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Research Article

Landscape structure and plague occurrence in black-tailed prairie dogs on grasslands of the western USA

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Abstract

Landscape structure influences the abundance and distribution of many species, including pathogens that cause infectious diseases. Black-tailed prairie dogs in the western USA have declined precipitously over the past 100 years, most recently due to grassland conversion and their susceptibility to sylvatic plague. We assembled and analyzed two long-term data sets on plague occurrence in black-tailed prairie dogs to explore the hypotheses that plague occurrence is associated with colony characteristics and landscape context. Our two study areas (Boulder County, Colorado, and Phillips County, Montana) differed markedly in degree of urbanization and other landscape characteristics. In both study areas, we found associations between plague occurrence and landscape and colony characteristics such as the amount of roads, streams and lakes surrounding a prairie dog colony, the area covered by the colony and its neighbors, and the distance to the nearest plague-positive colony. Logistic regression models were similar between the two study areas, with the best models predicting positive effects of proximity to plague-positive colonies and negative effects of road, stream and lake cover on plague occurrence. Taken together, these results suggest that roads, streams and lakes may serve as barriers to plague in black-tailed prairie dog colonies by affecting movement of or habitat quality for plague hosts or for fleas that serve as vectors for the pathogen. The similarity in plague correlates between urban and rural study areas suggests that the correlates of plague are not altered by uniquely urban stressors.

Introduction

Human activities such as urbanization and agriculture fragment and degrade native habitats, and it is well documented that native habitat loss and fragmentation pose serious threats to biological diversity and ecosystem services (Harrison and Bruna 1999; Chapin et al. 2000; Collinge 2001). Changes in landscape structure may also dramatically influence the rate of transmission and spread of infectious diseases (Wilson et al. 1994; Langlois et al. 2001; Allan et al. 2003). The interaction of habitat loss and fragmentation with disease occurrence may cause severe declines in wildlife populations, but this interaction is not well understood for most infectious diseases (Langlois et al. 2001; Schmidt and Ostfeld 2001; Allan et al. 2003).

Landscape structure may affect infectious disease dynamics by significantly altering the composition of ecological communities, thereby altering key ecological interactions involved in pathogen transmission pathways. For example, forest fragmentation in the northeastern United States shifts mammal communities toward domination by the white-footed mouse, *Peromyscus leucopus*, the most competent reservoir host for the spirochete that causes Lyme disease, thereby significantly increasing human risk of the disease (Allan et al. 2003; Ostfeld and LoGiudice 2003).

An increasingly common landscape configuration is that of native habitat surrounded by urban and suburban development (Theobald et al. 1997). With human population growth as high as 13% per year in some parts of the western United States (Riebsame 1997), the juxtaposition of native habitat and urban development in this region continues to increase. Yet relatively little is known about the effects of urban land uses on ecological communities (Blair and Launer 1997; Bock et al. 2002; Collinge et al. 2003) and on the dynamics of infectious diseases. Across the American west, conversion of native grasslands to urbanization and agriculture has severely reduced and fragmented available habitat for native species, and has precipitated population declines of many native species, including the black-tailed prairie dog, *Cynomys ludovicianus* (Samson and Knopf 1996; Knowles et al. 2002).

Black-tailed prairie dogs are exposed to multiple stressors across their geographic range, including habitat conversion, recreational shooting, poisoning, and plague (Miller and Cully 2001). These stressors have contributed to an approximately 98% reduction in prairie dog occurrence throughout their former range over the last 100 years (Miller and Cully 2001). In 2000 they were recognized as a candidate species for listing under the US Endangered Species Act (Gober 2000), but in 2004 were removed from the candidate list because current threats to the species were not as serious as previously believed (Federal Register 2004). Plague is strongly implicated in the decline of the species; unfortunately, little is known of plague dynamics in grassland ecosystems. One prerequisite for stemming further prairie dog declines is to develop predictive models of plague occurrence in prairie dog colonies. Such models may suggest testable hypotheses regarding the mechanisms of plague transmission in grassland ecosystems.

Our research centers on the interactions between habitat loss and fragmentation and disease occurrence in black-tailed prairie dogs. Sylvatic plague, caused by the bacterium *Yersinia pestis*, was introduced to North America from Asia c. 1900 and is now present throughout most of the western US (Barnes 1982; Gage et al. 1995; Antolin et al. 2002). Plague spreads through contact between flea vectors and mammalian hosts (Barnes 1982; Perry and Featherston 1997). Consistent observations of plague prevalence in small mammals such as deer mice (*Peromyscus maniculatus*) and California voles (*Microtus californicus)* that appear to be moderately resistant to the disease suggest that these animals may serve as maintenance or reservoir hosts in which plague persists in the enzootic portion of the plague cycle (Barnes et al. 1982; Gage et al. 1995). When plague enters prairie dog colonies, it causes nearly 100% mortality in black-tailed (*C. ludovicianus*) and Gunnison's (*C. gunnisoni*) prairie dogs (Cully 1997; Cully and Williams 2001) and high but more variable mortality in white-tailed (*C. leucurus*) (Anderson and Williams 1997) and Utah (*C. parvidens*) prairie dogs (Biggins, *pers. comm.*).

Previous studies suggest that prairie dogs are affected by the landscape context in which they occur. In a study of 22 prairie dog colonies sampled across an urbanization gradient in Boulder County, Colorado, prairie dog density within colonies increased as surrounding urbanization

increased (Johnson and Collinge 2004). It is not clear, however, how landscape structure and pathogen abundance and distribution interact to determine plague occurrence in fragmented grasslands. Our study examines the influence of landscape structure on plague occurrence in black-tailed prairie dogs, with the goal of increasing our understanding of the ecological risks of landscape alteration and disease introduction.

We investigated the importance of landscape structure for predicting plague occurrence in black-tailed prairie dogs in two landscapes, one fragmented by urbanization and one relatively unfragmented. We used disease occurrence data gathered by land managers over the past 20 years to explore two hypotheses: (1) plague occurrence in prairie dogs is related to colony size and isolation, and (2) plague occurrence in prairie dogs is related to landscape context. We predicted that large colonies near other colonies would be more likely to experience plague outbreaks because it is likely that plague enters colonies via movement of prairie dogs, sympatric reservoir hosts, or fleas. We also reasoned that if landscape features pose barriers to movement of prairie dogs, reservoir hosts, or fleas, then colonies surrounded by urbanization or other potential barriers would show lower plague occurrence than colonies in relatively continuous grassland. We explored univariate associations between plague occurrence and colony or landscape characteristics, and used a model-selection approach in order to identify combinations of variables that best explained plague occurrence in each study area. This exploratory analysis is intended to guide further investigation and the development of more educated hypotheses about how plague moves through the landscape.

