DISSERTATION

POPULATION GENETICS, FRAGMENTATION AND PLAGUE IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY LISA T. SAVAGE ENTITLED POPULATION GENETICS, FRAGMENTATION AND PLAGUE IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*) BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

POPULATION GENETICS, FRAGMENTATION AND PLAGUE IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

Black-tailed prairie dogs (*Cynomys ludovicianus*) have declined dramatically over the past century from habitat loss, poisoning, and plague, a disease caused by the bacterium *Yersinia pestis*. Because of these factors, populations have become fragmented, and, in areas with plague, exist in metapopulations, undergoing regular extinction and recolonization. The focus of this study was two primary sources of decline in black-tailed prairie dogs: habitat fragmentation and plague.

First, the genetic consequences of fragmentation from habitat loss and metapopulation dynamics resulting from plague were examined using six microsatellite loci and a 454 bp portion of the mitochondrial DNA control region. Prairie dog towns were sampled in 2000-2001 in two fragmented areas with plague in Colorado, in a naturally fragmented area without plague in South Dakota, and in a relatively unfragmented area without plague in South Dakota. To document temporal changes in genetic variability, prairie dogs were sampled on the Central Plains Experimental Range, Colorado in 1997, 2000 and 2001. This analysis found high levels of gene flow between populations, but that gene flow was inversely related to levels of landscape fragmentation. There was significant isolation by distance in the three fragmented sites, leading to the conclusion that conservation of genetic variability in fragmented populations of prairie dogs with and without plague should emphasize the maintenance of gene flow between populations.

Second, using long-term (1981-2005) monitoring of prairie dog towns on the Pawnee National Grasslands, Colorado, logistic regression models were fitted to examine factors influencing plague outbreaks, focusing on intertown connectivity, soils, and climate. The data revealed little spatial or temporal autocorrelation, but plague extinctions were spatially clustered and spatial dependence could be modeled by town connectivity. High summer temperatures were associated with reduced risk of plague. In spatial logit association models, increased summer rainfall raised the risk of plague events. However, plague outbreaks were not significantly linked with past precipitation in any models tested. As such, our models support the concept that plague occurrence depends upon direct climatic effects and not on a trophic cascade from lagged precipitation.

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CHAPTER I

INTRODUCTION

INTRODUCTION

Black-tailed prairie dog (*Cynomys ludovicianus*) populations have declined dramatically over the past century from habitat loss to agriculture and urban development, government poisoning programs for population control, and the introduction of the sylvatic plague (Miller et al. 1994; Luce 2003). While estimates of the extent of their decline vary, the land currently occupied by prairie dogs may be 5-10% within their historic range (Knowles et al. 2002; Vermiere et al. 2004; Forrest 2005). Black-tailed prairie dogs are an ecologically important species in the short and mixedgrass prairie ecosystems. And, because of their large effects on ecosystem-level functions relative to their abundance, they are considered keystone species by some researchers (Miller et al. 1994, 2000; Kotliar et al. 1999; Kotliar 2000; but see Stapp 1998; Vermiere et al. 2004). Prairie dogs alter grassland patch structure by increasing soil mixing, decreasing plant canopy height, changing plant species composition, and altering nutrient cycling on towns (Whicker and Detling 1988; Holland and Detling 1990). They increase landscape-level diversity by altering both plant and animal species composition as compared to off-colony sites. They have one obligate predator, the black-footed ferret (*Mustela nigripes*), are associated with two strongly facultative species, the mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*), and benefit other vertebrate species such as ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), swift fox (*Vulpes velox*), deer mice (*Peromyscus maniculatus*), grasshopper mice (*Onychomys leucogaster*), and horned larks (*Eremophila alpestris*) (Kotliar et al. 1999).

The resulting decline of black-tailed prairie dog populations induces landscape-level changes in prairie ecosystems, the most striking example of which is the near extinction of the black-footed ferret and the struggle to develop and maintain reintroduced populations of ferrets (Biggins and Godbey 2003). The following two chapters of this dissertation focus on two major sources of decline of prairie dogs: habitat fragmentation and plague, a disease caused by the bacterium *Yersinia pestis*. The first study looks at the interacting genetic consequences of fragmentation from habitat loss and metapopulation dynamics resulting from regular extinction and recolonization in areas where plague is present. The second study examines factors influencing plague outbreaks in prairie dog towns, focusing on soil moisture, climatic factors, and levels of connectivity of prairie dog towns to towns undergoing plague epizootics and to towns not experiencing plague epizootics. Where these two papers explicitly link is over the concepts of connectivity, dispersal and gene flow.

Fragmentation of populations involves both a decrease in population size and an increase in population isolation (Wilcove et al. 1986) accompanied by increases in the patchiness of populations across a landscape. The colonial nature of black-tailed prairie dogs makes them inherently patchily distributed over much of their range (Koford 1958), but habitat conversion and poisoning have increased landscape level patchiness. However, plague has transformed prairie dogs from relatively stable, patchily distributed populations to metapopulations (Roach et al. 2001). Metapopulations are defined as a series of local populations with independent population dynamics, connected via dispersal, where local populations are subject to extinction and subsequent recolonization (Hanski 1998). Fragmented populations and metapopulations exist on a continuum of patchiness and susceptibility to extinction. The line between highly fragmented populations in which small populations, due to population size, have an increased risk of extinction and where true metapopulations start is arbitrary. With black-tailed prairie dogs, however, fluctuations in population size are normal, though town extinctions from natural causes in areas without plague are rare (Barnes 1993; Wind Cave National Park historical files). Plague is the only known disease to cause extinctions of large prairie dog towns (Barnes 1993). In areas with plague, black-tailed prairie dog towns experience epizootics on a regular basis (Stapp et al. 2004), but these events are sporadic in that between epizootics, plague seemingly disappears from the landscape, and when epizootics reemerge, it is difficult to predict where they will take place (Anisimov 2004).

Fragmentation changes the dispersal equation by decreasing the number of potential dispersers, and by increasing the difficulty of dispersal to more isolated populations. On a genetic level, this decreases gene flow and can increase genetic differentiation between populations (Vos et al. 2001). Smaller population size as well as genetic drift can cause the loss of genetic variation (Frankham 1996). Metapopulation dynamics involve patchy or fragmented populations that also experience regular extinction and recolonization (Hanski 1998). In metapopulations, the extent of gene flow between populations and the genetic composition of dispersers, in addition to the extinction rate, are important determinants to maintaining genetic diversity (Barton and Whitlock 1997). Populations recolonized by a small number of individuals, with little subsequent dispersal, will have lower genetic variability and higher levels of genetic differentiation. However, regular gene flow following recolonization from a variety of populations will diminish the effects of extinction and recolonization in metapopulations, creating a genetic picture similar to that of populations that are simply fragmented. In the population genetic study, the total area of prairie dog towns within dispersal distance (10 km) of a sampled town (Knowles 1985) was used to estimate levels of fragmentation. Molecular markers were used to estimate levels of gene flow and measured how patterns of genetic diversity and differentiation changed over a gradient of fragmentation in areas with and without the plague. In all study sites, relatively high levels of dispersal between populations were found, but levels of dispersal were inversely related to levels of fragmentation. Fragmentation determined levels of gene flow.

In areas with plague, dispersal is a double-edged sword. While regular dispersal is necessary for metapopulations to persist following extinctions, dispersal by infected prairie dogs and their fleas is one of the possible mechanisms for transmitting plague between towns (Girard et al. 2004; Collinge et al. 2005), as is transmission of infected fleas by other rodent hosts and predators (Poland and Barnes 1979; Barnes 1993; Salkeld et al. 2007). Plague often occurs in clusters of prairie dog towns with short intertown distances (Anderson and Williams 1997; Cully and Williams 2001; Girard et al. 2004; Stapp et al. 2004; Collinge et al. 2005; Wagner et al. 2006). Lomolino et al. (2003) found that more isolated prairie dog towns in Oklahoma experienced fewer plague epizootics and persisted longer than towns with higher connectivity. In investigating the factors important to predicting plague outbreaks in prairie dog towns, this study measured connectivity of individual towns in relation to towns undergoing plague epizootics and to extant towns. Similar to the genetics study where high levels of dispersal were found, the modeling study found that levels of connectivity predicted whether individual colonies would undergo plague epizootics. As a town's connectivity to towns undergoing epizootics increased and its connectivity to extant towns simultaneously decreased, its own probability of undergoing a plague die-off increased. Thus, what is found genetically in prairie dog metapopulations is similar to the between-population spread of plague.

Another factor important to predicting epizootics was the water content of the soils, where fleas spend the majority of the pre-adult portion of their life-cycle (Krasnov et al. 2001). Towns with soils that could hold more moisture under dry conditions had a higher probability of undergoing plague epizootics than towns on soils with lower moisture-holding capacity. Climatic variables were also important to predicting plague outbreaks, with cool, moist summers and, to a lesser extent, warmer early springs promoting epizootics.

The predictions from the genetics and plague modeling studies coalesce in a recent plague epizootic that swept through our study site on the Central Plains Experimental Range (CPER), Colorado from the spring of 2006 to the summer of 2007. For the genetics study, six towns were measured on the CPER in 1997 and 2000, and five towns in 2001. When sampled in 1997, these towns were young, with an average age of 1.65 years, having just started the recolonization process. In 1997, the average town size was 4.1 ha. By 2001 it was 27.8 ha, and by 2005 average town size had risen to 103.9 ha (Figure 1.1). The results of the genetics study would predict that gene flow and thus dispersal between towns would be at an all-time high. Significant Mantel correlations between genetic distance from mitochondrial data and geographic distance predict that female prairie dogs would likely disperse along drainages, while the lack of correlation between genetic distance from microsatellite data and geographic distance predicts that prairie dogs, and in particular males, can eventually disperse to all sampled towns. Thus, with prairie dogs likely to disperse along drainages but also having the ability to reach all towns, and with prairie dogs one of the possible agents of intertown transmission of plague, along with other rodents and predators, plague transmission between towns may, at least in part, follow these patterns.

The results of the plague modeling study would predict that if plague started in this group of clustered towns, the connectivity to plagued towns would start to increase, thereby increasing the probability of die-offs in other towns within this cluster. The modeling study also predicts cool moist summers, and to a lesser extent warm early springs, help promote plague epizootics. Looking at 25 year averages for the CPER, the climatic conditions in the spring and summer of 2006 show that those time periods are just above normal across the board; in 2006 early spring temperature (March-April) was 8.5% above average, early summer temperature (June-July) was 7.4% above average, and summer precipitation (June 15-September 30) was 4.3% above average (Climate and Hydrology Database Projects 1981-2006). Early spring temperature in 2007 was even warmer, 11.6% above average. Thus, while warmer than average early springs may have helped trigger early plague epizootics, giving flea populations a head start by speeding development times (Silverman et al. 1981; Silverman and Rust 1983; Metzger and Rust 1997), the warmer than average early summer in 2006 may have temporarily suppressed epizootics because fleas do not complete development at high temperatures (> 35°C / 95°F) and fleas clear infection more readily and transmit plague less readily at temperatures greater than 28°C (Cavanaugh 1971; Kartman and Prince 1956). Epizootics probably accelerated once cooler weather returned in late August; this pattern of plague returning with the advent of cooler weather has been documented in human epizootics in India and Vietnam (India Plague Commission 1908; Cavanaugh and Marshall 1972). Thus, with high connectivity between prairie dog towns, adequate climatic conditions and the presence of plague, this area was ripe for a plague epizootic to move through its drainages. Following predictions, plague appeared in town 35 in the early spring of 2006, and moved north up the Little Owl Creek drainage (Figure 1.1) spreading sequentially to town 27 and then to town 22 (D. Tripp and M. Antolin, unpublished data). Jumping drainages to the Eastman drainage, which connects with the Owl Creek drainage, town 5 was undergoing an epizootic in early spring of 2007 that may have begun in the late fall, as was town 29, and town 30 was mostly inactive by the summer of 2007 (D. Tripp and M. Antolin, unpublished data). All of these towns on the CPER are now, in September of 2007, either extinct or much reduced in size, awaiting recolonization and a rebuilding of prairie dog populations.

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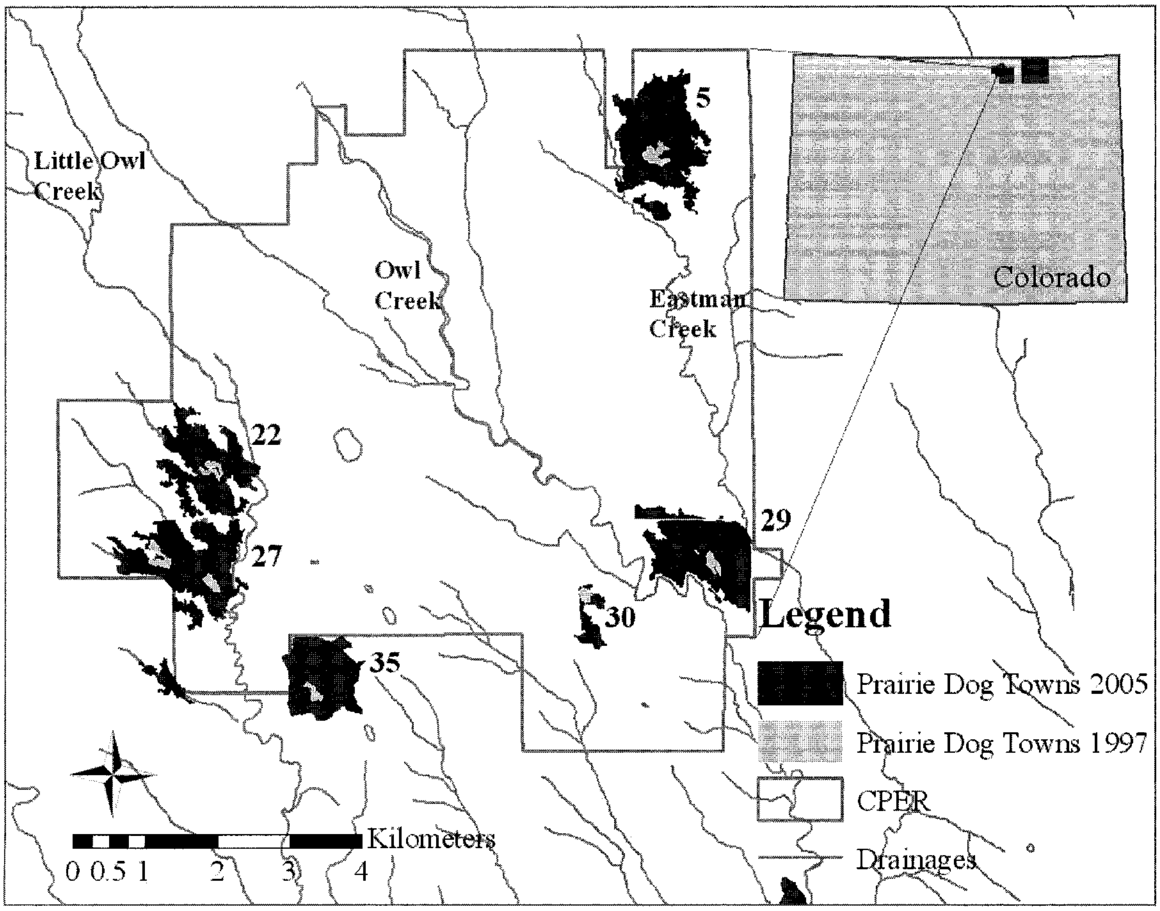

Figure 1.1. Black-tailed prairie dog towns on the Central Plains Experimental Range, Colorado in 1997 and 2005 in relation to drainages, which are used as dispersal corridors for prairie dogs. The large dark areas on the inset Colorado map indicate the extent of the Pawnee National Grassland, which includes a patchwork of federal, state and private land owners, with approximately 80,000 ha of federal ownership.

CHAPTER II

THE EFFECTS OF FRAGMENTATION AND METAPOPULATION DYNAMICS ON THE POPULATION GENETIC STRUCTURE OF BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

ABSTRACT

Black-tailed prairie dog populations have declined dramatically over the past century not only from habitat destruction and eradication efforts but also from the introduction of plague, caused by the bacterial pathogen *Yersinia pestis*, which causes 95-100% mortality in black-tailed prairie dog towns. Because of these factors, populations have become fragmented, involving both a decrease in population size and an increase in isolation of towns. In areas with plague, populations live in metapopulations, undergoing regular local extinction from plague and recolonization following epizootics. The objective of this study was to delineate the relationship between genetic variability and both fragmentation and metapopulation dynamics in black-tailed prairie dogs using six microsatellite loci and a 454 bp portion of the mitochondrial control region (mtDNA) in four to six prairie dog towns per study site. Black-tailed prairie dog towns were sampled in fragmented areas with plague (Central Plains Experimental Range, CO and Fort Collins, CO), in a naturally fragmented area without plague (Wind Cave National Park, SD), and in a well-connected, relatively unfragmented area without plague (Buffalo Gap National Grassland, SD) between June 2000 and April 2001. A temporal analysis was also performed, documenting changes in genetic variability in black-tailed prairie dogs on the Central Plains Experimental Range in June-December of 1997, 2000 and 2001. Observed heterozygosity (H_o) and gene diversity, from both microsatellites and mtDNA, did not differ between populations along a gradient of fragmentation, or between areas affected or unaffected by plague. Fragmentation was associated with both greater differentiation (F_{st}) and fewer individuals classified as migrants by assignment tests. The two fragmented sites that experience plague epizootics showed isolation by distance

between towns. Prairie dog populations in areas without plague had twice the number of mitochondrial haplotypes than in areas with plague. Conservation of genetic variability in fragmented populations of black-tailed prairie dogs with and without plague should emphasize the maintenance of gene flow between populations.

INTRODUCTION

Habitat fragmentation and loss is one of the primary factors in declining biodiversity world-wide (Harris 1984; Wilcox and Murphy 1985). Habitat fragmentation involves both a decrease in total amount of available habitat and an increase in isolation of remaining habitat (Wilcove et al. 1986). The resulting reduction in population size and increase in population isolation can have a number of consequences, including reduced gene flow and increased genetic differentiation between populations (Vos et al. 2001), loss of genetic variation (Frankham 1996), inbreeding depression (Falconer and Mackay 1996), population fluctuations, and susceptibility to extinction (Saccheri et al. 1998; Reed and Hobbs 2004).

For many species, multiple factors work in concert to reduce populations. In the case of black-tailed prairie dogs (*Cynomys ludovicianus*), which are diurnal, ground dwelling, colonial sciurids in North American short and mixed-grass prairies (Hollister 1916; Koford 1958), populations have declined dramatically over the past century not only from eradication efforts and habitat loss to agriculture and urban development, leading to increased habitat patchiness, smaller population size, and fluctuations in population size, but also from the introduction of plague (Luce 2003). Plague epizootics are caused by the bacterium *Yersinia pestis*, resulting in 95-100% mortality in black-tailed prairie dog towns (Van Putten and Miller 1999; Cully and Williams 2001; Stapp et al. 2004; Pauli et al. 2006). Introduced to the western coast of the United States at the turn of the century, plague spread quickly through native rodent populations and was first identified in black-tailed prairie dogs in Kansas in 1945 and in Texas in 1947 (Eskey and Haas 1940; Cully et al. 2000). Because plague causes large-scale die-offs, populations in regions with plague not only face the effects of fragmentation, they also experience metapopulation dynamics by undergoing regular local extinctions during outbreaks and recolonization in the following years (Cully and Williams 2001; Roach et al. 2001; Lomolino et al. 2003; Stapp et al. 2004; Pauli et al. 2006).

Whether a metapopulation can maintain genetic diversity in the face of regular extinction depends not only on the extinction rate, but also on the extent of gene flow between populations, the origins of dispersers, and the rapidity of recovery (Barton and Whitlock 1997). Genetic theory predicts that population bottlenecks from plague die-offs may cause the loss of alleles from populations and decrease heterozygosity and gene diversity. Prairie dog towns recovering from plague may experience inbreeding from small population size and genetic drift, a random sampling of alleles, both of which decrease genetic variability (Hedrick 2004). A significant loss of genetic variation could reduce fitness or could inhibit the ability of a population to respond to environmental change (Frankham 1996). Gene flow from dispersing individuals balances the forces of inbreeding and genetic drift and can restore genetic variation over time (Hedrick 2004), but the level of isolation in fragmented populations may affect the ability of individuals to migrate effectively and thus, genetic exchange.

Population genetic studies of black-tailed prairie dogs show that while plague causes a reduction in genetic diversity in towns that have undergone epizootics, subsequent dispersal and gene flow take place after initial colonization. Plague has been shown to significantly decrease genetic variability in towns recovering from plague epizootics compared with towns that did not experience die-offs (Trudeau et al. 2004). In the complex of recently recolonized towns in this study, older towns had lower genetic differentiation than younger towns (Roach et al. 2001), implying that initial colonization increased genetic differentiation between towns, but that gene flow over time reduced between-town differences. Additionally, when examining the relationship between genetic distance and geographic distance (Slatkin 1993), which can indicate the effects of dispersal and gene flow across a landscape on genetic differentiation, a young complex of prairie dogs showed a positive relationship between genetic and geographic distance (Roach et al. 2001) while older, stable complexes showed no isolation by distance (Chesser 1983; Daley 1992). This underscores the effects of gene flow in homogenizing populations over time. As such, the long-term maintenance of genetic variation in prairie dog metapopulations depends on the interplay between extinction and gene flow (Barton and Whitlock 1997).

The goal of this study was to examine the effects of both fragmentation and metapopulation dynamics on genetic variability in black-tailed prairie dogs. A regional analysis was performed, studying four prairie dog populations between June 2000 and April 2001 along a gradient of spatial fragmentation, with two fragmented sites in Colorado, where plague has been documented in prairie dogs since 1948 (Ecke and Johnson 1952), and one fragmented and one relatively unfragmented site in South Dakota, in areas with no documented plague die-offs (A. Smith, South Dakota Game, Fish and Parks (SDGFP), personal communication). The two Colorado sites are fragmented by land ownership and land use; the Central Plains Experimental Range is a mosaic of cattle-grazing intensity, while the city of Fort Collins has a prairie dog complex fragmented by urban development. In South Dakota, Wind Cave National Park has a complex of prairie dog towns naturally fragmented by pine-covered hills separating towns, and is bordered on the west by forested land that does not provide suitable habitat for prairie dogs. The park is also fragmented by land use in that it is bordered on the east and south by private land, where the few existing prairie dog towns are heavily controlled (A. Smith, SDGFP, personal communication). Buffalo Gap National Grassland, South Dakota borders Badlands National Park to the North and Pine Ridge Indian Reservation to the South, all of which have large populations of black-tailed prairie dogs. This site represents a large, relatively unfragmented population of black-tailed prairie dogs.

To place the regional analysis in the context of change in prairie dog populations through time, a temporal analysis was performed, sampling black-tailed prairie dogs on the Central Plains Experimental Range, CO in 1997, 2000 and 2001.

The objectives of this study were to estimate within-population genetic variation and the level of genetic structure among populations 1) along a gradient of fragmentation, 2) in populations that undergo metapopulation dynamics compared with populations that do not, and 3) within one population over time. The following predictions were made: 1) there should be a positive relationship between genetic differentiation and fragmentation, 2) that overall genetic variation (alleles, genotypes) may be the same in populations with and without plague because of gene flow and rapid recovery from population bottlenecks, but differentiation would be greater in Colorado, where prairie dogs have been converted to metapopulations, 3) the number of individuals classified as migrants should increase as the fragmentation decreases, 4) genetic differentiation should decrease through time with adequate dispersal between populations, and 5) the relationship between genetic and geographic distance should decrease as a complex ages, should be stronger in younger complexes than older complexes and stronger in more fragmented complexes than in less fragmented complexes.

MATERIALS AND METHODS

Study organism

Black-tailed prairie dogs are highly social, colonial, burrowing rodents that live in the short and mixed grass prairies of North America (Hollister 1916; Koford 1958). They live in coteries, harem-polygynous social breeding groups, consisting of 2-4 adult females, 1-2 adult males, yearlings and juvenile offspring (Hoogland 1995). Groups of coteries make up towns that are largely isolated populations (Dobson et al. 1997). Females are strongly philopatric, and generally remain in their natal coteries while yearling males usually disperse within towns to nearby coteries, although intertown dispersal by both males and females is occasionally observed (Hoogland 1982, 1995; Knowles 1985; Halpin 1987; Garret and Franklin 1988). Landscape features such as drainages, roads, and trails may facilitate dispersal across the landscape (Knowles 1985; Garrett and Franklin 1988; Roach et al. 2001) while urban and agricultural development, tall vegetation, and topographic variation may inhibit dispersal (Koford 1958; Johnson and Collinge 2004).

Population genetic studies of black-tailed prairie dog populations in New Mexico, Colorado, South Dakota and Montana show moderate genetic differentiation, with average F_{st} values ranging from 0.049 to 0.194 (Chesser 1983; Daley 1992; Roach 2001; Trudeau et al. 2004), with the highest estimates from samples that included widely spaced towns (50 km) well outside of the longest dispersal distance recorded for black-tailed prairie dogs of 10 km (Knowles 1985).

Despite having socially structured populations, black-tailed prairie dogs systematically avoid extreme inbreeding with close relatives at the coterie level, as demonstrated by observational studies and pedigrees (Hoogland 1982, 1992). Genetic data also show that black-tailed prairie dogs minimize inbreeding at the coterie level, but mate randomly at the colony level (individual-colony $F_{is} = 0$) (Dobson et al. 1997; Roach et al. 2001). Behavioral mechanisms that decrease inbreeding are male-biased dispersal of yearlings and adults, philopatry of females, the decreased probability that young females go into estrus if the father is in her natal coterie, and the recognition of close relatives through social learning (Dobson et al. 1997; Hoogland 1982, 1995).

Study Sites

Central Plains Experimental Range (CPER)

The CPER (Figure 2.1a) is located in Weld County, Colorado (elevation 1280-1950 m, 40° 48' N, 104° 40' W). It is administered by the USDA Agricultural Research Service, represents approximately 7,000 ha of publicly owned land with a checkerboard of grazing treatments established in 1939 to study the effects of grazing on sustainability of the shortgrass prairie, and is located in the northwestern corner of the Pawnee National Grassland. Both the Pawnee National Grassland and the CPER are research areas of the Shortgrass Steppe Long Term Ecological Research project at Colorado State University, funded since 1982 by the National Science Foundation. Black-tailed prairie dogs were sampled in 1997 (Roach et al. 2001), 2000 and 2001. Six towns were sampled in 1997 (average size 4.05 ha) and 2000 (average size 14.05 ha), and 5 towns were sampled in

2001 (average size 27.84 ha). In 2000, the western unit Pawnee National Grassland had 20 prairie dog towns totaling 195 ha. The towns on the CPER represent a young, fragmented complex of prairie dogs; the average town age in 2000 was 4.67 years. The use of rodenticide to control prairie dogs was halted in the 1970's.

City of Fort Collins

The city of Fort Collins (Figure 2.1b) is located in Larimer County, Colorado (elevation 1525 m, 40° 31' N, 105° 5' W). In 2000, the city of Fort Collins Natural Areas Program had 13 distinct prairie dog towns, totaling 171 ha, on remnant patches of shortgrass prairie interspersed with urban development, in an area of approximately 14,000 ha. Approximately 63% of prairie dog town area within the city limits was protected by the Natural Areas Program with the majority of remaining prairie dog town area found in 12 towns of 1 ha or more. We sampled three towns on Fort Collins Natural Areas and one town on Larimer County property (average size 24.33 ha) over a 10,000-ha area. These towns represent a young, fragmented complex of prairie dogs; the average town age was nine years. The Fort Collins Natural Areas program allows the use of rodenticide on a site by site basis to maintain prairie dog acreage levels and buffers in neighborhood properties (J. Shanihan, City of Fort Collins Natural Areas Program, personal communication).

Both the CPER and Fort Collins are situated in the shortgrass steppe ecosystem, which experiences low annual precipitation, between 18 and 55 cm of rain falling primarily from April to September (37 year average 33.37 cm) on the CPER (Climate and Hydrology Database Projects 1969-2006) and between 18 and 72 cm of rain falling in Fort Collins (60 year average 38.82 cm) (National Climate Data Center 1947-2007).

Vegetation on the shortgrass steppe is characterized by low-growing plants that tolerate grazing and drought. The most common plants are two C_4 grasses, blue grama (*Bouteloua gracilis)* and buffalo grass (*Buchloe dactyloides*), prickly pear (*Opuntia polyacantha*), yucca (*Yucca glauca)*, and several species of dwarf-shrubs. Vegetation is strongly dominated by blue grama, which contributes 60-80% of the plant cover, biomass, and net primary productivity (Milchunas et al. 1992).

Prairie dog towns on the shortgrass steppe are located within major dry stream channels and have population densities of approximately 25-28 prairie dogs/ha (Koford 1958; Magle et al. 2007). They are patchily distributed throughout the landscape and, because of plague outbreaks, experience metapopulation dynamics with regular town extinctions and recolonizations (Roach et al. 2001; Stapp et al. 2004; Antolin et al. 2006).

Wind Cave National Park

Wind Cave National Park, located in Custer County, South Dakota (elevation 1090 to 1530 m, 43° 35'N, 103° 25'W) encompasses an area of 11,400 ha, and has a complex of prairie dogs naturally fragmented by habitat and topography within the park, and fragmented by land use outside of the park. In 2000, Wind Cave had 553 ha of prairie dogs in 12 towns separated by ridgelines and Ponderosa pine forests, bordered by forested land to the west and private land to the east and south. Five towns (average size 79.06 ha) were sampled from this complex and one town from adjoining Custer State Park to obtain a measure of highly stable towns that were fragmented in an area without plague (Figure 2.1c); the average age of towns was 46 + years.

The climate is semi-arid, with 25-73 cm of annual precipitation (56 year average 45.11 cm), primarily during the growing season in local thunderstorms (Wind Cave records). The park is characterized by two major vegetation types, ponderosa pine forest and mixedgrass prairie. The mixedgrass prairie covers 75% of the park with a mixture of shortgrass and tallgrass prairie species including dominant grasses: western wheatgrass (*Agropyron smithii*), green needle grass (*Stipa viridula*), big and little bluestem (*Andropogon gerardi* and *Andropogon scoparius)*, side oats grama (*Bouteloua curtipendula*), blue grama, and buffalo grass (Froiland and Weedon 1990). Grasses constitute 80% of the biomass on the prairie, with forbs providing 20%. Forbs include prickly pear and yucca, among others. Plant composition of specific areas depends on annual precipitation; tallgrass species tend to dominate in wet years, while shortgrass species dominate in dry years (Froiland and Weedon 1990). Average prairie dog density is approximately 20-30 prairie dogs/ha (Hoogland 1995; D. Biggins, USGS, personal communication). No shooting is allowed within the park, although poisoning is allowed to maintain prairie dog acreage levels and to uphold a good-neighbor policy (B. Meunchau, Wind Cave, personal communication).

Buffalo Gap National Grassland, Wall Ranger District

The Wall Ranger District of Buffalo Gap National Grassland is located in Pennington County, South Dakota (770 to 820 m, 43° 43' N, 102° 17' W) and encompasses 240,000 ha. In 2000 the Wall District, with adjacent Badlands National Park, had approximately 215 prairie dog towns with a total area of 5,500 ha of prairie dogs: it represents a large, well-connected complex of prairie dogs. Prairie dog towns on Buffalo Gap experienced regular poisoning for population control prior to 1972, and in the late 1970's through the mid 1990's poisoning cycles caused fluctuations in town size (USDA Forest Service 2007) but sampled towns were continuously occupied since at least the 1970's (average town age 29 + years) (N. Eisenbraum, Buffalo Gap, personal communication). Prairie dogs were sampled in the Bouquet Table and Sage Creek allotments that border the southern edge of the Conata Basin, a black-footed ferret reintroduction site. Five towns (average size 38.38 ha) were sampled over a 3,600-ha area (Figure 2.1d).

The climate is semi-arid with average (50 yr) annual precipitation of 43.04 cm (National Climate Data Center 1957-2007). The vegetation of the sampling area is mixedgrass prairie dominated by western wheat grass, green needlegrass, and needle-and-thread (*Stipa comata*). The shortgrass element of the mixedgrass prairie (blue grama and buffalo grass) is patchy and increases in size during drought and overgrazed conditions (Froiland and Weedon 1990). Average prairie dog density is approximately 8-35 prairie dogs/ha (Severson and Plumb 1998).

Town mapping, landscape distances between towns, quantification of fragmentation

For the CPER, Wind Cave, and Buffalo Gap, surveys depended upon mapping the outermost active burrows of extant towns to determine town area and the geographic coordinates (centroids) of towns. Burrows were considered active if they were cleared of vegetation and cobwebs, had signs of fresh digging or excavation, and/or had the presence of fresh scat. For the city of Fort Collins, prairie dog town size and centroids were estimated from a digital photo taken in 1999, with town presence verified on the ground (City of Fort Collins, Geographic Information Services 1999). These maps were incorporated into a geographic information system (GIS) using ArcGIS Desktop 9.1 (Environmental Systems Research Institute 2005). All GIS layers used Universal Transverse Mercator projection, Zone 13, datum WGS84, in meters.

Prairie dogs may use drainages as dispersal corridors between towns (Garrett and Franklin 1988; Roach et al. 2001). Distances between towns along drainages were determined using United States Geological Survey (USGS) hydrography (1:24,000) digital line graphs by mapping the distance between centroids of towns along drainages (drainage distance). When drainage connections were too subtle to be included in the 1:24,000 drainage map, a hillshade layer of the USGS (1:10,000) digital elevation models was used to find the lowest elevation lines between larger drainages. Euclidean distances between all towns were also calculated. To quantify the degree of fragmentation at each study site, I calculated the total area of prairie dog towns within a 10-km buffer of the centroid of each sampled prairie dog town, and averaged that value over all sampled towns.

Black-tailed prairie dog sampling and DNA extraction

Black-tailed prairie dogs were live-trapped from June to December 1997 (Roach et al. 2001), 2000, and 2001 on the CPER. Prairie dogs were live-trapped from June-August 2000 in Wind Cave, from September-December 2000 in Fort Collins, and in April 2001 in Buffalo Gap (Table 2.1). Within each town, a transect was placed through the center of the town with clusters of 30 live-traps placed at four locations along it, sampling two sites at the edge of the town and two sites toward the center of the town. This trapping design ensured that prairie dog populations at each town were representatively sampled, with tail tissues obtained from approximately 16 adult males and 10 adult females, divided evenly between the four trapping clusters. I focused primarily on sampling male prairie dogs due to female philopatry within coteries and male-biased dispersal between coteries (Hoogland 1995). Sex-biased dispersal patterns result in females within coteries being more related than expected by random mating (Dobson et al. 1997). Each coterie includes 1-2 adult males, and thus captured males should have originated from different coteries within towns or are new migrants into towns, and will be representative of genotypes across the town. Thus, by focusing sampling of adult males I captured a more accurate picture of genetic diversity within and between towns.

I weighed, ear-tagged, and assessed the gender and reproductive status of each trapped prairie dog. A small sample of tail tissue was obtained by removing the posterior caudal vertebra (1 cm). Prior to removal, the tail was cleaned with antibacterial soap, a band tourniquet applied, and lidocaine administered as a local anesthetic. After tissue removal, the wound was sealed with surgical glue and stainless steel staples. Immediately after collection, tissue samples were placed in a storage buffer (1X STE: 0.1 M NaCl, 0.05M Tris-HCl (pH 7.5), 0.001 M EDTA) and stored at -80°C until processing. DNA was isolated from tail tissue using the CTAB (hexadecyltrimethylammonium bromide) procedure outlined by Black and DuTeau (1997). Extracted DNA was re-suspended and stored in TE (0.01 M Tris-HCl, 0.1 M EDTA (pH 8.0)). All procedures were reviewed and approved by the Colorado State University Institutional Animal Care and Use Committee.

Mitochondrial control region (mtDNA) marker and SSCP analysis

The mitochondrial control region is a noncoding region of the mitochondrial genome with a high level of variability (Aquadro and Greenberg 1983; Cann et al. 1984) making it ideal for population genetic studies. In developing a black-tailed prairie dog specific marker, the first amplifications were performed using “universal” primers described by Kocher et al. (1989): L15926 and H00651 (Table 2.2). PCR products were partially sequenced in both directions (Davis Sequencing, Davis, CA). Sequences were aligned using CLUSTAL W (Thompson et al. 1994) with a Bioedit interface (Hall 1997-2007). Black-tailed prairie dog specific primers were designed using Primer Premier 5 (Lalitha 2000) to amplify smaller portions of the resulting 980 bp section of the control region, dividing this segment of DNA into approximately four equal pieces of 200-300 bp, a length considered optimal for single strand conformation polymorphism (SSCP) analysis to detect single nucleotide polymorphisms (Orita et al. 1989; Hyashi 1991). Haplotypes with unique SSCP patterns were sequenced and checked for genetic variability. I amplified two 200-250 bp portions of the control region using primer pairs L19526 and ltsH200 (fragment A, 203 bp), and ltsL250 and ltsH250 (fragment B, 251 bp) which make up a contiguous 454 bp section of the control region (Figure 2.2). In fragment B, the mtDNA region flanked by primers ltsL250 and ltsH250, sequencing revealed one nucleotide with a T/C homoplasy that did not produce different bands on SSCP gels in eight haplotypes. I therefore designed a primer, ltsL140, which paired with ltsH250 to amplify a 140 bp section of fragment B; SSCP analysis distinguished whether the site contained a T or C (Figure 2.2).

PCR amplification was performed using M.J. Research PTC-100 thermocyclers in 25-μl volumes containing 30-90 ng DNA using the following protocol: initial denaturation for 5 min. at 95°C, followed by 35 cycles of 94°C for 40 sec., 48°C/ 50°C/ 54°C for 40 sec., 72°C for 1 min., and a final extension of 72°C for 10 min., with annealing temperatures of 48°C, 50°C and 54°C for the 140 bp, 200 bp and 250 bp segments, respectively.

For marker genotype scoring, PCR product was diluted 6 to 1 in stop buffer (10mM NaOH, 95% formamide, 0.05% bromophenol blue, 0.05% xylene cyanol), denatured for 5 min. at 95°C and then cold shocked on wet ice, causing the separated individual strands of DNA to anneal to themselves in different conformations depending on their nucleotide sequences. Aliquots were electrophoresed at 14 watts for 11 hours (140 bp segment of fragment B and 200 bp fragment A) and 16 hours (250 bp fragment B), in a neutral polyacrylamide gel (30% acrylamide, 2% bis-acrylamide) in 1X TBE buffer following Black and DuTeau (1997). Each gel was soaked in 2L of 10% glacial acetic acid for 20 min. to fix the DNA, and DNA was visualized by silver staining as described by Black and DuTeau (1997). Each sample was genotyped at each fragment by comparing DNA banding patterns with sample standards, and the fragment haplotypes were combined to identify the presence of 14 different haplotypes with 14 variable sites (Figure 2.3). These haplotypes were verified by sequencing two or more individuals per haplotype, except when a single unique individual was available for sequencing. The distribution of mtDNA control region haplotypes in each sampled population of black-tailed prairie dogs is shown in Table 2.3.

Microsatellite analysis

Microsatellites are highly variable nuclear markers consisting of tandem repeats of two to four base pairs. I amplified alleles at seven microsatellite loci that have been used previously in black-tailed prairie dogs: CGS 14, CGS 17, CGS 22, CGS 25, CGS 26, IGS 1 and IGS 6 (May et al. 1997; Stevens et al. 1997; Roach et al. 2001). PCR amplification was performed using M.J. Research PTC-100 thermocyclers in 25-μl volumes containing 30-90 ng DNA. The PCR protocols for the microsatellite markers followed Roach (1999). PCR product was diluted 1 to 1 in stop buffer, and denatured for 5 min. at 95°C. Aliquots were electrophoresed at 45-55 watts for 2-7 hours, depending on fragment length, in 8% denaturing polyacrylamide gels in 1X TBE buffer. Each gel was soaked in 2L of 10% glacial acetic acid for 20 min. to fix the DNA, and DNA was visualized by silver staining as described by Black and DuTeau (1997).

Each sample was genotyped by comparing PCR product with sample standards, and a subset of individuals with homozygous genotypes was sequenced to determine the exact repeat sequence and the length of each allele (Figure 2.4). I used at least one individual from Colorado and from South Dakota per sequenced allele. CGS 14, CGS 17, CGS 22, CGS 26 are made up of $(GT)_n$ repeats, IGS 1 and IGS 6 are made up of $(AC)_n$ repeats, and CGS 25 is made up of both $(GT)_n$ and $(GA)_n$ repeats. Sequencing revealed size homoplasy in two of seven loci. First, in IGS 6, different individuals within both Colorado and South Dakota had either a T or a C at two different nucleotide sites with the same overall repeat length. Therefore, the actual nucleotide sequence of each allele could not be discerned from the banding patterns on gels, and IGS 6 was omitted from all analyses. Second, in CGS 25, there was a split between South Dakota and Colorado in the allele with 19 repeats. In Colorado, this allele was $(GT)_{14}(GA)_{15}$ while in South Dakota this allele was $(GT)_{12}(GA)_{17}$. In other CGS 25 alleles sampled there were no differences found between individuals. Therefore, CGS 25 was included when performing individual site analyses, but omitted when making between site comparisons.

