each occupancy class on the colony. We then summed across colonies to determine the expected number of nests in each occupancy class, in order to account for variation among colonies in nest density. We used chi-squared tests ($\alpha = 0.05$) to compare the observed versus expected distribution of nests in each study area.

For the Comanche study area, we examined the distribution of 24 mountain plover nests found in 2005 on 10 prairie dog colonies encompassing 827 ha. For the Pawnee study area, we identified two colonies in 2003, one colony in 2005, one colony in 2006 and two colonies in 2007 (six different colonies) that were surveyed for mountain plovers after 6 previous years of documented colony expansion. We examined the distribution of 20 mountain plover nests on these six colonies, which encompassed 632 ha. For Phillips County, we analyzed nest distributions in 2003 and 2005 separately because a sufficiently large number of nests was sampled in each year. In 2003, we studied 114 mountain plover nests located on 22 prairie dog colonies encompassing 1,114 ha. In 2005, we studied 76 nests located on 15 prairie dog colonies encompassing 867 ha. For Phillips County in 2005, a more detailed analysis of nest distribution relative to prairie dog occupancy history was possible due to both the large sample of nests and the longer available record of prairie dog colony boundaries. For this survey, we additionally calculated the area of each colony occupied for 1–2, 3–4, 5–6, 7–8 and 9+ years.

To evaluate the influence of a recent epizootic plague outbreak in Phillips County, we also identified (1) all colonies that increased in size between 2002 and 2004, and for which at least one plover nest was documented in 2003 and/or 2005, and (2) all colonies that decreased by more than 50% between 2002 and 2004 due to apparent epizootic plague effects, and for which at least one plover nest was documented in 2003 and/or 2005. For this analysis, data were non-normally distributed so we used a Wilcoxon rank sum test ($\alpha = 0.05$) to compare the number of nests on expanding and declining colonies.

Results

Nests were found in all prairie dog colony age classes in proportion to expected distribution based on the area of each age class available for the Comanche study area ($\chi^2 = 0.08$, $df = 2$, $P = 0.96$; Fig. 3a), the Pawnee study area ($\chi^2 = 3.16$, $df = 2$, $P = 0.21$; Fig. 3b), and the Phillips County study area in 2003 ($\chi^2 = 4.17$, $df = 2$, $P = 0.12$; Fig. 3c) and 2005 ($\chi^2 = 0.07$, $df = 2$, $P = 0.97$; Fig. 3d). A more detailed analysis of nest distribution on expanding colonies in Phillips County in 2005 showed the same trends as the grouped analysis, with nests distributed across all colony age classes, including areas that had been occupied by prairie dogs for 9 or more years ($\chi^2 = 1.65$, $df = 4$, $P = 0.80$).

In the Comanche study area, we resurveyed four colonies in 2007 where nesting plovers were documented in 2005, and where prairie dogs were decimated by plague in 2006. In 2007, no live prairie dogs were observed at three of the four colonies, and only ~ 1 ha of active prairie dogs was observed at the fourth colony. In 2005, we documented a total of 13 plover nests on these four colonies. In 2007, we observed only one plover at one colony. The bird did not exhibit behaviors indicative of nesting adults, and no plovers were observed during subsequent visits to this site.

In the Phillips County study area, we identified 21 colonies that were expanding between the 2002 and 2004 colony surveys, and on which plover nests were found in 2003 or 2005. We also identified nine colonies that contracted substantially ($>50\%$; mean = 80%) between 2002 and 2004 due to apparent plague effects

Fig. 3 Comparison of the number of mountain plover nests observed versus expected in areas of prairie dog colonies with different lengths of prairie dog occupancy on the Comanche National Grassland, Colorado in 2005 (a), the Pawnee National Grassland, Colorado, during 2003–2007 (b) and in Phillips County, Montana in 2003 (c) and 2005 (d). Age classes refer to the length of time that prairie dogs had occupied different areas of the colonies prior to the nest survey (see Methods). In each case, mountain plover nests were distributed in proportion to the availability of the three age classes ($\chi^2 \leq 4.17$, $df = 2$, $P \geq 0.12$ for all comparisons)