Methods

Study areas

We selected two study areas within the range of the black-tailed prairie dog, one in Colorado and one in Montana, based on the availability of data on plague occurrence and prairie dog colony characteristics. These two study areas represent different landscape contexts: an urban corridor in northern Colorado vs. relatively undisturbed grassland in northeastern Montana (Figure 1).

The Colorado study area is located in Boulder County along the Front Range east of the Rocky Mountains. The population of Colorado has increased at a rate three times the national average since 1990 (U.S. Bureau of the Census 2000) and the Colorado Front Range, in particular, is one of the most rapidly urbanizing regions in the USA (Riebsame 1997). The City and County of Boulder own or manage properties comprising a total of approximately 12,000 ha of grassland habitats that are protected from development. There are approximately 1200 ha of active prairie dog colonies that lie within these properties. The mean and median colony sizes in this study area are 33.9 and 5.7 ha (Collinge et al. *unpublished data*). Prairie dog colonies in Boulder County are typically located in short- and mixed-grass prairies, all of which have historically been grazed by cattle. Short-grass prairies near Boulder are dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), pasture sagebrush (*Artemisia frigida*), and woolly plantain (*Plantago patagonica*), and mixed-grass prairies are dominated by blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), blazing star (*Liatris punctata*), prairie sage (*Artemisia ludoviciana*), and aster (*Aster falcatus*) (Bennett 1997; Collinge 2000).

The Montana study area is located in southern Phillips County. Southern Phillips County includes the Charles M. Russell (CMR) National Wildlife Refuge and a patchwork of Bureau of Land Management (BLM) parcels intermixed with private property. The CMR and BLM lands comprise approximately 400,000 ha and support slightly larger prairie dog colonies than those in our Colorado study area. The mean and median colony sizes in this area are 29.6 and 12.8 ha, respectively. This area is characterized by short- and mixed-grass prairies and sagebrush shrublands. Shrub-dominated areas include two common shrubs, big sagebrush (*Artemesia tridentata*) and greasewood (*Sarcobatus vermiculatus*) and grassland areas are dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), needle-and-thread (*Stipa comata*) and green needlegrass (*Stipa viridula*) (Reading and Matchett 1997). Cattle ranching and recreation are the dominant land uses in this area.

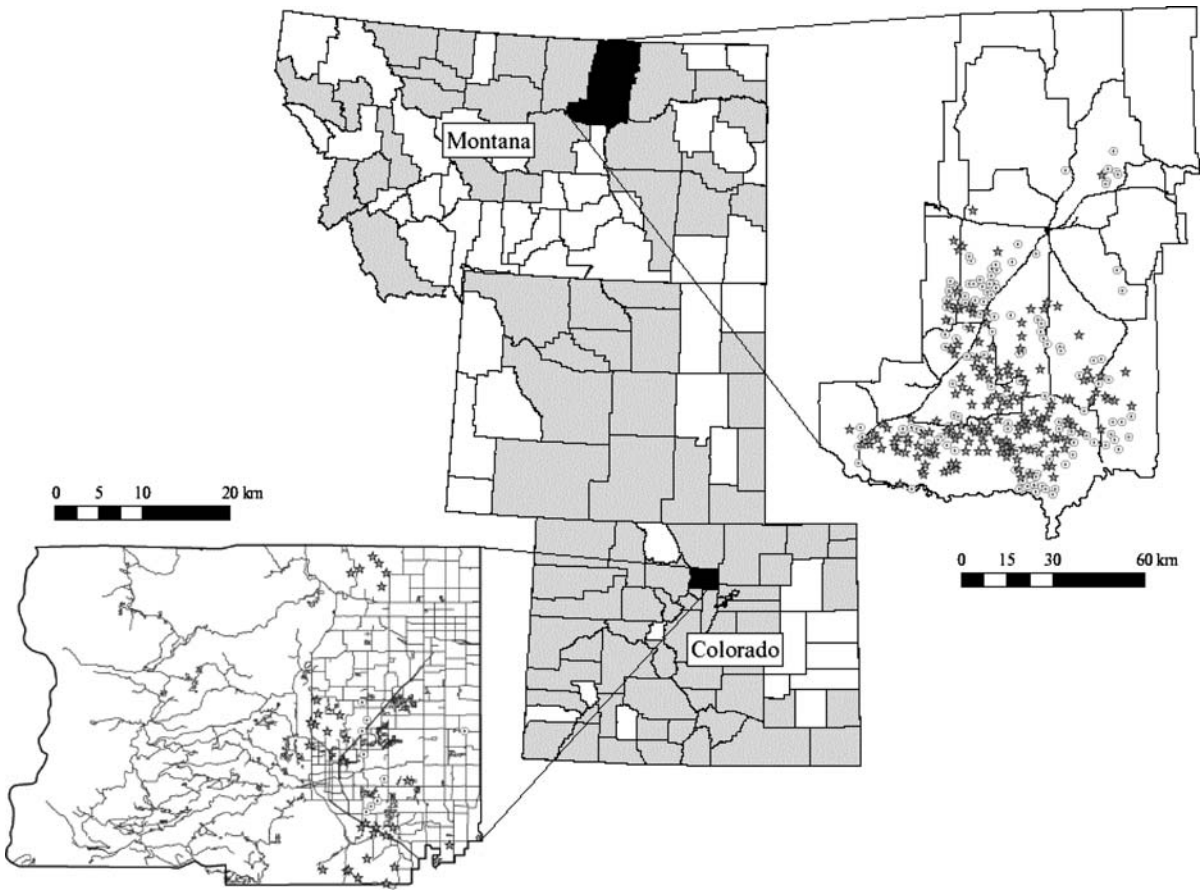

Figure 1. Boulder, Colorado and Phillips County, Montana study areas. The Centers for Disease Control has confirmed at least one occurrence of plague since 1970 in the counties shown in grey. Stars indicate plague-positive prairie dog colony locations and circles indicate plague-negatives. Major roads are indicated for reference.