Statistical Analysis

With observed genotype frequencies from microsatellite data, I tested for deviations from Hardy-Weinberg equilibrium and for linkage disequilibrium within each town at each locus using Bonferroni procedures to retain an overall type I error rate of 0.05 with FSTAT version 2.9.3.2 (Goudet 2001). After Bonferroni corrections, only one significant deviation from Hardy-Weinberg equilibrium was detected in one population at one locus (CGS 17, Wind Cave, Bison Flats) out of 124 total tests per locus, population and year, suggesting no systematic departure from Hardy-Weinberg equilibrium. Evidence of linkage disequilibrium was found between one pair of markers in one population (CGS 25 x CGS 26, PNG 2000) out of 75 total tests over all populations, suggesting no physical linkage of between genetic markers.

Observed heterozygosity, H_o, and gene diversity, $(1-\sum_{i=1}^{k} p_i^2, \text{for } k \text{ haplotypes each in frequency } p_i)$, were computed for each population with GDA (Lewis and Zaykin 2001). The level of genetic differentiation among populations was estimated by overall and pairwise F_{st} values (Weir and Cockerham 1984), as was the overall inbreeding coefficient, F_{it}, and the inbreeding coefficient within towns, F_{is}, using FSTAT version 2.9.3.2 (Goudet 2001), with 95% confidence intervals estimated by bootstrapping. I also calculated separate F_{st} values for adult males and females in each sampled population (Weir and Cockerham 1984).

For the mtDNA data, Nei's (1987) gene diversity, $(1-\sum_{i=1}^{k} p_i^2, \text{for } k \text{ haplotypes each in frequency } p_i)$, was computed using Arlequin version 3.1 (Excoffier 2005). Overall genetic differentiation among towns was estimated using Weir and Cockerham's (1984) estimator of F_{st}, and was jackknifed over populations to estimate 95% confidence intervals using GDA (Lewis and Zaykin 2001). Overall F_{st} (Weir and Cockerham 1984) was also calculated separately for adult males and females of each population. I calculated Reynolds et al. (1983) pairwise genetic distances (F_{st}) for haploid data between each of the sampled towns using Arlequin version 3.1 (Excoffier 2005).

To determine the probability that an individual prairie dog originated from its town of capture (source town) based on its multilocus genotype from microsatellite data, GeneClass 2 was used to perform assignment and exclusion tests (Cornuet et al. 1999). Assignment tests assign individuals to the population that maximizes the likelihood of their genotype. Individuals not assigned to their town of capture, but instead assigned to other towns in the system are inferred to be immigrants or direct descendents of immigrants (Cornuet et al. 1999). Chi-square tests were performed to test for differences in the numbers of individuals classified as migrants between sites and between years, and for differences in the numbers of males and females classified as migrants. Exclusion tests use Bayesian methods to generate probabilities that individuals belong to each population and compare probabilities to a threshold for exclusion from each sampled population. Individuals can thus be excluded from none, any, or all towns in the system, based on a designated rejection probability, which was set as the inverse of sample size. 10,000 simulated individuals were used per population. Exclusion tests determined how many individuals were excluded from all of the sampled towns and how many individuals were excluded from their source town but not from other sampled towns. All of these individuals were inferred to be immigrants or direct descendents of immigrants. Likewise, the number of individuals that assigned only to their source town was determined, as was the number of individuals that assigned to their source town as well as to other towns.

To test for isolation by distance, the relationship between landscape and genetic distance, and to test for differences in male and female dispersal across the landscape, I used Mantel general regression tests (Manley 1991). I regressed two geographic distances, drainage distance and Euclidian distance, with genetic distance, F_{st}, from both mtDNA and microsatellite data. Geographic distance was compared to $F_{st}/(1- F_{st})$ because of the linear relationship expected between the two distances in a two-dimensional habitat by putting the two distances on the same scale (Rousset 1997). The haploid mitochondrial genome is maternally inherited, allowing an estimate of how females disperse across the landscape; males carry their mother's mitochondrial DNA (mtDNA), so unless a male is a first generation migrant into a town, his mtDNA represents the mtDNA of either a resident female or a female who dispersed into the town. Diploid microsatellites are inherited from both parents, and allow estimates of how both females and males disperse across the landscape. 10,000 random permutations of the geographic distance matrices were performed to determine statistical significance of the observed Mantel correlations; significance levels were set as the proportion of permutations in which simulated correlation coefficients were equal to or greater than the observed value.

RESULTS

Spatial fragmentation

In the regional analysis, fragmentation of black-tailed prairie dogs on the CPER was higher than all other sites, with the lowest average prairie dog area within a 10-km buffer of sampled prairie dog towns (Figure 2.5a). This was followed by Fort Collins and

Wind Cave with slightly higher areas of prairie dogs within 10-km buffers of sampled prairie dog towns. None of the 95% confidence intervals for the three fragmented sites overlapped with that of Buffalo Gap, which had 4.8 times the area in Wind Cave, 9.4 times the area in Fort Collins, and 22.4 times the area on the CPER. In the temporal analysis on the CPER, the level of fragmentation decreased over time but 95% confidence intervals overlapped between all years (Figure 2.6a).

Overall numbers of alleles and haplotypes

The numbers of alleles per microsatellite locus ranged from four for CGS 26 to nine for CGS 14, with an average of 4.4 alleles per locus and population in the regional analysis and 3.9 alleles per locus and population in the temporal analysis. Overall, 14 mitochondrial haplotypes were sampled, with an average of 3.1 and 2.8 haplotypes per population in the regional and temporal analyses, respectively. More mitochondrial haplotypes were sampled in South Dakota than in Colorado, with 10 haplotypes in South Dakota, three of which were unique, and only five haplotypes in Colorado, with one relatively common haplotype shared between the two regions (Table 2.3).

Regional genetic analysis

Genetic diversity. For the regional analysis, observed heterozygosity, H_o, per population ranged from 0.553 for Wind Cave to 0.621 for Fort Collins with an average of 0.590 across all loci and populations (Table 2.4), while microsatellite gene diversity per population ranged from 0.554 for the CPER to 0.638 for Buffalo Gap with an average of 0.592. Microsatellite gene diversity did not differ between populations. MtDNA gene diversity ranged from 0.311 for Buffalo Gap to 0.605 for Wind Cave, with an overall average of 0.462 (Table 2.4). Although the Buffalo Gap had the lowest gene diversity of all sampled sites, it had seven mitochondrial haplotypes, the highest number of all populations sampled, but 95% confidence intervals for mtDNA gene diversity overlapped for all populations.

Inbreeding. Fragmented populations in Colorado had an overall excess of heterozygotes, with a negative F_{is}, but there was evidence of population-wide inbreeding in the two South Dakota populations that do not experience plague epizootics, Wind Cave ($F_{is} = 0.049$) and Buffalo Gap ($F_{is} = 0.042$: Table 2.5). In Wind Cave, the F_{is} of females ($F_{is} = 0.086$) was significantly different than zero while that of males was not ($F_{is} = 0.015$), while in Buffalo Gap the F_{is} of males was significantly different than zero ($F_{is} = 0.087$), but that of females ($F_{is} = -0.020$) was not, likely from random sampling error.

Genetic differentiation. Estimates of F_{st} between towns from microsatellites (Figure 2.5b) were lower in populations where towns were less isolated, i.e., where the area of prairie dog towns within dispersal distance was larger (Figure 2.5a). The CPER had the highest genetic differentiation ($F_{st} = 0.146$), followed by Fort Collins ($F_{st} = 0.098$) and Wind Cave ($F_{st} = 0.094$). Buffalo Gap had lower differentiation ($F_{st} = 0.016$) than all other sites (non-overlapping 95% confidence intervals). Genetic differentiation estimated from mtDNA shows a similar pattern (Figure 2.5c), with the three fragmented sites having higher F_{st} than the unfragmented site, Buffalo Gap, but only the CPER ($F_{st} = 0.430$) and Buffalo Gap ($F_{st} = 0.048$) had 95% confidence intervals that did not overlap. The 95% confidence intervals for F_{st} in males and females overlapped at all sites for both microsatellites and mtDNA (Table 2.5).

Assignment and exclusion tests. The percent of individuals identified as migrants (Table 2.6) was highest in the least fragmented site, with 19.15% of individuals not assigned to their source town on the CPER, followed by 23.08% for Fort Collins, 41.03% for Wind Cave, and increasing to 56.82% for Buffalo Gap. While the number of individuals identified as immigrants did not significantly differ between fragmented sites with plague in Colorado (CPER vs. Fort Collins: $\chi^2 = 3.0482$; $P = 0.085$), both had significantly fewer immigrants than the fragmented site without plague in South Dakota, Wind Cave ($P < 0.001$), and all fragmented sites were significantly different than the unfragmented site in South Dakota, Buffalo Gap ($P < 0.001$). χ^2 tests revealed no significant differences between the number of males and the number of females classified as immigrants (Table 2.6).

In exclusion tests, individuals excluded from all sampled towns are considered migrants from outside the study sample, while individuals excluded from their town of capture but not other sampled towns are considered migrants or direct descendents of migrants within the study population. The percent of immigrants identified by exclusion tests ranged from 2.1% for the CPER to 4.6% for Buffalo Gap (Table 2.7), with a trend of fragmented sites having fewer immigrants than the unfragmented site.

Landscape measures. In testing isolation by distance using landscape features, I found significant correlations between mtDNA F_{st} and both Euclidean (r = 0.75, $P = 0.0001$) and drainage distance (r = 0.86, $P = 0.0001$) on the CPER. There was no significant correlation between microsatellite F_{st} and either geographic distance (Table 2.8). This relationship was not consistent over all study sites. In Fort Collins, the correlation between mtDNA F_{st} and Euclidean distance was significant (r = 0.81, $P = 0.02$), but the correlation between mtDNA F_{st} and drainage distance was not significant, even though the correlation was slightly stronger (r = 0.86, $P = 0.079$). Also, the correlation between microsatellite F_{st} and drainage distance was significant (r = 0.71, P = 0.028). In Wind Cave, correlations between microsatellite F_{st} and both Euclidean (r = 0.85, P = 0.0001) and drainage distance (r = 0.79, P = 0.0001) were significant and positive. In Buffalo Gap, there were no significant relationships between genetic and geographic distance.

Temporal genetic analysis

Genetic diversity. Temporal analysis of microsatellite markers on the CPER revealed little change in observed heterozygosity, H_o (average of 0.561 over all loci and populations) or gene diversity (average of 0.564: Table 2.4). Mitochondrial gene diversity also did not change, with the same five haplotypes sampled in each year.

Inbreeding. The inbreeding coefficient, F_{is}, was less than zero in 2000 (F_{is} = -0.041) and overlapped zero in 1997 and 2001 (Table 2.5).

Genetic differentiation. Temporal estimates of F_{st} from microsatellite data (Figure 2.6b) decreased as the average total area of prairie dog towns within dispersal distance of sampled towns increased (Figure 2.6a). F_{st} estimated from microsatellites decreased through time, which was not true of the F_{st} estimated from mtDNA (Figure 2.6c), but 95% confidence intervals for F_{st} overlapped for both microsatellites and mtDNA across all time periods.

Assignment and exclusion tests. The percent of individuals classified as immigrants ranged from 17.3% in 1997 to 23.4% in 2001 (Table 2.6), increasing steadily over time, but did not significantly differ between years (χ^2 = 1.3; P = 0.525) or between the number of males and females classified as migrants. The total percent of immigrants identified by exclusion tests ranged from 2.1% in 2000 to 6.2% in 1997 (Table 2.7), with no significant differences between years ($\chi^2 = 2.37$; p = 0.323).

Landscape measures. In testing isolation by distance using landscape features, correlations between mtDNA F_{st} and both Euclidean and drainage distance were significant in all three years sampled (Table 2.8).

DISCUSSION

Fragmentation and metapopulation dynamics may impact genetic diversity and structure by decreasing a population's effective size, N_e, the size of an idealized breeding population that would lose genetic variation by genetic drift at the same rate as the study population (Wright 1931, 1938). In a long-term study in Wind Cave, Dobson et al. (2004) found that effective size was only slightly different than census number. The social structure of coteries, social breeding groups of one to two adult males and three to four highly related female kin and their offspring, actually slowed the loss of genetic diversity from this population. Black-tailed prairie dogs show considerable genetic differentiation between coteries, but no evidence of inbreeding at the level of whole towns (Dobson et al. 1997); thus, genetic differences at the coterie level may help maintain genetic diversity if members from more than one coterie survive population reductions from fragmentation (Daley 1992) or population bottlenecks from metapopulation dynamics.

Genetic effects of fragmentation

Multiple measures in this study showed that fragmentation impacted the amount of gene flow between prairie dog towns. It is logical to expect that areas with more prairie dogs within dispersal distance of towns will have more opportunities for gene flow. This is reflected in patterns of genetic differentiation from microsatellite data, which showed lower differentiation in the less fragmented Buffalo Gap population and over time in the CPER population. Genetic differentiation measured by mtDNA showed a similar pattern, but had wider confidence intervals than the microsatellite data because the estimates reflect variation in a single genetic marker.

Assignment tests also reflected the negative relationship between gene flow and fragmentation, where more individuals were identified as migrants or direct descendants of migrants in sites with greater fragmentation. Actual dispersal rates likely lie somewhere between the estimates from exclusion tests (2.1% for the CPER to 4.6% for Buffalo Gap) and the larger estimates from assignment tests (19% for the CPER and 56% for Buffalo Gap). The lower estimates from exclusion tests are similar to dispersal rates measured by Hoogland (1995), who intensively studied a single town in Wind Cave over 14 years and recorded an average of 3.5 dispersers per year (~3.9%), and by Garrett and Franklin (1988), who recorded between one and four (1.1%-4.2%) immigrants to a study town in Wind Cave per year. However, Knowles (1985) recorded high rates of dispersal (42% (10 individuals) and 15% in two different years) into a small prairie dog town on the Charles M. Russell National Wildlife Refuge in Montana.

The effects of fragmentation were seen in the results from Mantel correlations testing isolation by distance via distances across the landscape. All three fragmented sites displayed positive isolation by distance by both mtDNA and microsatellite data, while in the unfragmented site no correlations between genetic and geographic distance were significant. This implies that in Buffalo Gap, all towns sampled could potentially exchange migrants. In the three fragmented sites, patterns differed between sites. For towns in fragmented areas with plague, CPER and Fort Collins, I found positive and significant correlations between genetic distance from mtDNA and geographic distance, while I found weaker or non-significant correlations between microsatellite genetic distance and geographic distance. This implies that in these areas females move shorter distances, with males moving longer distances and potentially exchanging migrants among all sites. This agrees with a radio-tracking study in which males moved longer distances than females (Garrett and Franklin 1988). In Wind Cave, the only significant correlations were between genetic distance from microsatellite data and geographic distances. However, when the town in Wind Cave with the longest distance to its nearest neighbors was dropped from the analysis, no correlations remained significant. Thus, for the bulk of the towns in Wind Cave, there was no isolation by distance.

Contrary to my prediction, I did not find that isolation by distance decreased over time on the CPER, if anything, correlations between mitochondrial genetic distance and geographic distances showed an increasing trend over the five year sampling period.

Genetic effects of metapopulation dynamics

For most genetic estimates, I was unable to distinguish between fragmented sites that undergo metapopulation dynamics and fragmented sites that do not. For example, numbers of microsatellite alleles, observed heterozygosity, and gene diversity were similar between sites, and genetic differentiation was not significantly different between Fort Collins and Wind Cave. Metapopulation dynamics include regular population bottlenecks from the regular occurrence of extinction and recolonization (Hanski 1999). Populations recolonized by small numbers of individuals, with little subsequent dispersal, should have lower genetic variability and higher genetic differentiation. However, regular gene flow following recolonization from a number of sources will diminish the effects of extinction and recolonization in metapopulations, creating a genetic picture similar to that of populations that are simply fragmented (Barton and Whitlock 1997). The high gene flow inferred from assignment and exclusion tests in both the regional and temporal analyses, and from decreasing genetic differentiation over time on the CPER, suggest that in black-tailed prairie dogs metapopulation dynamics themselves do not increase genetic differentiation above that expected from just fragmentation.

While Wind Cave possesses a long-standing, older complex of prairie dogs with an average town age 46 + years, the prairie dogs towns on Buffalo Gap underwent periodic poisoning, approximately once every three years, from the late-1970's through the mid 1990's. This caused temporary reductions in town size but not complete town extinctions, and reductions were followed by rapid recovery (N. Eisenbraum, Buffalo Gap, personal communication; Buffalo Gap historical files). Declines in genetic diversity from population reductions in randomly mating populations depend on population size and time, following $H_t = H_o(1 - 1/2N_e)^t$, where H_o and H_t are the past and present heterozygosity, N_e is the effective population size, and t is time in generations (Hedrick 2004). This equation makes clear that the length of time spent in a population bottleneck dramatically affects the impact of a bottleneck on genetic diversity. Because prairie dog populations in Buffalo Gap recovered quickly from control efforts, the fluctuations in population size apparently did not have a strong impact on genetic diversity.

Regardless, I found three differences between the populations that undergo metapopulation dynamics from plague epizootics and those that do not. This implies that the population fluctuations on Buffalo Gap were not genetically equivalent to metapopulation dynamics. First, there were 10 mitochondrial haplotypes in South Dakota populations, which do not experience die-offs from plague, as compared to five haplotypes in Colorado populations, which regularly experience plague epizootics. Recent declines in effective population size will cause a reduction in numbers of alleles and gene diversity in polymorphic loci with loss of alleles occurring faster than the reduction in gene diversity (Luikart and Cornuet 1998). Thus, the lower numbers of mitochondrial haplotypes found in Colorado may be evidence of allelic loss caused by regular extinctions from plague. Additionally, it is interesting to note that three of the 10 haplotypes found in South Dakota were unique to Wind Cave, while four of the 10 haplotypes were unique to Buffalo Gap, with three haplotypes shared between the two sites. Despite fluctuations in population size, prairie dog towns on Buffalo Gap maintained rare alleles.

Second, while the fragmented sites with plague were either outbred ($F_{is} < 0$) or showed no sign of inbreeding ($F_{is} = 0$), both South Dakota populations had low but significant inbreeding coefficients ($F_{is} > 0$). Wind Cave possesses long standing, older towns that represent an equilibrial state, with more time to build inbreeding within their populations. The prairie dog towns in Buffalo Gap experienced population size fluctuations, but were still older than any of the towns sampled in Colorado. Behavioral observations (Hoogland 1995) and pedigree analyses (Dobson et al. 1997) demonstrate low levels of inbreeding in prairie dogs in Wind Cave at the colony level. While prairie dogs minimize inbreeding and are even slightly outbred at the coterie level, Dobson et al. (1997) found that prairie dogs do not minimize or promote inbreeding at the town level ($F_{is} \sim 0$). In contrast, the relatively young towns in Colorado represent a nonequilibrial state because new colonists into towns bring new genotypes and thus increase overall heterozygosity. Also, old towns have stable coterie structures with little change from year to year (Hoogland 1995) and will thus have standing genetic differences between coteries. Young towns, because they are newly formed and changing rapidly, will have less stable coterie structure over time. Trapping was designed to sample numerous coteries on each town, and thus could have resulted in an unintentional Wahlund effect, which is an increased frequency of homozygotes in a higher level of social structure because of missed population subdivision at a lower level of social structure (Dobson et al. 1997). This effect would be less pronounced on newly colonized towns within a metapopulation.

The third feature of populations that undergo metapopulation dynamics is significantly lower numbers of individuals classified as immigrants by assignment tests in fragmented sites with plague. The two sites in South Dakota have older towns that have had more time for gene flow to take place, and for the overall population to come to genetic equilibrium. However, if town age were the driving factor behind the number of individuals identified as immigrants, then Wind Cave, which has the oldest recorded ages of towns, should have higher rates of migration than Buffalo Gap, but this was not the case.

Genetic changes through time on the CPER

While there were no significant differences in fragmentation, genetic diversity, genetic differentiation, or the estimated numbers of migrants in the temporal analysis, multiple lines of evidence suggest significant gene flow among populations. Fragmentation and genetic differentiation from microsatellite data decreased through time, while the numbers of individuals identified as immigrants or descendants of immigrants by assignment tests increased through time. These patterns imply regular gene flow over time, which would allow for the numbers of migrants to build up in a population if individual migrants survive between sampling. Gene flow may increase with decreasing fragmentation because of the larger number of potential migrants in a less fragmented landscape.

Sex-biased dispersal

When testing for sex-biased dispersal in the number of individuals classified as immigrants by assignment tests, there were no significant differences between males and females. This supports previous findings that yearling males are the most common intertown dispersers, but adult males and females also disperse between towns (Knowles 1985; Garrett and Franklin 1988; Hoogland 1995). In fact, Garrett and Franklin (1988) observed more adult females than adult males moving between towns, and Hoogland's (1995) study of a town in Wind Cave over 14 years recorded 28 male and 21 female immigrants, although 46% of the male immigrants reproduced while only 24% of the female immigrants reproduced, so the effective migration rate was still male-biased.

While this study found no significant differences in the numbers of male and female migrants, the tests of isolation by distance do suggest male biased dispersal. On the CPER in all three years sampled, there were positive and significant correlations between genetic distance from mtDNA and geographic distance but not between genetic distance from microsatellite DNA and geographic distance. Because mtDNA is maternally inherited, the signal from mtDNA represents female dispersal even when sampled from adult males, unless a particular male was a first generation migrant.

Microsatellites are bi-parentally inherited and represent dispersal from both males and females. Thus, finding isolation by distance for mtDNA but not for microsatellite DNA implies that females are dispersing shorter distances, while males are able to disperse between all towns sampled.

In summary, this study found that fragmentation was associated with decreased gene flow between populations. While there was some evidence of differences among populations that undergo metapopulation dynamics and those that do not, there was not as strong a genetic signal from metapopulation dynamics. The gene flow taking place among towns appears to be large enough to quickly decrease the genetic signal that would come from recolonization after extinction. Certainly, gene flow on the CPER, in a period between plague epizootics, was high enough to reduce genetic differentiation to a level indistinguishable from that of Wind Cave, a fragmented population not subject to epizootics from plague. Similarly, Fort Collins, with an older set of prairie dog towns than the CPER, also represented a fragmented metapopulation whose level of genetic differentiation was indistinguishable from a fragmented population that did not cycle from plague. Since plague has been documented in more than half of the historic range of black-tailed prairie dogs (Cully and Williams 2001), metapopulation dynamics are now a permanent factor in the management of many prairie dog populations. The results of this study suggest that management of both metapopulation dynamics and fragmentation should include the preservation of gene flow among towns to maintain genetic diversity. In areas with plague, this must be balanced with the risks associated with inter-town dispersal of plague-infected prairie dogs and their fleas.

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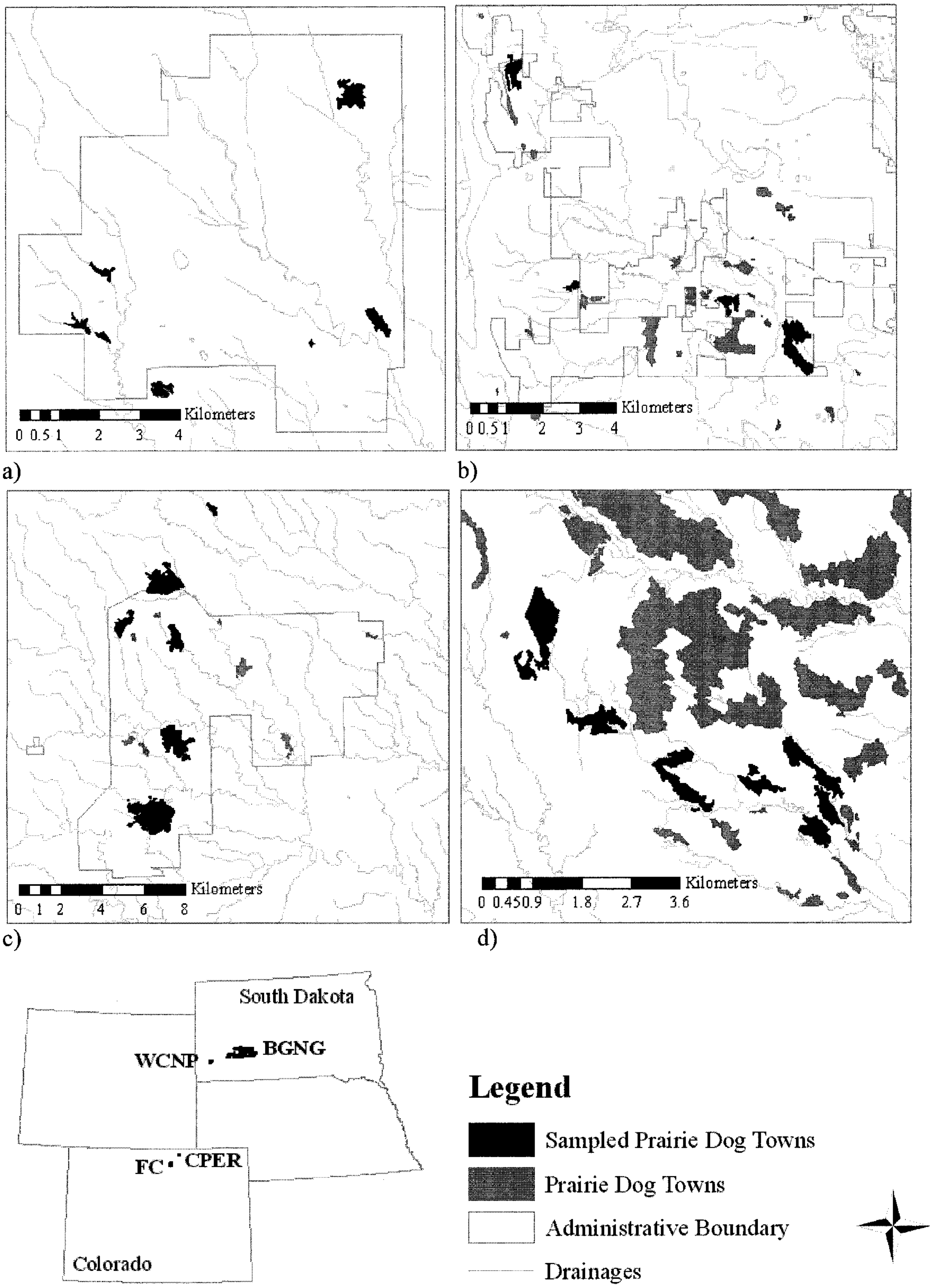

Figure 2.1. Black-tailed prairie dog towns on a) the Central Plains Experimental Range, CO, b) Fort Collins, CO, c) Wind Cave National Park, SD, and d) Buffalo Gap National Grassland, SD in 2000-2001.

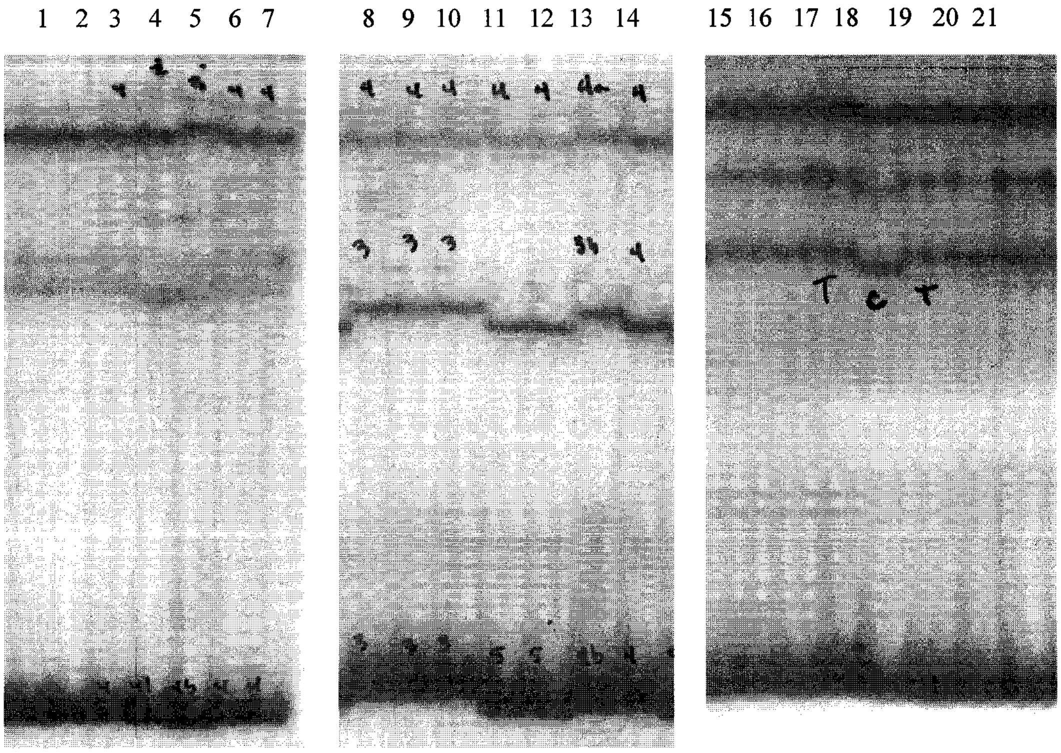

Figure 2.2. Single strand conformation polymorphism (SSCP) analysis of two fragments of the mitochondrial control region of black-tailed prairie dogs. Lanes 1-7 show variants of fragment A, 203 bp, lanes 8-14 show variants of fragment B, 251 bp, and lanes 15-21 show variants of a 140 bp section of fragment B which differentiate haplotypes with a single nucleotide difference.

	50	102	163	174	202	211	281	288	331	357	362	374	376	391
A	**T**	**--**	**A**	**T**	**G**	**A**	**C**	**--**	**A**	**T**	**C**	**--**	**T**	**T**
B	.	.	.	.	.	.	T	.	.	.	.	.	.	.
C	.	.	.	C	.	.	T	.	.	.	.	.	.	.
D	.	T	.	.	.	.	.	.	.	.	.	.	.	.
E	.	T	.	.	.	.	T	.	.	.	.	.	.	.
F	.	.	.	.	.	.	.	.	.	C	.	.	.	C
G	.	.	.	.	.	.	.	.	.	C	.	A	.	C
H	.	.	.	.	.	.	.	.	G	.	.	.	C	.
I	.	.	.	.	.	.	.	.	G	.	.	.	.	.
J	C	.	.	.	.	.	.	.	.	.	.	.	.	.
K	.	.	.	.	.	.	.	.	.	.	T	.	C	.
LS	.	.	.	.	.	.	.	G	.	.	.	.	.	.
MS	.	.	G	.	A	.	T	.	.	.	.	.	.	.
NS	C	.	.	.	.	C	.	.	.	.	.	.	.	.

Figure 2.3. Position and composition of variable sites of 14 haplotypes based on the sequencing and alignment of a 454 bp section of the mitochondrial control region of black-tailed prairie dogs.

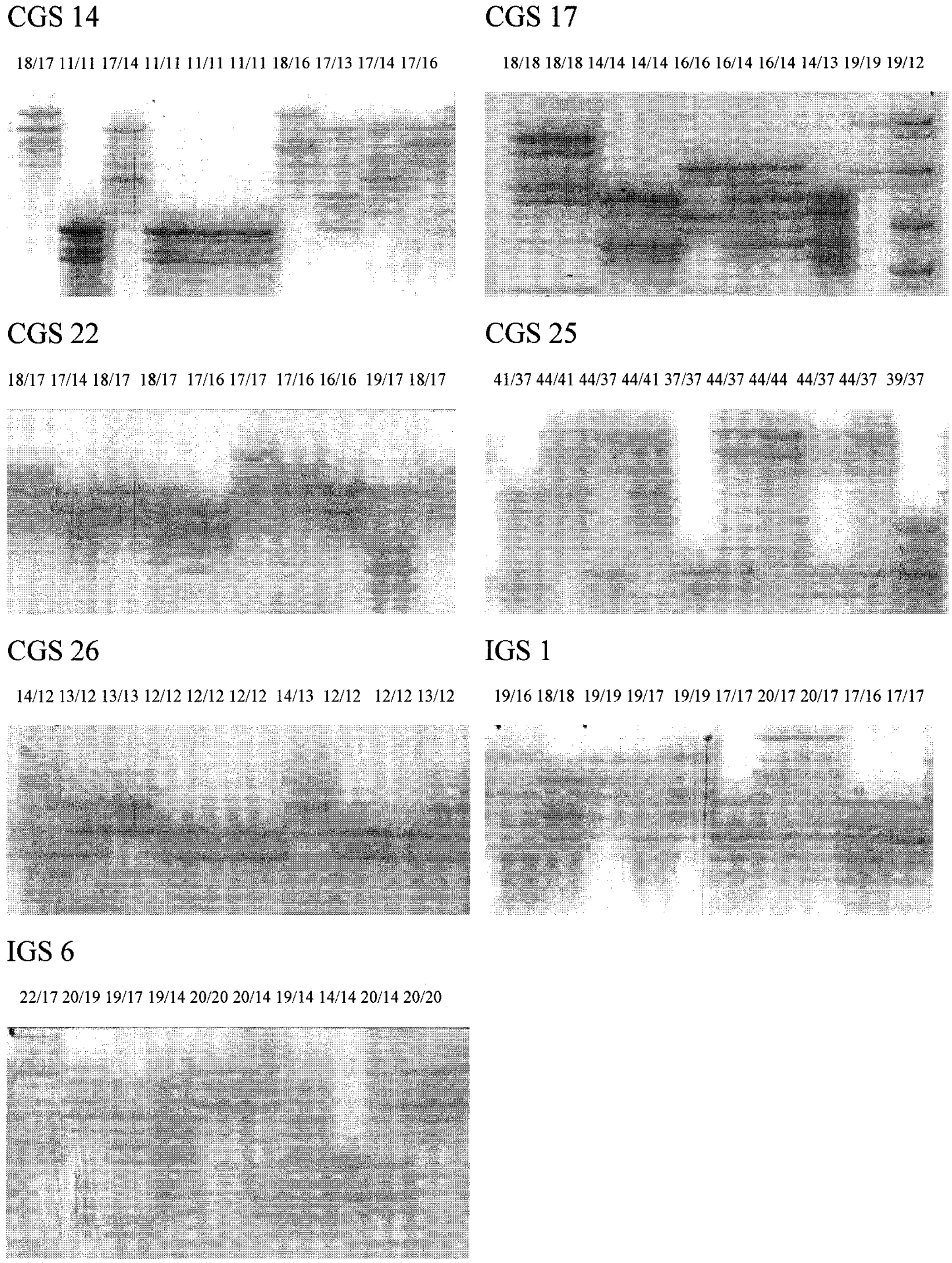

Figure 2.4. Examples of banding patterns of seven microsatellite loci in black-tailed prairie dogs. CGS 14, CGS 17, CGS 22, CGS 26 are made up of $(GT)_n$ repeats, IGS 1 and IGS 6 are made up of $(AG)_n$ repeats, and CGS 25 is made up of both $(GT)_n$ and $(GA)_n$ repeats. Microsatellites are codominant markers; the number of repeats in each set of alleles is listed above each lane.

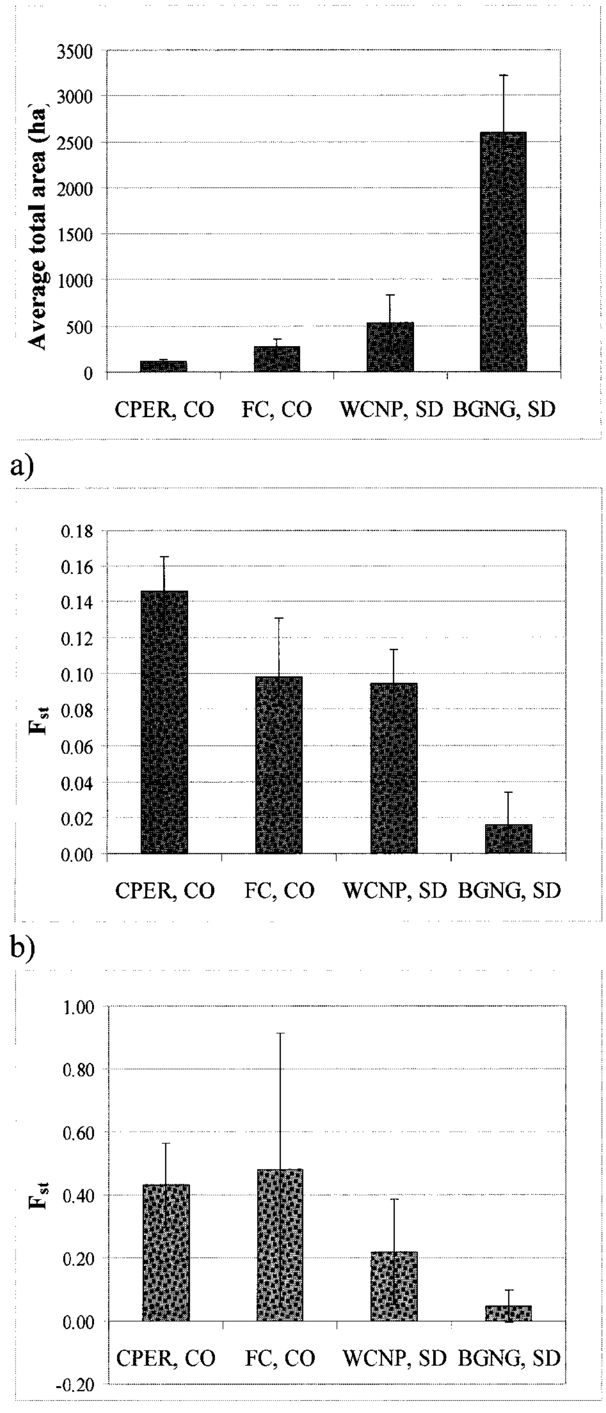

Figure 2.5. a) Fragmentation in 2000-2001, measured by the average total area of prairie dog towns within a 10-km buffer of the centroid of each sampled town at each site, and genetic differentiation (F_{st}) from b) microsatellite data and c) mtDNA for black-tailed prairie dogs in four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins, CO (FC); Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD). 95% confidence intervals shown.

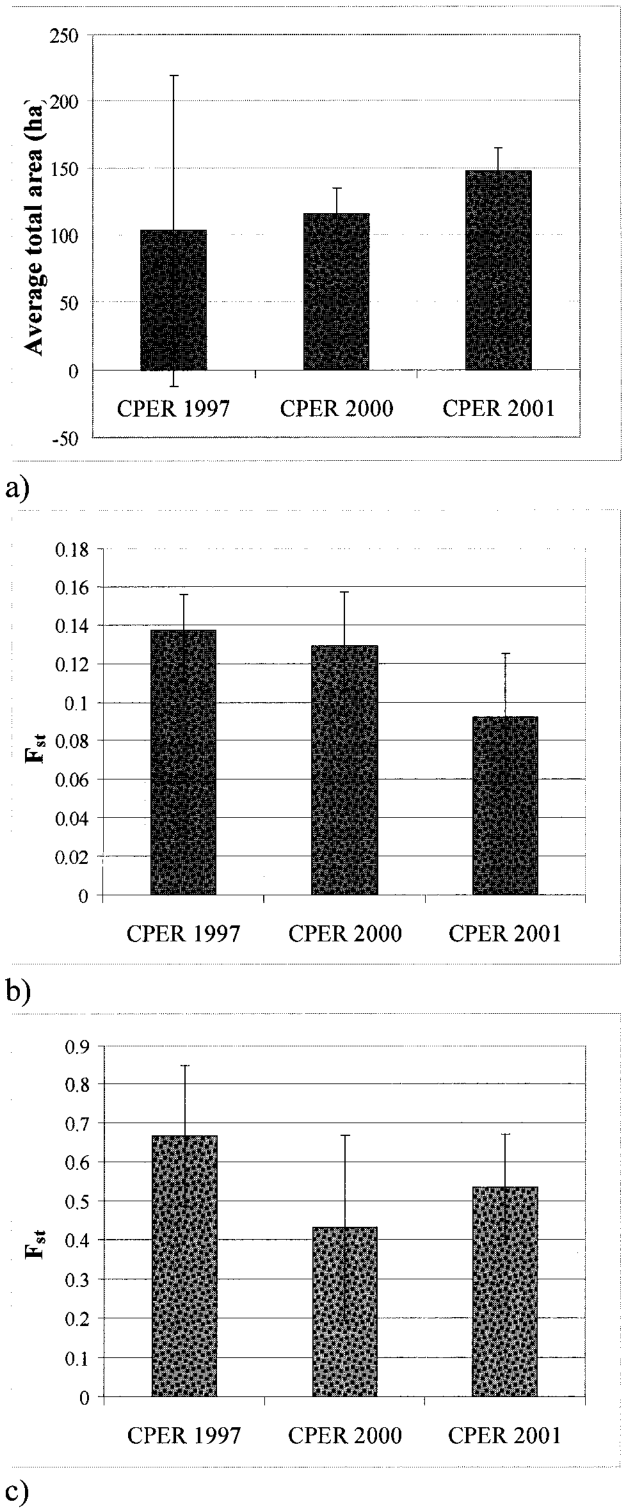

Figure 2.6. a) Fragmentation, measured by the average total area of prairie dog towns within a 10-km buffer of the centroid of each sampled town at each site, and genetic differentiation (F_{st}) from b) microsatellite data and c) mtDNA for black-tailed prairie dogs on the Central Plains Experimental Range (CPER), CO in 1997, 2000, and 2001. 95% confidence intervals shown.