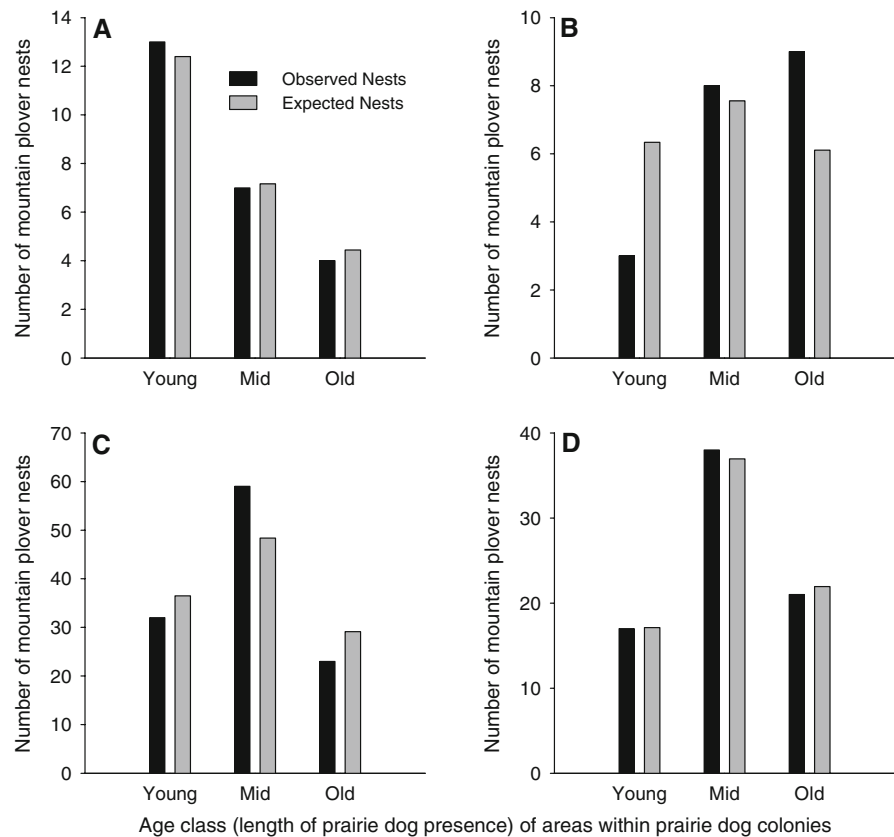


Table 2 Changes in colony size and number of mountain plover nests per colony (means with 1 SE in parentheses) for expanding versus plague-affected prairie dog colonies in Phillips County, Montana

	Number of colonies	Change in colony size			Change in nests per colony		
		2002 ha colony ⁻¹	2004 ha colony ⁻¹	Net change ha colony ⁻¹	2003 Nests colony ⁻¹	2005 Nests colony ⁻¹	Net change 2003–2005
Expanding colonies	21	44.2 (9.6)	54.0 (10.0)	9.8 (2.4)	4.4 (1.8)	4.1 (0.8)	−0.2 (1.3)
Plague-affected colonies	9	102.2 (24.2)	15.7 (5.9)	−86.4 (21.8)	2.8 (0.7)	0.4 (0.2)	−2.4 (0.8)

(Table 2). None of these colonies were extirpated completely between 2002 and 2004, but mean colony size declined from 102.2 ha in 2002 to 15.7 ha in 2004 (Table 2). The net change in number of nests per colony during 2003–2005 for declining colonies (mean = −2.44 nests colony⁻¹; median = −2.0 nests colony⁻¹) was significantly lower than the net change on expanding colonies (mean = −0.24 nests colony⁻¹; median = +1.0 nest colony⁻¹; Wilcoxon rank sum test, two-sided $P = 0.027$; Table 2).

Discussion

In mixed prairie, the abundance of forbs and subshrubs increases on older prairie dog colonies (Coppock et al. 1983; Archer et al. 1987) and preferential nesting by mountain plovers has been observed in portions of prairie dog colonies with increased cover of these plant functional groups (Olson and Edge 1985). In shortgrass steppe, older colonies contain more bare soil than young colonies or uncolonized

grassland (Hartley 2006) and mountain plovers often nest in portions of the landscape with high cover of bare soil (Knopf and Miller 1994; Shackford et al. 1999; Knopf and Rupert 1999). As a result, we originally hypothesized that mountain plovers would be confined to nesting in older areas of the colonies. In contrast, we found that across widely distributed sites in the western Great Plains, mountain plovers nested in both the youngest (colonized in the past 1–2 years) and the oldest (colonized more than 6–9 years) portions of prairie dog colonies in nearly direct proportion to the availability of these age classes.