Data on plague occurrence

For Boulder County, Colorado, we acquired data on plague occurrence in prairie dogs for the years 1981–2003 from the Centers for Disease Control (CDC), Boulder County Health Department records, and Boulder County wildlife managers. Data from CDC are the geographic locations (x, y coordinates) of prairie dogs or prairie dog fleas (primarily *Oropsylla hirsuta*) in which plague was detected. These data result from routine CDC investigations of prairie dog "die-offs" (*sensu* Cully and Williams 2001) in which colonies are rapidly and conspicuously decimated by plague. These data underestimate the actual number of prairie dog colonies affected by plague in a given year because CDC investigates only a sample of colonies involved in each spatio-temporal cluster of colony die-offs. Therefore, we supplemented these data with colony die-offs reported by Boulder County health officials and local wildlife managers who monitor local colonies due to their close proximity to urban areas.

Colonies on Boulder City Open Space properties have been regularly monitored and incorporated into grassland management plans since 1976 (M. Gershman, *personal communication*; City of Boulder Open Space and Mountain Parks 1996). In 1981, the Boulder County Health Department began regular flea collections from prairie dog burrows for plague surveillance (CDC, *unpublished data*). In 1986, wildlife managers in Boulder reported many colony die-offs. By screening fleas collected by Boulder County Health Department

officials, CDC confirmed that plague was present in each colony where wildlife managers had reported a die-off. These data, combined with the widespread observation that plague epizootics represent the only known natural cause of rapid colony die-offs (Gage et al. 1995; Hoogland 1995; Cully 1997; Cully and Williams 2001), give us confidence that die-offs observed by wildlife managers represent epizootics of plague. Using a combination of reports from County health officials and wildlife managers, we constructed a Geographic Information System (GIS) file with the locations of prairie dog colonies that were affected by plague (''plague-positive'' colonies) and those not affected by plague (''plague-negative'' colonies) throughout Boulder County from 1981 to 2003.

For southern Phillips County, Montana, observational data on plague occurrence on CMR and BLM lands have been collected since 1979 as part of a prairie dog population monitoring program associated with reintroduction of the black-footed ferret (*Mustela nigripes*). We collated plague data for the years 1992–2002 because no colony die-offs were observed in Phillips County prior to 1992 (Matchett, *unpublished data*).

Prairie dog colony characteristics

Wildlife managers in both study areas have mapped the locations of prairie dog colonies by hand or by Global Positioning System (GPS) for the past 10–20 years. The Colorado Division of Wildlife (CDOW) completed the earliest mapping of prairie dog colonies in Boulder County in 1993. Colonies were identified by aerial survey and colony locations were incorporated into a GIS data layer. In 1994, a major plague epizootic caused die-offs in most of Boulder's prairie dog colonies. In the following 2 years, the number of prairie dogs was very low and colonies were not mapped. In 1996, the City of Boulder Open Space Department began mapping prairie dog colonies annually and Boulder County Open Space department followed suit in 1997. These two agencies continue to map all colonies on their respective properties in September–October of each year for management purposes. Prairie dog colonies on Montana's CMR National Wildlife Refuge and BLM lands in southern Phillips County were mapped by hand on topographic maps every 2–3 years from 1979 to 1991, and mapped almost every year since 1992 using hand-held GPS receivers. In both study areas, colony perimeters were approximated wherever possible by mapping the locations of the outermost active prairie dog burrows. We obtained or developed GIS files based on these data.

To assess relationships between colony area, isolation and plague occurrence, we characterized each colony prior to each plague epizootic. In most cases, we were able to characterize each colony in the year prior to a plague epizootic. In some cases, colony characteristics were based on mapping performed 2–4 years prior to an epizootic. Our metrics of colony isolation were based on colony centroid, rather than perimeter, because the centroid tends to be more temporally stable and consistent across different measuring techniques (e.g., ground vs. aerial surveys). The density of colonies was low enough to justify centroid-based (rather than edge-based) metrics of isolation; e.g., even in Montana, where colony sizes and proximities were less constrained, the median distance from the centroid to the edge of a colony was c. 200 m, while the median distance between centroids of nearest neighboring colonies was c. 2600 m. We estimated the effective ''epizootic isolation'' of each colony as the centroid-based distance between it and the nearest colony that died off during the next epizootic. Distance to the nearest plague-positive colony was calculated as the distance between colonies prior to the epizootic. For example, the distance between a Boulder County colony that was plague-positive in 1994 and one that was plague-negative in 1994 was the distance between these two colonies in 1993.

Analyses of landscape context

We quantified landscape features at four scales (within radii of 1, 2, 3 and 5 km) around the centroid of each prairie dog colony. We used vector-based GIS files created by Boulder County, Phillips County BLM and the Montana Fish and Wildlife Service to quantify the coverage of water features, roads and prairie dog colonies, using methods described in Johnson and Collinge (2004). To quantify urbanization, we developed vector-based GIS files from raster-based, 30-m resolution GIS data

available from the Colorado GAP project (http://ndis1.nrel.colostate.edu/cogap/) and the Montana GAP project (http://gapserv.cr.usgs.gov/state/mt). From these data, we calculated the percent cover of urbanization, lakes (or reservoirs) and prairie dog colonies, and calculated the length of linear features (improved roads and streams or streambeds) surrounding each plague-positive and plague-negative colony at each spatial scale. We observed no differences in the results of our analyses whether we used percent cover of linear features or total length of linear features. We present here analyses using percent cover for all landscape variables for ease of presentation. For all spatial analyses we used ArcInfo version 8.3 (ESRI 2002).

Data analyses

We compared the percent cover of each land cover type (urbanization, roads, streams, lakes, and prairie dog colonies) between the Colorado and Montana study areas at each of the four spatial scales. Similarly, we compared the area, isolation (from the nearest die-off) and the percent cover of each land cover type between plague-positive and plague-negative colonies within each study area.