Table 2.1. Description of age, size, geographic isolation, sample sizes and presence of plague for black-tailed prairie dog towns sampled on the Central Plains Experimental Range (CPER), CO, Fort Collins (FC), CO, Wind Cave National Park (WCNP), SD and Buffalo Gap National Grassland (BGNG), SD.[*]

Study Site	**Year**	**No. of towns sampled**	**Ave. town age[§]**	**Ave. town size (ha)**	**Ave. total prairie dog area (ha) within 10 km buffer**	**Ave. distance to nearest neighboring town (km)**	n_{mean}	n_{tot}	**Plague Present**
CPER, CO	2000	6	4.67	14.1	115.5	2.4	23.5	141	Yes
FC, CO	2000	4	9 +	24.3	274.7	3.7	26.0	104	Yes
WCNP, SD	2000	6	46 +	79.1	534.9	3.3	26.0	156	No
BGNG, SD	2001	5	29.8 +	38.5	2592.8	1.5	26.4	132	No
CPER, CO	1997	6	1.67	4.1	103.3	2.4	13.4	81	Yes
CPER, CO	2000	6	4.67	14.1	115.5	2.4	23.5	141	Yes
CPER, CO	2001	5	5.67	27.8	146.9	3.3	24.8	124	Yes

[§] + indicates some towns had approximate ages because of lack of long term monitoring.

[*] Abbreviations: n_{mean} = average number of individuals sampled per town; n_{tot} = total number of individuals sampled.

Table 2.2. Amplification and Sequencing Primers

No.	**Primer**	**Primer Sequence ('5 - '3)**	**Pairs with (expected size)**
1	L15926	TCA AAG CTT ACA CCA GTC TTG TAA ACC	2 (980 bp); 3 (203 bp)
2	H00651	TAA CTG CAG AAG GCT AGG ACC AAA CCT	1 (980 bp)
3	ltsH200	AAT AAT GGC TTA ATG TGG AGG TG	1 (203 bp)
4	ltsL250	TAA TTG CAC CTC CAC ATT AAG C	5 (251 bp)
5	ltsH250	CAA CAT TGG TAG GGG ATA GTC ATT T	4 (251 bp); 6 (140 bp)
6	ltsL140	CGG GCT GAG GTA ATG TAT TAT G	5 (140 bp)

Table 2.3. Distribution of mitochondrial control region haplotypes in each sampled population of black-tailed prairie dogs: Fort Collins (FC), CO; Buffalo Gap National Grassland (BGNG), SD; Wind Cave National Park (WCNP), SD; Central Plains Experimental Range (CPER), CO.

Haplotype	**FC, CO**	**WCNP, SD**	**BGNG, SD**	**CPER, CO 1997**	**CPER, CO 2000**	**CPER, CO 2001**
A	41	53	108	2	2	5
B				37	46	47
C				7	15	11
D	35			7	35	40
E	28			23	33	21
F		49	7			
G		17				
H		11				
I		25	1			
J			7			
K			7			
LS		1				
MS			1			
NS			1			

Table 2.4. Genetic diversity of a) four black-tailed prairie dog populations (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) estimated by 5 microsatellite markers and one mitochondrial marker and b) black-tailed prairie dogs on the CPER in 1997, 2000, and 2001, estimated by 6 microsatellite markers and one mitochondrial marker, with 95% confidence intervals in parentheses.*

	Microsatellite Data					MtDNA		
	n	n_{tot}	A	H_o	*Gene Diversity*	A	*No. Hap.*	*Gene Diversity*
a) Regional Comparisons								
CPER, CO	23.5	141	3.767	0.588 (0.290, 0.886)	0.553 (0.280, 0.826)	3.17	5	0.477 (0.268, 0.686)
FC, CO	26.0	104	4.700	0.623 (0.339, 0.907)	0.610 (0.284, 0.936)	2.00	3	0.418 (0.058, 0.777)
WCNP, SD	26.0	156	3.867	0.553 (0.317, 0.789)	0.581 (0.316, 0.846)	3.67	6	0.605 (0.303, 0.906)
BGNG, SD	26.4	132	4.960	0.612 (0.372, 0.852)	0.639 (0.386, 0.892)	3.00	7	0.311 (0.100, 0.521)
Adult Males								
CPER, CO	12.5	75	3.200	0.585 (0.271, 0.899)	0.544 (0.307, 0.781)	2.67	5	0.456 (-0.039, 0.950)
FC, CO	14.0	56	4.300	0.640 (0.352, 0.928)	0.613 (0.278, 0.948)	2.00	3	0.448 (0.165, 0.731)
WCNP, SD	13.8	83	3.733	0.578 (0.382, 0.774)	0.593 (0.338, 0.848)	3.50	6	0.655 (0.356, 0.954)
BGNG, SD	13.8	69	4.240	0.569 (0.293, 0.845)	0.633 (0.389, 0.877)	2.40	5	0.310 (-0.034, 0.655)
Females								
CPER, CO	9.3	56	3.367	0.588 (0.277, 0.899)	0.550 (0.208, 0.892)	2.50	5	0.461 (0.138. 0.784)
FC, CO	10.3	41	3.950	0.612 (0.323, 0.901)	0.609 (0.323, 0.895)	1.75	3	0.386 (-0.123, 0.896)
WCNP, SD	10.8	65	3.567	0.530 (0.253, 0.807)	0.583 (0.315, 0.851)	2.83	5	0.559 (0.219, 0.900)
BGNG, SD	10.2	51	4.240	0.658 (0.413, 0.903)	0.645 (0.373, 0.917)	2.40	6	0.350 (0.175, 0.524)
b) Temporal Comparisons								
CPER 1997	13.4	81	3.583	0.568 (0.339, 0.797)	0.566 (0.360, 0.772)	2.00	5	0.251 (-0.205, 0.706)
CPER 2000	23.5	141	3.722	0.574 (0.299, 0.849)	0.545 (0.298, 0.792)	3.17	5	0.477 (0.268, 0.686)
CPER 2001	24.8	124	3.767	0.563 (0.373, 0.753)	0.561 (0.363, 0.759)	3.40	5	0.374 (0.104, 0.644)
Adult Males								
CPER 2000	12.5	75	3.194	0.579 (0.296, 0.862)	0.539 (0.326, 0.752)	2.67	5	0.456 (-0.039, 0.950)
CPER 2001	12.0	60	3.467	0.595 (0.473, 0.717)	0.589 (0.392, 0.784)	2.80	5	0.364 (-0.143, 0.871)
Females								
CPER 2000	9.3	56	3.278	0.562 (0.255, 0.869)	0.536 (0.224, 0.848)	2.50	5	0.461 (0.138. 0.784)
CPER 2001	10.4	52	3.133	0.526 (0.226, 0.826)	0.519 (0.282, 0.756)	2.60	5	0.423 (0.248. 0.598)

[*] Abbreviations: n = mean sample size; n_{tot} = total sample size; A = mean number of alleles or haplotypes per population; *No. Hap.* = total number of haplotypes sampled; H_o = observed heterozygosity.

Table 2.5. Genetic structure of black-tailed prairie dog populations in a) four study populations (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) and b) the CPER in 1997, 2000, and 2001 as measured by Weir and Cockerham's (1984) estimators of F statistics: F_{is} (f), F_{it} (F), and F_{st} (Θ), for microsatellite data and Weir and Cockerham's (1984) F_{st} (Θ) for mitochondrial haplotype data, with 95% confidence intervals in parentheses.

	Microsatellite Data			**MtDNA**
	F_{is}	F_{it}	F_{st}	F_{st}
a) Regional Comparisons				
CPER, CO	-0.054 (-0.079, -0.031)	0.100 (0.079, 0.125)	0.146 (0.122, 0.165)	0.431 (0.296, 0.566)
FC, CO	-0.019 (-0.066, 0.008)	0.081 (0.068, 0.097)	0.098 (0.082, 0.131)	0.480 (0.045, 0.915)
WCNP, SD	0.049 (0.002, 0.091)	0.139 (0.084, 0.183)	0.094 (0.072, 0.113)	0.220 (0.053, 0.387)
BGNG, SD	0.042 (0.012, 0.074)	0.058 (0.021, 0.098)	0.016 (0.006, 0.034)	0.049 (-0.002, 0.099)
Adult Males				
CPER, CO	-0.074 (-0.116, -0.021)	0.094 (0.079, 0.199)	0.156 (0.124, 0.177)	0.489 (0.179, 0.799)
FC, CO	-0.032 (-0.114,0.019)	0.075 (0.028, 0.122)	0.104 (0.071, 0.156)	0.465 (0.094, 0.837)
WCNP, SD	0.015 (-0.046, 0.065)	0.093 (0.020, 0.155)	0.078 (0.053, 0.107)	0.195 (0.023, 0.366)
BGNG, SD	0.087 (0.059, 0.125)	0.111 (0.077, 0.162)	0.027 (0.015, 0.043)	0.089 (-0.089, 0.267)
Females				
CPER, CO	-0.059 (-0.132, -0.006)	0.101 (0.047, 0.160)	0.152 (0.098, 0.212)	0.415 (0.267, 0.562)
FC, CO	-0.007 (-0.051, 0.028)	0.094 (0.052, 0.122)	0.100 (0.089, 0.115)	0.524 (-0.069, 1.118)
WCNP, SD	0.086 (0.024, 0.154)	0.171 (0.097, 0.231)	0.093 (0.062, 0.121)	0.254 (0.107, 0.401)
BGNG, SD	-0.020 (-0.058, 0.030)	-0.016 (-0.057, 0.024)	0.004 (-0.015, 0.030)	-0.002 (-0.065, 0.061)
b) Temporal Comparisons				
CPER 1997	-0.003 (-0.058, 0.041)	0.134 (0.048, 0.195)	0.137 (0.101, 0.163)	0.667 (0.429, 0.905)
CPER 2000	-0.041 (-0.068, -0.008)	0.093 (0.072, 0.115)	0.129 (0.086, 0.162)	0.431 (0.296, 0.566)
CPER 2001	-0.003 (-0.056, 0.040)	0.089 (0.029, 0.137)	0.092 (0.050, 0.123)	0.536 (0.408, 0.664)
Adult Males				
CPER 2000	-0.070 (-0.103, -0.026)	0.077 (0.038, 0.108)	0.137 (0.087, 0.169)	0.489 (0.178, 0.801)
CPER 2001	-0.003 (-0.064, 0.055)	0.073 (-0.015, 0.140)	0.076 (0.047, 0.100)	0.569 (0.319, 0.818)
Females				
CPER 2000	-0.033 (-0.101, 0.039)	0.106 (0.057, 0.157)	0.135 (0.079, 0.197)	0.421 (0.285, 0.557)
CPER 2001	-0.007 (-0.059, 0.066)	0.131 (0.065, 0.214)	0.137 (0.079, 0.190)	0.480 (0.335, 0.626)

Table 2.6. Results of assignment tests: percent of individual black-tailed prairie dogs which assigned correctly to their source town (town of capture), the percent which did not assign to their source town, inferred to be immigrants or direct descendants of immigrants, and the percent of males and females not correctly assigned to their source town for a) four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) in 2000-2001 and b) the CPER in 1997, 2000, and 2001. Sample sizes in parentheses.

a) Regional Comparisons	**CPER, CO**	**FC, CO**	**WCNP, SD**	**BGNG, SD**
Correctly assigned to source	80.85% (114/141)	76.92% (80/104)	58.97% (92/156)	43.18% (57/132)
Not assigned to source	19.15% (27/141)	23.08% (24/104)	41.03% (64/156)	56.82% (75/132)
Males not assigned to source	20.00% (17/85)	20.63% (13/63)	39.56% (36/91)	55.56% (45/81)
Females not assigned to source	17.86% (10/56)	26.83% (11/41)	43.08% (28/65)	58.82% (30/51)

b) Temporal Comparisons	**CPER 1997**	**CPER 2000**	**CPER 2001**
Correctly assigned to source	82.72% (67/81)	80.85% (114/141)	76.61% (95/124)
Not assigned to source	17.28% (14/81)	19.15% (27/141)	23.39% (29/124)
Males not assigned to source		20.00% (17/85)	26.39% (19/72)
Females not assigned to source		17.86% (10/56)	19.23% (10/52)

Table 2.7. Results of exclusion tests: percent of black-tailed prairie dogs classified as migrants or descendants of migrants (prairie dogs excluded from all sampled towns or excluded from the source town in which they were captured), the percent prairie dogs excluded from all towns except the source town, and the percent that was not excluded from the source town as well as other sampled towns for a) four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) in 2000-2001 and b) the CPER in 1997, 2000, and 2001. Sample sizes in parentheses.

a) Regional Comparisons	**CPER, CO**	**FC, CO**	**WCNP, SD**	**BGNG, SD**
Probability threshold	0.0071 (1/141)	0.0096 (1/104)	0.0064 (1/156)	0.0076 (1/132)
Exclude all sampled towns	0.71% (1/141)	1.92% (2/104)	0.00% (0/156)	0.00% (0/132)
Exclude source (but not other towns)	1.42% (2/141)	1.92% (2/104)	2.56% (4/156)	4.55% (6/132)
Exclude all towns except source	4.26% (6/141)	14.42% (15/104)	5.13% (8/156)	0.00% (0/132)
Can not exclude source and other towns	93.62% (132/141)	81.73% (85/104)	92.31% (144/156)	95.45% (126/132)

b) Temporal Comparisons	**CPER 1997**	**CPER 2000**	**CPER 2001**
Probability threshold	0.0123 (1/81)	0.0071 (1/141)	0.0081 (1/124)
Exclude all sampled towns	0.00% (0/81)	0.71% (1/141)	0.81% (1/124)
Exclude source (but not other towns)	6.17% (5/81)	1.42% (2/141)	3.23% (4/124)
Exclude all towns except source	8.64% (7/81)	4.26% (6/141)	7.26% (9/124)
Can not exclude source and other towns	85.19% (69/81)	93.62% (132/141)	88.71% (110/124)

Table 2.8. Mantel correlations between genetic distances ($F_{st}/(1-F_{st})$ from mitochondrial and microsatellite data) and geographic distances between black-tailed prairie dog towns for a) four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins, CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) in 2000-2001 and b) the CPER in 1997, 2000, and 2001.

Site	No. Towns Sampled	Genetic Distance	Geographic Distance	r	p
a) Regional Comparisons					
CPER, CO	6	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.748	0.0001
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.864	0.0001
		Micro. $F_{st}/(1-F_{st})$	Euclidean	0.051	0.3608
		Micro. $F_{st}/(1-F_{st})$	Drainage	-0.025	0.5979
FC, CO	4	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.81	0.0283
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.868	0.0787
		Micro. $F_{st}/(1-F_{st})$	Euclidean	0.522	0.2191
		Micro. $F_{st}/(1-F_{st})$	Drainage	0.708	0.0283
WCNP, SD	6	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.385	0.1135
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.288	0.1445
		Micro. $F_{st}/(1-F_{st})$	Euclidean	0.847	0.0001
		Micro. $F_{st}/(1-F_{st})$	Drainage	0.786	0.0001
BGNG, SD	5	Mito. $F_{st}/(1-F_{st})$	Euclidean	-0.342	0.1818
		Mito. $F_{st}/(1-F_{st})$	Drainage	-0.388	0.1419
		Micro. $F_{st}/(1-F_{st})$	Euclidean	-0.069	0.4962
		Micro. $F_{st}/(1-F_{st})$	Drainage	-0.065	0.4962
a) Temporal Comparisons					
CPER 1997	6	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.388	0.0413
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.452	0.031
		Micro. $F_{st}/(1-F_{st})$	Euclidean	-0.267	0.2062
		Micro. $F_{st}/(1-F_{st})$	Drainage	-0.231	0.1752
CPER 2000	6	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.748	0.0001
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.864	0.0001
		Micro. $F_{st}/(1-F_{st})$	Euclidean	0.033	0.3814
		Micro. $F_{st}/(1-F_{st})$	Drainage	-0.026	0.5876
CPER 2001	5	Mito. $F_{st}/(1-F_{st})$	Euclidean	0.796	0.0159
		Mito. $F_{st}/(1-F_{st})$	Drainage	0.884	0.0159
		Micro. $F_{st}/(1-F_{st})$	Euclidean	-0.582	0.1022
		Micro. $F_{st}/(1-F_{st})$	Drainage	-0.511	0.0551

APPENDIX 2.1

	Town	Town size (ha)	Total prairie dog area (ha) within 10 km buffer	Average Euclidean distance between towns (km)	Euclidean distance to nearest neighbor (km)	Average drainage distance between towns (km)	Drainage distance to nearest neighbor (km)
a) Regional Comparisons							
CPER, CO	5	30.91	111.41	7.3	5.5	33.5	8.7
	22	7.57	106.72	4.9	1.4	23.3	4.0
	27	12.48	108.73	5.1	1.4	23.6	4.0
	29	17.70	128.11	5.5	1.8	18.3	3.2
	30	1.04	128.11	4.6	1.8	21.4	3.2
	35	14.62	109.97	4.8	2.4	17.8	5.6
FC, CO	FC	57.41	286.85	6.4	2.2	11.4	3.1
	PD	14.73	308.23	5.0	2.2	11.5	3.1
	DX	21.38	213.06	8.4	5.9	16.8	14.7
	LF	3.80	290.57	5.5	4.3	13.9	13.5
WCNP, SD	BF	225.72	512.03	9.5	3.7	27.7	6.9
	ST	37.19	666.42	5.0	2.6	23.4	15.2
	RR	118.21	651.90	6.7	3.7	23.7	6.9
	CT	35.57	436.06	5.7	2.7	19.6	3.3
	PR	47.78	661.78	5.5	2.6	14.8	3.3
	WL	9.87	280.92	8.7	4.2	30.7	16.2
BGNG, SD	CU	55.25	2262.78	2.4	1.4	3.5	2.1
	LI	35.36	2407.90	2.6	1.1	3.9	1.8
	GA	59.65	3097.57	3.4	1.1	5.1	1.8
	RD	15.48	2507.74	2.8	1.9	4.1	2.7
	BR	26.70	2687.85	4.1	2.0	6.2	3.2
a) Temporal Comparisons							
CPER 1997	5	6.11	34.73	7.3	5.7	28.8	8.6
	22	3.23	46.81	4.9	1.4	21.1	3.9
	27	7.19	69.92	5.1	1.4	21.0	3.9
	29	2.19	155.36	4.6	1.8	21.3	3.1
	30	3.22	159.33	5.5	1.8	18.1	3.1
	35	2.37	153.85	4.8	2.4	17.8	5.5
CPER 2000	5	30.91	111.41	7.3	5.5	33.5	8.7
	22	7.57	106.72	4.9	1.4	23.3	4.0
	27	12.48	108.73	5.1	1.4	23.6	4.0
	29	17.70	128.11	5.5	1.8	18.3	3.2
	30	1.04	128.11	4.6	1.8	21.4	3.2
	35	14.62	109.97	4.8	2.4	17.8	5.6
CPER 2001	5	47.51	141.38	7.6	5.5	35.5	8.7
	22	17.74	141.38	4.8	1.4	22.4	4.0
	27	21.22	143.13	5.0	1.4	22.6	4.0
	29	34.71	163.35	6.4	5.5	22.0	8.7
	35	18.06	145.10	5.0	2.4	16.4	5.6

Appendix 2.1. Spatial characteristics of sampled towns in a) four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) and b) the CPER, CO in 1997, 2000 and 2001.

APPENDIX 2.2

				overall		CGS 14		CGS 17		CGS 22		CGS 26		IGS 1		mt control rgn	
	town	*n*	*A*	*He*	*Ho*	*a*	*He*	*a*	*He*	*a*	*He*	*a*	*He*	*a*	*He*	*a*	*GD*
PNG, CO	5	26	4.0	0.547	0.577	5	0.724	6	0.751	2	0.420	3	0.347	4	0.489	2	0.271
	22	27	4.4	0.617	0.674	5	0.688	8	0.784	3	0.558	2	0.439	4	0.610	3	0.467
	27	25	3.8	0.565	0.552	4	0.448	5	0.718	2	0.503	3	0.363	5	0.794	5	0.523
	29	25	3.6	0.516	0.512	4	0.559	5	0.756	3	0.516	2	0.217	4	0.534	3	0.573
	30	13	3.8	0.614	0.708	4	0.599	6	0.821	2	0.436	3	0.494	4	0.702	3	0.500
	35	25	3.0	0.464	0.504	3	0.468	5	0.653	2	0.302	2	0.458	3	0.437	3	0.527
FC, CO	FC	26	4.6	0.639	0.677	6	0.671	6	0.717	4	0.602	2	0.506	5	0.694	2	0.508
	PD	26	4.4	0.538	0.500	5	0.602	5	0.697	5	0.554	2	0.208	5	0.636	2	0.520
	DX	27	5.0	0.587	0.570	7	0.811	7	0.799	5	0.541	2	0.140	4	0.644	2	0.143
	LF	25	4.8	0.679	0.744	5	0.758	8	0.804	5	0.708	2	0.470	4	0.648	2	0.500
WCNP, SD	BF	27	4.2	0.663	0.570	5	0.712	6	0.744	4	0.677	2	0.509	4	0.681	4	0.667
	ST	25	4.2	0.585	0.648	6	0.811	6	0.801	3	0.492	2	0.392	4	0.424	2	0.333
	RR	26	4.2	0.651	0.592	5	0.703	6	0.832	4	0.654	2	0.509	4	0.562	5	0.775
	CT	27	3.8	0.542	0.556	5	0.578	5	0.723	3	0.672	2	0.308	4	0.427	3	0.530
	PR	25	3.8	0.594	0.520	4	0.707	6	0.670	3	0.636	2	0.330	4	0.635	4	0.667
	WL	26	3.0	0.449	0.431	4	0.437	3	0.649	3	0.534	2	0.266	3	0.358	4	0.655
BGNG, SD	CU	27	4.6	0.646	0.696	5	0.736	7	0.705	4	0.751	2	0.499	5	0.536	3	0.373
	LI	27	5.2	0.647	0.600	8	0.799	7	0.697	5	0.716	2	0.500	4	0.526	3	0.271
	GA	26	5.2	0.633	0.569	7	0.724	7	0.690	5	0.783	2	0.362	5	0.613	2	0.212
	RD	27	5.4	0.655	0.585	7	0.749	7	0.652	5	0.774	4	0.547	4	0.563	3	0.467
	BR	25	4.4	0.609	0.608	6	0.693	5	0.693	5	0.766	2	0.410	4	0.483	4	0.230

Appendix 2.2a. Town specific descriptive statistics for black-tailed prairie dog populations in a) four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD).*

*Abbreviations: n = mean sample size; *A* = mean number of alleles or haplotypes per population; H_o = observed heterozygosity; H_e = expected heterozygosity; *a* = number of alleles or haplotypes; *GD* = Gene Diversity, overall genetic diversity dependent on sample size.

				overall		CGS14		CGS17		CGS22		CGS26		IGS1		CGS 25		mt control rgn
	town	***n***	***A***	***He***	***Ho***	***a***	***He***	***a***	***He***	***a***	***He***	***a***	***He***	***a***	***He***	***a***	***He***	***a*** / ***GD***
CPER	5	15.0	3.5	0.551	0.578	4	0.657	5	0.776	2	0.495	3	0.495	3	0.355	4	0.521	2 / 0.133
1997	22	11.0	3.7	0.629	0.530	4	0.745	5	0.805	4	0.605	2	0.518	4	0.536	3	0.595	2 / 0.389
	27	14.0	3.0	0.494	0.476	4	0.522	3	0.670	3	0.495	2	0.143	3	0.596	3	0.544	1 / 0.000
	29	15.5	4.5	0.660	0.643	5	0.624	5	0.794	4	0.604	2	0.462	5	0.758	6	0.719	2 / 0.133
	30	10.0	3.8	0.609	0.700	4	0.722	5	0.744	3	0.200	3	0.667	4	0.639	4	0.650	2 / 0.200
	35	14.8	3.0	0.456	0.483	3	0.588	5	0.571	2	0.433	3	0.476	3	0.190	2	0.471	3 / 0.648
CPER	5	26	4.0	0.552	0.564	5	0.724	6	0.751	2	0.420	3	0.347	4	0.489	4	0.580	2 / 0.271
2000	22	27	4.2	0.603	0.648	5	0.688	8	0.784	3	0.558	2	0.439	4	0.610	3	0.532	3 / 0.467
	27	25	3.5	0.529	0.507	4	0.448	5	0.718	2	0.503	3	0.363	5	0.794	2	0.352	5 / 0.523
	29	25	3.8	0.528	0.547	4	0.559	5	0.756	3	0.516	2	0.217	4	0.534	5	0.583	3 / 0.573
	30	13	3.7	0.599	0.705	4	0.599	6	0.821	2	0.436	3	0.494	4	0.702	3	0.519	3 / 0.500
	35	25	3.2	0.462	0.473	3	0.468	5	0.653	2	0.302	2	0.458	3	0.437	4	0.453	3 / 0.527
CPER	5	25	3.7	0.591	0.533	4	0.708	6	0.766	2	0.508	3	0.421	3	0.588	4	0.564	2 / 0.153
2001	22	22	3.8	0.600	0.591	4	0.715	6	0.679	3	0.529	2	0.509	4	0.615	4	0.557	4 / 0.463
	27	27	3.7	0.542	0.562	5	0.417	5	0.744	2	0.504	3	0.396	5	0.783	2	0.407	4 / 0.390
	29	25	3.5	0.562	0.580	3	0.493	5	0.753	3	0.608	2	0.390	5	0.587	3	0.540	3 / 0.353
	35	25	4.2	0.510	0.547	5	0.569	7	0.746	3	0.476	3	0.513	3	0.338	4	0.412	4 / 0.510

Appendix 2.2b. Town specific descriptive statistics for black-tailed prairie dog populations on the Central Plains Experimental Range (CPER), CO in 1997, 2000 and 2001.*

*Abbreviations: n = mean sample size; *A* = mean number of alleles or haplotypes per population; H_o = observed heterozygosity; H_e = expected heterozygosity; *a* = number of alleles or haplotypes; *GD* = Gene Diversity, overall genetic diversity dependent on sample size.

APPENDIX 2.3

	Locus	*n*	*A*	*He*	*Ho*	F_{is} *(f)*	F_{it} *(F)*	F_{st} *(Θ)*
CPER, CO	CGS14	141	7	0.678	0.617	-0.060	0.115	0.165
	CGS17	141	8	0.814	0.766	-0.033	0.076	0.106
	CGS22	141	4	0.535	0.489	-0.066	0.112	0.167
	CGS26	141	3	0.438	0.383	-0.015	0.149	0.162
	IGS1	141	5	0.670	0.638	-0.092	0.071	0.149
	Overall	141	5.4	0.627	0.579	-0.054	0.100	0.146
	95% CI					(-0.079, -0.031)	(0.079, 0.125)	(0.122, 0.165)
FC, CO	CGS14	104	8	0.762	0.692	0.026	0.111	0.087
	CGS17	104	8	0.800	0.750	0.006	0.079	0.074
	CGS22	104	5	0.648	0.615	-0.027	0.073	0.097
	CGS26	104	2	0.382	0.375	-0.145	0.060	0.179
	IGS1	104	6	0.707	0.673	-0.027	0.070	0.094
	Overall	104	5.8	0.660	0.621	-0.019	0.081	0.098
	95% CI					(-0.066, 0.008)	(0.068, 0.097)	(0.082, 0.131)
WCNP, SD	CGS14	156	7	0.736	0.603	0.082	0.198	0.126
	CGS17	156	7	0.789	0.660	0.103	0.174	0.079
	CGS22	156	4	0.669	0.622	-0.016	0.086	0.100
	CGS26	156	2	0.422	0.359	0.070	0.164	0.101
	IGS1	156	5	0.541	0.519	-0.008	0.050	0.058
	Overall	156	5	0.631	0.553	0.049	0.139	0.094
	95% CI					(0.002, 0.091)	(0.084, 0.183)	(0.072, 0.113)
BGNG, SD	CGS14	132	8	0.747	0.735	0.008	0.018	0.010
	CGS17	132	8	0.691	0.659	0.041	0.048	0.007
	CGS22	132	5	0.766	0.689	0.090	0.103	0.014
	CGS26	132	4	0.487	0.432	0.072	0.124	0.057
	IGS1	132	5	0.545	0.545	-0.002	0.001	0.003
	Overall	132	6	0.647	0.612	0.042	0.058	0.016
	95% CI					(0.012, 0.074)	(0.021, 0.098)	(0.006, 0.034)

Appendix 2.3a. Locus specific descriptive statistics for microsatellite loci for black-tailed prairie dog populations in four study sites (Central Plains Experimental Range (CPER), CO; Fort Collins (FC), CO; Wind Cave National Park (WCNP), SD; Buffalo Gap National Grassland (BGNG), SD) in 2000-2001.*

*Abbreviations: n = sample size; *A* = mean number of alleles per population; H_o = observed heterozygosity; H_e = expected heterozygosity; Weir and Cockerham's (1984) F-statistics: F_{is} *(f)* = inbreeding coefficient; F_{it} *(F)* = overall fixation index; F_{st} *(Θ)* = fixation index.

	Locus	***n***	***A***	***He***	***Ho***	F_{is} ***(f)***	F_{it} ***(F)***	F_{st} ***(Θ)***
CPER 1997	CGS14	79	6	0.719	0.608	0.043	0.174	0.137
	CGS17	81	9	0.841	0.716	0.010	0.172	0.163
	CGS22	81	5	0.551	0.469	0.030	0.169	0.143
	CGS26	80	3	0.535	0.413	0.079	0.254	0.190
	IGS1	81	5	0.569	0.531	-0.050	0.087	0.131
	CGS25	80	6	0.606	0.650	-0.123	-0.064	0.052
	Overall	80.33	5.67	0.637	0.564	-0.003	0.134	0.137
	95% CI					(-0.058, 0.041)	(0.048, 0.195)	(0.101, 0.163)
	CGS14	141	7	0.678	0.617	-0.060	0.115	0.165
CPER 2000	CGS17	141	8	0.814	0.766	-0.033	0.076	0.106
	CGS22	141	4	0.535	0.489	-0.066	0.112	0.167
	CGS26	141	3	0.438	0.383	-0.015	0.149	0.162
	IGS1	141	5	0.670	0.638	-0.092	0.071	0.149
	CGS25	141	6	0.514	0.489	0.027	0.051	0.024
	Overall	141	5.5	0.608	0.564	-0.042	0.093	0.129
	95% CI					(-0.068, -0.008)	(0.072, 0.115)	(0.086, 0.162)
CPER 2001	CGS14	124	5	0.635	0.524	0.088	0.194	0.116
	CGS17	124	8	0.813	0.742	-0.004	0.108	0.111
	CGS22	124	4	0.547	0.524	0.001	0.051	0.051
	CGS26	124	3	0.481	0.500	-0.128	-0.021	0.095
	IGS1	124	5	0.663	0.597	-0.020	0.126	0.143
	CGS25	124	5	0.495	0.484	0.019	0.023	0.004
	Overall	124	5	0.606	0.562	-0.003	0.089	0.092
	95% CI					(-0.056, 0.040)	(0.029, 0.137)	(0.050, 0.123)

Appendix 2.3b. Locus specific descriptive statistics for microsatellite loci for black-tailed prairie dog populations on the Central Plains Experimental Range (CPER), CO in 1997, 2000 and 2001.*

*Abbreviations: n = sample size; *A* = mean number of alleles per population; H_o = observed heterozygosity; H_e = expected heterozygosity; Weir and Cockerham's (1984) F-statistics: F_{is} *(f)* = inbreeding coefficient; F_{it} *(F)* = overall fixation index; F_{st} *(Θ)* = fixation index.

CHAPTER III

THE INFLUENCE OF CLIMATE, SOILS, AND SPATIAL CONFIGURATION OF BLACK-TAILED PRAIRIE DOG TOWNS ON PLAGUE EPIZOOTICS

ABSTRACT

For plague outbreaks to occur, susceptible hosts, flea vectors and the plague bacterium (*Yersinia pestis*) must coincide in space, along with biotic and abiotic conditions that support pathogen transmission. Using a long-term data set (1981-2005) monitoring black-tailed prairie dog (*Cynomys ludovicianus*) town area and extinction on the shortgrass steppe in Northeastern Colorado, I investigated the link between climate and extinction of prairie dog towns in epizootics of plague. Previous studies indicated that plague outbreaks can be triggered by changes in spring and summer temperature and precipitation, microclimate of soils, and spatial configuration of both extant black-tailed prairie dog towns and towns undergoing plague epizootics. Results from logistic regression models indicated that plague extinctions were spatially clustered, but that spatial dependence could be modeled by town connectivity. Plague outbreaks were strongly associated with two measures of spatial configuration -- isolation from extant towns and proximity to towns undergoing extinction from plague -- and with soil moisture holding capacity as measured by 15 bar soil water content. Overall, little spatial and temporal autocorrelation was detected using spatial logit association models. In logistic regression models, lower risk of plague epizootics was predicted by high summer temperatures. In spatial logit association models, increased summer rainfall in the same year predicted plague events, but plague outbreaks were not significantly linked with past precipitation. As such, no evidence was found to support an indirect trophic-cascade model of plague outbreaks in wild rodent populations; rather, plague occurrence depends upon direct climate effects.

INTRODUCTION

Plague, a disease caused by the bacterium *Yersinia pestis*, was responsible for three large-scale human pandemics. The first, Justinian's plague (541-767 AD), ranged from central and southern Asia through the Middle East, Europe and North Africa (Pollitzer 1954). The second, the infamous Black Death (1346-1841) that killed up to one-third of the European population, originated in central Asia and spread from China, India and the Middle East through Europe and north Africa (Pollitzer 1954). The third pandemic, commonly referred to as the Modern Pandemic, 1860's to the present, originated in China, was identified in Hong Kong in 1894, and spread world-wide via ship-borne rats (Gage 1998). This greatly expanded the natural distribution of plague from portions of Asia and Africa to other parts of the world that include ground-dwelling rodents, establishing active foci in western North America, South America in the Andes and the coast of Brazil, southern Africa, Java and Madagascar (Gage 1998). The current distribution of plague includes all continents except Australia and Antarctica. While historically plague devastated human populations, it is primarily a disease of rodents and their fleas (Levy and Gage 1999).

Plague was introduced into the United States via San Francisco in 1900 and, later, in other ports along the Pacific Rim and became established in native rodent populations (Link 1955; Adjemian et al. 2007). It was identified in California ground squirrels (*Spermophilus beechii*) in 1908 (McCoy 1908) and spread quickly across the western United States, reaching all 15 states west of the 101st meridian by the 1940's (Barnes 1993). It was first identified in black-tailed prairie dogs (*Cynomys ludovicianus*) in

Kansas in 1945 and in Texas in 1947 (Eskey and Haas 1940; Miles et al. 1952; Cully et al. 2000).

Black-tailed prairie dogs are diurnal, ground dwelling, colonial sciurids that live in short and mixed-grass prairies. They are extremely susceptible to plague, which causes large-scale die-offs (epizootics) with 95-100% mortality (Cully and Williams 2001; Pauli et al. 2006). The speed of epizootics is thought to be facilitated by black-tailed prairie dogs' social habit of living in densely populated towns, frequent contact between individuals, and the sharing of burrows with favorable conditions for the survival and reproduction of fleas, the primary vectors of plague (Hoogland 1979; Webb et al. 2006). In conjunction with habitat conversion, poisoning, and recreational shooting, plague has played a significant role in the range-wide decline of prairie dog populations over the past century (Biggins and Kosoy 2001; Miller and Cully 2001).

Plague can be transmitted by infected fleas or direct contact between mammalian hosts (Gage and Kosoy 2005). For flea-borne transmission, the traditional model is via blocked fleas, where fleas with bacteremic blood meals develop a mass of multiplying bacteria enmeshed in a biofilm in their midgut and proventriculus (Hinnebush et al. 1996; Wang et al. 2004; Gage and Kosoy 2005). The mass partially or completely blocks the flow of ingested blood from the foregut to the midgut, causing the flea to starve, and results in repeated feeding attempts in which bacteria are regurgitated along with ingested blood (Bacot and Martin 1914; Bacot 1915). Blocked fleas usually die within a few days because of starvation and desiccation. However, recent models predict blocked fleas cannot drive epizootics in prairie dogs because of the long incubation period until the flea is infectious, and the short windows of time for 1) infectivity of fleas before flea death, and 2) sufficiently high host bacteremia before host death (Webb et al. 2006). These models predict that a short-term reservoir is required to drive epizootics (Webb et al. 2006).

Laboratory studies of both *Oropsylla hirsuta* and *Oropsylla tuberculatus cynomuris*, two of the primary prairie dog fleas in Colorado, demonstrated that both flea species are highly infective within the first 24 hours of a bacteremic blood meal, well before blockage occurs (Wilder 2007). If unblocked fleas can remain infectious for longer periods of time without suffering block-induced mortality, they could serve as the short-term reservoir necessary for epizootics in prairie dogs.

How plague persists between epizootics is not well understood, but it is commonly held that plague is maintained in an enzootic cycle involving partially resistant rodent hosts and their fleas, causing little host mortality (Barnes 1993; Gage and Kosoy 2005). Possible enzootic hosts in the shortgrass steppe of Colorado include the relatively abundant Northern grasshopper mice (*Onychomys leucogaster*), and to a lesser extent Ord's kangaroo rats (*Dipodomys irduu*) and deer mice (*Peromyscus maniculatus*), which are relatively scarce on prairie dog towns in the shortgrass steppe (Stapp 2007); all three display some degree of resistance to plague (Biggins and Kosoy 2001). Plague is thought to periodically spread to highly susceptible rodent hosts, like prairie dogs, causing epizootics with high host mortality, and amplification and spread of the bacterium (Gage and Kosoy 2005).

However, plague is difficult to detect between epizootics (Holmes et al. 2006; D. Tripp and M. Antolin, unpublished data) and evidence for distinct enzootic and epizootic cycles is lacking (Gage and Kosoy 2005). It is possible that plague exists at extremely low levels during interepizootic periods in the same hosts and fleas that experience epizootics (Gage and Kosoy 2005; Hanson et al. 2007). While the exact mechanism underlying the maintenance of plague between epizootics and the transfer between enzootic and epizootic states is poorly understood, epizootics may be triggered by favorable climatic conditions such as mild winters and cool summers when host populations are large (Parmenter et al. 1999; Enscore et al. 2002; Stapp et al 2004; Collinge et al. 2005b; Stenseth et al. 2006).

Human epidemics world-wide occur on a seasonal cycle and are strongly influenced by local climatic conditions (India Plague Commission 1908; Pollitzer 1954; Cavanaugh 1971). Human plague epidemics in India and Vietnam declined sharply when temperatures rose above 27°C (~80°F) (India Plague Commission 1908; Cavanaugh and Marshall 1972). While fleas thrive in moderate temperatures, survival declines at high temperatures (Silverman et al. 1981; Krasnov et al. 2001a), as does the ability of fleas to block and transmit plague (Kartman and Prince 1956; Cavanaugh 1971). High temperature influences not only the fleas but also the plague bacterium itself (Hinnebusch et al. 1998). More recently, human plague cases in Arizona and New Mexico were reported to be negatively associated with maximum daily summer temperatures and positively associated with time-lagged early spring and summer precipitation (Enscore et al. 2002). Black-tailed prairie dog town extinctions in Colorado were found to be associated with climate driven by El Nino Southern Oscillations, which have warmer December to February temperatures (Stapp et al. 2004). Black-tailed prairie dog town extinctions in Montana were associated with cooler summers and higher spring-summer precipitation in the previous year, although prairie dog town extinctions in Colorado were not (Collinge et al. 2005b). Epizootics in great gerbils in Kazakhstan were associated with warmer early springs and cooler, moist summers (Stenseth et al. 2006).

These findings lead to competing hypotheses as to the effects of precipitation and temperature on epizootics. The first is a temperature modulated trophic cascade hypothesis (Enscore et al. 2002; Collinge et al. 2005b) in which above average precipitation increases net primary productivity, leading to larger rodent and flea populations in the following 1 to 2 years, which, when combined with cool summer temperatures, leads to epizootics in rodents and an increase in human exposures. The second is a direct climate effects hypothesis in which climatic conditions influence plague die-offs within a calendar year; i.e. warm early springs and cool moist summers promote flea survival and reproduction in both seasons, setting up favorable conditions for die-offs within that year (Stenseth et al. 2006). This study seeks to determine which of these hypotheses best represents the epizootic patterns seen in black-tailed prairie dogs on the Pawnee National Grasslands (PNG) in Northeastern Colorado.