Our findings suggest that changes in vegetation and bare soil induced by multiple years of prairie dog presence are not required to create habitat in which plovers will nest. Rather, prairie dog presence and grazing activity, even in recently-colonized grassland, are sufficient to create nesting habitat. One possibility is that plovers utilize all portions of active colonies because vegetation remains cropped throughout the nesting and brood rearing season, thus maintaining conditions where plovers can effectively avoid predation. A second non-mutually exclusive possibility is that arthropod availability influences plover habitat use (Olson 1985; Schneider et al. 2006). For example, compared to grassland without prairie dogs, young grasshoppers can be more abundant on prairie dog colonies (Russell and Detling 2003). Densities of ground-dwelling arthropods are also enhanced in the immediate vicinity of prairie dog mounds (Davidson and Lightfoot 2007), and this microhabitat is distributed throughout active colonies.

Following plague-driven declines in prairie dog colonies, we found that mountain plover nesting activity declined relatively rapidly, within 1–2 years. This result is consistent with both the loss of the short-term influence of prairie dog grazing activity and the relatively rapid recovery of vegetative conditions that can occur on prairie dog colonies following plague (Hartley 2006). Taken together, our findings indicate that available plover nesting habitat associated with prairie dog colonies closely tracks the area actively occupied by prairie dogs each year. We note that this does not imply that all areas of active colonies are suitable habitat, as plovers also select relatively flat terrain for nesting (Graul 1975), and localized features of colonies such as topography may

influence suitability for plover nesting. However, our results do indicate that plague-driven fluctuations in the extent of active prairie dog colonies within the landscape also directly reflect fluctuations in the extent of prairie dog habitat used by nesting plovers.

Mountain plovers have been reported to exhibit strong philopatry in their breeding territory (Graul 1973, P. D. B. Skrade, unpublished data), but less is known about the distance individual plovers may move to new breeding locations in response to changing habitat conditions. Plague epizootics often affect clusters of prairie dog colonies located near one another, but can vary considerably in size of the area they affect within a year. Some landscape features such as lakes, rivers and high-traffic roads may serve as barriers to plague transmission, and at increasing densities can reduce the spatial extent of plague outbreaks (Collinge et al. 2005). Colony size and connectivity also strongly influence the occurrence and transmission of epizootic plague within the landscape (Stapp et al. 2004; Collinge et al. 2005; Antolin et al. 2006). These landscape features affecting spatial patterns of plague epizootics could in turn influence the nesting activity of mountain plovers.

In northern mixed prairie, where mountain plovers nest almost exclusively on prairie dog colonies, the spatial extent of plague epizootics may influence the degree to which plovers can shift from plague-affected colonies to other nearby active prairie dog colonies. In Phillips County, colonies affected by plague during 2002–2004 were all less than 7 km from a colony not affected by plague, and interannual movements among colonies separated by up to 15 km have been documented for banded plovers in this study area (S. Dinsmore, unpublished data). For plague epizootics that affect larger areas, the degree to which plovers may respond by moving longer distances or by nesting off of prairie dog colonies is not clear. A negative effect of plague on plover nesting activity in mixed prairie is consistent with our observation that the large decline in nests on plague-affected colonies during 2003–2005 was not balanced by an increase in nests on expanding colonies within the Phillips County study area (Table 2).

In shortgrass steppe, mountain plovers can nest in several habitat types with high cover of bare soil where prairie dogs are not present. In landscapes where plague affects an extensive area within a given year (e.g. ~200,000 ha of the Comanche study area

during 2006), the sustainability of mountain plover populations may depend upon the availability and quality of such alternate habitats as recently burned grasslands (Svingen and Giesen 1999) or agricultural fields (Knopf and Rupert 1999; Dreitz and Knopf 2007). Because plague incidence increases following years with above-average precipitation (Stapp et al. 2004), which coincides with increased grass production and fuel loads, prescribed burning may be one means to provide alternate plover nesting habitat in years and portions of the landscape where plague outbreaks have recently occurred. Given the presence of plague throughout the mountain plover's breeding range in the western Great Plains, important factors affecting plover populations may include landscape features determining the scale of plague outbreaks, the distance that plovers can move in response to changing habitat conditions, and the availability and quality of alternate breeding habitat within the landscape.

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