We used logistic regression to model plague occurrence as a function of multiple variables at each of the four spatial scales. Due to differences between study areas in available data, we were able to include more predictor variables in our regression models for the Montana study area. Our candidate models for the Montana study area included as predictor variables percent cover of lakes, streams, roads and prairie dog colonies within each spatial scale, pre-plague colony area, and pre-plague isolation from the nearest die-off. Our candidate models for the Colorado study area excluded colony area and colony cover as predictor variables (due to insufficient data), but included urban cover within each spatial scale.

Using these landscape variables, we created model sets for each study area based on hypotheses generated from previous research (Bock et al. 2002; Langlois et al. 2001; Staubach et al. 2001; Johnson and Collinge 2004). Previous research failed to provide further guidance on likely interactions among these predictor variables or on the scale at which each landscape variable may be related to plague occurrence. Although some predictors evidenced little quantitative difference between plague-positive and plague-negative colonies, we retained predictors based on their potential biological significance. For example, road cover differs only slightly between plague-positives and plague-negatives at some scales; but roads are narrow, linear features, so a small difference in road cover can represent a relatively large difference in the length of roads in the surrounding landscape. Furthermore, we found little correlation among landscape variables within scales. Therefore, we accepted as candidate models all combinations of one or more predictor variables, with the restriction that if multiple landscape variables were to appear in the same model they were to be measured at the same spatial scale (1, 2, 3 *or* 5 km from the colony centroid). Because this approach generated a large number of candidate models for each study area, our model-selection analysis must be considered exploratory. Our results may suggest but not confirm any relationships between these predictor variables and plague occurrence (Burnham and Anderson 2002; Anderson et al. 2001; Anderson and Burnham 2002).

We used Akaike's Information Criterion, corrected where necessary for small sample size (AIC_c), to determine the relative support for each model (Burnham and Anderson 2002). AIC is a maximum-likelihood estimate of model support that weighs model fit against the number of fitted parameters. Each model receives both a relative rank (AIC score) and a relative weight (Akaike weight). AIC scores can be used to compare the relative support for each model, given the data. The model with the lowest AIC score has highest support among the models tested, and any models with similarly low scores (difference less than c. 2–7, depending on application) may also be considered to have similar support, given the data. Akaike weights can be used to compare the relative importance of individual model parameters, by summing the relative weights of the models in which they appear (Burnham and Anderson 2002). We fit each model using SAS (SAS v. 8.2, SAS Institute 2001), but calculated AIC values independently, as recommended by Stafford and Strickland (2003).

Table 1. Landscape characteristics near prairie dog colonies in Boulder County, Colorado, and southern Phillips County, Montana.

Land cover type	Colorado	Montana
	Mean ± SE	Mean ± SE
Urbanization	11.95 ± 1.93	0
Roads	0.26 ± 0.02	0.05 ± 0.001
Streams	0.18 ± 0.01	0.06 ± 0.001
Lakes	3.20 ± 0.31	2.14 ± 0.24

Data shown are % cover of various land cover types within a 5-km radius of prairie dog colonies. $N = 42$ colonies for Colorado and 337 colonies for Montana. All land cover type percentages were significantly greater in Colorado than in Montana ($p < 0.001$). Means ± SE are presented.

Results

Univariate analyses

The landscape context of prairie dog colonies differed between study areas (Table 1). In Boulder County, Colorado, prairie dog colonies occur within a landscape that has been significantly altered by human activities. On average, urban land cover comprised nearly 12% of the total land cover within a 5-km radius of each colony. In Phillips County, Montana, urbanization comprised less than 0.001% of the surrounding landscape. Similarly, road cover in Colorado (0.26% within a 5-km radius) was five times higher than in Montana (0.05%). Streams and lakes also comprised significantly more of the surrounding landscape in Colorado than in Montana (Table 1).

Plague occurrence in both study areas was correlated with prairie dog colony characteristics (Figure 2). Colony area did not differ between plague-positive and plague-negative colonies in Colorado (Figure 2a), but in Montana plague-positive colonies were larger than plague-negative colonies (Figure 2b). In both study areas plague-positive colonies were closer to other plague-positive colonies than were plague-negative colonies (Figure 2c, d).

Landscape context correlated significantly with plague occurrence in both study areas, but in slightly different ways (Figure 3, Table 2). The most striking pattern from this analysis was that plague-negative colonies were surrounded by a higher cover of streams and lakes than were plague-positive

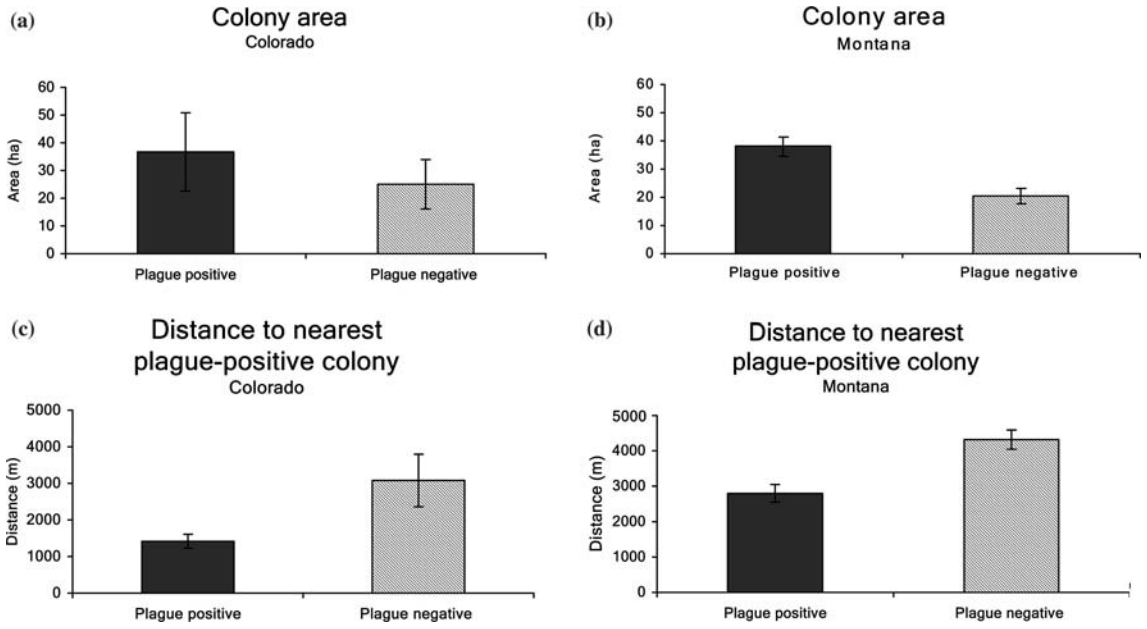

Figure 2. Characteristics of plague-positive and plague-negative prairie dog colonies in Colorado and Montana study areas. For Colorado, $N = 25$ plague-positive and eight plague-negative colonies for colony area, and $N = 33$ plague-positive and nine plague-negative colonies for distance to nearest plague-positive colony. For Montana, $N = 178$ plague-positive and 156 plague-negative colonies for colony area, and $N = 181$ plague-positive and 156 plague-negative colonies for distance to nearest plague-positive colony. Solid bars denote plague-positive colonies; hatched bars denote plague-negative colonies. Means ± 95% confidence intervals are presented.