In addition to climatic effects, I considered two other factors known to influence plague epizootics that have not been included in recent modeling efforts. The first is soil moisture, which may have a profound effect on flea developmental and survival rates, because larvae spend a large portion of their life cycle off mammalian hosts (Silverman and Rust 1983; Krasnov et al. 2001a; Krasnov et al. 2001b). The second is the spatial spread of plague epizootics across the landscape, as plague often occurs in clusters of prairie dog towns with short intertown distances (Anderson and Williams 1997; Cully and Williams 2001; Girard et al. 2004; Stapp et al. 2004; Collinge et al. 2005a; Wagner et al. 2006). Additionally, multiple studies have found that larger towns are more likely to experience plague die-offs than smaller towns (Cully et al. 2000; Cully and Williams 2001; Stapp et al. 2004; Collinge et al. 2005a). Plague is the only known natural cause of large town extinctions (Barnes 1993), and its introduction has left prairie dogs living in metapopulations, with regular episodes of town extinction and recolonization (Roach et al. 2001; Stapp et al. 2004). Consequently, the area and connectivity of towns change year to year and could influence the likelihood of plague epizootics in any particular town.

The clustering of prairie dog towns and plague epizootics complicates statistical analyses of their dynamics. While prairie dog towns have relatively discrete boundaries, the possibility remains that risk of plague is not statistically independent among towns in a locality. Spatial autocorrelation occurs when closely spaced sampling points are more similar to each other than distantly spaced ones; for example, when towns with small intertown distances all undergo epizootics in the same year. Similarly, temporal autocorrelation occurs when sampling points in a time series are influenced by the status of the same points in previous time steps; for example, if precipitation in previous years influences current plague epizootics. Both patterns of autocorrelation violate standard assumptions in regression, with overestimates of the degrees of freedom and underestimates of error (Burton et al. 1998).

Spatial and temporal autocorrelation were accounted for using three approaches. First, logistic regression models were used to predict town extinctions based on town area and connectivity, soil characteristics, and climatic variables, assuming independence of observations and no correlation structure in the data. Second, yearly spatial autocorrelation was assessed by running spatial logit association models with the same dependent variables but with observations clustered spatially, assuming that towns closer together are more alike than distant towns. Third, temporal autocorrelation was assessed via spatial logit association models with the same dependent variables but with observations clustered temporally, assuming that towns are correlated with themselves through time.

In summary, I sought to determine the relationship between black-tailed prairie dog town extinctions from plague and climatic factors (i.e., current and lagged spring and summer precipitation, current spring and summer temperature), soil moisture-holding capacity, and spatial factors (i.e., town area, connectivity to extant towns and to towns undergoing plague extinctions), while accounting for spatial or temporal autocorrelation in the data. Using a 25-year data set (1981-2005) of black-tailed prairie dog town area, location, and extinction on the Pawnee National Grasslands in Northeastern Colorado, models were parameterized on data from 1981-2003, and validated with data from 2004-2005.

MATERIALS AND METHODS

Study Site

The study site on the Pawnee National Grasslands (PNG) (Figure 3.1) is located in Weld County, Colorado (elevation 1280-1950 m), where our research group has conducted studies of plague and prairie dogs since 1997 (Roach et al. 2001; Antolin et al. 2002; Stapp et al. 2004). The PNG is administered by the United States Forest Service (USFS) and represents approximately 80,000 ha of publicly owned land embedded within a checkerboard of lands under federal, state, and private ownership. It is divided into eastern and western units (Pawnee and Crow Valley, respectively) that comprise different drainage systems and are separated by a 16-km wide strip of private land. A greater proportion of the western Crow Valley Unit is contiguous federal grassland (46%) than is the eastern Pawnee Unit (18%). The Central Plains Experimental Range (CPER), located on the northwestern corner of the PNG, is a research area established in 1939 and administered by the US Department of Agriculture / Agricultural Research Service to study the effects of grazing on sustainability of the shortgrass prairie. Both the PNG and CPER are research areas of the Shortgrass Steppe Long Term Ecological Research (SGS-LTER) project at Colorado State University, funded since 1982 by the National Science Foundation.

The PNG is situated in the shortgrass steppe ecosystem. Shortgrass steppe experiences low annual precipitation with between 30 and 50 cm of rain falling primarily from April to September. Vegetation is characterized by low-growing plants that tolerate grazing and drought. The most common plants are two species of C_4 grasses, blue grama (*Bouteloua gracilis)* and buffalo grass (*Buchloe dactyloides*), prickly pear (*Opuntia polyacantha*), yucca (*Yucca glauca)*, and several species of dwarf-shrubs. Vegetation is dominated by blue grama, which contributes 60-80% of the plant cover, biomass, and net primary productivity (Milchunas et al. 1992).

Prairie dog towns on the shortgrass steppe are located within major dry stream channels and have population densities of approximately 25-28 prairie dogs/ha (Koford 1958; Magle et al. 2007). They are patchily distributed throughout the landscape and, because of plague outbreaks, experience metapopulation dynamics with regular town extinction and recolonization (Roach et al. 2001; Stapp et al. 2004; Antolin et al. 2006).

Prairie dog surveys and mapping

Seventy-five prairie dog towns were surveyed by the U.S. Forest Service on the PNG between 1981 and 2005. Starting in 1995, nine additional towns on the CPER were surveyed by the SGS-LTER after prairie dogs recolonized the area. All surveys mapped the outermost active burrows of extant towns in the late summer and fall of each year to determine town area and the geographic coordinates of the centroids of towns. Burrows were considered active if they were cleared of vegetation and cobwebs, had signs of fresh digging or excavation, and/or had the presence of fresh scat. Surveys performed between 1981 and 1994 were mapped using survey equipment, with distances to nearby landmarks recorded to serve as ground controls. In 1999 the coordinates of these landmarks were recorded using a global positioning system (GPS) unit, and the paper maps were digitized, scaled to area based on the ground control points, and incorporated into a geographic information system (GIS) using ArcGIS Desktop 9.1 (Environmental Systems Research Institute 2005). Surveys performed after 1994 were mapped using a GPS and entered into a GIS.

Prairie dogs may use drainages as dispersal corridors between towns (Garrett and Franklin 1988; Roach et al. 2001). Distances between towns along drainages were determined using United States Geological Survey (USGS) hydrography (1:24,000) digital line graphs by mapping the distance between the average centroids of pairs of towns along drainages (drainage distance). When drainage connections were too subtle to be included in the 1:24000 drainage map, a hillshade layer of the USGS (1:10,000) digital elevation models was used to find the lowest elevation lines between larger drainages. All GIS layers used Universal Transverse Mercator projection, Zone 13, datum WGS84, in meters.

In three instances the mapped data were adjusted. First, prairie dogs recolonized six different locations on the CPER for one to two years before the towns were mapped for the first time. Four towns started in 1995 and two more towns started in 1996; all were first mapped in 1997. Because town age was known from monitoring, but maps did not exist for each town, circular buffers were created around the same centroid as the mapped towns in 1997 with areas back-adjusted so that towns were half the area of the mapped town in the previous year, and one quarter the area of the mapped town two years previous. Similarly, on the CPER, towns were not mapped in 1998 and 2001. With GPS data from previous and subsequent years for each of these gaps, buffers were created around an average centroid with the average area of the previous and subsequent year for each town.

Second, individual town buffers were created in seven other instances on the PNG where it was noted that towns existed but were not mapped at that time, often because the towns were very small. The buffers were centered on the previous or subsequent year's centroid or at a location based on explicit spatial references in Forest Service records, with the estimated areas noted by Forest Service staff. One town had an estimated area in 1992, was not monitored for a year, and then was mapped in 1994. For 1992 the town was buffered around the mapped 1994 centroid, with the area in 1992 from the notes. The area in 1993 was the average from 1992 and 1994.

Third, for three years (2002-2004) the mapped area of town 66 indicated growth far beyond an exponential growth curve fitted to data from all towns from 1981 to 2005

(Figure 3.2a). The mapped area returned to just under the fitted curve in 2005. With these data, the standard interpretation of the area decrease between 2004 and 2005 was a town die-off from plague, but in this instance this was not deemed likely for the following reasons: 1) the soils at town 66 leave strong burrow structures that decompose slowly, and if not observed carefully, could be misinterpreted as an active burrow when not actually in use by prairie dogs, thus creating an overestimate of town area, 2) when mapped in 2005, it was noted that prairie dogs were at low densities on this town, 3) prairie dogs were living in small clusters making it difficult to map the true area of the town and easy to overestimate the town area, 4) the town is in close proximity to a town on public land that experiences heavy shooting pressure, so this town may be held at lower densities than normal from shooting, and 5) the mapped areas from 2000, 2001 and 2005 closely match the exponential growth curve derived from all PNG towns between 1981-2005, while the 2002-2004 mapped areas diverge greatly (Figure 3.2b). Given these reasons, modeled values for town area for 2002-2004 were substituted for the GPS data for town 66.

Town Extinctions and Epizootics

In this study, the term die-off refers to a population crash, while, die-off from plague is used to refer to a decline in a prairie dog population caused by plague. The term epizootic refers to a verified outbreak of plague in a black-tailed prairie dog population. Verification consists of a positive test for the presence of the F1 antigen, produced by the plague bacterium, that has been isolated from a prairie dog carcass or a positive mouse inoculation or culture, a positive polymerase chain reaction (PCR) test for the presence of plague DNA isolated from a flea, or a positive blood test for presence of antibodies to plague in mammals sampled on prairie dog towns (Chu 2000). There are nine verified plague epizootics in this dataset from 2003 to 2005 (courtesy of the Center for Disease Control, Fort Collins, CO).

The term extinction refers to a prairie dog town that has no evidence of live prairie dogs for at least some period of time. From 1981-2005, there were fifty-three instances in which towns were present in one year and were not active in the next, but the die-offs were not verified to have been caused by plague; these are referred to as extinctions. In six instances, evidence of a die-off of the town was noted during mapping, in which case the extinction was counted in the year of the die-off, not in the following year. Four towns that had large decreases in area from the previous year were also counted as extinctions. Not every plague epizootic results in an extinction; individual prairie dogs do survive epizootics. However, the nature of this dataset does not contain the detail necessary to identify towns with small numbers of survivors, so towns that may have had a few surviving prairie dogs are included in the term extinction.

I am confident that large town extinctions were caused by plague. Black-tailed prairie dogs are highly susceptible to plague, with mortality rates of 95-100% during plague epizootics (Cully and Williams 2001; Pauli et al. 2006), and plague is the only known disease to cause town extinctions over a short time period (Barnes 1993). While larger towns have a higher probability of undergoing an epizootic (Cully et al. 2000; Cully and Williams 2001; Lomolino and Smith 2001; Collinge et al. 2005a), plague can eradicate both small and large towns (Roach et al. 2001; Stapp et al. 2004; Wagner et al. 2006). The other main cause of town die-offs, poisoning, was officially stopped on the PNG in the 1970's. This dataset lacks direct bacteriologic or serologic evidence of plague for every extinction, so some errors in our data set remain from extinctions of small towns that were caused by factors other than plague, such as unauthorized poisoning, predation, demographic stochasticity, or other factors (Stapp et al. 2004). Error was reduced by excluding town extinctions where poisoning or predation was recorded by PNG staff. In four instances evidence of unauthorized poisoning of small towns was noted (average town area 0.65 ha); in two instances predation was the likely extinction cause (average town area 0.13 ha). Analyses and interpretation of results account for this source of error.

Independent Variables

Prairie dog town area. Town area was measured as the minimum convex polygon of the outermost active burrows of each town in each year. From 1981-2005, town size ranged from 0.02 ha to 252.99 ha, with an average town size of 17.70 ha.

Prairie dog town connectivity. Town connectivity, a metric of structural landscape connectivity that emphasizes town area and intertown distance, provides a measure of how well connected or how isolated towns are within the prairie dog complex in a given year. I calculated the connectivity of towns to all extant towns in year t, as well as the connectivity of towns to all towns undergoing plague extinctions in year t. Because the area of towns was not recorded in the year epizootics took place, the area of the extinct towns in the previous year was used to measure connectivity. The connectivity of each prairie dog town in each year was calculated as:

$$\text{Connectivity of town } j:\ S_j = \sum_{i=1}^{k} P_i A_i \exp(-d_{ij}), i \neq j,$$

where P_i denotes whether a town is active ($P_i = 1$) or extinct ($P_i = 0$), A_i is the area (ha) of town i, and d_{ij} is the drainage distance (km) between town j and town i. The units of connectivity, S_j, are ha (Ovaskainen and Hanski 2004). Because the PNG is comprised of two units that are separated by a 16 km strip of private land and reside in different drainages (Figure 3.3), and because genetic analyses show plague strains from the two units of the PNG are genetically distinct, implying rare dispersal of plague between units (Lowell 2007), the units were treated as separate systems and connectivity estimates were limited to towns within each unit.

Climate. Daily and monthly total precipitation (mm) and daily absolute maximum air temperature (°C) were recorded at seven weather stations across the PNG (Figure 3.3) (National Climate Data Center 1981-2005; Climate and Hydrology Database Projects 1981-2006). Two weather stations were located on the Eastern section of the PNG (New Raymer and New Raymer 21 N) and five were located on or near the Western unit of the PNG (SGS11, SGS12, ARS HQ, Briggsdale and Nunn) (Figure 3.3). Because weather stations SGS11 and SGS12 are located only 122 m apart, their climate data were averaged.

Precipitation. Average spring and summer precipitation for Eastern and Western units of the PNG were calculated from total rainfall from 1 March through 15 June and from 16 June through 30 September (Figure 3.4). Daily precipitation data were used to calculate the total rainfall in the first and second halves of June, while monthly precipitation data was used for monthly totals for March through May, and July through September. Rainfall was averaged from two weather stations (New Raymer and New Raymer 21N) for the Eastern PNG and four weather stations (SGS11/SGS12, ARS HQ, Briggsdale, and Nunn) for the Western PNG. The current year's precipitation should relate to direct effects of moisture on flea reproduction and survival, and the previous year's precipitation should correlate with the potential of rainfall to increase food availability and thus the populations of susceptible rodent hosts. The current and previous year's precipitation were not combined in individual models to avoid collinearity of multiple variables derived from the same data (Legendre and Legendre 1998).

In years that weather stations missed recording data, the weather stations were not included in the averages. For SGS 11 and SGS 12, which were treated as one weather station because of their close proximity, nine individual months of data were missing from the March through September period over the 25-year study period, but in no instances were data missing from both stations simultaneously; these nine monthly averages only contained data from one station. Three months of data were missing from the March through September period for all other weather stations. June of 1982 was missing for Briggsdale, but because there were three other weather stations in operation on the Western unit at that time, Briggsdale was removed from the average for that year. April and May of 1986 were missing for New Raymer, which was the only weather station functioning on the Eastern Unit at that time. The average monthly rainfall of all other weather stations was substituted for those two months because they were similar across weather stations, instead of the long-term monthly average precipitation (1948-2004) for New Raymer which was highly divergent (>30mm) from the rainfall found at the other weather stations.

Temperature. Average spring temperature (March to April) and average summer temperature (June to July) were calculated for the Eastern and Western units of the PNG (Figure 3.5) using daily maximum temperatures.

An index of summer "hotness" was also calculated based on the yearly degree days above 26.7°C (80°F) and 32.2°C (90°F) for the Eastern and Western units. Degree days are the sum of days per calendar year that reached maximum daily temperatures higher than the cutoffs. A temperature index, $\boldsymbol{T_{dd}}$, which is the ratio of degree days over 26.7°C divided by the degree days over 32.2°C, was calculated. A hotter year would result in a smaller $\boldsymbol{T_{dd}}$, while a cooler year would result in a larger $\boldsymbol{T_{dd}}$.

Four of the seven weather stations (New Raymer (1.1 yrs), New Raymer 21N (6.4 yrs), SGS12 (6.3 yrs), Nunn (8.9 yrs)) were not continuously in service over the entire time-course of this study, and especially missed daily maximum temperatures (1236 days), resulting in missing data for 14.9% (9533 out of 63917 days) of daily maximum temperature observations. Because of the strong linear relationships for daily maximum temperature between weather stations (Figure 3.6), we used multiple imputation to account for the missing data, which predicts missing values by using a predictive distribution given the relationship between all observed variables and an underlying model for the type of data used (Schafer 1997). Imputations were implemented in S-Plus, version 6.2 (Insightful Corporation 2003). These imputes, or predictions, were substituted into the original data to create a completed set of maximum daily temperatures and multiple such imputed data sets were created.

Three imputed datasets were used for this analysis. Statistical analyses were carried out on each dataset to produce a set of top models. Normally, the parameters of imputed models are averaged over the completed data sets for overall estimates, and overall standard errors are calculated for each parameter using within-imputation variance and between-imputation variance to incorporate the additional uncertainty

(Schafer 1997). However, because the analysis compared three different types of models, made predictions for the 2004-2005 data based on models parameterized on the 1981-2003 data, and, most importantly, because the results from the three imputations were in strong agreement (Table 3.1), the final analysis was produced from a single imputation. Additionally, models were run with the raw data and compared with the same models using the imputed data; the imputed data provided more stable, less variable results.

Soils. Hot and dry summer conditions negatively impact flea survival and reproduction (Stenseth et al. 2006), and the microclimate provided by burrow systems buffers both ambient temperatures and humidity (Wilcolmb 1954). Under the dry conditions normally found on the PNG, prairie dog towns on soils with a greater capacity to hold water may have a higher susceptibility to plague, because low to moderate levels of soil moisture, as compared with no soil moisture, have been shown to dramatically increase survival rates in larval fleas (Silverman and Rust 1983). In statistical analyses, soils in the previous time step was used because the soil measure was dependent on the area of prairie dog towns, and towns that went extinct in a particular year had an area of zero.

A soils map was created using the soil horizon with the maximum 15 bar water content, the weight percentage of water soils retain in their pore spaces at 15 bars of pressure, commonly called the wilting point of plants (U.S. Department of Agriculture, Natural Resources Conservation Service 2005), for soil series within a soil polygon at any depth up to 1.6 m across the PNG. The maximum depth measured in the soil survey was 1.52 m, with a mean soil depth of 1.24 m (SD 0.46 m) across the PNG. The field capacity or 1/3 bar soil water content was subtracted from the available water capacity for each soil horizon to calculate -15 bar soil water content for each soil horizon, and the layer with the minimum -15 bar soil water content for each polygon was identified. For ease of interpretation we used the absolute value of the -15 bar water content, so that larger values denote larger water holding capacity at 15 bars of pressure. This measures the soil layer that will hold the most water under dry conditions. I overlaid the prairie dog coverage for each year on this soils map and performed zonal statistics using Spatial Analyst in ArcMap 9.1 (Environmental Systems Research Institute 2005) to find the average maximum 15 bar soil water content for each prairie dog town extant in each year. Data on soil components at different depths was from the Northern Weld County Soil Survey (Soil Survey Staff, Natural Resources Conservation Service, U.S. Department of Agriculture 1982).

Multicollinearity

I tested for multicollinearity in the independent variables by calculating variance inflation factors (VIF), which measure the number of times the variance of a parameter estimate is raised from multicollinearity relative to what it would be without multicollinearity. In logistic regression, VIF values above 2.5 may be cause for concern (Allison 1999).

Model Selection

While evidence of links between climatic variation and plague dynamics mounts (Parmenter et al. 1999; Enscore et al. 2002; Stapp et al. 2004; Collinge et al. 2005b, Stenseth et al. 2006), this analysis focused on how spatial factors (town area, town connectivity to extant towns and to extinctions from plague) and soils may interact with climatic factors (current spring and summer temperature, and current and lagged spring and summer precipitation) to influence town extinctions from plague.

More specifically, this study compared two competing hypotheses regarding climate. First, it tested a "direct climate effects" hypothesis, that precipitation and temperature conditions would influence plague die-offs within a given calendar year; i.e. that a warm early spring and cool moist summer would promote flea survival and reproduction in both seasons and set up favorable conditions for epizootics within a given year (Stenseth et al. 2006). Second, it tested a "temperature-modulated trophic cascade" hypothesis (Enscore et al. 2002; Collinge et al. 2005b) that above-average precipitation increases net primary productivity, fueling rodent and flea populations in the following one to two years, which, when combined with a cool summer, create favorable conditions for epizootics to occur. Figure 3.7 shows the temporal relationship between plague year, temperature year, and spring and summer climatic variables considered in the models.

The independent variables considered were town connectivity to extant towns, $\boldsymbol{CE}$, town connectivity to plagued towns, $\boldsymbol{CP}$, town area, $\boldsymbol{A}$, 15 bar soil water content, $\boldsymbol{S}$, three temperature variables: average spring temperature $\boldsymbol{T_{sp}}$, average summer temperature $\boldsymbol{T_{su}}$, degree days 26.7°C /degree days 32.2°C, $\boldsymbol{T_{dd}}$, and four precipitation variables: average spring precipitation in plague year t, $\boldsymbol{P_{sp}}$, average summer precipitation in plague year t, $\boldsymbol{P_{su}}$, average spring precipitation lagged one year, $\boldsymbol{P_{sp-1}}$, and average summer precipitation lagged one year, $\boldsymbol{P_{su-1}}$. Interactions between soils and current and lagged precipitation were also examined.

A backward stepwise model selection procedure was performed in S-Plus version 6.2 (Insightful Corporation 2003) starting with a global model. At each step, partial t-tests were performed, the variable with the smallest t-statistic was removed from the equation, and a chi-square test was used to test for differences between the larger and the reduced model. If this test was not significant, the reduced model was accepted, and variables were eliminated until no variables could be removed without a chi-square test significant at $\alpha = 0.05$. This procedure was run with two sets of temperature variables, either spring and summer temperature or degree days 26.7°C /degree days 32.2°C and on two sets of precipitation variables, the current year's precipitation or the previous year's precipitation. The different temperature variables were not tested simultaneously, nor were the current and previous year's precipitation, to avoid problems with multicollinearity from variables derived from the same data (Legendre and Legendre 1998).

Statistical Analysis

Generalized linear modeling (GLM). GLM logistic regression was used to generate models, with town extinction from plague in calendar year *t* as the dependent variable. The model takes the form (Neter et al. 1996):

$$E\{Y_i\} = \pi_i = \frac{e^{\beta_0+\beta_1 x_1+\ldots+\beta_{p-1}x_{p-1}}}{1+e^{\beta_0+\beta_1 x_1+\ldots+\beta_{p-1}x_{p-1}}},$$

where $x_1, \ldots, x_{p-1}$ are independent predictor variables and $\beta_1, \ldots, \beta_{p-1}$ are logistic coefficients. The logit transformation of the probability of town extinction from plague, π_i, produces an alternate, linear form of the logistic response function:

$$\text{logit}(\pi) = \log_e\left(\frac{\pi}{1-\pi}\right) = \beta_0 + \beta_1 x_1 + \ldots + \beta_{p-1}x_{p-1}$$

Generalized Estimation Equations (GEE) and spatial and temporal autocorrelation. GLM assumes that observations are independent and does not consider autocorrelation between the n observations. Autocorrelations describe systematic patterns in the spatial or temporal distribution of variables. Failing to account for autocorrelation violates the assumption of independence of observations, resulting in overestimates of the number of degrees of freedom and underestimates of error in regression coefficients. In essence, not accounting for autocorrelation extracts more information from the data than really exists (Burton et al. 1998).

Generalized estimation equations (GEE) were developed to extend GLM to accommodate correlated data, particularly binary or count data (Hanley et al. 2003). GEE use weighted combinations or clusters of observations to identify the correlation structure in the data and thus extract the proper amount of information. Observations are clustered spatially or temporally, and observations within clusters are correlated, while the clusters are independent. To test for spatial autocorrelation, towns were clustered within years; while testing for temporal autocorrelation, time was clustered within towns.

A correlation matrix has the following characteristics: 1) independence: no correlations between clusters, 2) exchangeable: clustered observations have no order within clusters, 3) unstructured: the number of observations per cluster is small in a balanced and complete design, 4) auto-regressive: correlation is a function of time between observations, and 5) fixed: the correlation matrix is user defined (Horton and Lipsitz 1999).

Overall, this analysis investigated three possible correlation structures in the data. First, the original GLM models ignored spatial and temporal autocorrelation, assuming independence of observations. Second, GEE models tested for spatial autocorrelation by assuming that clusters of neighboring towns within a plague year are correlated. Third, GEE models tested for temporal autocorrelation by assuming that individual towns are correlated with themselves through time.

Spatial Autocorrelation in GEE models: Moran's I. In each time period, *t*, Moran's *I* (Cliff and Ord 1973; Haining 1980) was calculated to test the null hypothesis of no spatial correlation in the distribution of extinct towns. Moran's *I* identified departures from spatial randomness over all towns in the system, defined as

$$I_{YZ} = \frac{n}{2W} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}(y_i - \bar{y})(y_j - \bar{y})}{\sum_{i=1}^{n}(y_i - \bar{y})^2},$$

where y_i is the status (0 – active, 1 - extinct) of town *i, n* is the number of towns in time period *t,* w_{ij} is a scalar that quantifies the degree of spatial association or proximity between locations *i* and *j*, or a 0-1 variable indicating that locations *i* and *j* are within some distance range of each other, and *W,* the spatial weights matrix, is the sum of all n^2 values of w_{ij}. The matrix *W* took the form of a block diagonal matrix, where the diagonal elements represent the towns in the western and eastern portion of the study area (Figure 3.3). The two sides of the study area reside in separate drainages and are separated by a 16 km strip of private land. In addition, recent genetic analyses show that plague strains from the two units are genetically distinct (Lowell 2007), which implies rare dispersal of plague between units. Therefore it was assumed the two groups of towns were spatially independent. In calculating Moran's *I* three different spatial weights matrices were evaluated. The first was based on inverse distance between towns, while the two spatial weight matrices were binary 0,1 matrices. The binary spatial weights matrices were based on limiting distances of 10 km and 30 km. For example, if the distance between two towns was ≤ 10 km, their weight was 1, otherwise weights were 0's. Distances between towns were based on drainage distance (km) (Figure 3.3). Values of Moran's *I* vary from negative one to one, with negative one indicating negative spatial autocorrelation, zero indicating no spatial autocorrelation, and one indicating positive spatial autocorrelation.

Another statistic commonly used to evaluate spatial autocorrelation is the partial Moran's *I* which checks for correlation between individual towns and all other towns:

$$I_i = \frac{n}{2W} \frac{\sum_{j=1}^{n} w_{ij}(y_i - \bar{y})(y_j - \bar{y})}{\sum_{i=1}^{n} (y_i - \bar{y})^2}.$$

If a significant spatial autocorrelation was observed in a given time period, the partial Moran's *I* statistic was used to provide a measure of an individual town's correlation with its neighbors.

Model validation. The performance of models was evaluated using receiver operating characteristic (ROC) curves, a technique with increasing applications in recent ecological studies such as modeling habitat and species distributions (Pearce and Ferrier 2000; Gibson et al. 2004; Eyre and Buck 2005; Claessens et al. 2006; Greaves et al. 2006). ROC curves plot the true positive rate (sensitivity) against the false positive rate (1-specificity) at threshold probabilities that increase incrementally from zero to one for models predicting binary observations (Fielding and Bell 1997). The closer the curve is to the upper left corner of the graph, the higher the discrimination accuracy of the model. That is to say, the accuracy of a model is greater when the true-positive rate is higher for a given false-positive rate (Swets et al. 2000). The area under the curve (AUC) measures overall model accuracy and is independent of the arbitrary probability threshold that, in this study, determines whether a town has gone extinct from plague or not. The AUC varies from 0.5, indicating accuracy no better than chance, to 1.0 for 100% accuracy.

I also computed a threshold-dependent measure of model performance, total model accuracy, the total proportion of the sample that was correctly predicted by the model at the decision threshold. The point that maximizes the true positive rate and minimizes the false positive rate was used as the cutoff probability or decision threshold for determining whether a model predicted that a town went extinct in a given year.

The measures of predictive performance were used to evaluate model accuracy for the 1981-2003 data, as well as for the 2004-2005 data, which were excluded from initial analyses to be used for model validation.

k-fold cross-validation. Because the test data were only from a two-year period, k-fold cross validation was used to determine how consistently models will perform on future data. In k-fold cross validation, the complete dataset D is randomly divided into k, mutually exclusive sets or folds ($D_1, D_2, \ldots D_k$) that are approximately equal in size. Each model is trained and tested k times. Each time one fold of the data, D_i, is withheld, the model is trained on the remaining D-D_i dataset, and then is tested on the D_i test set. The cross-validation accuracy estimate is the average of the k individual accuracies (Kohavi 1995). A 10-fold cross validation process was performed using S-Plus version 6.2 (Insightful Corporation 2003).

RESULTS

Three temperature imputations

In the GLM analysis, backward stepwise model selection produced the same top model in each of three temperature imputations (Table 3.1). Coefficient estimates and standard errors showed a high degree of agreement, as did estimates of the area under the ROC curve for both the 1981-2003 data and for predictions from 2004-2005 and overall model accuracies. Because the model results from the three imputations were so similar, and because models were used not only to find the best fit to the 1981-2003 data but to predict plague epizootics in the 2003-2004 data, I randomly chose one imputation, imputation one, and performed the analysis using parameters from this imputation, rather than averaging the coefficients from the three imputations.

GLM

Backward stepwise selection on four sets of models which differed by temperature variable, either spring and summer temperature or degree days 26.7°C /degree days 32.2°C, and by precipitation variable, the current year's precipitation or the previous year's precipitation, resulted in the same top model in all sets (Table 3.1a). Extinctions on prairie dog towns were predicted by two spatial factors, connectivity to extant towns and to plague extinctions, by 15 bar soil water content, and by summer temperature. Extinction was more likely for towns whose connectivity to extant towns dropped while their connectivity to towns going extinct increased. Extinction was also more likely on towns with soils that hold more moisture under dry conditions and in years with cool summer temperatures. Although it appears that cooler summers overall (larger degree days 26.7°C/degree days 32.2°C) and warmer springs also increase plague, only summer temperature was significant at $\alpha = 0.05$. Town size, current and lagged spring and summer precipitation, and the interactions between precipitation and soils were not significant predictors of town extinctions from plague.

The results from this model selection procedure were in agreement with an information-theoretic approach to model evaluation which used Akaike's Information Criterion (AIC) values to determine the best-fitting, most parsimonious models (Burnham and Anderson 2002). The methods and results for that analysis are found in Appendix 3.1, with complete model sets listed in Appendices 3.2, 3.3 and 3.4.

GLM Model Performance. The area under the ROC curve (AUC), a threshold-independent measure of model accuracy, was 0.769 for the 1981-2003 data, and 0.952 for the 2004-2005 validation data for the top GLM model. The ROC curves are shown in Figure 3.8. Overall model accuracy, a threshold-dependent measure of model performance, was 0.723 for the 1981-2003 data and 0.802 for the 2004-2005 validation data. 10-fold cross-validation predicted an average accuracy of 0.686, which is much lower than the 0.802 accuracy achieved by the top model on the 2004-2005 data.

GEE testing for spatial and temporal autocorrelation

The GEE models accounting for spatial or temporal autocorrelation performed nearly identically to the GLM that assumed no correlation structure in the data. Parameter estimates are summarized in Table 3.2. Important variables included connectivity to extant towns, soils, and summer precipitation. Town extinction was more likely for towns isolated from extant towns, on soils that hold more moisture under dry conditions, and with elevated summer precipitation. In the spatial model, spatial autocorrelation within years was estimated at 0.032. This weak correlation suggests a lack of spatial autocorrelation among towns within a given year, and agrees with the general lack of spatial autocorrelation measured by Moran's I. In the temporal model, temporal correlations were observed for individual towns, but accounting for this correlated error structure did not significantly improve the fit of the model. That the models with spatial and temporal autocorrelation did not provide better fits to the data suggests that variability of extinctions among towns is as great as the variability among years.

In the GEE models, summer precipitation was the only climatic variable that predicted plague, while in the top GLM model summer temperature was the significant predictor. These two results are not contradictory because the models have different functions, and summer temperature and precipitation are inversely correlated ($r = -0.55$), with hot summers having less rainfall. Thus, cool, moist summers were associated with an increased probability of town extinctions from plague.

GEE testing for spatial autocorrelation: Moran's I

Overall spatial autocorrelation ($P < 0.05$) was observed in only two time periods: 1992 and 1999, but in 1998 the p-value for the Moran's I statistic was 0.06. Partial Moran's I for those years are plotted in Figures 3.9a through 3.11a. In 1992 the strongest spatial autocorrelations were observed in the eastern portion of the study area, while the towns in the western portion of the study all exhibited weak spatial autocorrelation. In contrast, in 1998 and 1999, most towns showed a strong spatial autocorrelation with their neighbors. Individual towns in 1992, 1998, and 1999 experienced spatial autocorrelation, but on a global level for most years, the probability of a town going extinct from plague was spatially independent of the status of their neighbors when town connectivity was modeled explicitly.

DISCUSSION

The results from this study indicate that the spatial configuration of both extant prairie dog towns and towns experiencing extinctions from plague may influence the probability that individual towns will experience a die-off from plague. When testing for spatial autocorrelation, little additional spatial variation was identified when town connectivity was modeled explicitly. Contrary to the trophic cascade hypothesis, no significant temporal autocorrelation was found, implying that conditions in previous years had little influence on plague outcomes in subsequent years. More specifically, this study found no evidence for lagged precipitation influencing plague outbreaks, but instead that summer temperature and precipitation within the same year influence plague occurrence. In addition, 15 bar soil water content was a predictor of plague outbreaks. Lastly, town area was not found to be a strong predictor of plague in prairie dog towns, nor were there significant interactions between soils and current or lagged precipitation.

Spatial configuration of prairie dog towns

Connectivity to extant towns and to towns going extinct from plague both predicted plague occurrence, and reflected the common finding that plague occurs in clusters of prairie dog towns with short intertown distances (Anderson and Williams 1997; Cully and Williams 2001; Girard et al. 2004; Stapp et al. 2004; Collinge et al. 2005a; Wagner et al. 2006). This clustered pattern of plague suggests that plague epizootics greatly amplify the amount of plague in the environment, increasing the probability of the spread of plague by dispersing prairie dogs, other widely dispersing rodent hosts, and/or predators like coyotes and swift fox (Poland and Barnes 1979; Barnes 1993; Gage et al. 1994; Cully et al. 2000; Girard et al. 2004; Collinge et al. 2005a; Salkeld et al. 2007).

At the same time that plague epizootics were clustered, plague was also scattered, with individual towns undergoing epizootics while neighbors were unaffected, also a finding in other studies of plague in prairie dogs (Anderson and Williams 1997; Cully and Williams 2001; Girard et al. 2004). This suggests the occurrence of long-distance dispersal of plague-positive fleas by predators such as coyotes, swift foxes, badgers or raptors (Poland and Barnes 1979; Barnes 1993; Cully et al. 2000; Girard et al. 2004; Salkeld et al. 2007), or the possibility that plague is regionally widespread and is coordinately triggered by environmental conditions like ones described here. Genetic evidence supporting both scenarios was found in Gunnison's prairie dogs in Arizona (Girard et al. 2004). Reservoirs where plague could persist between epizootics remain unidentified.

Connectivity to towns undergoing extinctions from plague was not as important in the GEE models. In GLM models, both connectivity to extant towns and connectivity to plagued towns were significant predictors, but it was not possible to fit GEE models when connectivity to plagued towns was included. It is likely that this variable became redundant within the GEE models.

Spatial autocorrelation

Tests of spatial autocorrelation in GEE spatial logit association models that included connectivity to extant towns detected significant spatial autocorrelation in only two of 22 years (Figures 3.9-3.11). Thus a single biologically sensible spatial variable accounted for most of the spatial variation in our system and little additional large-scale spatial variation could be detected. The detection of some large scale spatially correlated variation hints at local factors that may influence spatial clustering of epizootics, such as town-specific precipitation and temperature, prairie dog population density, fine-scale variation in soils, and seasonal flea abundance. Our research group is actively investigating many town-specific factors that will allow development of models that may help predict localized clustering of plague.

Temporal autocorrelation

Using GEE spatial logit association models, no significant temporal autocorrelation was found in this system, implying that past climatic conditions and spatial states did not significantly influence the probability of extinctions from plague in the current year; rather, current climatic conditions, connectivity and soils were more influential in triggering plague epizootics in prairie dog towns. This finding runs contrary to the trophic cascade hypothesis, which emphasizes the effects of past precipitation on rodent population size as a primary driver of epizootics. Instead, the lack of temporal autocorrelation in this system shifts the emphasis towards the effects of current climatic conditions on flea survival and reproduction and on the plague bacterium in driving epizootics. This concurs with a long-term study of plague in great gerbils in Kazakhstan, which found a predictive relationship between epizootics and past abundance of gerbils, implying that high host abundance is necessary for epizootics to take place but other factors must also drive epizootics (Davis et al. 2004). Warmer early spring temperatures and cooler, wetter summers in the current year also predicted plague outbreaks in great gerbils, supporting the effects of the current year's climate on plague outbreaks (Stenseth et al. 2006). Thus, while rodent abundance undoubtedly plays a role in plague dynamics (Davis et al. 2004), past precipitation may not be a useful proxy for rodent abundance.

15 bar soil water content

Our results suggest that the microclimate of the soils, as measured by 15 bar soil water content, may be an important factor in predicting plague outbreaks on prairie dog towns. Soils have the potential to greatly impact flea populations because fleas spend most of their pre-adult life cycle off-host. The soil water content of burrow soils may impact flea development and survival via the relative humidity of burrows. Research on the effects of relative humidity on both cat fleas (*Ctenocephalides felis*) and two Xenopsylla species found that flea larvae did not survive below 40-50% relative humidity, and that eggs and larvae developed faster and had higher survival rates with increasing relative humidity (Silverman et al. 1981; Krasnov et al. 2001a; Krasnov et al. 2001b). Increasing relative humidity did not affect development times of the pupal period, when pupae are protected by the cocoon and are more resistant to desiccation (Krasnov et al. 2001b). Additionally, soil moisture itself can impact flea survival; even at low ambient relative humidity (12%), increasing soil moisture of sand or sandy clay from zero to one percent increased larval survival from zero to 100%, while with silty clay, larval survival increased at five percent soil moisture because of the ability of clay to bind water, making it unavailable at low levels (Silverman and Rust 1983). In contrast, high soil moisture can be deleterious because water saturates soil interstitial spaces and prevents gaseous transfer (Silverman and Rust 1983). Because the shortgrass steppe is a semi-arid ecosystem, water-saturation of soils is not a typical state. Our results suggest that towns with soils that retain more moisture under dry conditions may be more likely to succumb to plague than towns with drier soils. Under the dry conditions normally found on the shortgrass steppe, soils that retain more moisture may potentially increase survival and speed development of fleas, but the exact mechanism underlying the association between 15 bar soil moisture and extinctions from plague needs to be determined with future sampling and experiments.

Climatic variables: temperature

In logistic regression models, prairie dog town extinctions from plague were negatively associated with summer temperature, and, to a lesser extent, were positively associated with early spring temperature. These results agree with a wealth of research on the effects of temperature on flea development and survival, on the ability of fleas to clear plague infections, and on the plague bacterium itself. First, like relative humidity, a temperature window promotes flea development and survival, and both low and high temperatures have adverse affects on the flea life cycle. Cat fleas, *Ctenocephalides felis*, do not complete development in temperatures less than 10°C (50°F) and greater than 35°C (95°F), and within this temperature window development time from egg to hatched adult slows with decreasing temperature (Silverman et al. 1981; Silverman and Rust 1983; Metzger and Rust 1997). Similar temperature results have been found with *Xenopsylla cheopis*, the oriental rat flea, which is the main plague vector in many epidemics in Asia, Africa, and South America (Pollitzer 1954; Margalit and Shulov 1972). Thus, both low spring temperatures and high summer temperatures can have negative effects on flea development and depress flea population size. In addition, in newly emerged adult fleas, survival time was inversely related to temperature (Krasnov et al. 2002), providing both a means for adults to overwinter at lower temperatures, and for the stemming of epizootics at higher temperatures. Future experiments are necessary to determine the specific effects of temperature on prairie dog fleas.

Second, at higher ambient temperatures (>28°C) fleas clear infection more readily and fail to block (Cavanaugh 1971; Kartman and Prince 1956), most likely because of the effects of temperature on the bacterium itself. Because the life cycle of *Y. pestis* requires the establishment of a transmissible infection in fleas at low ambient temperatures as well as in mammalian hosts at higher mammalian body temperatures, *Y. pestis* displays different gene expression profiles at 26°C versus 37°C. Lower temperatures promote genes required to survive in the flea midgut and to produce a biofilm that aids in the aggregation of bacteria and blockage of the flea midgut, while higher temperatures promote genes required to thwart a vertebrate host's innate immune system and cause a high bacteremia (Perry and Fetherston 1997; Hinnebusch 2005). Interestingly, the temperature regulation of biofilm formation at high temperatures is not transcriptional, but is caused by high temperatures decreasing the stability of the proteins involved in biofilm formation (Perry et al. 2004).

