



Factors associated with long-term changes in distribution of black-tailed prairie dogs in northwestern Mexico

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ABSTRACT

The area occupied by colonies of the black-tailed prairie dog (*Cynomys ludovicianus*; BTPD henceforth) in northwestern Mexico was dramatically reduced between 1988 and 2005. We conducted a quantitative assessment of the distributional changes of these BTPD colonies during the periods 1988–2000 and 2000–2005 focusing on the potential roles of plant biomass, landscape configuration, habitat loss, and habitat suitability. We used remote sensing and GIS tools to characterize habitat and landscape conditions at areas of extinction and persistence at the beginning of each period. Based on this information, we contrasted areas of extinction and persistence within single BTPD colonies, and used logistic regression to model extinction of entire colonies. The greatest levels of reduction, fragmentation and extinction of colonies occurred between 1988 and 2000. The trend of reduction continued between 2000 and 2005 because the largest colony became smaller and fragmented, driving the area down, however, the rest of the towns showed a marginal increase. During the first period, extinction of entire colonies was higher in smaller colonies occupying low-biomass areas. Both extinction models and raw data indicate that colony area lost to agriculture and urbanization was relatively low for both periods. Because the period exhibiting the highest colony area loss coincided with a severe period of drought (1994–1995), we hypothesized that an unusually high food shortage could be the driving force behind this generalized reduction in colonies. Our results suggest that BTPD populations are sensitive to size and isolation effects mainly in the context of severe drought. Because changes in precipitation have profound impacts on plant productivity and composition in arid ecosystems, BTPD populations at the southernmost edge of their geographic range are especially vulnerable to drought and desertification processes, and therefore to climate disruption.

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1. Introduction

For thousands of years, the black-tailed prairie dog (BTPD), *Cynomys ludovicianus*, has shaped the structure of extensive grassland communities of North America. In historical times, the BTPD inhabited vast areas of the Great Plains, from southern Saskatchewan, Canada, to northwestern Chihuahua and northeastern Sonora, Mexico (Hall, 1980; Hoogland, 1995). Despite climatic and environmental fluctuations during the late Pleistocene in North America, the geographic range of BTPDs in the United States remained relatively stable over the last 40,000 years (Lomolino and

Smith, 2001). In the 19th century, the geographic range of BTPDs was estimated at more than 160 million ha, of which roughly 30 million ha were effectively occupied by BTPD colonies (Proctor et al., 2006; Vermeire et al., 2004). However, after European settlement in the Great Plains, BTPD populations declined rapidly. At present, the total area occupied by BTPD colonies is approximately 2% of the area occupied 100–200 years ago; similarly, total population numbers have declined more than 95% during the same period (Miller et al., 2007; Proctor et al., 2006; but see Vermeire et al., 2004). Poisoning campaigns promoted by the United States government, along with habitat loss, exotic sylvatic plague (*Yersinia pestis*) epizootics, and recreational shooting have been documented as the main causes of these population crashes (Hoogland, 2006).

Decline of BTPD populations has resulted in area reduction and increased isolation of individual colonies. In the 19th century,

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individual colonies larger than 20,000 ha were apparently common, with some exceptional colonies occupying more than 2 million ha (Knowles et al., 2002). In contrast, by the beginning of the 21st century, only five colony complexes occupied more than 4000 ha (Proctor et al., 2006). As remnant colonies become smaller and more isolated, local populations become more sensitive to stochastic processes and likely exhibited reduced immigration rates (Lomolino et al., 2003). Such processes might further increase the extinction probability of remnant local populations and reduce recolonisation rates of suitable habitat patches, which could therefore compromise the long-term persistence of entire colony complexes (Lomolino et al., 2003; Lomolino and Smith, 2001).

Declines of BTPD populations and colony size are well documented for most North American regions (Proctor et al., 2006). In northwestern Mexico, BTPD populations extended over an area of 560,000 ha at the beginning of the 20th century (Mearns, 1907). By late 1980s, the two most important colonies in Sonora were extirpated, whereas colonies in Chihuahua were reduced to about 55,000 ha (Ceballos et al., 1993). The colonies in northwestern Chihuahua were the largest prairie dog colonies left in the continent, and as such their conservation value was immense. Unfortunately, those colonies declined by about 64% between 1988 and 2000 (Marcé, 2001). By analysing area changes in a subsample of colonies, Marcé (2001) concluded that most reduction and fragmentation of colonies occurred between 1988 and 1996. Qualitative data and casual observations suggested that agriculture, poisoning associated with cattle ranching, and shrub encroachment, were responsible for population declines in Chihuahua (Ceballos et al., 1993; List, 1997; Marcé, 2001). Despite its tremendous decline in area, this system of colonies still constitutes one of the three largest BTPD colony complexes and includes the largest colony in North America (Ceballos et al., 2005; Proctor et al., 2006).