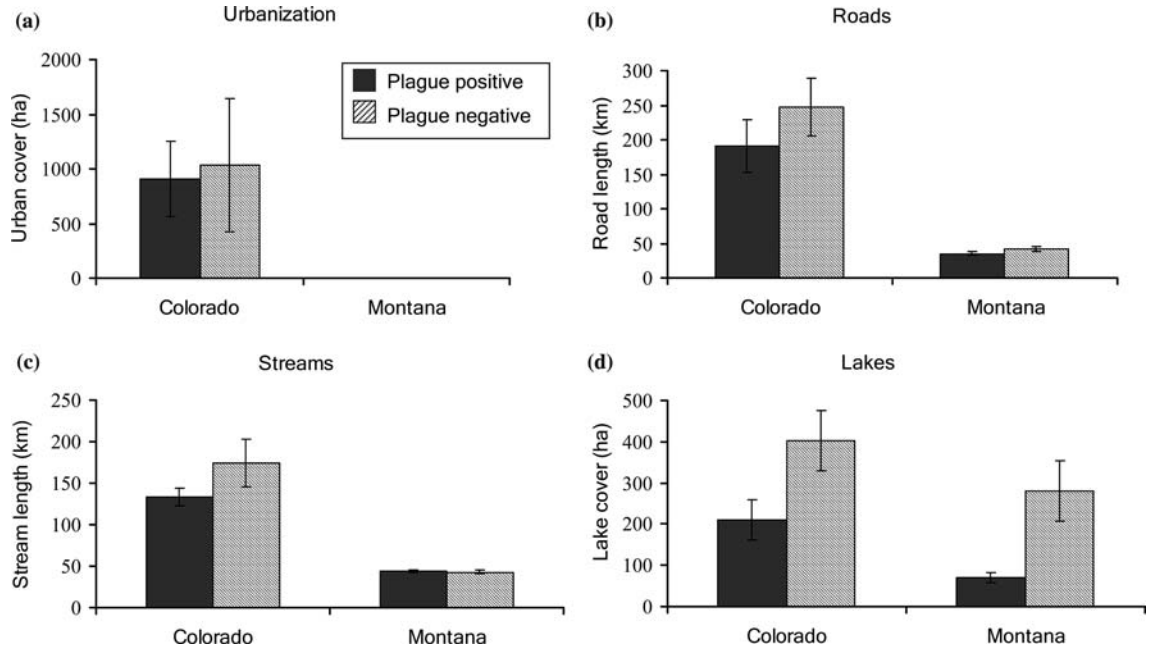

Figure 3. Characteristics of the landscape within a 5-km radius surrounding plague-positive and plague-negative prairie dog colonies in Colorado and Montana study areas. For Colorado, $N = 33$ plague-positive and nine plague-negative colonies. For Montana, $N = 181$ plague-positive and 156 plague-negative colonies. Solid bars denote plague-positive colonies; hatched bars denote plague-negative colonies. Means ± 95% confidence intervals are presented.

Table 2. Percent cover of various land-cover types within 1-, 2-, and 3-km zones surrounding plague-positive and plague-negative prairie dog colonies.

Land cover and scale	Colorado		Montana	
	Plague-positive colonies	Plague-negative colonies	Plague-positive colonies	Plague-negative colonies
Urbanization (1 km)	5.65 ± 5.88	0	0	0
Urbanization (2 km)	5.72 ± 4.95	2.41 ± 1.73	0	0
Urbanization (3 km)	7.76 ± 4.67	6.61 ± 4.55	0	0
Roads (1 km)	0.14 ± 0.05	0.18 ± 0.04	0.05 ± 0.007	0.05 ± 0.008
Roads (2 km)	0.16 ± 0.05	0.24 ± 0.04	0.05 ± 0.004	0.05 ± 0.006
Roads (3 km)	0.19 ± 0.05	0.28 ± 0.05	0.05 ± 0.003	0.05 ± 0.005
Streams (1 km)	**0.16 ± 0.03**	**0.30 ± 0.05**	0.05 ± 0.006	0.06 ± 0.008
Streams (2 km)	**0.16 ± 0.03**	**0.28 ± 0.04**	**0.05 ± 0.004**	**0.06 ± 0.005**
Streams (3 km)	**0.17 ± 0.02**	**0.25 ± 0.05**	**0.05 ± 0.003**	**0.06 ± 0.004**
Lakes (1 km)	**1.56 ± 1.19**	**16.90 ± 9.64**	1.15 ± 0.49	1.53 ± 0.65
Lakes (2 km)	**1.73 ± 0.98**	**10.03 ± 5.14**	**1.07 ± 0.30**	**2.42 ± 1.02**
Lakes (3 km)	**2.32 ± 0.93**	**7.53 ± 1.93**	**1.01 ± 0.24**	**3.03 ± 1.04**
Prairie dog colonies(1 km)	16.96 ± 6.85	11.63 ± 4.65	**12.26 ± 2.12**	**8.25 ± 1.63**
Prairie dog colonies (2 km)	12.20 ± 3.88	7.51 ± 1.61	4.86 ± 0.76	3.76 ± 0.69
Prairie dog colonies (3 km)	11.24 ± 3.19	7.87 ± 2.41	3.46 ± 0.50	2.71 ± 0.45

For Colorado, $N = 33$ plague-positive and 9 plague-negative colonies for all variables except for % prairie dog colonies in the surrounding landscape, where $N = 25$ plague-positive and 8 plague-negative colonies. For Montana, $N = 181$ plague-positive and 156 plague-negative colonies for all variables except for % prairie dog colonies in the surrounding landscape, where $N = 178$ plague-positive and 156 plague-negative colonies. Means ± 95% CI are presented. Non-overlapping CIs are indicated in bold.

colonies in both study areas at almost every spatial scale (Figure 3c, d; Table 2). Urbanization of the landscape surrounding prairie dog colonies was not related to plague occurrence in the Colorado study area (Figure 3, Table 2). The Montana study area contained very little urban land cover (Table 2), so

we were unable to make this comparison. Road cover tended to be higher around plague-negative colonies, especially at smaller spatial scales in the urban Colorado landscape (Table 2) and at the largest spatial scale in the relatively roadless Montana landscape (Figure 3). Plague occurrence was positively associated with prairie dog colony cover at scales of 1 km (Table 2) and 5 km (not shown) in the Montana study area.