However, this mechanism of high temperatures decreasing block formation and increasing the clearance of infection in fleas presupposes that the primary mode of flea-borne transmission is via blocked fleas, which is true for epidemics caused by *Xenopsylla cheopis.* However, early phase transmission, which likely causes epizootic spread of plague in prairie dogs (Eisen et al. 2006; Wilder 2007), takes place prior to blockage formation. Further research is necessary to delineate the role of temperature in early phase transmission as well as the effects of temperature on the life cycle of prairie dog fleas.

Climatic variables: precipitation

In the GEE models, increased summer precipitation in the current year predicted plague outbreaks while in the GLM models, no current or lagged precipitation variables were significant predictors of plague. The lack of association between extinctions from plague and lagged precipitation concurs with the lack of temporal autocorrelation in our system and runs contrary to the trophic cascade hypothesis. This differs from a study of human plague cases in which lagged early spring precipitation was associated with increased numbers of human plague cases in the northwestern New Mexico while lagged early spring, lagged summer, and unlagged early spring precipitation were associated with increased numbers of human plague cases in northeastern Arizona (Enscore et al. 2002). In a study of black-tailed prairie dogs, Collinge et al. (2005b) found support for the trophic-cascade model in their Montana study area, where cooler summers and increased spring-summer precipitation in the previous year were associated with plague occurrence. However, in their Colorado study area, they found a negative association between precipitation in the previous year and plague occurrence, a result they concluded was spurious. They hypothesized that variability in the timing of peak precipitation may break the potential for a trophic cascade in rodent numbers and thus plague prevalence (Collinge et al. 2005b). However, using precipitation as an indirect method of measuring rodent abundance is not universally supported (Brown and Ernest 2002). Brown and Ernest (2002) found that rodent population dynamics did not exhibit simple "bottom-up" regulation because of the complexity of interactions between large numbers of environmental variables (i.e., magnitude and timing of rainfall events, temperature, herbivory, predation).

It is possible that locations of our weather stations are not specific enough to capture the range of spatial variability in precipitation that could cause individual towns to undergo epizootics. On the shortgrass steppe, summer precipitation falls in few but intense rainfall events unevenly spread across the landscape that may have disproportionate effects on individual towns (Lehmer et al. 2006). Lehmer et al. (2006) documented a case in which prairie dogs sampled on one town on the CPER that received less precipitation than all other surrounding towns displayed thermoregulatory behavior consistent with hibernation. This would allow animals to reduce water loss associated with the metabolic requirements of digesting and assimilating excessively dry forage as well as provide energy savings from maintaining lower body temperatures. If localized climatic conditions can alter the water content in vegetation on individual prairie dog towns enough to induce hibernation in a single town while not in nearby towns, they may also affect soil moisture levels enough to affect flea populations and the intensity of plague epizootics. Installing small precipitation gauges on prairie dog towns, especially towns with high connectivity levels, could provide valuable town-specific climatic data that would further elucidate the relationship between precipitation and plague.

Town area

Town area was not a strong predictor of town extinctions. While some studies have found that larger towns have a higher probability of plague epizootics (Cully et al. 2000; Cully and Williams 2001; Stapp et al. 2004; Collinge et al. 2005a), others have found town area to be a poor predictor (Wagner et al. 2006). Both of these findings could suggest the influence of plague on population dynamics, because prairie dog populations without plague outbreaks have greater persistence if they are larger (Lomolino and Smith 2001; Scott-Morales et al. 2004). However, a lack of association may stem from problems with using prairie dog town area as a proxy for actual prairie dog population size. For example, in drought conditions, town area could increase without an increase in actual population number. Population size estimates would be a useful measure for future researchers.

Differences in performance between 2004-2005

In our two performance measures, AUC and overall model accuracy, the top GLM model performed better on the 2004-2005 data than it did on the 1981-2003 data, while kfold cross-validation predicted accuracies similar to those found in the 1981-2003 data. The two year sample was not completely representative of the longer term sample, in part from the data improving in accuracy in 2004 and 2005, where eight of nine town extinctions were verified by the CDC to have been caused by plague through plague-positive fleas or prairie dogs (courtesy of the Center for Disease Control, Fort Collins, CO). While I am confident that the mid to large town extinctions in this dataset were caused by plague, it is possible that some of the small town extinctions were caused by other factors, introducing some error into the dataset. However, models parameterized on the 1981-2003 data performed very well on the 2004-2005 data, indicating that the noise in the original data did not diminish the predictability of resulting models.

Future directions of study

This study raises several questions for future study. First, it suggests that the ability of soils to hold moisture under dry conditions may increase the probability of plague epizootics in individual prairie dog towns. While soils with larger 15 bar soil water content will hold a larger amount of water than soils with smaller 15 bar soil water content, the exact mechanism of how increased 15 bar soil water content would affect a larval flea developing in the soils is unknown. In addition, this measure of soil water content was based on large scale soil survey data. It is possible that finer investigation of soil composition at different soil depths and measurements from specific locations, such as nest cavities where flea larvae are found, could reveal specific soil qualities important for flea survival and maintenance of plague. Possibilities include the composition of the soils (percent sand, silt, clay and organic matter), thermal properties of soils, and the different rates at which materials, in particular water, diffuse through soils of different compositions. Survivability experiments with prairie dog flea larvae in soils of different compositions with varying levels of soil water could provide a mechanism for soil associations with plague epizootics.

Combined with localized precipitation data for individual towns, more detailed soil data could reveal an interaction with soils and precipitation. On an annual basis, the pattern of soil water distribution varies by soil depth (Sala et al. 1992). Surface soils (0-2.5 cm) show no seasonal pattern of water availability because of the high level of evaporation; soils at this depth are almost always dry. Intermediate-depth soils (15-45 cm) follow seasonal patterns of precipitation with water availability building through the early spring and peaking in May and June (Sala et al. 1992). Deep soil layers (45-60 cm) are wet only in the late spring, the period with the highest interannual variability in precipitation and thus deep soil water potential. Dry years have shallow water distributions, while in wet years wet conditions can reach 120-135 cm (Sala et al. 1992).

Thus, climatic variability directly affects the soil moisture and potentially the relative humidity of cavities in deeper soils where prairie dog burrows and nests may be found and may prove to be important in predicting plague outbreaks in individual prairie dog towns.

Second, the results of this study suggest that the current year's summer climate may be important in modulating the occurrence of plague epizootics in prairie dogs, and suggest a central role for fleas in epizootics. As discussed above, the model of transmission by blocked fleas, with high temperatures affecting the stability of proteins required for biofilm formation necessary for blockage (Perry et al. 2004), may not fit plague transmission in prairie dogs, since two of the main prairie dog fleas most effectively transmit plague within the first 24 hours of an infectious blood meal (Wilder 2007) and models predict a short-term reservoir is necessary to sustain epizootics in prairie dogs (Webb et al. 2006). Nevertheless, high temperatures seem to depress plague epizootics in this system as well. Future studies investigating the effects of temperature on prairie dog flea development and survival, on the fleas' ability to clear infection, and on the plague bacterium itself within the context of early phase transmission will help elucidate the role of temperature in epizootics in prairie dogs.

Third, in this dataset, the seasonal timing of epizootics is not delineated. However, flea species vary seasonally (Anderson and Williams 2001), and research in the last four years has shown that there may be two periods of high plague activity, spring/summer and fall, with different suites of flea species involved (D. Tripp and M. Antolin, personal communication). Epizootics have also been noted starting in individual towns with a drop in summer temperatures (D. Tripp and M. Antolin, personal communication). Evidence from India and Vietnam (India plague commission 1908; Cavanaugh and Marshall 1972) demonstrates plague epidemics stopping with the onset of hot weather, then restarting once cooler climatic conditions occur. Finer scale research will allow for better identification of the climatic conditions present during epizootics and for differentiation of seasonal dynamics.

Lastly, this research emphasizes the spatial nature of plague epizootics. Susceptible hosts, flea vectors and the plague bacterium must coincide in space, along with the proper biotic and abiotic conditions to support pathogen transmission. This study shows that plague can both cluster in space and also affect widely spaced prairie dog towns, raising questions about why extinction hotspots are so pronounced in certain years, as well as the question of where and how plague is maintained between epizootics. While the models presented here suggest that soil moisture and climatic triggers may be important to epizootics, and that epizootics greatly amplify plague in the environment leading to clusters of towns going extinct, the location of plague between epizootics remains unknown.

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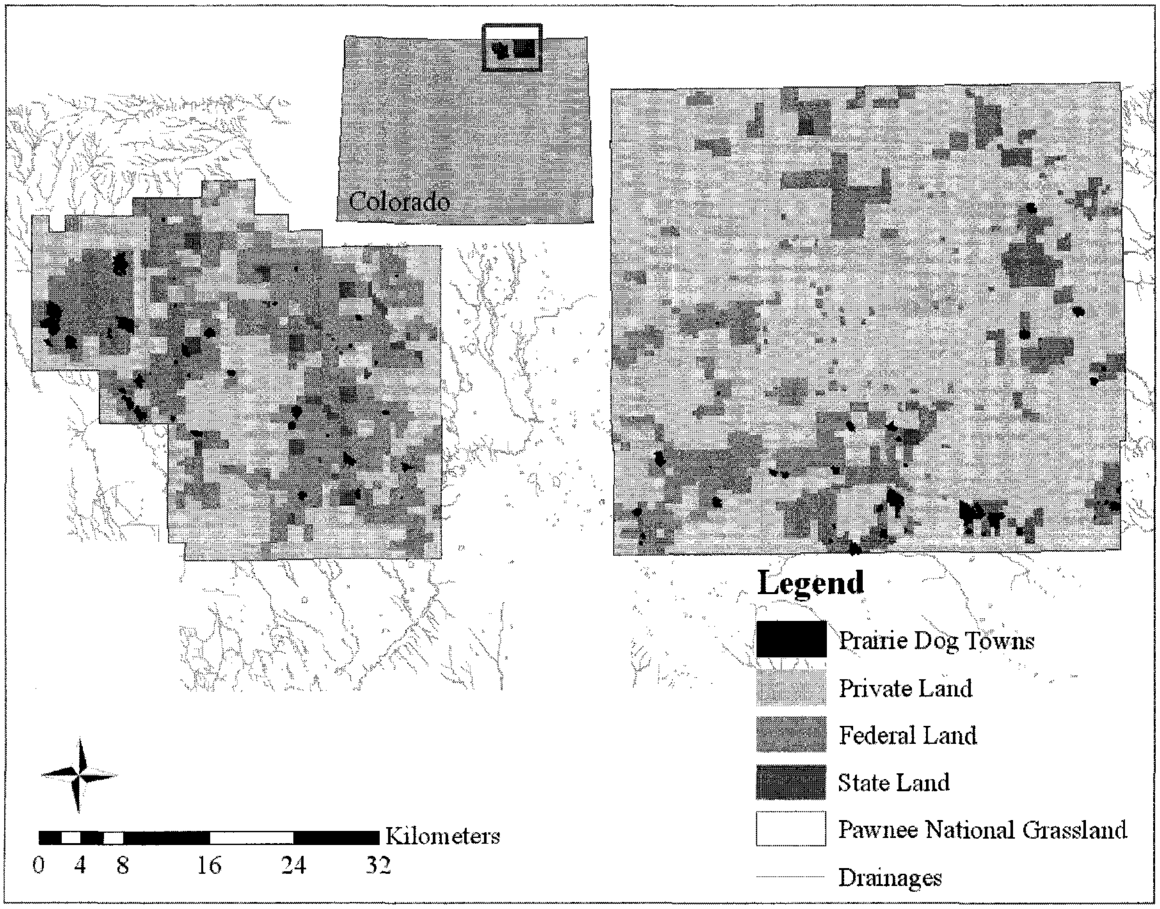


Figure 3.1. Land ownership on the Pawnee National Grassland. Largest recorded area of black-tailed prairie dog towns shown (1981-2005).

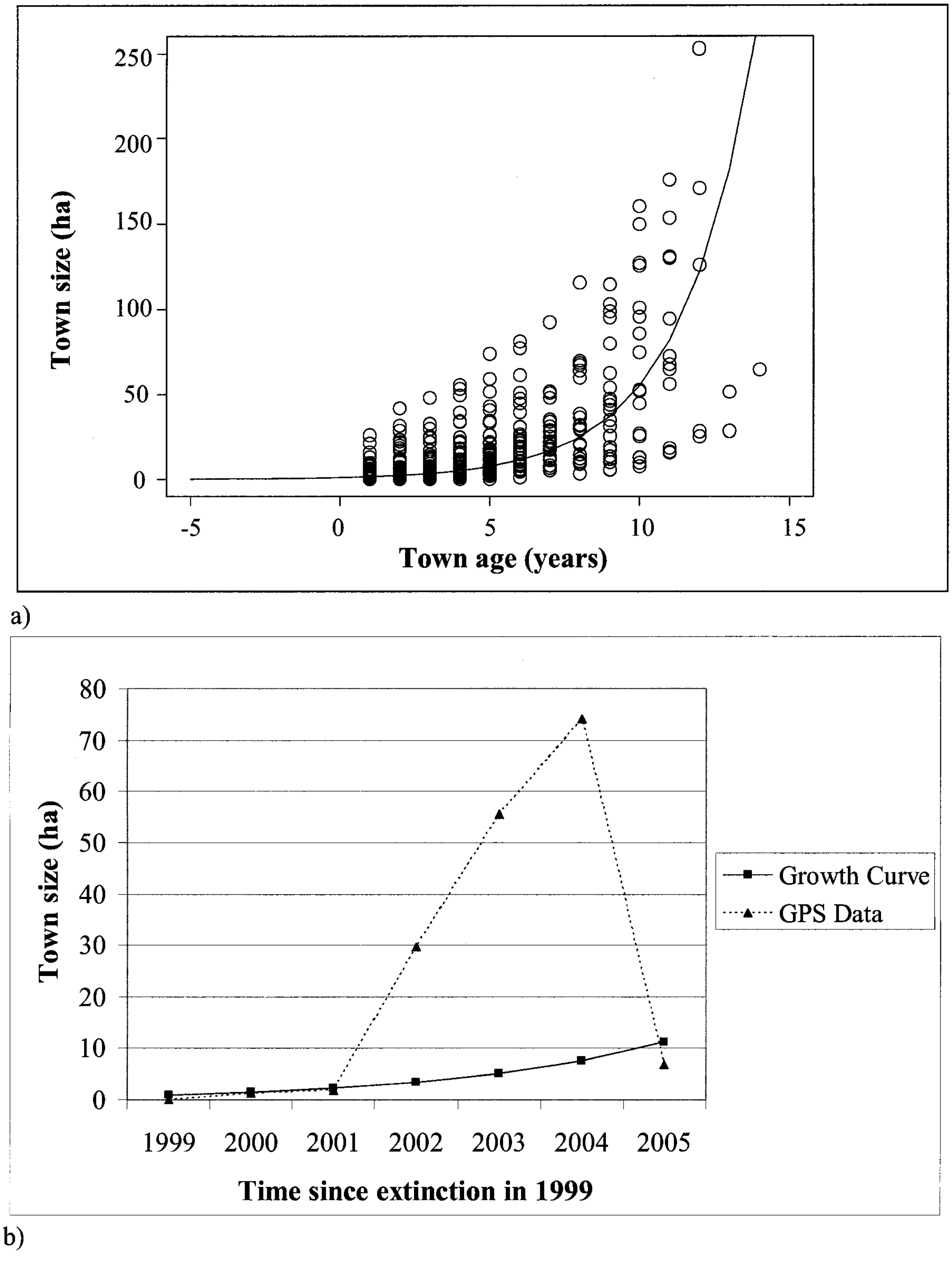


Figure 3.2. a) Exponential curve fitted to growth of black-tailed prairie dog towns between 1981 and 2005 on the Pawnee National Grassland, Colorado. b) Comparison of growth curve with GPS data for town 66 from 1999 to 2005.

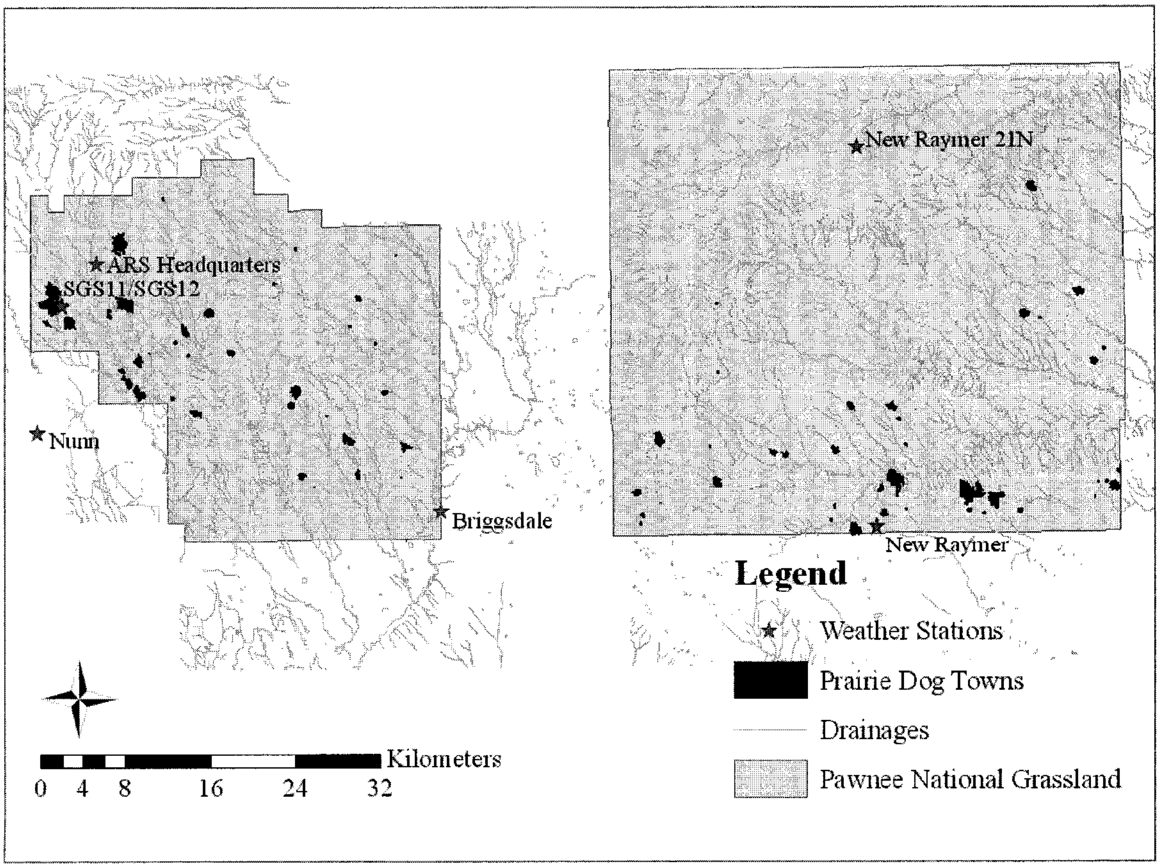
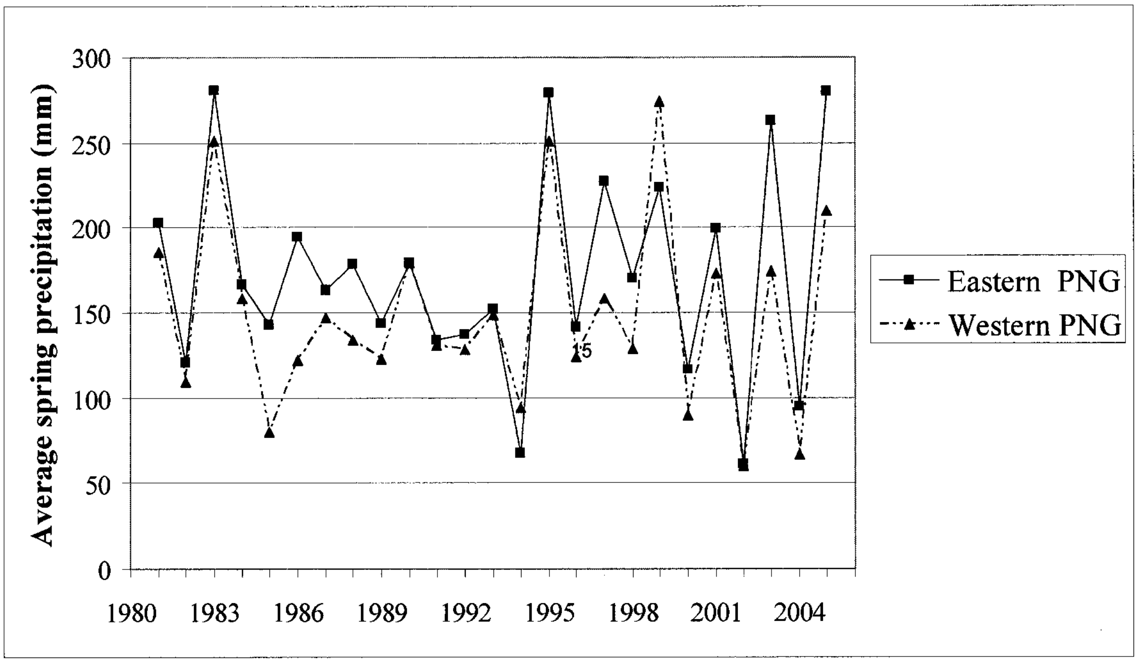


Figure 3.3. Largest recorded area of black tailed prairie dog towns (1981-2005) in relation to weather stations and drainages on the Pawnee National Grassland, Colorado. Prairie dogs may use drainage networks to move between towns.



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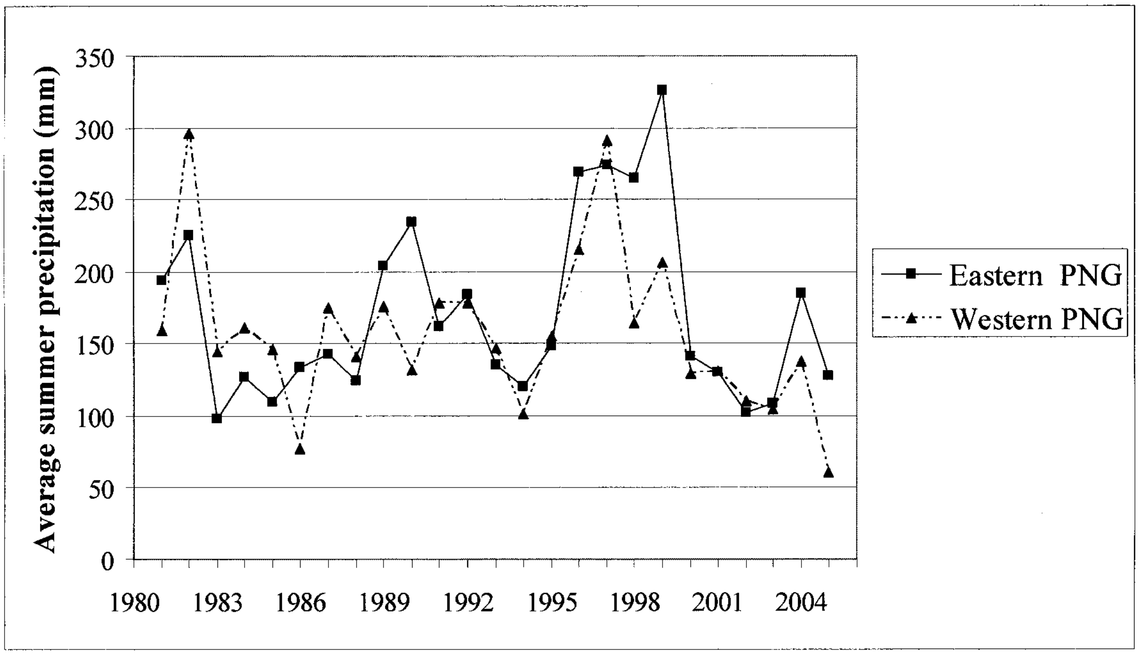

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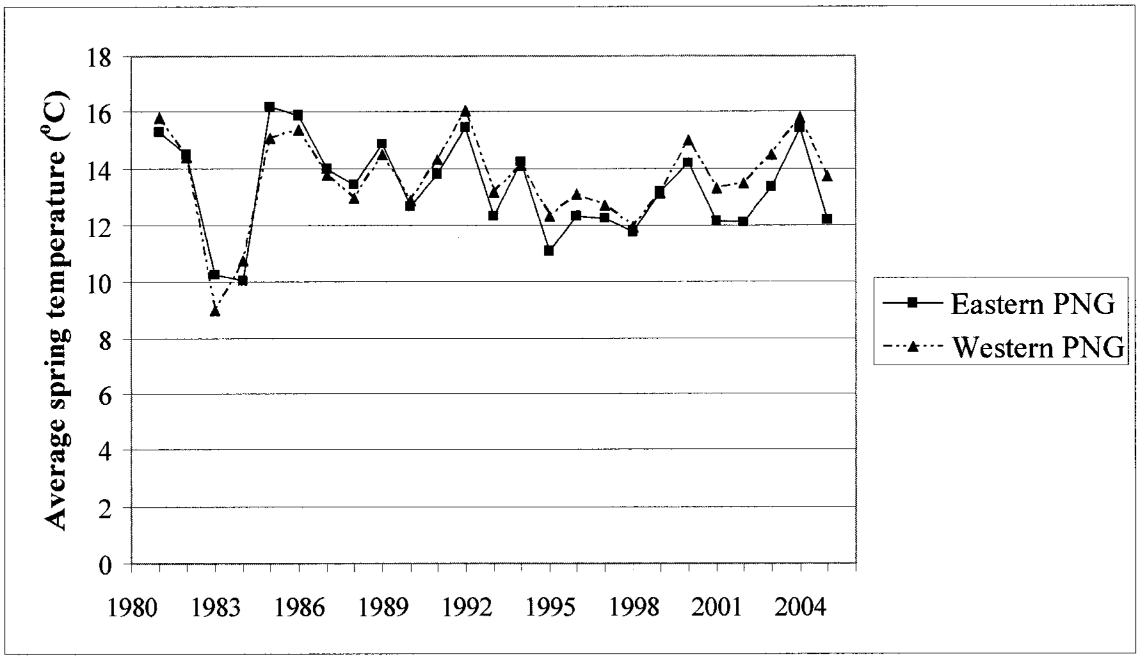
Figure 3.4. a) Average spring precipitation (1 March-15 June), b) average summer precipitation (16 June-30 September) for the eastern and western units of the Pawnee National Grassland, Colorado, 1981-2005.



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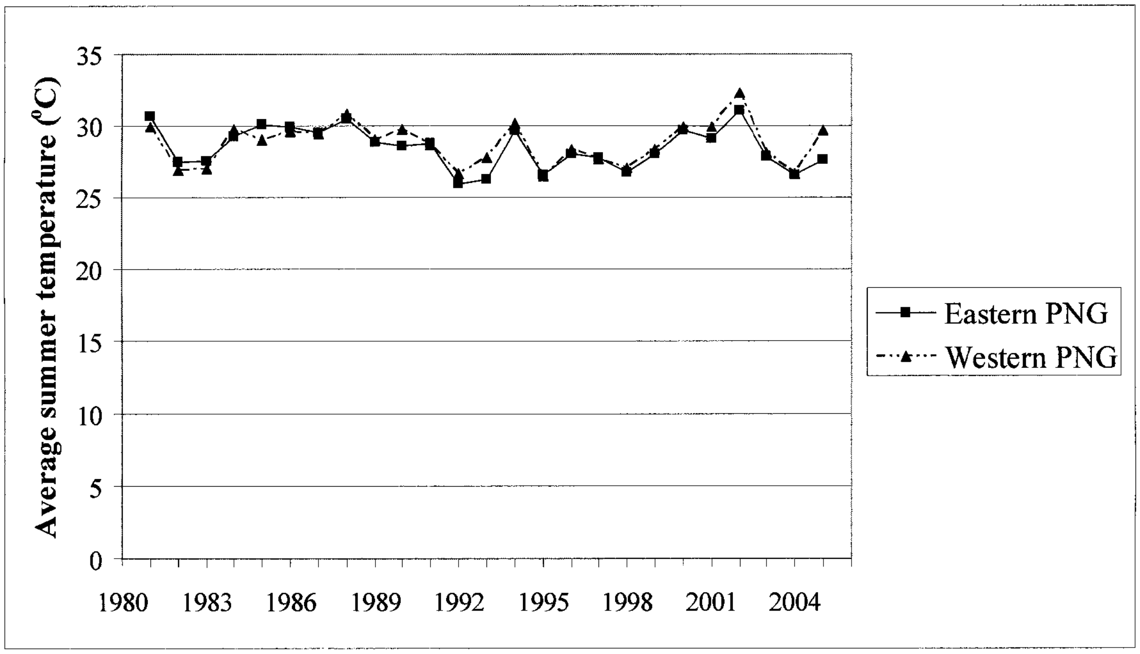

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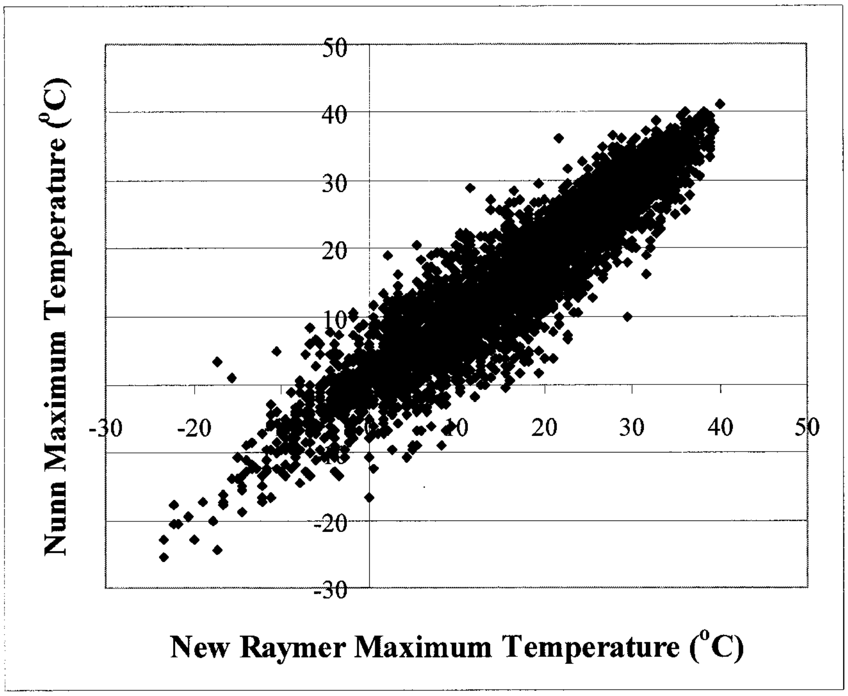
Figure 3.5. a) Average early spring temperature (March-April), and b) average early summer temperature (June-July) for the eastern and western units of the Pawnee National Grassland, Colorado, 1981-2005.



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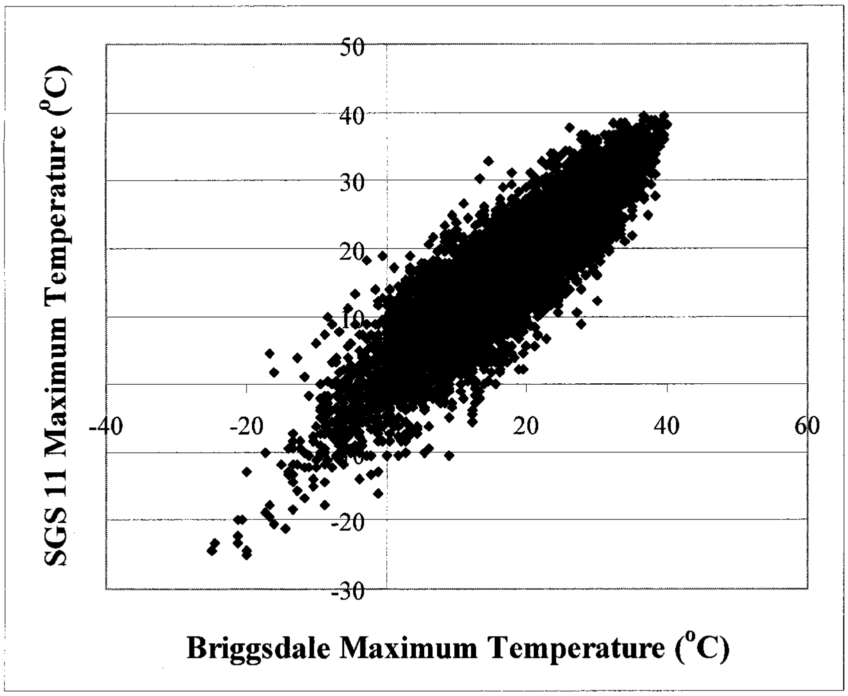

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Figure 3.6. Two examples of daily maximum temperature relationships between pairs of weather stations on the Pawnee National Grassland, Colorado: a) relationship between Nunn and New Raymer weather stations, and b) relationship between Briggsdale and SGS 11 weather stations.

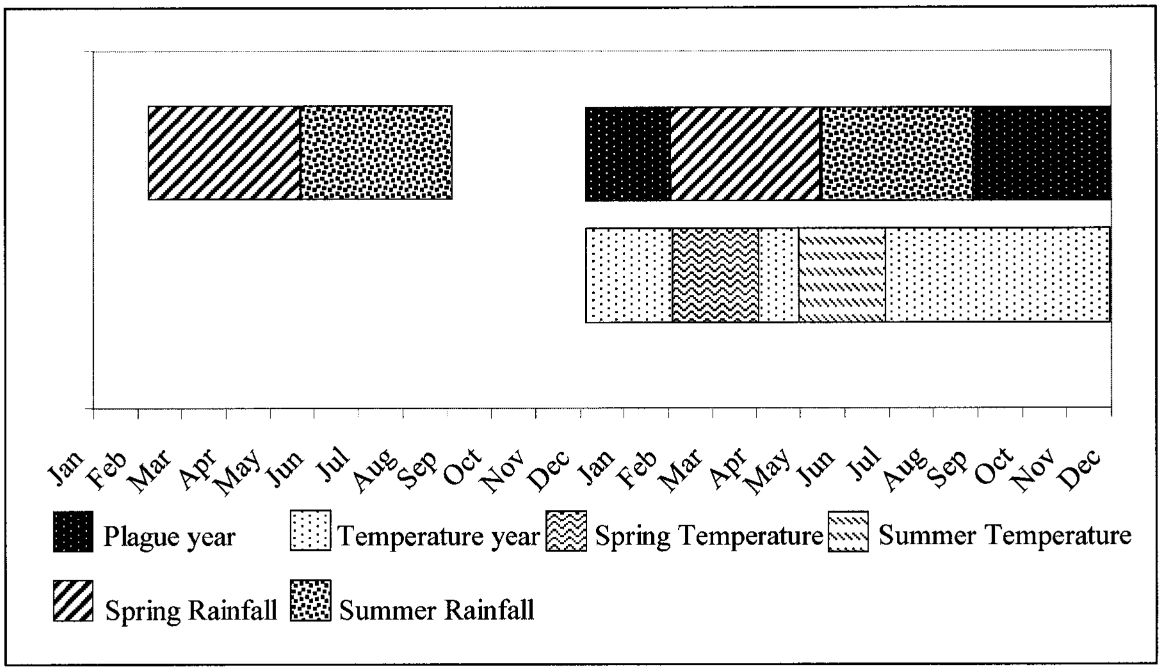
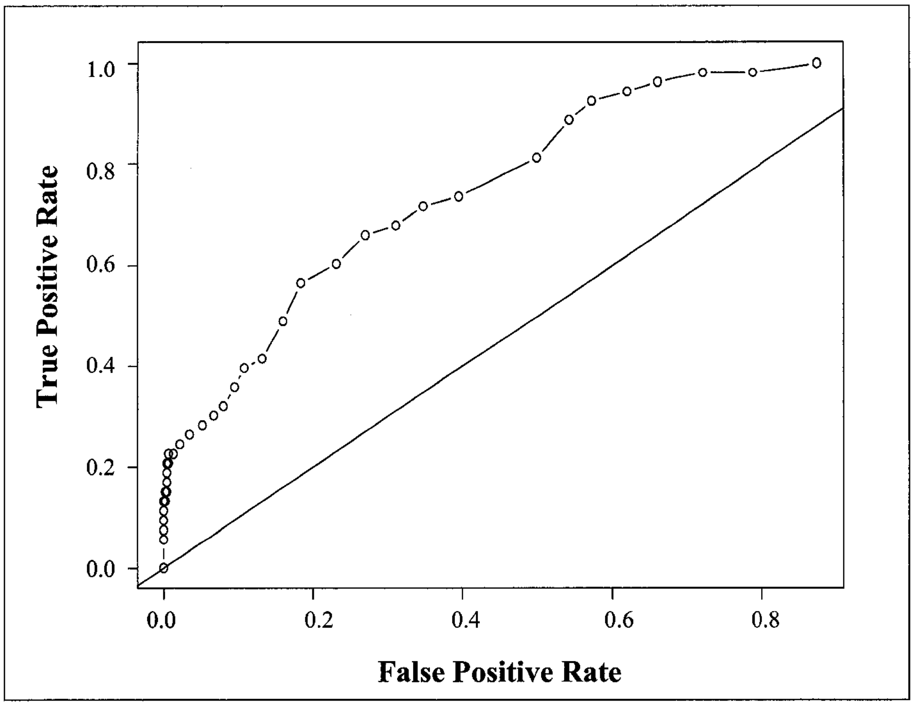


Figure 3.7. Temporal relationship between climatic parameters and modeled plague years for models explaining black-tailed prairie dog town extinctions: Plague year = 1 January - 31 December, Temperature year = 1 Jan-31 December, Spring Temperature = 1 March-30 April average temperature, Summer Temperature = 1 June-31 July average temperature, Spring Rainfall = 1 March- 15 June total precipitation, Summer Rainfall = 16 June- 30 September total precipitation.



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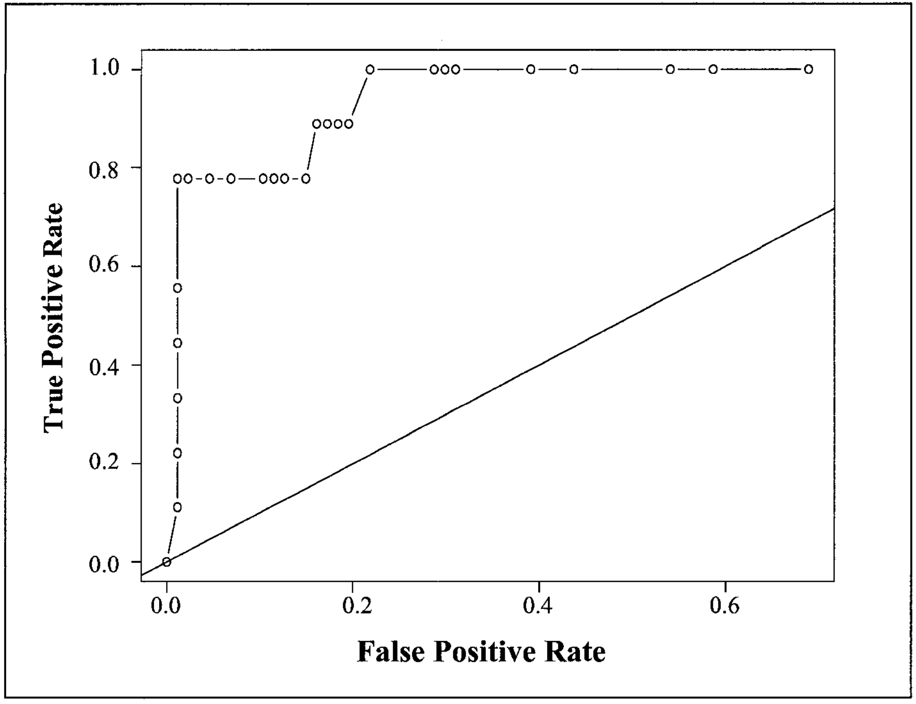

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Figure 3.8. Area under the ROC Curve (AUC) for GLM logistic regression model predicting extinctions from plague in black-tailed prairie dog towns for a) 1981-2003 data and b) 2004-2005 data.