The BTPD colonies of northwestern Chihuahua occupy a desert grassland region at the southernmost limit of the species' geographic range. Available information suggests that the environmental conditions faced by southern BTPD populations may differ significantly from those faced at more northern latitudes (Avila-Flores et al., 2010; Facka et al., 2008, 2010; Truett et al., *in press*). Because desert grasslands occupy the driest and warmest portions of the Great Plains, they exhibit lower primary productivity as well as higher occurrence of warm-season plant species and shrubs than other North American grassland communities (Sims et al., 1978). Therefore, BTPD populations at the southern limit of distribution could face the most severe habitat alterations, like reductions in plant productivity, loss of the plant species they feed upon, and increases in shrub cover (Ceballos et al., 2010). Although processes of gradual desertification and shrub encroachment have been observed in northwestern Chihuahua, presumably due to the combined effects of drought and overgrazing by cattle (Ceballos et al., 2010; List, 1997), it is unknown to what extent these changes have affected BTPD distribution.

We used distributional data of BTPDs for the years 1988, 2000 and 2005, in combination with remote sensing and GIS tools, to identify the habitat and landscape factors associated with the declines in occupancy of BTPD populations of northwestern Chihuahua, Mexico. We evaluated the potential roles of landscape configuration (colony area and degree of isolation), habitat suitability, habitat loss, and plant biomass (measured using the Normalized Difference Vegetation Index (NDVI) as a proxy), on the observed changes in distribution (extinction or persistence within spatial units) of BTPD colonies during the periods 1988–2000 (when most severe drought occurred) and 2000–2005 (moderate drought). Due to the nature of our data, we could not separate the effects of overgrazing by cattle and drought, through their effects on plant biomass, on extinction/persistence patterns (however, they are most likely to be synergistic). We predicted that

extinction within spatial units for a given period would be associated with small colony areas, increased isolation, low habitat suitability, higher habitat loss, and low plant biomass. Because our study area is located in one of the driest and hottest portions of the BTPD geographic range, we expected to find a strong impact of plant biomass on BTPD distribution during the most critical period of drought (1988–2000).

2. Study area and methods

Colonies considered in this study correspond to regions I–III of BTPD geographic range as defined by Ceballos et al. (1993), which encompass municipalities of Janos, Ascensión, Casas Grandes, and Nuevo Casas Grandes, at the northwest portion of the state of Chihuahua, Mexico. The division of the colonies in three zones was originally done to facilitate analysis, it does not respond to ecological attributes. For simplicity, we considered all colonies in the three regions as a single complex despite the fact that several of them are relatively isolated. The study area includes the core of the Biosphere Reserve of Janos, which is one of the top priority areas for conservation of vertebrates in Mexico (Ceballos et al., 2005). The region represents the northwestern limit of the Chihuahuan Desert in Mexico, and is bordered to the south and west by mountain chains of the Sierra Madre Occidental. The area is dominated by a mosaic of desert grasslands and shrublands, with interspersed patches of savannahs, riparian vegetation, agricultural lands, and human settlements. Vegetation is dominated by annual forbs, annual grasses, perennial grasses, and shrubs (Desmond, 2004). Climate is temperate arid with hot summers and cold winters, with extreme historical temperatures ranging from -15 to 50 °C, and a mean annual temperature of 15.7 °C. The mean annual precipitation is 307 mm, with most rainfall occurring from July to September and occasional snow showers in winter (García, 1973). The region was strongly influenced by a widespread and persistent drought, which started in 1994 and extended over western North America (Stahle et al., 2009). Incomplete records from the weather station of Ascensión, Chihuahua (45 km away from the centre of the complex), and data recorded on site between 1993 and 1996 show that annual precipitation dropped to 50–200 mm (unpublished data, Servicio Meteorológico Nacional, Mexico; List, 1997). However, scarcity of recent data precluded separate estimates of average precipitation for periods 1988–2000 and 2000–2005.

Cattle ranching and agriculture are the primary economic activities of the region. In recent years, farmers have replaced traditional farming with mechanized irrigation agriculture. Most grasslands and shrublands in private and communal lands are currently used for livestock grazing and often are overstocked and exposed to continuous grazing. Recent declines in plant biomass production and grass abundance, increases of shrub encroachment, and acceleration of erosion processes have been considered consequences of overgrazing by cattle (Ceballos et al., 2005, 2010; Desmond, 2004). However, it is unknown to what extent this desertification process was intensified by the prolonged regional drought.