Multiple regression analyses

We used logistic regression to model plague occurrence as a function of multiple colony and landscape context variables, with similar results for both study areas. For the Colorado study area, the model of plague occurrence with most support included negative effects of stream and lake cover at the 3-km scale (Table 3). Several other models with similar support included negative effects of urbanization and roads at the 3-km scale, and distance to the nearest plague-positive colony. For the Montana study area, the model with most support included negative effects of lake cover at the 5-km scale and distance to the nearest plague-positive colony, and positive effects of colony area (Table 3). Other models with similar support included negative effects of stream and road cover, also at the 5-km scale.

For the Colorado study area, the predictor with highest relative importance across all candidate models was lake cover, followed closely by stream cover (Table 4). For the Montana study area, where there was sufficient data to include colony area and isolation as predictors in some candidate models, lake cover, colony area, and colony isolation from plague were tied for highest relative importance (Table 4).

By using a weighted average of the models in Table 3, we can fit plague occurrence quite well for the Colorado study area and moderately well for the Montana study area (Figure 4). We used Akaike weights to weight the predictions of our regression models (Burnham and Anderson 2002). For the Colorado study area, observed values were 99% concordant with modeled values, and the difference between modeled and observed values was less than 0.5 for 97% of plague-positive colonies and 89% of plague-negative colonies. For the Montana study area, observed values were 79% concordant with modeled values, and the difference between modeled and observed values was less than 0.5 for 81% of plague-positive colonies and 56% of plague-negative colonies (Figure 4). Note that Figure 4 represents model fit rather than prediction.

Table 3. Logistic regression models of plague occurrence in prairie dog colonies in Colorado and Montana study areas.

Predictors of plague occurrence (sign of regression coefficient)	AIC_c	$dAIC_c$	Akaike weight	Scaled R^2
(a) Colorado				
% lake (−), % stream (−)	19.85	0	0.27	0.84
% lake (−), % stream (−), isolation (−)	20.50	0.65	0.19	0.87
% lake (−), % stream (−), % road (−)	22.05	2.20	0.09	0.85
% lake (−), % stream (−), isolation (−), % road (−)	22.07	2.22	0.09	0.89
% lake (−), % stream (−), % urban (−)	22.42	2.57	0.07	0.84
% lake (−), % stream (−), isolation (−), % urban (−)	22.55	2.70	0.07	0.88
(b) Montana	AIC	dAIC	Akaike weight	Scaled R^2
% lake (−), area (+), isolation (−)	375.27	0.00	0.26	0.33
% lake (−), area (+), isolation (−), % stream (−)	375.58	0.31	0.22	0.34
% lake (−), area (+), isolation (−), % road (−)	376.65	1.38	0.13	0.34
% lake (−), area (+), isolation (−), % stream (−), % road (−)	377.10	1.83	0.10	0.34
% lake (−), area (+), isolation (−), % colony (+)	377.17	1.90	0.10	0.33
% lake (−), area (+), isolation (−), % stream (−), % colony (+)	377.49	2.22	0.09	0.34

We analyzed 121 models for Colorado and 243 models for Montana. Candidate models for Colorado included one scale-independent model (based on colony isolation), and 30 models based on at least one of four scale-dependent variables (% lake, stream, road and urban cover). The candidate models for Montana included three scale-independent models (based on colony area, isolation, or both), and 60 models based on at least one of four scale-dependent predictor variables (% lake, stream, road and colony cover). For Colorado, all of the models presented here were based on variables measured at the 3-km scale, and for Montana, variables measured at the 5-km scale.