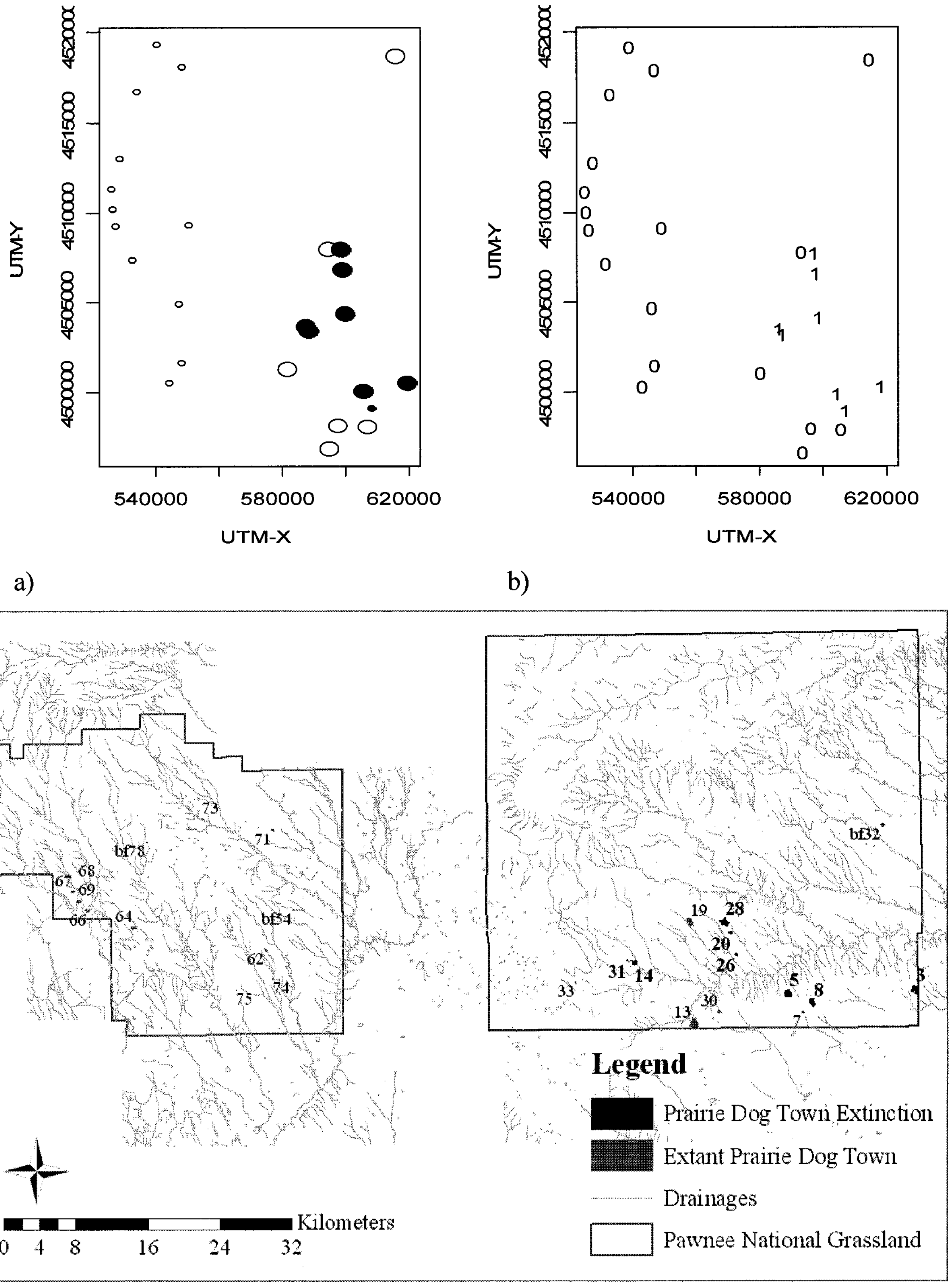

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Figure 3.9. a) Plot of the partial Moran's I statistic for prairie dog towns in 1992, b) spatial distribution showing plague status of towns, and c) map of towns with extinct town numbers in bold. In a) large and small circles represent strong and weak spatial autocorrelation with neighbors. Open and solid circles represent negative and positive spatial autocorrelation with neighbors. In b) 1 = extinct, 0 = extant towns.

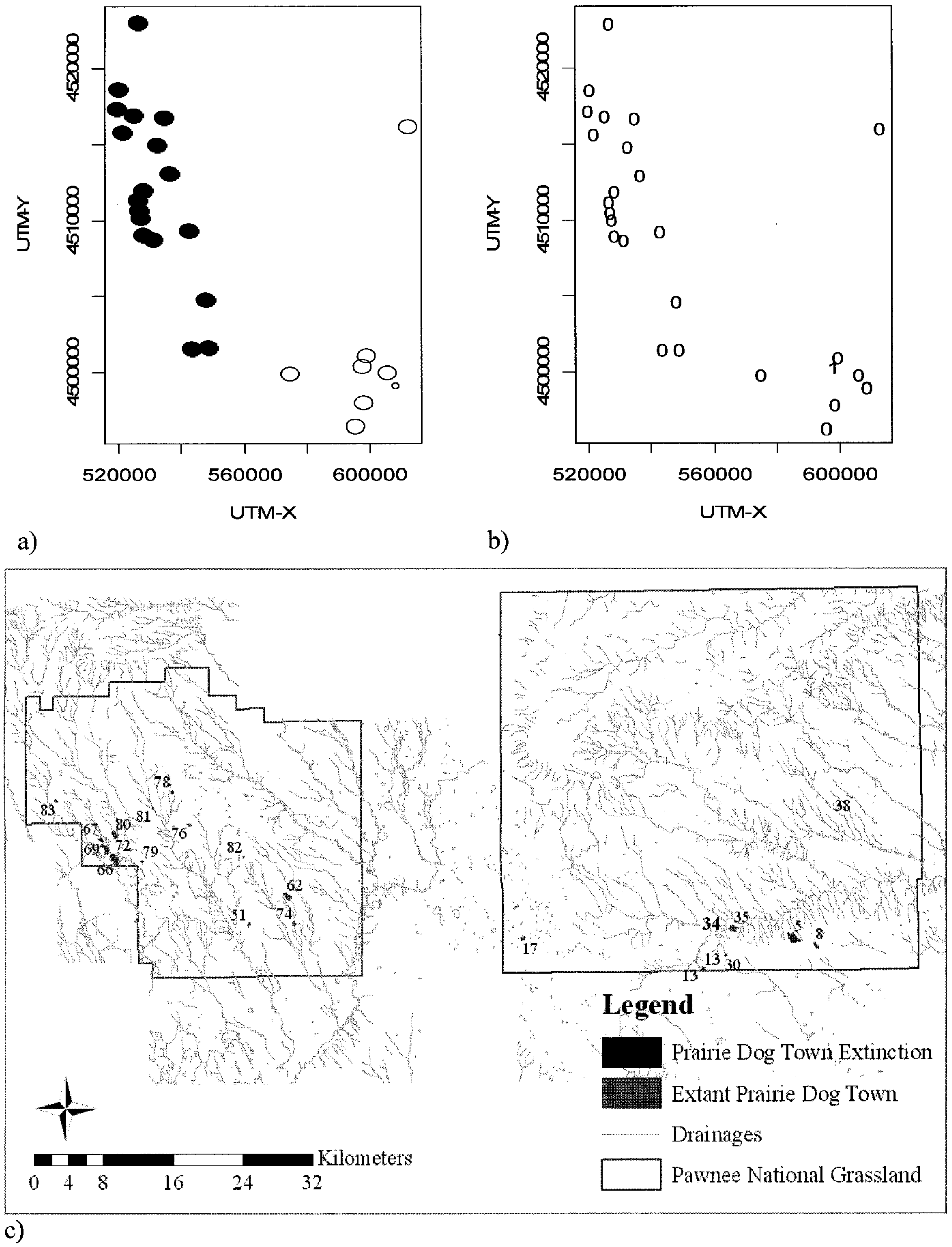


Figure 3.10. a) Plot of the partial Moran's I statistic for prairie dog towns in 1998, b) spatial distribution showing plague status of towns, and c) map of towns with extinct town numbers in bold. In a) large and small circles represent strong and weak spatial autocorrelation with neighbors. Open and solid circles represent negative and positive spatial autocorrelation. In b) 1 = extinct, 0 = extant towns.

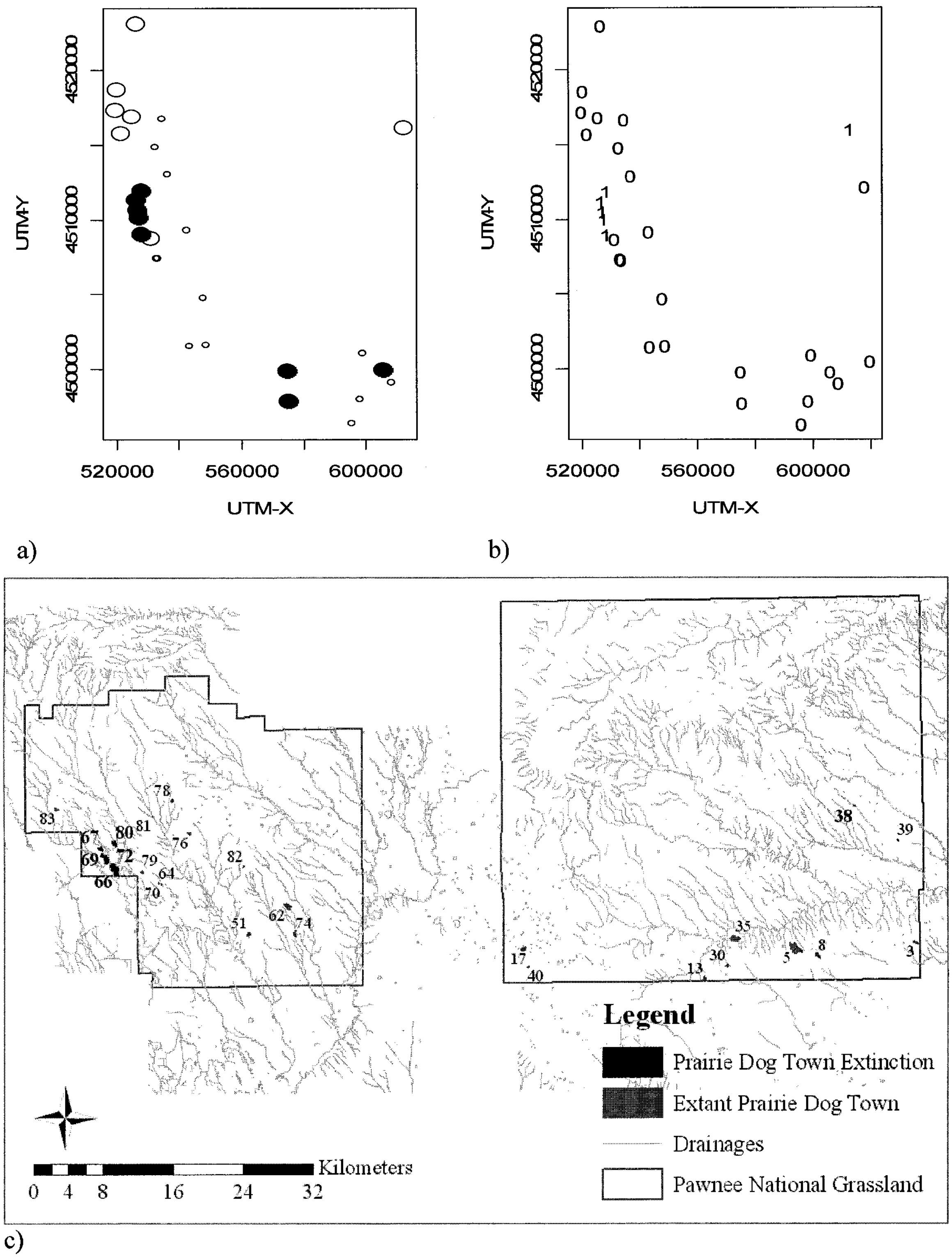


Figure 3.11. a) Plot of the partial Moran's I statistic for prairie dog towns in 1999, b) spatial distribution showing plague status of towns, and c) map of towns with extinct town numbers in bold. In a) large and small circles represent strong and weak spatial autocorrelation with neighbors. Open and solid circles represent negative and positive spatial autocorrelation. In b) 1 = extinct, 0 = extant towns.

Table 3.1. Model coefficients, standard errors, overall accuracy (Acc.), and area under the ROC curve (AUC) for GLM logistic regression models describing the probability of extinction from plague of individual prairie dog towns for three temperature imputations: a) imputation 1, b) imputation 2 and c) imputation 3.

Variable	**Coefficient**	**SE**	**Acc.**	**AUC**
a) Temperature Imputation 1				
Intercept	5.905	3.310	0.723	0.769
Connectivity: extant towns	-1.430	0.633		
Connectivity: plague extinctions	1.261	0.461		
15 bar soil water content	1.249	0.518		
Summer temperature, imputation 1	-0.331	0.117		
b) Temperature Imputation 2				
Intercept	5.819	3.314	0.721	0.770
Connectivity: extant towns	-1.426	0.632		
Connectivity: plague extinctions	1.262	0.461		
15 bar soil water content	1.249	0.518		
Summer temperature, imputation 2	-0.328	0.117		
c) Temperature Imputation 3				
Intercept	5.573	3.302	0.721	0.768
Connectivity: extant towns	-1.452	0.637		
Connectivity: plague extinctions	1.267	0.461		
15 bar soil water content	1.239	0.518		
Summer temperature, imputation 3	-0.319	0.117		

Table 3.2. Model coefficients, standard errors, overall accuracy (Acc.), and area under the ROC curve (AUC) for GEE spatial-temporal logit models describing the probability of extinction from plague of individual prairie dog towns for a) the independence model, b) the model accounting for spatial autocorrelation and c) the model accounting for temporal autocorrelation.

Variable	Coefficient	SE	Acc.	AUC
a) Independence Model				
Intercept	-4.137	0.772	0.459	0.774
Connectivity: extant towns	-1.623	0.725		
Summer precipitation	0.004	0.003		
15 bar soil water content	1.304	0.406		
b) Spatial Autocorrelation				
Intercept	-4.126	0.727	0.455	0.763
Connectivity: extant towns	-1.477	0.675		
Summer precipitation	0.004	0.003		
15 bar soil water content	1.286	0.393		
c) Temporal Correlation				
Intercept	-4.140	0.782	0.459	0.774
Connectivity: extant towns	-1.623	0.733		
Summer precipitation	0.004	0.002		
15 bar soil water content	1.304	0.484		

APPENDIX 3.1

Appendix 3.1. Methods and results from AIC analysis of plague extinctions in black-tailed prairie dog towns on the Pawnee National Grasslands, CO from 1981-2005.

METHODS

Model Selection

The independent variables included in our models were town connectivity to extant towns, CE, town connectivity to plagued towns, CP, town area, A, 15 bar soil water content, S, three temperature variables: average spring temperature T_{sp}, average summer temperature T_{su}, degree days 26.7°C /degree days 32.2°C, T_{dd}, and four precipitation variables: average spring precipitation in plague year t, P_{sp}, average summer precipitation in plague year t, P_{su}, average spring precipitation lagged one year, P_{sp-1}, and average summer precipitation lagged one year, P_{su-1}.

A set of models was created to encompass competing hypotheses by combining clusters of variables. First, sets of spatial variables were created by taking combinations of connectivity to extant towns, connectivity to plagued towns, and town area. I added to these sets 15 bar soil water content and one of the three temperature variables, then combined them with sets of this year's precipitation or last year's precipitation. This resulted in three sets of 103 models, one for each of the temperature variables. One final set of 286 models was created that included both spring and summer temperature. Because 11 models had no temperature variables and were included in each model set, a total of 376 models were tested.

In addition to the original sets of models comparing the effects of connectivity to extant towns and connectivity to plagued towns, I also analyzed models with overall connectivity to all towns in a given year, including both extant and plagued towns. An additional 16 models with overall connectivity to models from the spring and summer temperature set were tested.

I acknowledge that the large number of models tested puts this analysis on the exploratory end of the spectrum, and that it runs the risk of spurious or accidental correlations (Burnham and Anderson 2002; Haig 2003). However, the variables included in the models were carefully considered to keep the number of variables examined to a minimum, with specific hypotheses to be tested by each grouping of variables. While the model set does incorporate highly related models, the likely situation of multiple models with equally good fits to the data can be addressed by using a multi-model approach (Burnham and Anderson 2002).

Multi-model inference approach

A multi-model inference approach was used to rank models (Burnham and Anderson 2002) rather than determining a single "best" model. With a set of highly related models, the "best" model could vary considerably between replicate datasets by chance alone with misleading inference from any single model (Burnham and Anderson 2002). A multi-model approach allows information from all of the models that fit the data well to be retained.

An information-theoretic approach to evaluate models was employed, using Akaike's Information Criterion (AIC) values to determine the best-fitting, most parsimonious models. The AIC value was calculated as,

$$\mathrm{AIC} = -2\log(L(\hat{\theta}|data)) + 2K$$

where $\log(L(\hat{\theta}|data))$ is the maximized log-likelihood of unknown parameters given the data and the model, and K is the total number of estimated regression parameters (Burnham and Anderson 2002).

Models were ranked by AIC, and ΔAIC values were calculated by subtracting the AIC value from the model with the lowest AIC value from each model's AIC value. The top model has a ΔAIC of zero, and all other models have ΔAIC greater than zero (Burnham and Anderson 2002).

Akaike weights were calculated as

$$w_i = \frac{\exp(-\frac{1}{2}\Delta AIC_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta AIC_i)},$$

where exp(-1/2 ΔAIC) is the likelihood of each model, given the data. The Akaike weights of all models sum to one, and indicate the relative weight of evidence of each model relative to the entire set (Burnham and Anderson 2002). If no individual model is clearly superior to the others (with $w_i > .9$), as was the case here, then model averaging is recommended to allow inference based on a set of models. Model averaging was performed over the entire set of models and applied to the top model. Parameter coefficients were weighted over all models in which the predictor occurs as follows:

$$\hat{\bar{\beta}} = \frac{\sum_{i=1}^{R} w_i I_j(g_i)\hat{\beta}_{j,i}}{w_+(j)},$$

$$w_+(j) = \sum_{i=1}^{R} w_i I_j(g_i),$$

and

$$I_j(g_i) = \begin{matrix} 1 \text{ if predictor } x_j \text{ is in model } g_i \\ 0 \text{ otherwise} \end{matrix}$$

where $\hat{\beta}_{j,i}$ is the estimated coefficient of parameter x_j in model g_i. The coefficients were averaged over all models in which the predictor occurs. They were weighted by the Akaike weights and the sum of the weighted coefficients was divided by the sum of the weights of all models in which the predictor occurred. When model averages were calculated for a subset of the models, the Akaike weights were renormalized so that they summed to 1.

The unconditional variance estimator for each model was calculated as

$$\hat{\text{var}}(\hat{\bar{\theta}}) = \left[\sum_{i=1}^{R} w_i \sqrt{\hat{\text{var}}(\hat{\theta} | g_i) + (\hat{\theta}_i - \hat{\bar{\theta}})^2} \right]^2 ,$$

with

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \theta_i ,$$

where $\hat{\bar{\theta}}$ is the modeled averaged coefficient estimate and $\hat{\theta}_i$ is the coefficient estimate for model g_i (Burnham and Anderson 2002).

To determine the relative importance of individual variables, a balanced set of models was created that included all possible combinations of six variables, so that each of our variables had an equal number of appearances over the model set, and the Akaike weights of all models in which each variable appeared was summed.

RESULTS

GLM: Information-theoretic approach

Model sets with precipitation included. Four model sets that used different temperature measures were tested: degree days 26.7°C/degree days 32.2°C, spring temperature, summer temperature, and combined spring and summer temperature.

Prairie dog town extinctions were predicted by two spatial factors, connectivity to extant towns and to plagued towns, and by 15 bar soil water content. Model averaged coefficients, unconditional standard errors and 95% confidence intervals for the four temperature model sets are in Table 3A.1. In all model sets, town extinction was more likely for towns whose connectivity to extant towns dropped while their connectivity to plagued towns increased, and was more likely on towns with soils with higher water contents under dry conditions. AIC ranks and weights for the 95% confidence set for all model sets are shown in rank order in Table 3A.2. All models in the 95% confidence sets included both connectivity measures, suggesting they were the most important variables in predicting town extinctions. Models using any of the temperature measures in combination with the two connectivity measures and 15 bar soil water content had ΔAIC ≤ 6.7, suggesting the importance of 15 bar soil water content in predicting town extinctions.

There was also support for the effects of summer temperature on plague outbreaks (Table 3A.1). Although it appears that cooler summers overall (larger degree days 26.7°C/degree days 32.2°C) and warmer springs also increase plague, only summer temperature had 95% confidence intervals that did not overlap zero.

There was little support for the effect of town area in the model sets. Similarly, there was little for the effects of precipitation or lagged precipitation on town extinctions. The coefficients for spring precipitation and lagged spring precipitation were not stable across model sets, but variance inflation factors of 1.01 and 1.28 were well below the cutoff threshold of 2.5 that would indicate that multicollinearity was concerning (Allison 1999). While the relationship between summer precipitation and town extinction was stable and positive, a negative association between lagged summer precipitation and plague outbreaks was found which, while stable, directly contradicts the trophic-cascade hypothesis. I currently have no explanation for how low moisture in the previous year would increase plague outbreaks; this is potentially a spurious result. Additionally, none of the precipitation variables were strong predictors of plague outbreaks, and 95% confidence intervals for all precipitation variables in all model sets overlapped zero (Table 3A.1). To reduce the noise created by having models with insignificant variables included in them, precipitation variables were eliminated from model sets in subsequent analyses.

Model sets without precipitation. Model sets without precipitation show the same pattern as model sets with precipitation, with two spatial factors, connectivity to extant and to plagued towns, and 15 bar soil water content as the most important factors predicting plague outbreaks (Table 3A.3). Town extinction was more likely for towns isolated from extant towns and well connected to plagued towns, and was more likely on towns with soils that hold more moisture under dry conditions. Connectivity to extant towns and connectivity to plagued towns were included in all models of the 95% confidence set of models, suggesting they were the most important in predicting town extinctions. In fact, connectivity variables were such strong predictors that groups of models could be ranked by AIC value depending on their connectivity variables, with models including both connectivity variables ranking highest, then models with just connectivity to plagued towns, followed by models with connectivity to extant towns, and lastly, by models with only climatic factors. All models with a $\Delta AIC \leq 4$ contained the variable 15 bar soil water content, suggesting that it too was important in predicting plague outbreaks (Table 3A.4).

Town area also appeared in half of all models in the 95% confidence set, with larger towns being more likely to suffer extinctions (Table 3A.4), but in all model sets the 95% confidence intervals for the model averaged coefficient for town area overlapped zero (Table 3A.5).

Temperature, in particular summer temperature, and to a lesser degree spring temperature, was important in predicting plague outbreaks in prairie dog towns. There was a positive relationship between degree days 26.7°C/degree days 32.2°C and town extinction, a positive relationship between early spring temperature and town extinction, and a negative relationship between summer temperature and town extinction (Table 3A.4). The combined spring and summer temperature model set had the lowest AIC values, followed by the summer temperature model set, the spring temperature model set, and the degree days 26.7°C/degree days 32.2°C set.

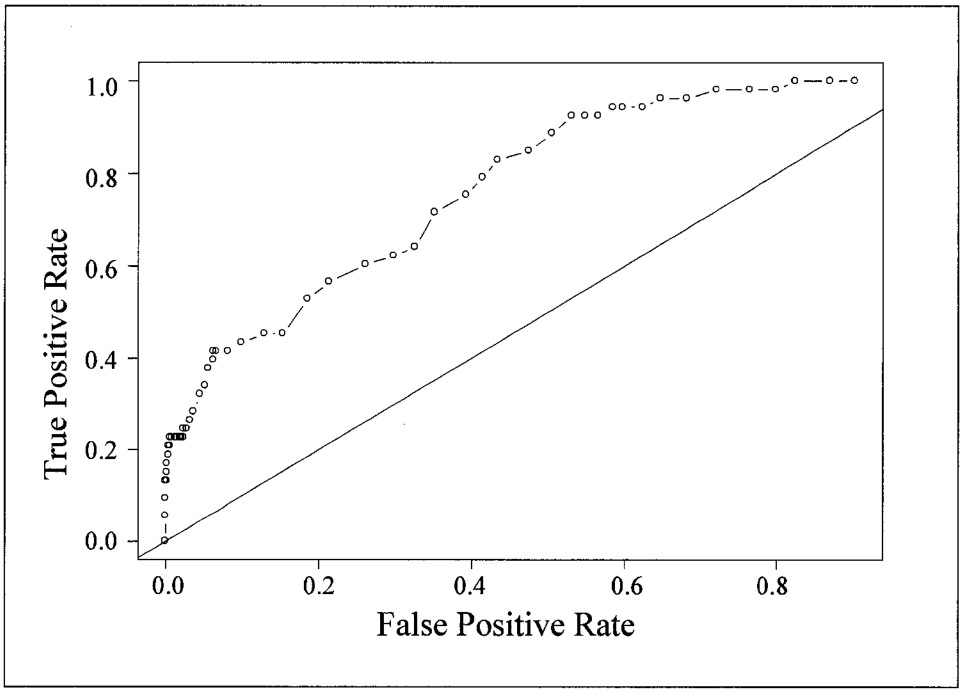
The relative importance of predictor variables in the spring and summer temperature model set were generally high: connectivity to extant towns (0.9986) and connectivity to plagued towns (0.9999) had predictor weights close to 1, 15 bar soil water content (0.9613) and summer temperature (0.9750) also had high predictor weights, with lower values for spring temperature (0.6336) and town area (0.3412).

Looking more closely at the spring and summer temperature model set, which was the best performing model set, the 95% confidence set of models contains six models within ΔAIC<7.3 (Table 3A.5), and a top model with an Akaike weight of 0.402, suggesting considerable uncertainty. Thus, model averaging was used to expand inference to a larger model set (Burnham and Anderson 2002). Averaging was performed on the entire set of models and model averaged coefficients were applied to the top model (Table 3A.5). The model averaged top model included variables connectivity to extant towns, connectivity to plagued towns, 15 bar soil water content, spring temperature and summer temperature. The ROC curves for the 1981-2003 and 2004-2005 data are shown in Figure 3A.1.

GLM Model Performance. The area under the ROC curve serves as a threshold-independent measure of model accuracy. The values for the 1981-2003 data from 0.708 to 0.781 while the values for the 2004-2005 data range from 0.900 to 0.980 (Table 3A.7). For the 1981-2003 data, the model achieving the highest AUC for every model set was a model that included spatial variables (connectivity to extant towns and to plagued towns), town area, 15 bar soil water content, and temperature. When testing models on the 2004-2005 data, the models with the highest AUC included spatial variables, town area, 15 bar soil water content, but not temperature variables. However, two to four models in each model set scored within one percent of the top model's AUC. Thus, multiple models perform almost equally for both the 1981-2003 and the 2004-2005 data, suggesting model selection uncertainty and lending support to inference based on model averaging. The model averaged top model had an AUC value for the 1981-2003 data of 0.78 and an AUC value for the 2004-2005 of 0.95 (Table 3A.5).

Overall model accuracy for the 95% certainty set of models ranged from 0.471 to 0.746 for the 1981-2003 data, and from 0.792 to 0.969 for the 2004-2005 data (Table 3A.7). As with the AUC values, these performance measures score consistently higher on the 2004-2005 data that on the 1981-2003 data. The 10-fold cross validation produced overall model accuracies that varied between 0.508 and 0.745 (Table 3A.7) but did not point to a single model with better predictive power than others.

Additional connectivity: connectivity to extant and plagued towns. An additional model set compared the effects of connectivity to extant towns and connectivity to plagued towns with overall connectivity to all towns in a given year, including both extant and plagued towns. When the models were ranked by AIC, a clear pattern emerged. First, models cluster together depending on the connectivity variables used; models including both connectivity to plagued towns and to extant towns ranked the highest followed by models containing only connectivity to plagued towns. These are followed by models containing only connectivity to extant towns. Models with overall connectivity and models with only climatic variables ranked the lowest (see Appendix iii). The model averaged coefficients, unconditional standard errors and 95% confidence intervals for this model set are in Table 3A.8.



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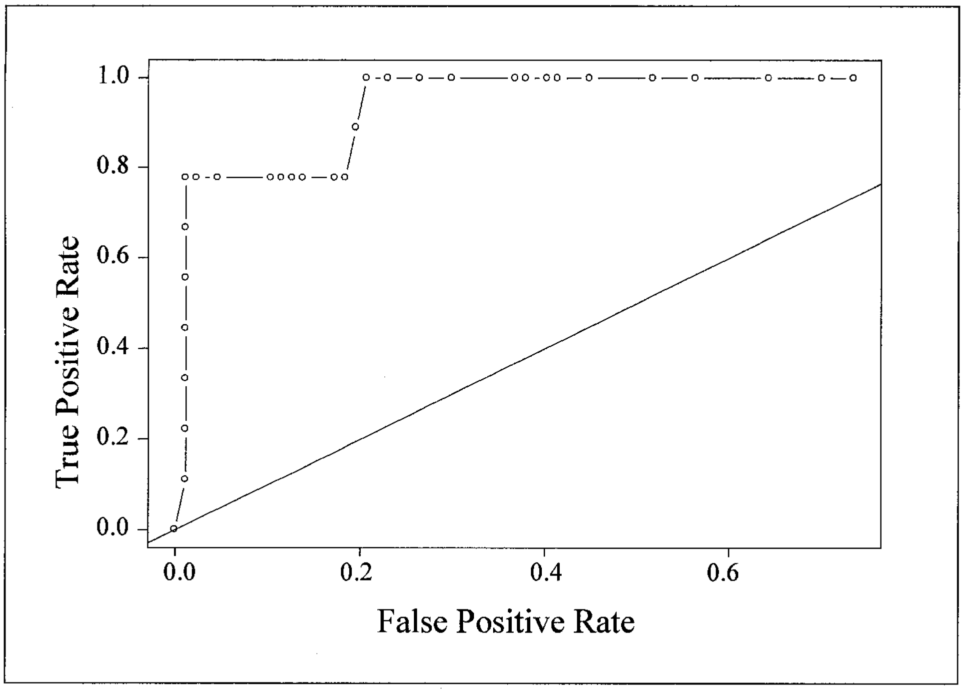

b)

Figure 3A.1. Receiver operating characteristic curves for spring and summer temperature model set for model averaged AIC top ranked model with model coefficients averaged over entire model set for a) 1981-2003 data and b) 2004-2005 data.

Table 3A.1. Model averaged coefficients, unconditional standard errors and 95% confidence intervals for model sets that include precipitation variables. Model sets vary according to temperature variable: a) degree days 26.7°C/degree days 32.2°C, b) spring temperature c) summer temperature and d) spring and summer temperature. Model averages were taken over entire model sets.

Variable	Coefficient	Uncond. SE	- 95%CI	+ 95%CI
a) Degree days 26.7/Degree days 32.2				
Intercept	-3.709	0.911	-5.495	-1.924
Connectivity: extant towns	-1.499	0.653	-2.778	-0.220
Connectivity: plagued towns	1.279	0.484	0.331	2.228
Area	0.007	0.008	-0.009	0.024
15 bar soil water content	1.180	0.519	0.163	2.196
Degree days 26.7/32.2	0.117	0.081	-0.042	0.277
Average Spring Precipitation	0.000	0.003	-0.006	0.006
Average Summer Precipitation	0.002	0.003	-0.004	0.007
Average Spring Precipitation Lagged 1 year	-0.002	0.003	-0.008	0.004
Average Summer Precipitation Lagged 1 year	-0.002	0.003	-0.008	0.005
b) Spring Temperature				
Intercept	-4.981	2.037	-8.973	-0.990
Connectivity: extant towns	-1.543	0.666	-2.849	-0.237
Connectivity: plagued towns	1.446	0.458	0.548	2.344
Area	0.009	0.008	-0.007	0.025
15 bar soil water content	1.095	0.512	0.091	2.098
Average Spring Temperature	0.151	0.121	-0.087	0.388
Average Spring Precipitation	0.001	0.003	-0.005	0.008
Average Summer Precipitation	0.004	0.003	-0.001	0.009
Average Spring Precipitation Lagged 1 year	-0.002	0.003	-0.008	0.004
Average Summer Precipitation Lagged 1 year	-0.001	0.003	-0.007	0.006
c) Summer Temperature				
Intercept	6.882	3.758	-0.483	14.247
Connectivity: extant towns	-1.431	0.632	-2.670	-0.192
Connectivity: plagued towns	1.250	0.465	0.338	2.163
Area	0.007	0.008	-0.009	0.024
15 bar soil water content	1.244	0.524	0.217	2.270
Average Summer Temperature	-0.356	0.125	-0.601	-0.111
Average Spring Precipitation	-0.003	0.003	-0.009	0.003
Average Summer Precipitation	0.000	0.003	-0.006	0.006
Average Spring Precipitation Lagged 1 year	0.001	0.003	-0.005	0.007
Average Summer Precipitation Lagged 1 year	-0.005	0.003	-0.011	0.002

Table 3A.1. continued:

Variable	Coefficient	Uncond. SE	- 95%CI	+ 95%CI
d) Spring and Summer Temperature				
Intercept	5.607	4.026	-2.284	13.498
Connectivity: extant towns	-1.419	0.625	-2.643	-0.194
Connectivity: plagued towns	1.179	0.467	0.263	2.096
Area	0.007	0.008	-0.009	0.024
15 bar soil water content	1.254	0.524	0.227	2.281
Average Spring Temperature	0.188	0.118	-0.044	0.420
Average Summer Temperature	-0.370	0.126	-0.617	-0.124
Average Spring Precipitation	-0.002	0.003	-0.009	0.005
Average Summer Precipitation	0.001	0.003	-0.005	0.007
Average Spring Precipitation Lagged 1 year	0.001	0.003	-0.006	0.007
Average Summer Precipitation Lagged 1 year	-0.004	0.003	-0.011	0.003

Table 3A.2. Summary of 95% confidence interval sets of models in AIC-based model selection for plague die-offs on black-tailed prairie dog towns, with models in rank order; the table also shows the maximized log-likelihood function (log($\mathscr{L}$)), number of predictor variables (*K*), AIC differences (ΔAIC_i) and Akaike weights (w_i). Table includes results for model sets which include precipitation variables and which vary by the temperature variables a) degree days 26.7°C/degree days 32.2°C, b) spring temperature, c) summer temperature and d) spring and summer temperature.

Model	Variables	-2log($\mathscr{L}$)	*K*	AIC	ΔAIC_i	w_i
a) Degree Days 26.7/Degree Days 32.2						
m87	$CE + CP + S + T_{dd}$	281.16	5	291.16	0.000	0.157
m100	$CE + CP + S$	284.15	4	292.15	0.987	0.096
m35	$CE + CP + S + T_{dd} + P_{su-1}$	280.20	6	292.20	1.041	0.093
m90	$CE + CP + A + S + T_{dd}$	280.41	6	292.41	1.250	0.084
m48	$CE + CP + S + T_{dd} + P_{sp-1}$	280.61	6	292.61	1.445	0.076
m9	$CE + CP + S + T_{dd} + P_{su}$	280.89	6	292.89	1.728	0.066
m22	$CE + CP + S + T_{dd} + P_{sp}$	281.15	6	293.15	1.983	0.058
m103	$CE + CP + A + S$	283.25	5	293.25	2.087	0.055
m38	$CE + CP + A + S + T_{dd} + P_{su-1}$	279.51	7	293.51	2.343	0.049
m74	$CE + CP + S + T_{dd} + P_{sp-1} + P_{su-1}$	279.91	7	293.91	2.747	0.040
m51	$CE + CP + A + S + T_{dd} + P_{sp-1}$	279.97	7	293.97	2.810	0.038
m12	$CE + CP + A + S + T_{dd} + P_{su}$	280.06	7	294.06	2.897	0.037
m25	$CE + CP + A + S + T_{dd} + P_{sp}$	280.41	7	294.41	3.245	0.031
m61	$CE + CP + S + T_{dd} + P_{sp} + P_{su}$	280.89	7	294.89	3.728	0.024
m77	$CE + CP + A + S + T_{dd} + P_{sp-1} + P_{su-1}$	279.30	8	295.30	4.134	0.020
m64	$CE + CP + A + S + T_{dd} + P_{sp} + P_{su}$	280.05	8	296.05	4.891	0.014
m97	$CE + CP + A$	289.06	4	297.06	5.900	0.008
m84	$CE + CP + A + T_{dd}$	287.12	5	297.12	5.959	0.008

Table 3A.2. continued

Model	Variables	$-2\log(\mathcal{L})$	K	AIC	ΔAIC_i	w_i
b) Spring Temperature						
m100	CE + CP + S	284.15	4	292.15	0.000	0.146
m9	CE + CP + S + T_{sp} + P_{su}	280.58	6	292.58	0.431	0.118
m87	CE + CP + S + T_{sp}	282.81	5	292.81	0.659	0.105
m103	CE + CP + A + S	283.25	5	293.25	1.100	0.084
m12	CE + CP + A + S + T_{sp} + P_{su}	279.51	7	293.51	1.360	0.074
m90	CE + CP + A + S + T_{sp}	281.87	6	293.87	1.723	0.062
m48	CE + CP + S + T_{sp} + P_{sp-1}	282.27	6	294.27	2.123	0.051
m61	CE + CP + S + T_{sp} + P_{sp} + P_{su}	280.43	7	294.43	2.280	0.047
m22	CE + CP + S + T_{sp} + P_{sp}	282.49	6	294.49	2.335	0.046
m35	CE + CP + S + T_{sp} + P_{su-1}	282.74	6	294.74	2.594	0.040
m64	CE + CP + A + S + T_{sp} + P_{sp} + P_{su}	279.42	8	295.42	3.270	0.029
m51	CE + CP + A + S + T_{sp} + P_{sp-1}	281.47	7	295.47	3.317	0.028
m25	CE + CP + A + S + T_{sp} + P_{sp}	281.63	7	295.63	3.478	0.026
m38	CE + CP + A + S + T_{sp} + P_{su-1}	281.82	7	295.82	3.667	0.023
m74	CE + CP + S + T_{sp} + P_{sp-1} + P_{su-1}	282.27	7	296.27	4.123	0.019
m97	CE + CP + A	289.06	4	297.06	4.913	0.013
m6	CE + CP + A + T_{sp} + P_{su}	285.32	6	297.32	5.169	0.011
m77	CE + CP + A + S + T_{sp} + P_{sp-1} + P_{su-1}	281.47	8	297.47	5.316	0.010
m94	CE + CP	291.53	3	297.53	5.381	0.010
m84	CE + CP + A + T_{sp}	287.57	5	297.57	5.419	0.010
c) Summer Temperature						
m35	CE + CP + S + T_{su} + P_{su-1}	273.53	6	285.53	0.000	0.160
m87	CE + CP + S + T_{su}	275.62	5	285.62	0.093	0.152
m22	CE + CP + S + T_{su} + P_{sp}	274.47	6	286.47	0.934	0.100
m90	CE + CP + A + S + T_{su}	274.97	6	286.97	1.442	0.078
m38	CE + CP + A + S + T_{su} + P_{su-1}	273.02	7	287.02	1.486	0.076
m74	CE + CP + S + T_{su} + P_{sp-1} + P_{su-1}	273.19	7	287.19	1.655	0.070
m9	CE + CP + S + T_{su} + P_{su}	275.62	6	287.62	2.084	0.056
m48	CE + CP + S + T_{su}+ P_{sp-1}	275.62	6	287.62	2.093	0.056
m25	CE + CP + A + S + T_{su} + P_{sp}	273.69	7	287.69	2.155	0.054
m61	CE + CP + S + T_{su} + P_{sp}+ P_{su}	274.46	7	288.46	2.933	0.037
m77	CE + CP + A + S + T_{su} + P_{sp-1}+ P_{su-1}	272.58	8	288.58	3.049	0.035
m12	CE + CP + A + S + T_{su}+ P_{su}	274.95	7	288.95	3.414	0.029
m51	CE + CP + A + S + T_{su} + P_{sp-1}	274.96	7	288.96	3.432	0.029
m64	CE + CP + A + S + T_{su} + P_{sp} + P_{su}	273.68	8	289.68	4.144	0.020
m100	CE + CP + S	284.15	4	292.15	6.619	0.006

Table 3A.2. continued:

Model	**Variables**	**$-2\log(\mathcal{L})$**	***K***	**AIC**	**ΔAIC_i**	**w_i**
d) Spring and Summer Temperature						
m87 sp&su	CE + CP + S + T_{sp} + T_{su}	272.45	6	284.45	0.000	0.115
m35 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{su-1}	271.30	7	285.30	0.859	0.075
m35 su	CE + CP + S + T_{su} + P_{su-1}	273.53	6	285.53	1.086	0.067
m87 su	CE + CP + S + T_{su}	275.62	5	285.62	1.180	0.064
m90 sp&su	CE + CP + A + S + T_{sp} + T_{su}	271.87	7	285.87	1.422	0.057
m22 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp}	272.35	7	286.35	1.909	0.044
m9 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{su}	272.42	7	286.42	1.970	0.043
m48 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp-1}	272.44	7	286.44	2.000	0.042
m22 su	CE + CP + S + T_{su} + P_{sp}	274.47	6	286.47	2.020	0.042
m38 sp&su	CE + CP + A + S + T_{sp} + T_{su} + P_{su-1}	270.81	8	286.81	2.365	0.035
m90 su	CE + CP + A + S + T_{su}	274.97	6	286.97	2.528	0.033
m38 su	CE + CP + A + S + T_{su} + P_{su-1}	273.02	7	287.02	2.572	0.032
m74 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	271.03	8	287.03	2.584	0.032
m74 su	CE + CP + S + T_{su} + P_{sp-1} + P_{su-1}	273.19	7	287.19	2.742	0.029
m9 su	CE + CP + S + T_{su}+ P_{su}	275.62	6	287.62	3.170	0.024
m48 su	CE + CP + S + T_{su} + P_{sp-1}	275.62	6	287.62	3.179	0.023
m25 su	CE + CP + A + S + T_{su} + P_{sp}	273.69	7	287.69	3.241	0.023
m25 sp&su	CE + CP + A + S + T_{sp} + T_{su} + P_{sp}	271.72	8	287.72	3.279	0.022
m12 sp&su	CE + CP + A + S + T_{sp} + T_{su} + P_{su}	271.81	8	287.81	3.365	0.021
m51 sp&su	CE + CP + A + S + T_{sp} + T_{su} + P_{sp-1}	271.86	8	287.86	3.412	0.021
m61 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp} + P_{su}	272.33	8	288.33	3.886	0.016
m77 sp&su	CE + CP + A + S + T_{sp} + T_{su}+ Ps_{p-1} + P_{su-1}	270.45	9	288.45	4.006	0.016
m61 su	CE + CP + S + T_{su} + P_{sp} + P_{su}	274.46	7	288.46	4.019	0.015
m77 su	CE + CP + A + S + T_{su} + P_{sp-1} + Psu-1	272.58	8	288.58	4.136	0.015
m12 su	CE + CP + A + S + T_{su} + P_{su}	274.95	7	288.95	4.500	0.012
m51 su	CE + CP + A + S + T_{su} + P_{sp-1}	274.96	7	288.96	4.518	0.012
m64 su	CE + CP + A + S + T_{su} + P_{sp} + P_{su}	273.68	8	289.68	5.230	0.008
m64 sp&su	CE + CP + A + S + T_{sp} + T_{su} + P_{sp} + P_{su}	271.68	9	289.68	5.233	0.008
m84 sp&su	CE + CP + A + T_{sp} + T_{su}	279.55	6	291.55	7.100	0.003

[*] Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil water content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July); P_{sp} = average spring precipitation (March 1-June 15); P_{su} = average summer precipitation (June 16-September 30); $P_{sp(t-1)}$ = average spring precipitation (March 1-June 15) lagged one year; $P_{su(t-1)}$ = average summer precipitation (June 16-September 30) lagged one year.