2.1. Prairie dog colony maps

We used BTPD colony maps generated in previous studies for the years 1988 and 2000 (Ceballos et al., 1993; Marcé, 2001), along with new maps produced in 2005. In 1988, colonies were located for the first time through ground expeditions and interviews with local people; then, colony borders (places where conspicuous burrows could be seen on one side but not in the other) were mapped on 1:50,000 topographic maps after aerial and ground surveys (Ceballos et al., 1993). Colonies El Cuervo and Salto de Ojo were

edited from the digitised original maps to exclude large areas covered with agriculture in 1988. In September 1999, general locations of most colonies were recorded with a GPS-unit through aerial surveys. Parallel straight-line flights separated by 1.25 km were performed to delineate the borders of the largest colony of the complex (“El Cuervo”, roughly 15,000 ha by that time); after ground-verification of a small section of this colony, it was estimated that the error of aerial mapping was approximately 500 m (the same error was assumed for colony maps generated in 1988; *Marcé, 2001*). Between September 1999 and March 2000, most of the colonies previously detected by airplane were mapped on the ground, either by foot or vehicle, recording in a GPS-unit the coordinates of active burrows forming the boundary every 150 m (*Marcé, 2001*). For simplicity, maps generated both in 1999 and 2000 are referred to as corresponding to year 2000. Between May and December 2005, we searched from the ground almost all colonies registered during the 1988 and 2000 surveys; during these surveys we found some colonies not recorded in previous years. In 2005, all colony boundaries were mapped from the ground as in 2000. For analytical purposes, colony polygons separated by <100 m were considered as a single colony, assuming that BTPD individuals do not move more than 100 m during their daily activities (*Hoogland, 1995*).

2.2. Land cover and plant biomass maps

We gathered Landsat-5 and -7 scenes (processed with the standard terrain correction) covering the study area from the US Geological Survey Global Visualization Viewer website (<http://glovis.usgs.gov/>). We used Landsat TM scenes from 1990 and 1991 to describe plant biomass and land cover attributes of colonies in 1988; Landsat ETM+ scenes from 1999 and 2000 to describe attributes in 2000; and Landsat GLS scenes (which combine ETM+ and TM data) from 2005 to describe attributes in 2005. The three image types had six visible and infrared bands and a resolution of 30 m. Metadata associated with scenes indicated that all of them were originally recorded during the local rainy season, specifically between June 17 and October 21. We used programs ENVI (ITT Visual Information Solutions, Pearl East Circle Boulder, CO, USA) and ERDAS Imagine (ERDAS Inc., Norcross, GA, USA) to process and classify images. Hereafter, mosaics produced with 1990–1991, 1999–2000 and 2005 scenes will be referred to as 1988, 2000 and 2005 mosaics to match the year of colony mapping.

We calculated the Normalized Difference Vegetation Index (NDVI) to produce a relative estimate of the standing-crop biomass in 1988, 2000, and 2005. This widely used vegetation index uses near-infrared and red bands to estimate “greenness”, producing standardized values between -1 and $+1$ (*Jensen, 2007*). We produced land cover maps from supervised classifications of Landsat mosaics based on decision-tree algorithms (*Portillo-Quintero and Sánchez-Azofeifa, 2010*). This method was preferred over signature-based supervised classification because of its higher mapping accuracy capabilities (*Portillo-Quintero and Sánchez-Azofeifa, 2010*) and because it was difficult to identify unique signatures for cover types in the study area. Land cover types considered in this study were: grassland, shrubland, temperate forest, active agricultural land, inactive (abandoned) agricultural land, water body, barren ground, and urban area. Decision-tree algorithms were produced based on the See5 algorithm to classify 400–500 reference locations per year (1988, 2000, 2005) using information from an elevation model, the year-specific NDVI images, and the original Landsat mosaics (bands 2, 3, 4, 5 and 7). Land cover type of reference locations was determined directly in the field for part of 2000 (R. List unpub. data) and most of 2005 locations; cover type of most 2000 and all 1988 locations was defined by visual examination of satellite images based on identifiable features (towns, crops,

water, prairie dog towns), unchanged habitat patches, and information provided by local people. Decision-tree algorithms were then uploaded in ENVI to classify the entire 1988, 2000 and 2005 mosaics. Final edition and filtering of raster images was performed in ERDAS Imagine, and resulting maps were converted to vector format to facilitate analyses. Overall classification accuracy of final maps was 76.8% for 1988, 77.6% for 2000, and 76.1% for 2005.