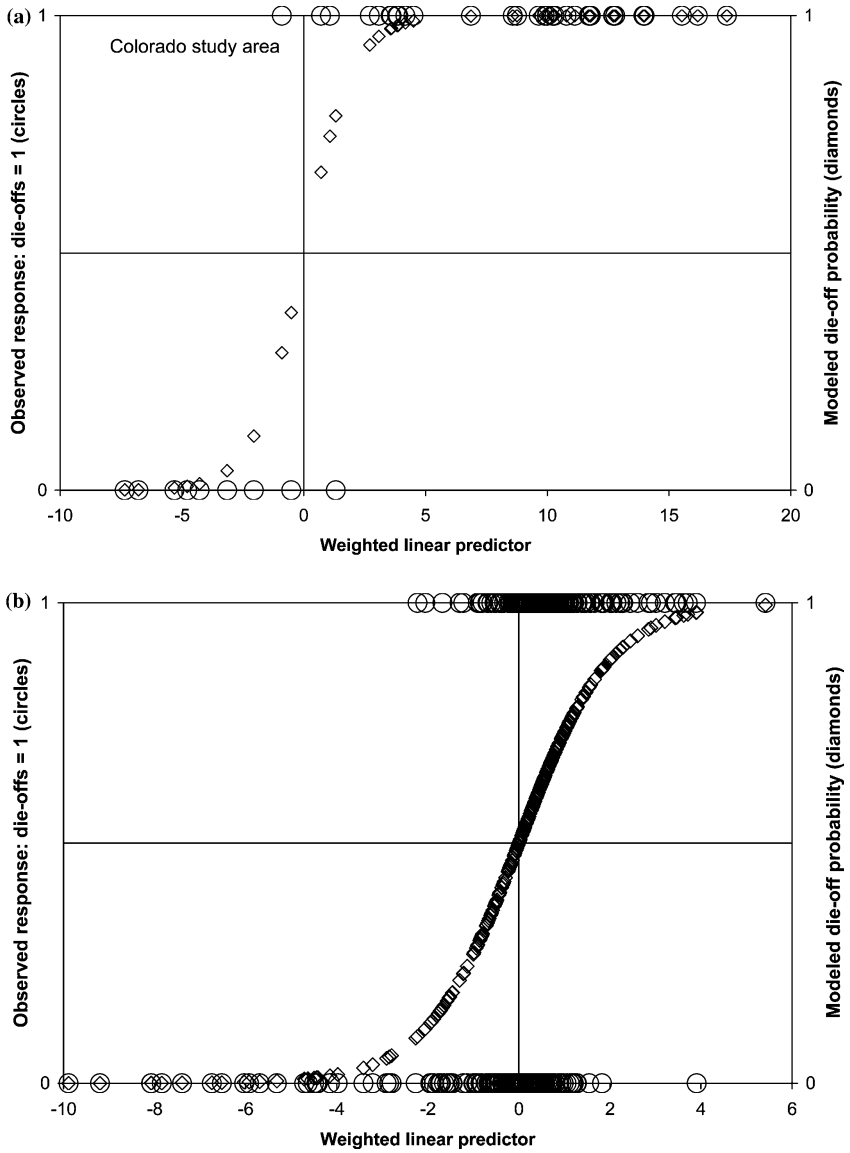

Figure 4. Observed and predicted values of plague occurrence from logistic regression models of the (a) Colorado and (b) Montana study areas. The "weighted linear predictor" was a weighted average of the models shown in Table 3. For Colorado, this predictor included effects of colony isolation and percent cover of lakes, streams, roads and urbanization within 3 km of the focal colony; and for Montana this predictor included effects of colony area, isolation from the nearest colony die-off, and percent cover of lakes, streams, roads and prairie dog colonies within 5 km of the focal colony. For the Colorado study area, percent concordant = 99% and |predicted-observed| was <0.5 for 95% of all colonies (97% of plague-positives, 89% of plague-negatives). For the Montana study area, percent concordant = 79% and |predicted-observed| was <0.5 for 70% of all colonies (81% of plague-positives, 56% of plague-negatives).

Discussion

Our analyses of two disparate regions revealed some striking similarities in correlates of plague occurrence in prairie dogs over the past 10–20 years. Despite notable differences in the overall characteristics of the two study sites, our results suggest a common set of predictive variables. In both urban and rural landscapes, the presence of plague in a colony was positively associated with plague occurrence in an adjacent colony. In both study areas, the cover of lakes or reservoirs,

Table 4. Relative importance of predictive variables (Burnham and Anderson 2002).

Variable	Colorado	Montana
Urban	0.28	N/A
Roads	0.34	0.33
Streams	0.99	0.46
Lakes	1	1
Colony cover	N/A	0.28
Isolation from plague	N/A	1
Colony area	N/A	1

The higher the value, the greater the relative support for models including this variable as a predictor of plague occurrence.

streams and roads in the landscape surrounding colonies was negatively associated with plague occurrence. In both study areas, the relationship between landscape structure and plague occurrence was most evident at larger spatial scales (Table 2).

Colony size and isolation

Colony area was not associated with plague occurrence in the Colorado study area, but was correlated with plague occurrence in the Montana study area, where plague-positive colonies were 'larger' (i.e., covered more area) than plague-negative colonies. This result for Montana is consistent with two other studies of plague in black-tailed prairie dogs, both of which found that larger colonies were more likely to experience plague than smaller colonies (Cully and Williams 2001; Lomolino and Smith 2001). Colony size may positively correlate with plague occurrence for several reasons that are not mutually exclusive. Common associates of prairie dogs and putative reservoir hosts, such as deer mice (Barnes 1982), may be more abundant on large colonies than small colonies (Collinge et al. in prep.), which would increase the probability of contact between infective hosts and prairie dogs. Rates of prairie dog dispersal may be higher to large colonies than small colonies, perhaps because of greater habitat suitability, thereby increasing the probability that a large colony will attract a dispersing prairie dog that is either infected or infested with infected fleas. Correspondingly, prairie dog density may differ between large and small colonies, altering levels of stress and susceptibility to infection. Large colonies may also be more likely to attract rodent-consuming predators, such as coyotes, badgers, or raptors, which are known to occasionally harbor fleas from their prey and could therefore carry infected rodent fleas between colonies (Hubbard 1947). Consistent with our univariate results, colony area was included in all of our best regression models for the Montana study area.

Colony isolation, measured as the distance to the nearest plague-positive prairie dog colony, was negatively correlated with plague occurrence in both study areas. Colonies with plague tended to be clustered in space, such that plague-positive colonies were closer to other plague-positive colonies than were plague-negative colonies. This spatial clustering suggests at least two hypotheses to explain plague dynamics among colonies. One hypothesis is that plague initially enters a colony at random, independent of its proximity to other colonies. Once plague establishes in a colony, it may be much more likely to spread to nearby colonies than to colonies further away. A second hypothesis is that plague may simultaneously enter neighboring colonies, due to high pathogen prevalence and an abundance of flea vectors and reservoir hosts in the greater landscape. In other words, plague may simultaneously enter groups of colonies, or colony complexes, based on characteristics of the landscape at the scale of complexes, rather than individual colonies. Our results for colony isolation and plague occurrence are intriguing because they suggest either that there are distinct phases of plague spread across these landscapes or that plague occurs at larger spatial scales than a single colony in the landscape matrix.

Landscape context and plague occurrence

Plague occurrence in prairie dog colonies was significantly related to landscape context, but in somewhat unexpected ways. In the Colorado study area, urban cover in the surrounding landscape was not correlated with plague occurrence, except perhaps as a conditioning variable in our multiple regression models. But the cover of roads, streams, and lakes were all negatively associated with plague occurrence in this urban landscape. In the relatively rural, roadless, and less riparian Montana study area, plague was negatively associated with the cover of lakes, and negative effects of

roads and streams were also implicated in the best models of plague occurrence. Note that for linear features like roads and streams, differences of only 0.05% cover results in a difference of approximately 10% in the total length of the linear feature in the landscape. Therefore, small differences in cover of linear features may be biologically meaningful in the context of disease occurrence.