Table 3A.3. Model averaged coefficients, unconditional standard errors and 95% confidence intervals for model sets that do not include precipitation variables. Model sets vary according to temperature variable: a) degree days 26.7°C/degree days 32.2°C, b) spring temperature c) summer temperature and d) spring and summer temperature. Model averages were taken over entire model sets.

Variable	Coefficient	Uncond. SE	- 95%CI	+ 95%CI
a) Degree Days 26.7/Degree Days 32.2				
Intercept	-3.670	0.814	-5.265	-2.075
Connectivity: extant towns	-1.521	0.656	-2.808	-0.235
Connectivity: plagued towns	1.354	0.483	0.407	2.302
Area	0.008	0.008	-0.008	0.025
15 bar soil water content	1.149	0.514	0.140	2.157
Degree days 26.7/32.2	0.136	0.077	-0.016	0.287
b) Spring Temperature				
Intercept	-4.021	1.427	-6.817	-1.224
Connectivity: extant towns	-1.567	0.671	-2.882	-0.252
Connectivity: plagued towns	1.495	0.455	0.604	2.386
Area	0.009	0.008	-0.007	0.025
15 bar soil water content	1.093	0.511	0.092	2.095
Average Spring Temperature	0.133	0.115	-0.092	0.358
c) Summer Temperature				
Intercept	5.502	3.547	-1.450	12.454
Connectivity: extant towns	-1.445	0.637	-2.695	-0.196
Connectivity: plagued towns	1.275	0.466	0.361	2.188
Area	0.007	0.008	-0.009	0.024
15 bar soil water content	1.219	0.522	0.196	2.243
Average Summer Temperature	-0.328	0.117	-0.558	-0.098
d) Spring and Summer Temperature				
Intercept	4.652	4.203	-3.586	12.891
Connectivity: extant towns	-1.425	0.662	-2.722	-0.128
Connectivity: plagued towns	1.182	0.513	0.176	2.188
Area	0.007	0.008	-0.009	0.023
15 bar soil water content	1.243	0.533	0.199	2.287
Average Spring Temperature	0.199	0.115	-0.026	0.424
Average Summer Temperature	-0.355	0.121	-0.593	-0.118

Table 3A.4. Summary of 95% confidence interval sets of models in AIC-based model selection for plague die-offs on black-tailed prairie dog towns, with models in rank order. Table includes results for model sets which do not include precipitation variables and which vary by the temperature variables a) degree days 26.7°C/degree days 32.2°C, b) spring temperature, c) summer temperature and d) spring and summer temperature.*

Model	**Variables**	**$-2\log(\mathcal{L})$**	**K**	**AIC**	**ΔAIC_i**	**w_i**
a) Degree Days 26.7/Degree Days 32.2						
m87	CE + CP + S + T_{dd}	281.16	5	291.16	0.000	0.372
m100	CE + CP + S	284.15	4	292.15	0.987	0.227
m90	CE + CP + A + S + T_{dd}	280.41	6	292.41	1.250	0.199
m103	CE + CP + A + S	283.25	5	293.25	2.087	0.131
m97	CE + CP + A	289.06	4	297.06	5.900	0.019
m84	CE + CP + A + T_{dd}	287.12	5	297.12	5.959	0.019
b) Spring Temperature						
m100	CE + CP + S	284.15	4	292.15	0.000	0.334
m87	CE + CP + S + T_{sp}	282.81	5	292.81	0.659	0.240
m103	CE + CP + A + S	283.25	5	293.25	1.100	0.193
m90	CE + CP + A + S + T_{sp}	281.87	6	293.87	1.723	0.141
m97	CE + CP + A	289.06	4	297.06	4.913	0.029
m94	CE + CP	291.53	3	297.53	5.381	0.023
c) Summer Temperature						
m87	CE + CP + S + T_{su}	275.62	5	285.62	0.000	0.608
m90	CE + CP + A + S + T_{su}	274.97	6	286.97	1.349	0.310
m100	CE + CP + S	284.15	4	292.15	6.526	0.023
m84	CE + CP + A + T_{su}	282.25	5	292.25	6.628	0.022
d) Spring and Summer Temperature						
m87 sp&su	CE + CP + S + T_{sp} + T_{su}	272.45	6	284.45	0.000	0.402
m87 su	CE + CP + S + T_{su}	275.62	5	285.62	1.180	0.223
m90 sp&su	CE + CP + A + S + T_{sp} + T_{su}	271.87	7	285.87	1.422	0.197
m90 su	CE + CP + A + S + T_{su}	274.97	6	286.97	2.528	0.114
m84 sp&su	CE + CP + A + T_{sp} + T_{su}	279.55	6	291.55	7.100	0.012
m81 sp&su	CE + CP + T_{sp} + T_{su}	281.78	5	291.78	7.336	0.010

*Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil water content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July); $\log(\mathcal{L})$ = maximized log-likelihood function; K = number of predictor variables; ΔAIC_i = AIC differences; w_i = Akaike weights.

Table 3A.5. Model averaged coefficients, unconditional standard errors, 95% confidence intervals, overall model accuracy (Acc.) and AUC for Spring and Summer Temperature model set without precipitation for AIC top ranked model with model coefficients and unconditional standard errors based on entire model set.

Variables	Coef.	SE	- 95%CI	+ 95%CI	Acc.	AUC
a) AIC Top Ranked Model					0.593	0.780
Intercept	4.652	4.203	-3.586	12.891		
Connectivity: extant towns	-1.425	0.662	-2.722	-0.128		
Connectivity: plagued towns	1.182	0.513	0.176	2.188		
Area	0.007	0.008	-0.009	0.023		
15 bar soil water content	1.243	0.533	0.199	2.287		
Average Spring Temperature	0.199	0.115	-0.026	0.424		
Average Summer Temperature	-0.355	0.121	-0.593	-0.118		

Table 3A.6. Model accuracy and AUC for 1981-2003 data and 2004-2005 data, and k-fold cross validation average accuracy for the top 8 AIC ranked models in four temperature model sets: a) degree days 26.7°C/degree days 32.2°C, b) spring temperature, c) temperature summer temperature, and d) spring and summer temperature which do include models with precipitation variables.*

		1981-2003 data		2004-2005 data		
Model	**Variables**	**Acc.**	**AUC**	**Acc.**	**AUC**	**k-fold Acc.**
a) Degree Days 26.7/Degree Days 32.2						
m87	CE + CP + S + T_{dd}	0.471	0.734	0.844	0.958	0.565
m100	CE + CP + S	0.543	0.724	0.906	0.961	0.508
m35	CE + CP + S + T_{dd} + P_{su-1}	0.484	0.740	0.969	0.954	0.539
m90	CE + CP + A + S + T_{dd}	0.640	0.744	0.958	0.980	0.588
m48	CE + CP + S + T_{dd} + P_{sp-1}	0.442	0.740	0.865	0.973	0.533
m9	CE + CP + S + T_{dd} + P_{su}	0.448	0.743	0.854	0.958	0.602
m22	CE + CP + S + T_{dd} + P_{sp}	0.483	0.736	0.844	0.963	0.629
m103	CE + CP + A + S	0.547	0.731	0.958	0.980	0.663
b) Spring Temperature						
m100	CE + CP + S	0.543	0.724	0.906	0.961	0.508
m9	CE + CP + S + T_{sp} + P_{su}	0.822	0.751	0.969	0.951	0.692
m87	CE + CP + S + T_{sp}	0.746	0.741	0.969	0.950	0.592
m103	CE + CP + A + S	0.545	0.731	0.958	0.980	0.663
m12	CE + CP + A + S + T_{sp} + P_{su}	0.810	0.755	0.875	0.969	0.641
m90	CE + CP + A + S + T_{sp}	0.566	0.746	0.948	0.976	0.643
m48	CE + CP + S + T_{sp} + P_{sp-1}	0.469	0.739	0.948	0.962	0.688
m61	CE + CP + S + T_{sp} + P_{sp} + P_{su}	0.457	0.749	0.969	0.954	0.610
c) Summer Temperature						
m35	CE + CP + S + T_{su} + P_{su-1}	0.804	0.777	0.792	0.950	0.751
m87	CE + CP + S + T_{su}	0.723	0.769	0.802	0.952	0.706
m22	CE + CP + S + T_{su} + P_{sp}	0.707	0.776	0.802	0.950	0.659
m90	CE + CP + A + S + T_{su}	0.620	0.769	0.958	0.966	0.706
m38	CE + CP + A + S + T_{su} + P_{su-1}	0.523	0.775	0.938	0.962	0.731
m74	CE + CP + S + T_{su} + P_{sp-1} + P_{su-1}	0.560	0.776	0.792	0.948	0.673
m9	CE + CP + S + T_{su} + P_{su}	0.719	0.769	0.813	0.953	0.671
m48	CE + CP + S + T_{su} + P_{sp-1}	0.723	0.769	0.813	0.953	0.477
d) Spring and Summer Temperature						
m87 sp&su	CE + CP + S + T_{sp} + T_{su}	0.605	0.774	0.792	0.948	0.665
m35 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{su-1}	0.516	0.779	0.802	0.948	0.716
m35 su	CE + CP + S + T_{su} + P_{su-1}	0.804	0.777	0.792	0.950	0.751
m87 su	CE + CP + S + T_{su}	0.723	0.769	0.802	0.952	0.686
m90 sp&su	CE + CP + A + S + T_{sp} + T_{su}	0.517	0.781	0.823	0.955	0.641
m22 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp}	0.562	0.778	0.802	0.948	0.649
m9 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{su}	0.517	0.776	0.802	0.949	0.645
m48 sp&su	CE + CP + S + T_{sp} + T_{su} + P_{sp-1}	0.514	0.774	0.792	0.948	0.667

*Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil water content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July); P_{sp} = average spring precipitation (March 1-June 15); P_{su} = average summer precipitation (June 16-September 30); $P_{sp(t-1)}$ = average spring precipitation (March 1-June 15) lagged one year; $P_{su(t-1)}$ = average summer precipitation (June 16-September 30) lagged one year.

Table 3A.7. Model accuracy and AUC for 1981-2003 data and 2004-2005 data, and k-fold cross validation average accuracy for the top 8 AIC ranked models in four temperature model sets: a) degree days 26.7°C/degree days 32.2°C, b) spring temperature, c) temperature summer temperature, and d) spring and summer temperature which do not include models with precipitation variables.*

		1981-2003 data		2004-2005 data		
Model	**Variables**	**Acc.**	**AUC**	**Acc.**	**AUC**	**k-fold Acc.**
b) Spring Temperature						
m100	CE + CP + S	0.543	0.724	0.906	0.961	0.508
m87	CE + CP + S + T_{sp}	0.746	0.741	0.969	0.950	0.592
m103	CE + CP + A + S	0.545	0.731	0.958	0.980	0.663
m90	CE + CP + A + S + T_{sp}	0.566	0.746	0.948	0.976	0.643
m97	CE + CP + A	0.610	0.739	0.958	0.977	0.608
m94	CE + CP	0.531	0.708	0.958	0.916	0.551
c) Summer Temperature						
m87	CE + CP + S + T_{su}	0.723	0.769	0.802	0.952	0.706
m90	CE + CP + A + S + T_{su}	0.620	0.769	0.958	0.966	0.706
m100	CE + CP + S	0.543	0.724	0.906	0.961	0.508
m84	CE + CP + A + T_{su}	0.607	0.744	0.948	0.961	0.706
m81	CE + CP + T_{su}	0.744	0.738	0.969	0.907	0.745
m103	CE + CP + A + S	0.545	0.731	0.958	0.980	0.663
a) Degree Days 26.7/Degree Days 32.2						
m87	CE + CP + S + T_{dd}	0.471	0.734	0.844	0.958	0.565
m100	CE + CP + S	0.543	0.724	0.906	0.961	0.508
m90	CE + CP + A + S + T_{dd}	0.640	0.744	0.958	0.980	0.588
m103	CE + CP + A + S	0.547	0.731	0.958	0.980	0.663
m97	CE + CP + A	0.610	0.739	0.958	0.977	0.608
m84	CE + CP + A + T_{dd}	0.746	0.715	0.948	0.976	0.590
d) Spring and Summer Temperature						
m87 sp&su	CE + CP + S + T_{sp} + T_{su}	0.605	0.774	0.792	0.948	0.665
m87 su	CE + CP + S + T_{su}	0.723	0.769	0.802	0.952	0.686
m90 sp&su	CE + CP + A + S + T_{sp} + T_{su}	0.517	0.781	0.823	0.955	0.641
m90 su	CE + CP + A + S + T_{su}	0.620	0.769	0.958	0.966	0.665
m84 sp&su	CE + CP + A + T_{sp} + T_{su}	0.672	0.750	0.948	0.956	0.716
m81 sp&su	CE + CP + T_{sp} + T_{su}	0.729	0.745	0.969	0.900	0.714

* Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil water content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July).

Table 3A.8. Model averaged logistic regression coefficients and unconditional standard errors for model set containing three connectivity variables: connectivity to both extant and plagued towns, connectivity to extant towns and connectivity to plagued towns, predicting extinctions in prairie dog towns. Coefficients and unconditional standard errors based on entire model set.

Variable	**Coefficient**	**Uncond. SE**	**- 95%CI**	**+ 95%CI**
Intercept	4.652	3.623	-2.449	11.753
Connectivity: extant and plagued towns	0.043	0.060	-0.074	0.160
Connectivity: extant towns	-1.425	0.626	-2.653	-0.198
Connectivity: plagued towns	1.182	0.468	0.264	2.100
Area	0.007	0.008	-0.009	0.024
15 bar soil water content	1.243	0.523	0.217	2.268
Average spring temperature	0.199	0.115	-0.025	0.424
Average summer temperature	-0.355	0.121	-0.593	-0.118

APPENDIX 3.2

Appendix 3.2. Results of AIC based model selection for plague occurrence in black-tailed prairie dog towns in a 286 model set which includes spring and summer temperature and spring and summer precipitation variables. The AIC weights of the 95% confidence set are highlighted.*

model	k	AIC	ΔAIC	£(g_i|data)	w_i	parameters	int	CE	CP	A	S	T_{sp}	T_{su}	P_{sp}	P_{su}	P_{sp-1}	P_{su-1}
sp&su m87	6	284.45	0.000	1.000	0.115	$CE + CP + S + T_{sp} + T_{su}$	4.365	-1.404	1.122		1.282	0.201	-0.375				
sp&su m35	7	285.30	0.859	0.651	0.075	$CE + CP + S + T_{sp} + T_{su} + P_{su-1}$	6.127	-1.405	1.110		1.296	0.172	-0.403				-0.0035
su m35	6	285.53	1.086	0.581	0.067	$CE + CP + S + T_{su} + P_{su-1}$	7.942	-1.427	1.215		1.286		-0.379				-0.0045
su m87	5	285.62	1.180	0.554	0.064	$CE + CP + S + T_{su}$	5.905	-1.430	1.261		1.249		-0.331				
sp&su m90	7	285.87	1.422	0.491	0.057	$CE + CP + A + S + T_{sp} + T_{su}$	4.216	-1.431	1.109	0.007	1.213	0.200	-0.369				
sp&su m22	7	286.35	1.909	0.385	0.044	$CE + CP + S + T_{sp} + T_{su} + P_{sp}$	4.963	-1.400	1.139		1.286	0.184	-0.382	-0.0010			
sp&su m9	7	286.42	1.970	0.373	0.043	$CE + CP + S + T_{sp} + T_{su} + P_{su}$	4.033	-1.400	1.122		1.280	0.203	-0.367		0.0005		
sp&su m48	7	286.44	2.000	0.368	0.042	$CE + CP + S + T_{sp} + T_{su} + P_{sp-1}$	4.371	-1.403	1.123		1.282	0.201	-0.375			0.0001	
su m22	6	286.47	2.020	0.364	0.042	$CE + CP + S + T_{su} + P_{sp}$	7.542	-1.414	1.267		1.272		-0.372	-0.0033			
sp&su m38	8	286.81	2.365	0.306	0.035	$CE + CP + A + S + T_{sp} + T_{su} + P_{su-1}$	5.907	-1.429	1.098	0.006	1.232	0.172	-0.396				-0.0034
su m90	6	286.97	2.528	0.282	0.033	$CE + CP + A + S + T_{su}$	5.773	-1.463	1.254	0.007	1.177		-0.327				
su m38	7	287.02	2.572	0.276	0.032	$CE + CP + A + S + T_{su} + P_{su-1}$	7.736	-1.454	1.208	0.006	1.221		-0.372				-0.0043
sp&su m74	8	287.03	2.584	0.275	0.032	$CE + CP + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	6.697	-1.375	1.112		1.309	0.168	-0.426			0.0017	-0.0043
su m74	7	287.19	2.742	0.254	0.029	$CE + CP + S + T_{su} + P_{sp-1} + P_{su-1}$	8.500	-1.390	1.213		1.305		-0.405			0.0019	-0.0052
su m9	6	287.62	3.170	0.205	0.024	$CE + CP + S + T_{su} + P_{su}$	5.736	-1.429	1.262		1.248		-0.327		0.0003		
su m48	6	287.62	3.179	0.204	0.023	$CE + CP + S + T_{su} + P_{sp-1}$	5.912	-1.430	1.262		1.249		-0.332			0.0001	
su m25	7	287.69	3.241	0.198	0.023	$CE + CP + A + S + T_{su} + P_{sp}$	7.502	-1.444	1.255	0.008	1.195		-0.369	-0.0034			
sp&su m25	8	287.72	3.279	0.194	0.022	$CE + CP + A + S + T_{sp} + T_{su} + P_{sp}$	4.971	-1.426	1.128	0.007	1.216	0.178	-0.378	-0.0013			
sp&su m12	8	287.81	3.365	0.186	0.021	$CE + CP + A + S + T_{sp} + T_{su} + P_{su}$	3.750	-1.426	1.109	0.007	1.208	0.202	-0.357		0.0007		
sp&su m51	8	287.86	3.412	0.182	0.021	$CE + CP + A + S + T_{sp} + T_{su} + P_{sp-1}$	4.246	-1.427	1.110	0.007	1.214	0.200	-0.371			0.0003	
sp&su m61	8	288.33	3.886	0.143	0.016	$CE + CP + S + T_{sp} + T_{su} + P_{sp} + P_{su}$	4.649	-1.397	1.138		1.284	0.186	-0.375	-0.0010	0.0005		
sp&su m77	9	288.45	4.006	0.135	0.016	$CE + CP + A + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	6.550	-1.394	1.099	0.007	1.242	0.167	-0.422			0.0020	-0.0043
su m61	7	288.46	4.019	0.134	0.015	$CE + CP + S + T_{su} + P_{sp} + P_{su}$	7.478	-1.413	1.267		1.272		-0.370	-0.0032	0.0001		
su m77	8	288.58	4.136	0.126	0.015	$CE + CP + A + S + T_{su} + P_{sp-1} + P_{su-1}$	8.356	-1.413	1.205	0.007	1.237		-0.402			0.0021	-0.0051
su m12	7	288.95	4.500	0.105	0.012	$CE + CP + A + S + T_{su} + P_{su}$	5.486	-1.462	1.255	0.007	1.174		-0.319		0.0005		
su m51	7	288.96	4.518	0.104	0.012	$CE + CP + A + S + T_{su} + P_{sp-1}$	5.806	-1.459	1.255	0.007	1.178		-0.330			0.0003	
su m64	8	289.68	5.230	0.073	0.008	$CE + CP + A + S + T_{su} + P_{sp} + P_{su}$	7.303	-1.443	1.255	0.008	1.193		-0.364	-0.0034	0.0003		
sp&su m64	9	289.68	**5.233**	0.073	0.008	$CE + CP + A + S + T_{sp} + T_{su} + P_{sp} + P_{su}$	4.519	-1.422	1.127	0.007	1.211	0.181	-0.367	-0.0013	0.0007		
sp&su m84	6	291.55	7.100	0.029	0.003	$CE + CP + A + T_{sp} + T_{su}$	4.331	-1.399	1.224	0.012		0.183	-0.317				
sp&su m81	5	291.78	7.336	0.026	0.003	$CE + CP + T_{sp} + T_{su}$	4.582	-1.326	1.253			0.184	-0.321				
m100	4	292.15	7.705	0.021	0.002	$CE + CP + S$	-3.376	-1.564	1.522		1.127						
su m84	5	292.25	7.808	0.020	0.002	$CE + CP + A + T_{su}$	5.990	-1.438	1.362	0.012			-0.288				
su m81	4	292.55	8.109	0.017	0.002	$CE + CP + T_{su}$	6.209	-1.358	1.384				-0.291				
sp m9	6	292.58	8.137	0.017	0.002	$CE + CP + S + T_{sp} + P_{su}$	-6.344	-1.485	1.389		1.139	0.166			0.0041		
sp&su m32	7	292.73	8.281	0.016	0.002	$CE + CP + A + T_{sp} + T_{su} + P_{su-1}$	5.688	-1.391	1.215	0.012		0.163	-0.338				-0.0029
sp m87	5	292.81	8.364	0.015	0.002	$CE + CP + S + T_{sp}$	-5.155	-1.543	1.442		1.119	0.132					
su m32	6	292.82	8.379	0.015	0.002	$CE + CP + A + T_{su} + P_{su-1}$	7.530	-1.421	1.329	0.012			-0.320				-0.0037
sp&su m29	6	292.83	8.389	0.015	0.002	$CE + CP + T_{sp} + T_{su} + P_{su-1}$	6.046	-1.319	1.244			0.162	-0.344				-0.0032
su m29	5	292.96	8.515	0.014	0.002	$CE + CP + T_{su} + P_{su-1}$	7.849	-1.342	1.350				-0.326				-0.0039
su m19	6	293.15	8.709	0.013	0.001	$CE + CP + A + T_{su} + P_{sp}$	7.553	-1.414	1.358	0.013			-0.325	-0.0032			
m103	5	293.25	8.805	0.012	0.001	$CE + CP + A + S$	-3.374	-1.608	1.522	0.008	1.046						
sp&su m6	7	293.40	8.956	0.011	0.001	$CE + CP + A + T_{sp} + T_{su} + P_{su}$	3.616	-1.393	1.222	0.013		0.187	-0.300		0.0011		
sp&su m19	7	293.42	8.976	0.011	0.001	$CE + CP + A + T_{sp} + T_{su} + P_{sp}$	5.040	-1.393	1.239	0.013		0.164	-0.326	-0.0012			
sp m12	7	293.51	9.065	0.011	0.001	$CE + CP + A + S + T_{sp} + P_{su}$	-6.403	-1.525	1.381	0.009	1.050	0.169			0.0043		
sp&su m45	7	293.54	9.099	0.011	0.001	$CE + CP + A + T_{sp} + T_{su} + P_{sp-1}$	4.343	-1.398	1.224	0.012		0.183	-0.318			0.0001	
su m16	5	293.70	9.251	0.010	0.001	$CE + CP + T_{su} + P_{su}$	7.572	-1.339	1.386				-0.323	-0.0028			
sp&su m3	6	293.71	9.265	0.010	0.001	$CE + CP + T_{sp} + T_{su} + P_{su}$	4.087	-1.321	1.253			0.186	-0.310		0.0008		
sp&su m16	6	293.74	9.295	0.010	0.001	$CE + CP + T_{sp} + T_{su} + P_{sp}$	4.979	-1.323	1.263			0.173	-0.326	-0.0007			
sp&su m42	6	293.76	9.316	0.009	0.001	$CE + CP + T_{sp} + T_{su} + P_{sp-1}$	4.531	-1.333	1.252			0.184	-0.317			-0.0004	
sp m90	6	293.87	9.428	0.009	0.001	$CE + CP + A + S + T_{sp}$	-5.185	-1.583	1.438	0.008	1.036	0.134					
su m6	6	294.17	9.722	0.008	0.001	$CE + CP + A + T_{su} + P_{su}$	5.503	-1.437	1.363	0.013			-0.276		0.0009		
su m45	6	294.25	9.808	0.007	0.001	$CE + CP + A + T_{su} + P_{sp-1}$	5.991	-1.438	1.362	0.012			-0.288			0.0000	
sp m48	6	294.27	9.829	0.007	0.001	$CE + CP + S + T_{sp} + P_{sp-1}$	-4.842	-1.560	1.418		1.107	0.135				-0.0022	
sp m61	7	294.43	9.986	0.007	0.001	$CE + CP + S + T_{sp} + P_{sp} + P_{su}$	-6.763	-1.481	1.369		1.138	0.184		0.0012	0.0040		
sp m22	6	294.49	10.040	0.007	0.001	$CE + CP + S + T_{sp} + P_{sp}$	-5.804	-1.532	1.413		1.118	0.159		0.0018			
su m3	5	294.52	10.075	0.006	0.001	$CE + CP + T_{su} + P_{su}$	5.909	-1.356	1.385				-0.284		0.0005		
sp&su m71	8	294.52	10.076	0.006	0.001	$CE + CP + A + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	6.155	-1.362	1.214	0.012		0.161	-0.358			0.0015	-0.0036
su m42	5	294.53	10.080	0.006	0.001	$CE + CP + T_{su} + P_{sp-1}$	6.140	-1.367	1.383				-0.286			-0.0005	
su m71	7	294.61	10.166	0.006	0.001	$CE + CP + A + T_{su} + P_{sp-1} + P_{su-1}$	7.967	-1.389	1.326	0.012			-0.341			0.0015	-0.0042
sp m35	6	294.74	10.299	0.006	0.001	$CE + CP + S + T_{sp} + P_{su-1}$	-4.923	-1.542	1.445		1.117	0.124					-0.0008
sp&su m68	7	294.76	10.311	0.006	0.001	$CE + CP + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	6.332	-1.300	1.244			0.161	-0.356			0.0009	-0.0036
su m68	6	294.88	10.434	0.005	0.001	$CE + CP + T_{su} + P_{sp-1} + P_{su-1}$	8.118	-1.322	1.349				-0.338			0.0009	-0.0043
su m58	7	295.09	10.642	0.005	0.001	$CE + CP + A + T_{su} + P_{sp} + P_{su}$	7.091	-1.412	1.360	0.013			-0.314	-0.0032	0.0008		
sp&su m58	8	295.29	10.846	0.004	0.001	$CE + CP + A + T_{sp} + T_{su} + P_{sp} + P_{su}$	4.312	-1.387	1.237	0.013		0.168	-0.310	-0.0011	0.0011		
sp m64	8	295.42	10.975	0.004	0.000	$CE + CP + A + S + T_{sp} + P_{sp} + P_{su}$	-6.723	-1.522	1.366	0.009	1.052	0.183		0.0010	0.0041		
sp m51	7	295.47	11.022	0.004	0.000	$CE + CP + A + S + T_{sp} + P_{sp-1}$	-4.904	-1.595	1.417	0.008	1.031	0.136				-0.0019	
sp m25	7	295.63	11.183	0.004	0.000	$CE + CP + A + S + T_{sp} + P_{sp}$	-5.745	-1.573	1.413	0.008	1.038	0.158		0.0015			
su m55	6	295.67	11.229	0.004	0.000	$CE + CP + T_{su} + P_{sp} + P_{su}$	7.310	-1.338	1.387				-0.317	-0.0028	0.0004		
sp&su m55	7	295.68	11.230	0.004	0.000	$CE + CP + T_{sp} + T_{su} + P_{sp} + P_{su}$	4.471	-1.319	1.262			0.176	-0.315	-0.0006	0.0008		
sp m38	7	295.82	11.373	0.003	0.000	$CE + CP + A + S + T_{sp} + P_{su-1}$	-4.973	-1.582	1.441	0.008	1.035	0.127					-0.0007
sp m74	7	296.27	11.829	0.003	0.000	$CE + CP + S + T_{sp} + P_{sp-1} + P_{su-1}$	-4.828	-1.559	1.419		1.107	0.134				-0.0022	-0.0001

Appendix 3.2 continued:

model	k	AIC	ΔAIC	£(g_i|data)	w_i	parameters	int	CE	CP	A	S	T_{sp}	T_{su}	P_{sp}	P_{su}	P_{sp-1}	P_{su-1}
m97	4	297.06	12.619	0.002	0.000	CE + CP + A	-2.204	-1.577	1.600	0.013							
sp&su m86	5	297.25	12.802	0.002	0.000	CP + S + T_{sp} + T_{su}	3.740		1.179		1.196	0.229	-0.373				
sp m6	6	297.32	12.875	0.002	0.000	CE + CP + A + T_{sp} + P_{su}	-5.204	-1.494	1.454	0.014		0.169			0.0041		
sp m77	8	297.47	13.022	0.001	0.000	CE + CP + A + S + T_{sp} + P_{sp-1} + P_{su-1}	-4.885	-1.595	1.418	0.008	1.031	0.136				-0.0019	-0.0001
m94	3	297.53	13.086	0.001	0.000	CE + CP	-2.060	-1.487	1.609								
sp m84	5	297.57	13.124	0.001	0.000	CE + CP + A + T_{sp}	-4.074	-1.549	1.511	0.013		0.137					
sp m3	5	298.07	13.620	0.001	0.000	CE + CP + T_{sp} + P_{su}	-4.952	-1.413	1.475			0.164			0.0039		
sp m81	4	298.07	13.626	0.001	0.000	CE + CP + T_{sp}	-3.890	-1.464	1.525			0.135					
sp&su m34	6	298.21	13.766	0.001	0.000	CP + S + T_{sp} + T_{su} + P_{su-1}	5.242		1.174		1.202	0.201	-0.395				-0.0031
sp&su m89	6	298.96	14.513	0.001	0.000	CP + A + S + T_{sp} + T_{su}	3.612		1.174	0.004	1.148	0.230	-0.369				
su m34	5	299.07	14.623	0.001	0.000	CP + S + T_{su} + P_{su-1}	7.393		1.305		1.191		-0.368				-0.0042
sp m45	6	299.10	14.650	0.001	0.000	CE + CP + A + T_{sp} + P_{sp-1}	-3.758	-1.566	1.489	0.012		0.139				-0.0021	
sp&su m8	6	299.13	14.685	0.001	0.000	CP + S + T_{sp} + T_{su} + P_{su}	3.077		1.179		1.194	0.234	-0.359		0.0010		
su m86	4	299.13	14.685	0.001	0.000	CP + S + T_{su}	5.629		1.344		1.165		-0.329				
sp&su m47	6	299.15	14.706	0.001	0.000	CP + S + T_{sp} + T_{su} + P_{sp-1}	3.873		1.181		1.200	0.229	-0.383			0.0009	
sp&su m21	6	299.17	14.725	0.001	0.000	CP + S + T_{sp} + T_{su} + P_{sp}	4.320		1.191		1.198	0.214	-0.382	-0.0009			
sp m58	7	299.25	14.809	0.001	0.000	CE + CP + A + T_{sp} + P_{sp} + P_{su}	-5.471	-1.493	1.441	0.014		0.180		0.0008	0.0040		
sp m42	5	299.33	14.884	0.001	0.000	CE + CP + T_{sp} + P_{sp-1}	-3.514	-1.491	1.499			0.136				-0.0026	
sp m19	6	299.37	14.921	0.001	0.000	CE + CP + A + T_{sp} + P_{sp}	-4.571	-1.542	1.488	0.013		0.158		0.0014			
sp&su m73	7	299.44	14.997	0.001	0.000	CP + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	6.287		1.172		1.219	0.193	-0.436			0.0028	-0.0045
sp m32	6	299.51	15.062	0.001	0.000	CE + CP + A + T_{sp} + P_{su-1}	-3.867	-1.546	1.513	0.013		0.132					-0.0008
sp m16	5	299.74	15.299	0.000	0.000	CE + CP + T_{sp} + P_{sp}	-4.530	-1.456	1.497			0.161		0.0018			
sp m55	6	299.91	15.462	0.000	0.000	CE + CP + T_{sp} + P_{sp} sp + P_{su}	-5.374	-1.412	1.455			0.182		0.0013	0.0038		
sp&su m37	7	299.97	15.525	0.000	0.000	CP + A + S + T_{sp} + T_{su} + P_{su-1}	5.082		1.169	0.004	1.158	0.202	-0.390				-0.0031
su m21	5	299.98	15.530	0.000	0.000	CP + S + T_{su} + P_{sp}	7.395		1.338		1.176		-0.374	-0.0032			
sp m29	5	299.99	15.541	0.000	0.000	CE + CP + T_{sp} + P_{su-1}	-3.650	-1.462	1.528			0.128					-0.0009
su m73	6	300.15	15.709	0.000	0.000	CP + S + T_{su} + P_{sp-1} + P_{su-1}	8.380		1.296		1.216		-0.412			0.0029	-0.0054
sp&su m11	7	300.80	16.360	0.000	0.000	CP + A + S + T_{sp} + T_{su} + P_{su}	2.845		1.173	0.005	1.142	0.236	-0.352		0.0012		
sp&su m50	7	300.82	16.373	0.000	0.000	CP + A + S + T_{sp} + T_{su} + P_{sp-1}	3.764		1.174	0.005	1.148	0.230	-0.381			0.0011	
sp&su m24	7	300.84	16.398	0.000	0.000	CP + A + S + T_{sp} + T_{su} + P_{sp}	4.315		1.187	0.005	1.146	0.212	-0.379	-0.0011			
su m89	5	300.85	16.403	0.000	0.000	CP + A + S + T_{su}	5.546		1.343	0.004	1.118		-0.326				
su m37	6	300.85	16.408	0.000	0.000	CP + A + S + T_{su} + P_{su-1}	7.279		1.304	0.004	1.149		-0.364				-0.0041
su m47	5	301.04	16.596	0.000	0.000	CP + S + T_{su} + P_{sp-1}	5.756		1.345		1.169		-0.339			0.0009	
sp&su m60	7	301.07	16.624	0.000	0.000	CP + S + T_{sp} + T_{su} + P_{sp} + P_{su}	3.633		1.189		1.195	0.221	-0.367	-0.0008	0.0010		
sp&su m76	8	301.08	16.634	0.000	0.000	CP + A + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	6.184		1.165	0.005	1.166	0.194	-0.434			0.0031	-0.0046
sp m71	7	301.09	16.650	0.000	0.000	CE + CP + A + T_{sp} + P_{sp-1} + P_{su-1}	-3.737	-1.566	1.490	0.012		0.138				-0.0020	-0.0001
su m8	5	301.10	16.654	0.000	0.000	CP + S + T_{su} + P_{su}	5.334		1.346		1.164		-0.322		0.0005		
sp m68	6	301.33	16.883	0.000	0.000	CE + CP + T_{sp} + P_{sp-1} + P_{su-1}	-3.495	-1.491	1.500			0.136				-0.0025	-0.0001
su m24	6	301.58	17.140	0.000	0.000	CP + A + S + T_{su} + P_{sp}	7.390		1.335	0.005	1.121		-0.373	-0.0034			
su m76	7	301.82	17.374	0.000	0.000	CP + A + S + T_{su} + P_{sp-1} + P_{su-1}	8.315		1.294	0.005	1.165		-0.411			0.0032	-0.0054
su m60	6	301.96	17.518	0.000	0.000	CP + S + T_{su} + P_{sp} + P_{su}	7.192		1.339		1.175		-0.369	-0.0032	0.0003		
sp&su m63	8	302.71	18.267	0.000	0.000	CP + A + S + T T_{sp} sp + T_{su} + P_{sp} + P_{su}	3.526		1.185	0.005	1.141	0.220	-0.362	-0.0010	0.0011		
su m50	6	302.72	18.275	0.000	0.000	CP + A + S + T_{su} + P_{sp-1}	5.695		1.344	0.005	1.119		-0.337			0.0011	
su m11	6	302.80	18.355	0.000	0.000	CP + A + S + T_{su} + P_{su}	5.179		1.346	0.004	1.114		-0.317		0.0006		
sp&su m80	4	303.38	18.937	0.000	0.000	CP + T_{sp} + T_{su}	4.178		1.300			0.214	-0.332				
sp&su m85	5	303.56	19.113	0.000	0.000	CE + S + T_{sp} + T_{su}	5.851	-1.496			1.461	0.241	-0.448				
su m63	7	303.56	19.115	0.000	0.000	CP + A + S + T_{su} + P_{sp} + P_{su}	7.102		1.336	0.005	1.118		-0.365	-0.0034	0.0005		
sp&su m83	5	303.90	19.455	0.000	0.000	CP + A + T_{sp} + T_{su}	3.908		1.282	0.009		0.218	-0.328				
sp&su m88	6	304.05	19.608	0.000	0.000	CE + A + S + T_{sp} + T_{su}	5.650	-1.554		0.010	1.355	0.239	-0.440				
sp&su m33	6	304.09	19.649	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{su-1}	7.740	-1.501			1.476	0.207	-0.477				-0.0038
sp&su m28	5	304.42	19.973	0.000	0.000	CP + T_{sp} + T_{su} + P_{su-1}	5.525		1.295			0.191	-0.351				-0.0031
sp&su m20	6	304.68	20.234	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{sp}	4.193	-1.513			1.447	0.292	-0.431	0.0030			
sp&su m36	7	304.75	20.308	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{su-1}	7.417	-1.555		0.009	1.375	0.207	-0.467				-0.0035
su m80	3	304.88	20.430	0.000	0.000	CP + T_{su}	6.148		1.456				-0.299				
sp&su m31	6	305.04	20.593	0.000	0.000	CP + A + T_{sp} + T_{su} + P_{su-1}	5.184		1.278	0.009		0.195	-0.345				-0.0029
su m28	4	305.14	20.693	0.000	0.000	CP + T_{su} + P_{su-1}	7.668		1.425				-0.330				-0.0039
sp m8	5	305.14	20.694	0.000	0.000	CP + S + T_{sp} + P_{su}	-7.249		1.426		1.084	0.210			0.0045		
sp&su m2	5	305.23	20.786	0.000	0.000	CP + T_{sp} + T_{su} + P_{su} su	3.450		1.299			0.220	-0.316		0.0012		
sp&su m15	5	305.31	20.867	0.000	0.000	CP + T_{sp} + T_{su} + P_{sp}	4.722		1.310			0.200	-0.339	-0.0009			
sp&su m41	5	305.34	20.894	0.000	0.000	CP + T_{sp} + T_{su} + P_{sp-1}	4.273		1.300			0.214	-0.339			0.0006	
sp&su m7	6	305.38	20.933	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{su}	5.095	-1.486			1.456	0.245	-0.431		0.0012		
sp&su m23	7	305.43	20.985	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{sp}	4.235	-1.568		0.009	1.350	0.282	-0.425	0.0025			
su m83	4	305.45	21.009	0.000	0.000	CP + A + T_{su}	5.967		1.446	0.009			-0.297				
sp&su m46	6	305.50	21.053	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{sp-1}	5.773	-1.507			1.458	0.241	-0.442			-0.0007	
sp&su m5	6	305.66	21.217	0.000	0.000	CP + A + T T_{sp} sp + T_{su} + P_{su}	2.977		1.280	0.010		0.225	-0.308		0.0014		
sp&su m18	6	305.75	21.302	0.000	0.000	CP + A + T_{sp} + T_{su} + P_{sp}	4.716		1.295	0.010		0.197	-0.340	-0.0013			
m99	3	305.75	21.308	0.000	0.000	CP + S	-3.627		1.589		1.067						
sp&su m44	6	305.77	21.327	0.000	0.000	CP + A + T_{sp} + T_{su} + P_{sp-1}	4.065		1.281	0.010		0.218	-0.340			0.0011	
sp&su m10	7	305.78	21.332	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{su}	4.704	-1.543		0.010	1.345	0.245	-0.418		0.0015		
su m33	5	305.79	21.345	0.000	0.000	CE + S + T_{su} + P_{su-1}	10.199	-1.529			1.476		-0.457				-0.0051
su m31	5	305.83	21.383	0.000	0.000	CP + A + T_{su} + P_{su-1}	7.427		1.416	0.009			-0.326				-0.0037
sp m86	4	305.83	21.387	0.000	0.000	CP + S + T_{sp}	-5.857		1.484		1.059	0.165					
su m15	4	305.84	21.390	0.000	0.000	CP + T_{su} + P_{su}	7.753		1.449				-0.339	-0.0031			
sp&su m67	6	305.90	21.460	0.000	0.000	CP + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	6.335		1.292			0.187	-0.383			0.0023	-0.0041
sp&su m72	7	305.99	21.544	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	8.089	-1.481			1.483	0.203	-0.491			0.0010	-0.0042
sp&su m49	7	306.04	21.597	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{sp-1}	5.617	-1.558		0.010	1.355	0.239	-0.437			-0.0003	
su m18	5	306.18	21.737	0.000	0.000	CP + A + T_{su} + P_{sp}	7.753		1.435	0.010			-0.341	-0.0034			
sp&su m70	7	306.27	21.825	0.000	0.000	CP + A + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	6.171		1.271	0.010		0.190	-0.386			0.0029	-0.0042