At least three mechanisms could explain these striking patterns of plague occurrence in relation to roads, streams and lakes. First, roads, streams and lakes may act as barriers to movement of prairie dogs, fleas, or other grassland rodents that serve as reservoir hosts for plague. With fewer infective animals moving to a particular colony, the likelihood of the pathogen reaching the colony would be lowered. Alternatively, roads, streams and lakes may modify the microclimate or habitat quality of nearby prairie dog colonies such that abundance and distribution of the plague pathogen, vectors, or reservoir hosts may be altered. Finally, roads, streams and lakes may be associated with topographical and/or vegetative features that affect animal community structure or the potential for movement of plague vectors.

Given current information, the effect of roads on prairie dog movement is debatable. There is some evidence that black-tailed prairie dogs disperse along roads in the Montana study area (Knowles 1985; J. Grensten, *unpublished data*), which would suggest that roads should not pose a significant barrier to movement of prairie dogs. In the urban Colorado study area, however, roads surrounding prairie dog colonies are usually paved and have moderate to heavy automobile traffic, which increases the probability of mortality for prairie dogs that disperse across or along them. Finally, genetic analysis of black-tailed prairie dogs in the Pawnee National Grasslands of northern Colorado suggests that dispersal through the vegetation adjacent to ephemeral stream corridors is more likely than along roads (Roach et al. 2001). Thus, it appears that roads may either facilitate or inhibit successful movement of prairie dogs, depending on the landscape setting.

It is even less clear how roads, streams, or lakes may affect movement of other species in this system. For example, field research on several plague hosts (mice, voles, rats, chipmunks) suggests that landscape features such as wooded fencerows (Bennett et al. 1994) and vegetated corridors (LaPolla and Barrett 1993; Lidicker and Koenig 1996) may affect movement. There is little information on small mammal movement in relation to roads, streams, and lakes, however, and none for the species that are associated with prairie dog colonies and potentially serve as reservoir hosts for plague in either the Colorado or Montana study area. It is possible that predators, such as coyotes, foxes, or badgers, may move flea vectors and plague bacteria among prairie dog colonies and that their movement may be affected by the presence of roads, streams, and lakes, but we have no data with which to evaluate this possibility for our study areas.

Predictive models

Our logistic regression models derive from an exploratory analysis of virtually all combinations of one or more predictor variables for which we had data and reason to suspect an association with plague occurrence. The results should be useful for developing predictions and testing specific hypotheses.

The top six models for each study area were quite similar (Table 3) and biologically sensible. For the Colorado study area, our models included negative effects of distance to the nearest plague-positive colony and cover of roads, streams and lakes at the 3-km scale. Two models included negative effects of urban land cover, which may indicate that the plague-inhibiting effects of other variables may be more potent in urban areas. Three models included a negative effect of distance to the nearest plague-positive colony, which suggests that plague tends to occur in colonies that are in close proximity to one another. For the Montana study area, the best predictors of plague occurrence were similar to those for Colorado, except for the scale of the landscape variables and the inclusion of colony area in all of the models for Montana (recall that we lacked the data necessary to include colony area as a predictor in Colorado models). All six Montana models included negative effects of lake cover at the 5-km scale and three included negative effects of stream cover at the 5-km scale, rather than at the 3-km scale implicated in Colorado. This difference in scale seems reasonable given the lower density of streams and lakes at the Montana study site (Table 1). If water or other features associated

with riparian habitats act as barriers to the spread of plague, then epizootics should spread over larger scales where streams and lakes are sparse. Alternatively, this difference in scale may be due to the relative proximity of colonies in the Colorado study area. Where colonies are close together, there can be little distinction between the landscape context of plague-positive and plague-negative colonies at the largest spatial scale. Finally, the effect of colony isolation was similar in Montana and Colorado models. Plague occurrence was negatively related to a colony's isolation from plague-positive colonies, again suggesting the possibilities for plague spread among colonies or for relatively large epizootics occurring in the matrix in which these colonies are embedded.

Does landscape structure affect general patterns of disease occurrence?

The influence of landscape structure on disease dynamics has been studied in relatively few other systems. For example, landscape context influenced the occurrence of alveolar echinococcosis in foxes in northwestern Germany (Staubach et al. 2001). In contrast to our specific results, foxes infected with *Echincoccus multilocularis* occurred closer to rivers than uninfected foxes. There were no differences between uninfected and infected foxes in distance to lakes, forests, villages, or streets (Staubach et al. 2001), again in contrast with our results that showed a significant negative association between cover of roads, streams, and lakes and plague occurrence.

Studies of Lyme disease in fragmented forests of the northeastern USA have shown that forest patch area is inversely correlated with the density of vectors and with pathogen prevalence of vectors. These two factors combined serve to increase risk of Lyme disease in humans that live near small compared to large forest fragments (Allan et al. 2003). Smaller forest patches support relatively larger populations of white-footed mice (*Peromyscus leucopus*), the most competent reservoir host for *Ixodes scapularis* ticks, probably because the mice are tolerant of declines in patch area and because predators and competitors tend to be absent in small forest patches.

Landscape composition (the types of patches present in the landscape) and landscape configuration (the spatial arrangement of patches) significantly influenced the prevalence of Sin Nombre virus in deer mice, *Peromyscus maniculatus*, at 101 sites across Canada (Langlois et al. 2001). These authors analyzed landscape context within 1-, 2-, and 4-km radii from deer mouse trapping locations and found that the well-supported models included landscape variables measured at the 1-km scale. They concluded that landscape structure had stronger effects on virus incidence than other variables that are often correlated with Sin Nombre virus, such as climate and season.

In summary, we conclude that prairie dog colony characteristics and landscape context were significantly correlated with plague occurrence in two study areas that occur in quite different landscape settings. The general similarities in plague correlates between urban and rural study areas suggest that the correlates of plague are not altered by uniquely urban stressors. Our research group is currently studying the abundance and distribution of prairie dogs, other mammalian reservoir hosts, flea vectors, and the prevalence of *Y. pestis* and other bacterial pathogens in varied landscape contexts, which should provide further insights into disease dynamics in relation to landscape structure. We are also considering metrics of landscape structure other than 'percent cover' that may better describe how landscape structure may facilitate contact processes and the percolation of epidemics through the landscape.

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