Appendix 3.2 continued:

model	k	AIC	ΔAIC	£(g_i|data)	w_i	parameters	int	CE	CP	A	S	T_{sp}	T_{su}	P_{sp}	P_{su}	P_{sp-1}	P_{su-1}
sp&su m59	7	306.42	21.979	0.000	0.000	CE + S + T_{sp} + T_{su} + P_{sp} + P_{su}	3.243	-1.502			1.441	0.299	-0.410	0.0031	0.0014		
su m36	6	306.44	21.993	0.000	0.000	CE + A + S + T_{su} + P_{su-1}	9.926	-1.590		0.009	1.375		-0.448				-0.0048
sp m11	6	306.47	22.024	0.000	0.000	CP + A + S + T_{sp} + P_{su}	-7.352		1.422	0.007	1.014	0.216			0.0046		
sp&su m75	8	306.55	22.102	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	7.902	-1.528		0.010	1.381	0.203	-0.486			0.0015	-0.0042
su m67	5	306.58	22.139	0.000	0.000	CP + T_{su} + P_{sp-1} + P_{su-1}	8.423		1.419				-0.364			0.0023	-0.0048
su m2	4	306.82	22.379	0.000	0.000	CP + T_{su} + P_{su}	5.787		1.458				-0.290		0.0006		
su m85	4	306.83	22.383	0.000	0.000	CE + S + T_{su}	7.957	-1.526			1.430		-0.406				
sp m60	6	306.83	22.389	0.000	0.000	CP + S + T_{sp} + P_{sp} + P_{su}	-7.823		1.403		1.090	0.234		0.0017	0.0043		
su m41	4	306.84	22.398	0.000	0.000	CP + T_{su} + P_{sp-1}	6.233		1.456				-0.305			0.0005	
su m70	6	307.02	22.573	0.000	0.000	CP + A + T_{su} + P_{sp-1} + P_{su-1}	8.342		1.406	0.009			-0.367			0.0028	-0.0049
sp&su m62	8	307.09	22.644	0.000	0.000	CE + A + S + T_{sp} + T_{su} + P_{sp} + P_{su}	3.132	-1.556		0.009	1.340	0.291	-0.401	0.0027	0.0017		
sp&su m54	6	307.18	22.731	0.000	0.000	CP + T_{sp} + T_{su} + P_{sp} + P_{su}	3.964		1.308			0.207	-0.323	-0.0008	0.0011		
su m88	5	307.20	22.758	0.000	0.000	CE + A + S + T_{su}	7.815	-1.595		0.010	1.322		-0.400				
sp m21	5	307.26	22.816	0.000	0.000	CP + S + T_{sp} + P_{sp}	-6.689		1.450		1.068	0.200		0.0023			
sp m89	5	307.29	22.845	0.000	0.000	CP + A + S + T_{sp}	-5.922		1.482	0.006	0.996	0.170					
m102	4	307.31	22.862	0.000	0.000	CP + A + S	-3.624		1.593	0.005	1.010						
su m44	5	307.35	22.905	0.000	0.000	CP + A + T_{su} + P_{sp-1}	6.115		1.446	0.009			-0.307			0.0010	
su m5	5	307.35	22.910	0.000	0.000	CP + A + T_{su} + P_{su}	5.462		1.449	0.009			-0.284		0.0009		
sp&su m57	7	307.54	23.090	0.000	0.000	CP + A + T_{sp} + T_{su} + P_{sp} + P_{su}	3.755		1.292	0.010		0.206	-0.319	-0.0012	0.0014		
sp m47	5	307.54	23.091	0.000	0.000	CP + S + T_{sp} + P_{sp-1}	-5.653		1.470		1.055	0.168				-0.0016	
su m72	6	307.59	23.149	0.000	0.000	CE + S + T_{su} + P_{sp-1} + P_{su-1}	10.596	-1.501			1.488		-0.476			0.0013	-0.0056
sp m34	5	307.72	23.278	0.000	0.000	CP + S + T_{sp} + P_{su-1}	-5.562		1.488		1.057	0.156					-0.0010
su m54	5	307.80	23.355	0.000	0.000	CP + T_{su} + P_{sp} + P_{su}	7.431		1.450				-0.331	-0.0031	0.0005		
su m57	6	308.11	23.662	0.000	0.000	CP + A + T_{su} + P_{sp} + P_{su}	7.277		1.437	0.010			-0.329	-0.0034	0.0008		
su m75	7	308.12	23.671	0.000	0.000	CE + A + S + T_{su} + P_{sp-1} + P_{su-1}	10.434	-1.554		0.010	1.386		-0.472			0.0017	-0.0055
sp m63	7	308.25	23.801	0.000	0.000	CP + A + S + T_{sp} + P_{sp} + P_{su}	-7.832		1.402	0.006	1.023	0.236		0.0015	0.0044		
su m7	5	308.73	24.288	0.000	0.000	CE + S + T_{su} + P_{su}	7.487	-1.523			1.427		-0.394		0.0008		
su m20	5	308.77	24.328	0.000	0.000	CE + S + T_{su} + P_{sp}	8.267	-1.522			1.434		-0.413	-0.0006			
su m46	5	308.77	24.329	0.000	0.000	CE + S + T_{su} + P_{sp-1}	7.878	-1.537			1.426		-0.399			-0.0007	
sp m24	6	308.81	24.368	0.000	0.000	CP + A + S + T_{sp} + P_{sp}	-6.671		1.452	0.005	1.010	0.201		0.0021			
su m10	6	309.04	24.592	0.000	0.000	CE + A + S + T_{su} + P_{su}	7.193	-1.593		0.010	1.315		-0.385		0.0011		
sp m50	6	309.07	24.628	0.000	0.000	CP + A + S + T_{sp} + P_{sp-1}	-5.740		1.470	0.005	0.997	0.172				-0.0014	
su m23	6	309.08	24.632	0.000	0.000	CE + A + S + T_{su} + P_{sp}	8.287	-1.589		0.010	1.326		-0.412	-0.0010			
sp m37	6	309.19	24.743	0.000	0.000	CP + A + S + T_{sp} + P_{su-1}	-5.640		1.486	0.006	0.994	0.161					-0.0010
su m49	6	309.19	24.748	0.000	0.000	CE + A + S + T_{su} + P_{sp-1}	7.782	-1.600		0.010	1.321		-0.398			-0.0003	
sp m73	6	309.52	25.072	0.000	0.000	CP + S + T_{sp} + P_{sp-1} + P_{su-1}	-5.538		1.473		1.055	0.163				-0.0014	-0.0004
sp m2	4	309.84	25.398	0.000	0.000	CP + T_{sp} + P_{su}	-5.869		1.513			0.206			0.0042		
sp m5	5	309.88	25.437	0.000	0.000	CP + A + T_{sp} + P_{su}	-6.178		1.498	0.011		0.216			0.0044		
sp m 80	3	310.24	25.791	0.000	0.000	CP + T_{sp}	-4.632		1.566			0.167					
m93	2	310.26	25.812	0.000	0.000	CP	-2.368		1.675								
sp m83	4	310.53	26.087	0.000	0.000	CP + A + T_{sp}	-4.857		1.556	0.010		0.174					
su m59	6	310.69	26.242	0.000	0.000	CE + S + T_{su} + P_{sp} + P_{su}	7.789	-1.519			1.431		-0.401	-0.0006	0.0008		
m96	3	310.70	26.257	0.000	0.000	CP + A	-2.482		1.673	0.009							
su m62	7	310.93	26.482	0.000	0.000	CE + A + S + T_{su} + P_{sp} + P_{su}	7.656	-1.586		0.010	1.319		-0.396	-0.0009	0.0011		
sp m76	7	311.05	26.604	0.000	0.000	CP + A + S + T_{sp} + P_{sp-1} + P_{su-1}	-5.615		1.474	0.005	0.996	0.167				-0.0012	-0.0005
sp m54	5	311.63	27.185	0.000	0.000	CP + T_{sp} + P_{sp} + P_{su}	-6.337		1.494			0.226		0.0015	0.0040		
sp m57	6	311.77	27.321	0.000	0.000	CP + A + T_{sp} + P_{sp} + P_{su}	-6.511		1.484	0.011		0.230		0.0011	0.0043		
sp m15	4	311.80	27.354	0.000	0.000	CP + T_{sp} + P_{sp}	-5.341		1.538			0.196		0.0020			
sp m41	4	311.87	27.424	0.000	0.000	CP + T_{sp} + P_{sp-1}	-4.399		1.551			0.169				-0.0017	
sp&su m82	5	312.05	27.602	0.000	0.000	CE + A + T_{sp} + T_{su}	5.914	-1.536		0.016		0.226	-0.389				
sp m28	4	312.08	27.638	0.000	0.000	CP + T_{sp} + P_{su-1}	-4.311		1.570			0.158					-0.0012
sp m18	5	312.22	27.775	0.000	0.000	CP + A + T_{sp} + P_{sp}	-5.438		1.533	0.009		0.198		0.0017			
sp m44	5	312.32	27.877	0.000	0.000	CP + A + T_{sp} + P_{sp-1}	-4.667		1.545	0.009		0.176				-0.0013	
sp m31	5	312.41	27.960	0.000	0.000	CP + A + T_{sp} + P_{su-1}	-4.564		1.560	0.010		0.166					-0.0011
sp&su m30	6	313.05	28.606	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{su-1}	7.311	-1.531		0.015		0.203	-0.409				-0.0031
sp&su m17	6	313.37	28.925	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{sp}	4.429	-1.553		0.015		0.269	-0.372	0.0026			
sp&su m4	6	313.57	29.127	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{su}	4.719	-1.523		0.016		0.233	-0.362		0.0019		
sp m67	5	313.84	29.390	0.000	0.000	CP + T_{sp} + P_{sp-1} + P_{su-1}	-4.258		1.555			0.164				-0.0015	-0.0006
sp&su m43	6	314.02	29.580	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{sp-1}	5.861	-1.543		0.016		0.225	-0.384			-0.0004	
sp m70	6	314.28	29.838	0.000	0.000	CP + A + T_{sp} + P_{sp-1} + P_{su-1}	-4.518		1.550	0.009		0.170				-0.0011	-0.0007
sp&su m79	4	314.35	29.901	0.000	0.000	CE + T_{sp} + T_{su}	6.210	-1.407				0.225	-0.393				
su m30	5	314.80	30.358	0.000	0.000	CE + A + T_{su} + P_{su-1}	9.856	-1.573		0.015			-0.395				-0.0041
su m82	4	314.82	30.376	0.000	0.000	CE + A + T_{su}	8.206	-1.588		0.016			-0.361				
sp&su m56	7	314.83	30.381	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{sp} + P_{su}	3.104	-1.539		0.015		0.280	-0.344	0.0028	0.0021		
sp&su m69	7	314.95	30.504	0.000	0.000	CE + A + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}	7.640	-1.510		0.016		0.201	-0.423			0.0010	-0.0035
sp&su m27	5	315.14	30.699	0.000	0.000	CE + T_{sp} + T_{su} + P_{su-1}	7.752	-1.403				0.201	-0.416				-0.0034
sp&su m14	5	315.18	30.734	0.000	0.000	CE + T_{sp} + T_{su} + P_{sp}	4.313	-1.429				0.282	-0.373	0.0034			
sp m59	6	315.45	31.007	0.000	0.000	CE + S + T_{sp} + P_{sp} + P_{su}	-9.040	-1.558			1.286	0.294		0.0050	0.0050		
sp m62	7	315.58	31.133	0.000	0.000	CE + A + S + T_{sp} + P_{sp} + P_{su}	-8.964	-1.636		0.011	1.173	0.292		0.0045	0.0051		
sp m10	6	315.90	31.455	0.000	0.000	CE + A + S + T_{sp} + P_{su}	-7.417	-1.640		0.012	1.168	0.226			0.0056		
sp&su m1	5	316.05	31.604	0.000	0.000	CE + T_{sp} + T_{su} + P_{su}	5.278	-1.397				0.231	-0.372		0.0015		
sp&su m40	5	316.19	31.743	0.000	0.000	CE + T_{sp} + T_{su} + P_{sp-1}	6.067	-1.428				0.225	-0.381			-0.0012	
sp m7	5	316.31	31.869	0.000	0.000	CE + S + T_{sp} + P_{su}	-7.299	-1.558			1.295	0.219			0.0054		
su m4	5	316.51	32.063	0.000	0.000	CE + A + T_{su} + P_{su}	7.389	-1.584		0.016			-0.342		0.0015		
su m69	6	316.67	32.226	0.000	0.000	CE + A + T_{su} + P_{sp-1} + P_{su-1}	10.186	-1.547		0.015			-0.411			0.0011	-0.0045
su m17	5	316.75	32.303	0.000	0.000	CE + A + T_{su} + P_{sp}	8.560	-1.582		0.016			-0.369	-0.0008			
su m43	5	316.79	32.343	0.000	0.000	CE + A + T_{su} + P_{sp-1}	8.133	-1.597		0.015			-0.356			-0.0005	

Appendix 3.2 continued:

model	k	AIC	ΔAIC	£(g_i|data)	w_i	parameters	int	CE	CP	A	S	T_{sp}	T_{su}	P_{sp}	P_{su}	P_{sp-1}	P_{su-1}
sp&su m53	6	316.79	32.349	0.000	0.000	$CE + T_{sp} + T_{su} + P_{sp} + P_{su}$	3.211	-1.419				0.291	-0.350	0.0036	0.0017		
su m27	4	316.92	32.478	0.000	0.000	$CE + T_{su} + P_{su-1}$	10.198	-1.433					-0.399				-0.0044
sp m20	5	317.06	32.616	0.000	0.000	$CE + S + T_{sp} + P_{sp}$	-7.737	-1.610			1.262	0.257		0.0054			
sp&su m66	6	317.14	32.694	0.000	0.000	$CE + T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	7.824	-1.398				0.201	-0.419			0.0002	-0.0035
su m79	3	317.22	32.773	0.000	0.000	$CE + T_{su}$	8.408	-1.446					-0.362				
sp m23	6	317.45	33.001	0.000	0.000	$CE + A + S + T_{sp} + P_{sp}$	-7.640	-1.692		0.010	1.159	0.255		0.0051			
su m56	6	318.45	34.001	0.000	0.000	$CE + A + T_{su} + P_{sp} + P_{su}$	7.720	-1.579		0.016			-0.349	-0.0007	0.0015		
sp m88	5	318.57	34.130	0.000	0.000	$CE + A + S + T_{sp}$	-5.754	-1.711		0.011	1.151	0.176					
sp m85	4	318.70	34.254	0.000	0.000	$CE + S + T_{sp}$	-5.681	-1.626			1.269	0.171					
su m66	5	318.91	34.465	0.000	0.000	$CE + T_{su} + P_{sp-1} + P_{su-1}$	10.298	-1.425					-0.404			0.0003	-0.0045
su m40	4	319.04	34.591	0.000	0.000	$CE + T_{su} + P_{sp-1}$	8.236	-1.469					-0.349			-0.0012	
su m1	4	319.04	34.595	0.000	0.000	$CE + T_{su} + P_{su}$	7.796	-1.443					-0.347		0.0011		
sp m46	5	319.19	34.747	0.000	0.000	$CE + S + T_{sp} + P_{sp-1}$	-5.198	-1.662			1.255	0.176				-0.0035	
su m14	4	319.22	34.770	0.000	0.000	$CE + T_{su} + P_{su}$	8.477	-1.445					-0.364	-0.0001			
m98	3	319.29	34.842	0.000	0.000	$CE + S$	-3.370	-1.654			1.284						
m101	4	319.30	34.852	0.000	0.000	$CE + A + S$	-3.364	-1.744		0.011	1.170						
sp m49	6	319.40	34.960	0.000	0.000	$CE + A + S + T_{sp} + P_{sp-1}$	-5.309	-1.736		0.010	1.147	0.180				-0.0031	
sp m36	6	320.55	36.104	0.000	0.000	$CE + A + S + T_{sp} + P_{su-1}$	-5.617	-1.710		0.011	1.151	0.172					-0.0005
sp m33	5	320.66	36.218	0.000	0.000	$CE + S + T_{sp} + P_{su-1}$	-5.515	-1.625			1.268	0.165					-0.0006
su m53	5	321.04	36.594	0.000	0.000	$CE + T_{su} + P_{sp} + P_{su}$	7.838	-1.442					-0.348	-0.0001	0.0011		
sp m72	6	321.13	36.683	0.000	0.000	$CE + S + T_{sp} + P_{sp-1} + P_{su-1}$	-5.417	-1.662			1.256	0.186				-0.0038	0.0008
sp m56	6	321.20	36.752	0.000	0.000	$CE + A + T_{sp} + P_{sp} + P_{su}$	-7.563	-1.630		0.016		0.289		0.0045	0.0050		
sp m75	7	321.34	36.899	0.000	0.000	$CE + A + S + T_{sp} + P_{sp-1} + P_{su-1}$	-5.516	-1.737		0.010	1.148	0.189				-0.0034	0.0008
sp m4	5	321.42	36.972	0.000	0.000	$CE + A + T_{sp} + P_{su}$	-6.083	-1.627		0.017		0.227			0.0055		
sp m17	5	322.97	38.528	0.000	0.000	$CE + A + T_{sp} + P_{sp}$	-6.317	-1.686		0.015		0.256		0.0050			
sp m53	5	323.54	39.091	0.000	0.000	$CE + T_{sp} + P_{sp} + P_{su}$	-7.477	-1.494				0.292		0.0052	0.0047		
sp m82	4	323.98	39.535	0.000	0.000	$CE + A + T_{sp}$	-4.518	-1.696		0.016		0.182					
sp m1	4	324.56	40.112	0.000	0.000	$CE + T_{sp} + P_{su}$	-5.705	-1.486				0.217			0.0052		
sp m43	5	324.72	40.270	0.000	0.000	$CE + A + T_{sp} + P_{sp-1}$	-4.033	-1.728		0.015		0.183				-0.0032	
sp m14	4	324.88	40.431	0.000	0.000	$CE + T_{sp} + P_{sp}$	-6.293	-1.538				0.259		0.0056			
m95	3	324.98	40.530	0.000	0.000	$CE + A$	-2.034	-1.735		0.016							
sp m30	5	325.95	41.505	0.000	0.000	$CE + A + T_{sp} + P_{su-1}$	-4.381	-1.695		0.016		0.178					-0.0005
sp m79	3	326.65	42.208	0.000	0.000	$CE + T_{sp}$	-4.237	-1.546				0.175					
sp m69	6	326.66	42.215	0.000	0.000	$CE + A + T_{sp} + P_{sp-1} + P_{su-1}$	-4.210	-1.731		0.015		0.190				-0.0035	0.0007
sp m40	4	326.80	42.355	0.000	0.000	$CE + T_{sp} + P_{sp-1}$	-3.688	-1.595				0.178				-0.0038	
m92	2	327.50	43.053	0.000	0.000	CE	-1.853	-1.575									
sp m27	4	328.60	44.153	0.000	0.000	$CE + T_{sp} + P_{su-1}$	-4.055	-1.544				0.170					-0.0007
sp m66	5	328.75	44.302	0.000	0.000	$CE + T_{sp} + P_{sp-1} + P_{su-1}$	-3.867	-1.597				0.185				-0.0041	0.0007
sp&su m91	3	328.79	44.343	0.000	0.000	$T_{sp} + T_{su}$	5.757					0.260	-0.404				
sp&su m39	4	329.63	45.183	0.000	0.000	$T_{sp} + T_{su} + P_{su-1}$	7.134					0.235	-0.422				-0.0032
sp&su m26	4	329.84	45.398	0.000	0.000	$T_{sp} + T_{su} + P_{sp}$	3.986					0.310	-0.383	0.0030			
sp&su m13	4	330.31	45.867	0.000	0.000	$T_{sp} + T_{su} + P_{su}$	4.579					0.270	-0.379		0.0019		
sp&su m52	4	330.79	46.342	0.000	0.000	$T_{sp} + T_{su} + P_{sp-1}$	5.767					0.260	-0.405			0.0001	
sp&su m65	5	331.23	46.782	0.000	0.000	$T_{sp} + T_{su} + P_{sp} + P_{su}$	2.549					0.326	-0.354	0.0033	0.0021		
sp&su m78	5	331.29	46.846	0.000	0.000	$T_{sp} + T_{su} + P_{sp-1} + P_{su-1}$	7.772					0.231	-0.447			0.0018	-0.0040
su m39	3	332.46	48.019	0.000	0.000	$T_{su} + P_{su-1}$	9.971						-0.403				-0.0043
su m91	2	332.89	48.441	0.000	0.000	T_{su}	8.343						-0.371				
su m78	4	334.04	49.595	0.000	0.000	$T_{su} + P_{sp-1} + P_{su-1}$	10.597						-0.431			0.0019	-0.0050
su m13	3	334.67	50.226	0.000	0.000	$T_{su} + P_{su}$	7.699						-0.355		0.0012		
su m26	3	334.85	50.409	0.000	0.000	$T_{su} + P_{sp}$	8.593						-0.376	-0.0005			
su m52	3	334.89	50.441	0.000	0.000	$T_{su} + P_{sp-1}$	8.340						-0.370			0.0000	
su m65	4	336.65	52.203	0.000	0.000	$T_{su} + P_{sp} + P_{su}$	7.920						-0.360	-0.0004	0.0012		
sp m65	4	337.97	53.520	0.000	0.000	$T_{sp} + P_{sp} + P_{su}$	-8.469					0.339		0.0052	0.0050		
sp m13	3	339.14	54.696	0.000	0.000	$T_{sp} + P_{su}$	-6.719					0.267			0.0054		
sp m26	3	339.80	55.356	0.000	0.000	$T_{sp} + P_{sp}$	-7.084					0.295		0.0056			
sp m91	2	341.80	57.353	0.000	0.000	T_{sp}	-5.055					0.212					
sp m52	3	342.73	58.281	0.000	0.000	$T_{sp} + P_{sp-1}$	-4.685					0.216				-0.0028	
sp m39	3	343.69	59.242	0.000	0.000	$T_{sp} + P_{su-1}$	-4.797					0.205					-0.0009
sp m78	4	344.72	60.277	0.000	0.000	$T_{sp} + P_{sp-1} + P_{su-1}$	-4.735					0.218				-0.0029	0.0002
			Σ	**8.688**													

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[*] Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area, S = average maximum 15 bar soil water content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July); P_{sp} = average spring precipitation (March 1-June 15); P_{su} = average summer precipitation (June 16-September 30); $P_{sp(t-1)}$ = average spring precipitation (March 1-June 15) lagged one year; $P_{su(t-1)}$ = average summer precipitation (June 16-September 30) lagged one year.

APPENDIX 3.3

Appendix 3.3. Results of AIC based model selection for plague occurrence in black-tailed prairie dog towns in a 51 model set which includes spring and summer temperature but does not include spring and summer precipitation variables. The AIC weights of the 95% confidence set of models are highlighted.[*]

model	k	AIC	ΔAIC	£(g_i|data)	w_i	parameters	int	CE	CP	A	S	T_{sp}	T_{su}
sp&su m87	6	284.45	0.000	1.000	0.402	**CE + CP + S + T_{sp} + T_{su}**	4.365	-1.404	1.122		1.282	0.201	-0.375
su m87	5	285.62	1.180	0.554	0.223	**CE + CP + S + T_{su}**	5.905	-1.430	1.261		1.249		-0.331
sp&su m90	7	285.87	1.422	0.491	0.197	**CE + CP + A + S + T_{sp} + T_{su}**	4.216	-1.431	1.109	0.007	1.213	0.200	-0.369
su m90	6	286.97	**2.528**	0.282	0.114	CE + CP + A + S + T_{su}	5.773	-1.463	1.254	0.007	1.177		-0.327
sp&su m84	6	291.55	7.100	0.029	0.012	CE + CP + A + T_{sp} + T_{su}	4.331	-1.399	1.224	0.012		0.183	-0.317
sp&su m81	5	291.78	7.336	0.026	0.010	CE + CP + T_{sp} + T_{su}	4.582	-1.326	1.253			0.184	-0.321
m100	4	292.15	7.705	0.021	0.009	CE + CP + S	-3.376	-1.564	1.522		1.127		
su m84	5	292.25	7.808	0.020	0.008	CE + CP + A + T_{su}	5.990	-1.438	1.362	0.012			-0.288
su m81	4	292.55	8.109	0.017	0.007	CE + CP + T_{su}	6.209	-1.358	1.384				-0.291
sp m87	5	292.81	8.364	0.015	0.006	CE + CP + S + T_{sp}	-5.155	-1.543	1.442		1.119	0.132	
m103	5	293.25	8.805	0.012	0.005	CE + CP + A + S	-3.374	-1.608	1.522	0.008	1.046		
sp m90	6	293.87	9.428	0.009	0.004	CE + CP + A + S + T_{sp}	-5.185	-1.583	1.438	0.008	1.036	0.134	
m97	4	297.06	12.619	0.002	0.001	CE + CP + A	-2.204	-1.577	1.600	0.013			
sp&su m86	5	297.25	12.802	0.002	0.001	CP + S + T_{sp} + T_{su}	3.740		1.179		1.196	0.229	-0.373
m94	3	297.53	13.086	0.001	0.001	CE + CP	-2.060	-1.487	1.609				
sp m84	5	297.57	13.124	0.001	0.001	CE + CP + A + T_{sp}	-4.074	-1.549	1.511	0.013		0.137	
sp m81	4	298.07	13.626	0.001	0.000	CE + CP + T_{sp}	-3.890	-1.464	1.525			0.135	
sp&su m89	6	298.96	14.513	0.001	0.000	CP + A + S + T_{sp} + T_{su}	3.612		1.174	0.004	1.148	0.230	-0.369
su m86	4	299.13	14.685	0.001	0.000	CP + S + T_{su}	5.629		1.344		1.165		-0.329
su m89	5	300.85	16.403	0.000	0.000	CP + A + S + T_{su}	5.546		1.343	0.004	1.118		-0.326
sp&su m80	4	303.38	18.937	0.000	0.000	CP + T_{sp} + T_{su}	4.178		1.300			0.214	-0.332
sp&su m85	5	303.56	19.113	0.000	0.000	CE + S + T_{sp} + T_{su}	5.851	-1.496			1.461	0.241	-0.448
sp&su m83	5	303.90	19.455	0.000	0.000	CP + A + T_{sp} + T_{su}	3.908		1.282	0.009		0.218	-0.328
sp&su m88	6	304.05	19.608	0.000	0.000	CE + A + S + T_{sp} + T_{su}	5.650	-1.554		0.010	1.355	0.239	-0.440
su m80	3	304.88	20.430	0.000	0.000	CP + T_{su}	6.148		1.456				-0.299
su m83	4	305.45	21.009	0.000	0.000	CP + A + T_{su}	5.967		1.446	0.009			-0.297
m99	3	305.75	21.308	0.000	0.000	CP + S	-3.627		1.589		1.067		
sp m86	4	305.83	21.387	0.000	0.000	CP + S + T_{sp}	-5.857		1.484		1.059	0.165	
su m85	4	306.83	22.383	0.000	0.000	CE + S + T_{su}	7.957	-1.526			1.430		-0.406
su m88	5	307.20	22.758	0.000	0.000	CE + A + S + T_{su}	7.815	-1.595		0.010	1.322		-0.400
sp m89	5	307.29	22.845	0.000	0.000	CP + A + S + T_{sp}	-5.922		1.482	0.006	0.996	0.170	
m102	4	307.31	22.862	0.000	0.000	CP + A + S	-3.624		1.593	0.005	1.010		
sp m 80	3	310.24	25.791	0.000	0.000	CP + T_{sp}	-4.632		1.566			0.167	
m93	2	310.26	25.812	0.000	0.000	CP	-2.368		1.675				
sp m83	4	310.53	26.087	0.000	0.000	CP + A + T_{sp}	-4.857		1.556	0.010		0.174	
m96	3	310.70	26.257	0.000	0.000	CP + A	-2.482		1.673	0.009			
sp&su m82	5	312.05	27.602	0.000	0.000	CE + A + T_{sp} + T_{su}	5.914	-1.536		0.016		0.226	-0.389
sp&su m79	4	314.35	29.901	0.000	0.000	CE + T_{sp} + T_{su}	6.210	-1.407				0.225	-0.393
su m82	4	314.82	30.376	0.000	0.000	CE + A + T_{su}	8.206	-1.588		0.016			-0.361
su m79	3	317.22	32.773	0.000	0.000	CE + T_{su}	8.408	-1.446					-0.362
sp m88	5	318.57	34.130	0.000	0.000	CE + A + S + T_{sp}	-5.754	-1.711		0.011	1.151	0.176	
sp m85	4	318.70	34.254	0.000	0.000	CE + S + T_{sp}	-5.681	-1.626			1.269	0.171	
m98	3	319.29	34.842	0.000	0.000	CE + S	-3.370	-1.654			1.284		
m101	4	319.30	34.852	0.000	0.000	CE + A + S	-3.364	-1.744		0.011	1.170		
sp m82	4	323.98	39.535	0.000	0.000	CE + A + T_{sp}	-4.518	-1.696		0.016		0.182	
m95	3	324.98	40.530	0.000	0.000	CE + A	-2.034	-1.735		0.016			
sp m79	3	326.65	42.208	0.000	0.000	CE + T_{sp}	-4.237	-1.546				0.175	
m92	2	327.50	43.053	0.000	0.000	CE	-1.853	-1.575					
sp&su m91	3	328.79	44.343	0.000	0.000	T_{sp} + T_{su}	5.757					0.260	-0.404
su m91	2	332.89	48.441	0.000	0.000	T_{su}	8.343						-0.371
sp m91	2	341.80	57.353	0.000	0.000	T_{sp}	-5.055					0.212	
			Σ	**2.487**									

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[*] Abbreviations: CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil moisture content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July).

APPENDIX 3.4

Appendix 3.4. Results of AIC based model selection for plague occurrence in black-tailed prairie dog towns in spring and summer temperature model set (without precipitation) expanded with a set of models which include the variable connectivity to plague and extant towns.*

model	k	AIC	ΔAIC	£($g_i \mid$data)	w_i	parameters	intercpt	CE+P	CE	CP	A	S	T_{sp}	T_{su}
sp&su m87	6	284.45	0.000	1.000	0.402	CE + CP + S + T_{sp} + T_{su}	4.365		-1.404	1.122		1.282	0.201	-0.375
su m87	5	285.62	1.180	0.554	0.223	CE + CP + S + T_{su}	5.905		-1.430	1.261		1.249		-0.331
sp&su m90	7	285.87	1.422	0.491	0.197	CE + CP + A + S + T_{sp} + T_{su}	4.216		-1.431	1.109	0.007	1.213	0.200	-0.369
su m90	6	286.97	2.528	0.282	0.114	CE + CP + A + S + T_{su}	5.773		-1.463	1.254	0.007	1.177		-0.327
sp&su m84	6	291.55	7.100	0.029	0.012	CE + CP + A + T_{sp} + T_{su}	4.331		-1.399	1.224	0.012		0.183	-0.317
sp&su m81	5	291.78	7.336	0.026	0.010	CE + CP + T_{sp} + T_{su}	4.582		-1.326	1.253			0.184	-0.321
m100	4	292.15	7.705	0.021	0.009	CE + CP + S	-3.376		-1.564	1.522		1.127		
su m84	5	292.25	7.808	0.020	0.008	CE + CP + A + T_{su}	5.990		-1.438	1.362	0.012			-0.288
su m81	4	292.55	8.109	0.017	0.007	CE + CP + T_{su}	6.209		-1.358	1.384				-0.291
sp m87	5	292.81	8.364	0.015	0.006	CE + CP + S + T_{sp}	-5.155		-1.543	1.442		1.119	0.132	
m103	5	293.25	8.805	0.012	0.005	CE + CP + A + S	-3.374		-1.608	1.522	0.008	1.046		
sp m90	6	293.87	9.428	0.009	0.004	CE + CP + A + S + T_{sp}	-5.185		-1.583	1.438	0.008	1.036	0.134	
m97	4	297.06	12.619	0.002	0.001	CE + CP + A	-2.204		-1.577	1.600	0.013			
sp&su m86	5	297.25	12.802	0.002	0.001	CP + S + T_{sp} + T_{su}	3.740			1.179		1.196	0.229	-0.373
m94	3	297.53	13.086	0.001	0.001	CE + CP	-2.060		-1.487	1.609				
sp m84	5	297.57	13.124	0.001	0.001	CE + CP + A + T_{sp}	-4.074		-1.549	1.511	0.013		0.137	
sp m81	4	298.07	13.626	0.001	0.000	CE + CP + T_{sp}	-3.890		-1.464	1.525			0.135	
sp&su m89	6	298.96	14.513	0.001	0.000	CP + A + S + T_{sp} + T_{su}	3.612			1.174	0.004	1.148	0.230	-0.369
su m86	4	299.13	14.685	0.001	0.000	CP + S + T_{su}	5.629			1.344		1.165		-0.329
su m89	5	300.85	16.403	0.000	0.000	CP + A + S + T_{su}	5.546			1.343	0.004	1.118		-0.326
sp&su m80	4	303.38	18.937	0.000	0.000	CP + T_{sp} + T_{su}	4.178			1.300			0.214	-0.332
sp&su m85	5	303.56	19.113	0.000	0.000	CE + S + T_{sp} + T_{su}	5.851		-1.496			1.461	0.241	-0.448
sp&su m83	5	303.90	19.455	0.000	0.000	CP + A + T_{sp} + T_{su}	3.908			1.282	0.009		0.218	-0.328
sp&su m88	6	304.05	19.608	0.000	0.000	CE + A + S + T_{sp} + T_{su}	5.650		-1.554		0.010	1.355	0.239	-0.440
su m80	3	304.88	20.430	0.000	0.000	CP + T_{su}	6.148			1.456				-0.299
su m83	4	305.45	21.009	0.000	0.000	CP + A + T_{su}	5.967			1.446	0.009			-0.297
m99	3	305.75	21.308	0.000	0.000	CP + S	-3.627			1.589		1.067		
sp m86	4	305.83	21.387	0.000	0.000	CP + S + T_{sp}	-5.857			1.484		1.059	0.165	
su m85	4	306.83	22.383	0.000	0.000	CE + S + T_{su}	7.957		-1.526			1.430		-0.406
su m88	5	307.20	22.758	0.000	0.000	CE + A + S + T_{su}	7.815		-1.595		0.010	1.322		-0.400
sp m89	5	307.29	22.845	0.000	0.000	CP + A + S + T_{sp}	-5.922			1.482	0.006	0.996	0.170	
m102	4	307.31	22.862	0.000	0.000	CP + A + S	-3.624			1.593	0.005	1.010		
sp m 80	3	310.24	25.791	0.000	0.000	CP + T_{sp}	-4.632			1.566			0.167	
m93	2	310.26	25.812	0.000	0.000	CP	-2.368			1.675				
sp m83	4	310.53	26.087	0.000	0.000	CP + A + T_{sp}	-4.857			1.556	0.010		0.174	
m96	3	310.70	26.257	0.000	0.000	CP + A	-2.482			1.673	0.009			
sp&su m82	5	312.05	27.602	0.000	0.000	CE + A + T_{sp} + T_{su}	5.914		-1.536		0.016		0.226	-0.389
sp&su m79	4	314.35	29.901	0.000	0.000	CE + T_{sp} + T_{su}	6.210		-1.407				0.225	-0.393
su m82	4	314.82	30.376	0.000	0.000	CE + A + T_{su}	8.206		-1.588		0.016			-0.361
su m79	3	317.22	32.773	0.000	0.000	CE + T_{su}	8.408		-1.446					-0.362
sp m88	5	318.57	34.130	0.000	0.000	CE + A + S + T_{sp}	-5.754		-1.711		0.011	1.151	0.176	
sp m85	4	318.70	34.254	0.000	0.000	CE + S + T_{sp}	-5.681		-1.626			1.269	0.171	
m98	3	319.29	34.842	0.000	0.000	CE + S	-3.370		-1.654			1.284		
m101	4	319.30	34.852	0.000	0.000	CE + A + S	-3.364		-1.744		0.011	1.170		
cn11	5	320.92	36.477	0.000	0.000	CEP + S + T_{sp} + T_{su}	4.833	0.045				1.353	0.283	-0.441
cn12	6	322.09	37.642	0.000	0.000	CEP + A + S + T_{sp} + T_{su}	4.656	0.043			0.007	1.274	0.285	-0.435
sp m82	4	323.98	39.535	0.000	0.000	CE + A + T_{sp}	-4.518		-1.696		0.016		0.182	
m95	3	324.98	40.530	0.000	0.000	CE + A	-2.034		-1.735		0.016			
cn7	4	325.70	41.255	0.000	0.000	CEP + S + T_{su}	7.500	0.029				1.331		-0.398
sp m79	3	326.65	42.208	0.000	0.000	CE + T_{sp}	-4.237		-1.546				0.175	
cn8	5	326.90	42.457	0.000	0.000	CEP + A + S + T_{su}	7.429	0.027			0.006	1.255		-0.395
m92	2	327.50	43.053	0.000	0.000	CE	-1.853		-1.575					
sp&su m91	3	328.79	44.343	0.000	0.000	T_{sp} + T_{su}	5.757						0.260	-0.404
cn10	5	328.97	44.521	0.000	0.000	CEP + A + T_{sp} + T_{su}	5.044	0.057			0.012		0.278	-0.395
cn9	4	329.79	45.342	0.000	0.000	CEP + T_{sp} + T_{su}	5.354	0.062					0.273	-0.398
su m91	2	332.89	48.441	0.000	0.000	T_{su}	8.343							-0.371
cn6	4	333.60	49.154	0.000	0.000	CEP + A + T_{su}	8.015	0.041			0.011			-0.365
cn5	3	334.29	49.845	0.000	0.000	CEP + T_{su}	8.149	0.047						-0.365
cn3	4	335.56	51.117	0.000	0.000	CEP + S + T_{sp}	-6.736	0.069				1.196	0.226	
cn4	5	336.31	51.869	0.000	0.000	CEP + A + S + T_{sp}	-6.858	0.067			0.008	1.104	0.236	
cn15	3	337.57	53.125	0.000	0.000	CEP + S	-3.662	0.053				1.215		
cn16	4	338.59	54.146	0.000	0.000	CEP + A + S	-3.655	0.051			0.007	1.134		
cn2	4	341.03	56.581	0.000	0.000	CEP + A + T_{sp}	-5.715	0.077			0.012		0.244	
sp m91	2	341.80	57.353	0.000	0.000	T_{sp}	-5.055						0.212	
cn1	3	342.11	57.664	0.000	0.000	CEP + T_{sp}	-5.386	0.081					0.231	
cn14	3	343.72	59.270	0.000	0.000	CEP + A	-2.362	0.061			0.011			
cn13	2	344.42	59.977	0.000	0.000	CEP	-2.225	0.066						
			Σ	2.487										

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*Abbreviations: CE+P = connectivity to both extant and plagued towns; CE = connectivity to extant towns; CP = connectivity to plagued towns; A = town area; S = average maximum 15 bar soil moisture content; T_{dd} = degree days 26.7°C/degree days 32.2°C; T_{sp} = average spring temperature (March-April); T_{su} = average summer temperature (June-July).