2.3. Spatial and statistical analyses

2.3.1. Study design

We analysed patterns of extinction and persistence of colony areas separately for each of two periods: 1988–2000 and 2000–2005. For analytical purposes, we only selected colonies whose distribution was known (mapped) both at the beginning and end of a given period (hereafter these colonies will be referred to as focal colonies). The total number of focal colonies included in analyses was 23 for 1988–2000 and 43 for 2000–2005. We used the term “fragment” for referring to small colonies within the area which in the previous survey was a single larger colony. Because the effort and strategies employed to search colonies were not consistent each year, we could not assume with certainty that colonies detected for the first time either in 2000 or in 2005 were indeed new colonies; consequently we did not make any attempt to analyse patterns of colonization.

We identified the habitat (land cover and vegetation attributes inside colonies) and landscape (spatial context) variables associated with extinction and persistence at colony areas employing two different analytical approaches: (1) contrasting habitat conditions between portions of colonies where BTPDs became extinct with portions of the same colonies where BTPDs persisted; and (2) modelling occurrence of extinction of entire colonies based on their habitat and landscape attributes. We also modelled occurrence of extinction at equal-sized spatial units (500 × 500-m cells) based on habitat and landscape attributes; however, we do not report results of this analysis because they were strongly influenced by spatial autocorrelation (results of this analysis are described by *Avila-Flores, 2009*). In all cases, colony attributes for a given period were described based on their conditions at the beginning of the period rather than on their rates of change. In the case of vegetation-related attributes (NDVI, cover of grassland, cover of shrubland, cover of barren areas), we avoided using rates of change as explanatory variables because conditions measured at the end of a period could be a consequence rather than a cause of prairie dog extinction. Only anthropogenic variables (cover of agricultural and urban lands) were analysed as rates of change because their condition at the end of the period was independent of prairie dog presence or absence. All spatial analyses were performed in ArcGIS 8.1 and statistical analyses in S-Plus and Stata.

2.3.2. Extinction vs. persistence within colonies

Areas of persistence and extinction were identified by overlapping maps of focal colonies delineated at the beginning and end of each period. In the resulting composite maps, overlap areas were defined as areas of persistence, whereas areas that no longer had burrows present were defined as areas of extinction. We overlapped polygons of extinction and persistence with NDVI and land cover maps at the start of each period to describe initial environmental conditions on each. For each polygon, we calculated the average NDVI value as well as the proportion covered by grasslands, shrublands and barren lands. We used two-tailed paired *t*-tests to compare initial habitat conditions of extinct and persistent areas.

2.3.3. Modelling extinction of entire colonies

Focal colonies were classified either as extinct or persistent for each period. Persistence was defined solely on the basis of

continued presence of a given colony both at the beginning and end of a given period, not distinguishing between colony expansions or reductions. We overlaid NDVI and land cover maps with colony maps at the start of the period in order to describe initial habitat conditions of colonies. Habitat attributes included: average NDVI; percent cover of grasslands, shrublands and barren lands (ha); and percent change (ha) in cover of (active and inactive) agricultural and urban lands. Landscape (area and isolation) effects were estimated by including initial colony area and initial number of neighbour colonies within 3 km (from the edge of colony). Buffer distance was chosen based on the fact that BTPDs rarely disperse more than 3 km (Garret and Franklin, 1988).

We used logistic regression to model extinction of colonies separately for each period. We created four logistic regression models, each representing a different hypothesis of extinction of BTPD colonies, based on different combinations of explanatory variables: (1) plant biomass model (NDVI values and cover of barren areas); (2) habitat suitability model (cover of grasslands and shrublands); (3) habitat loss model (change in cover of urban and agricultural lands); and (4) landscape model (colony area and number of neighbour colonies within 3 km). We included an additional model which combined the most significant variables in the previous models and in univariate models (combined model). We used the Akaike's Information Criterion for small samples (AIC_c), ΔAIC_c and AIC_c weights (w_i) to select the model that best explains extinction of entire colonies. Pseudo- R^2 was calculated to evaluate overall model fit.

3. Results

3.1. Long-term changes in prairie dog distribution

The total area occupied by BTPD colonies in northwestern Chihuahua declined greatly between 1988 and 2005 (Fig. 1; Table 1). By 2000, the area occupied by BTPDs represented approximately 44% of the area occupied in 1988, and by 2005 it represented 24% of the 1988 area. As expected for this level of decline, reduction of colony area was accompanied by increased fragmentation of colonies: 23 focal colonies that were recorded in 1988 resulted in 36 colonies by 2005 (Fig. 1). Because not all colonies were consistently surveyed in all years, accurate estimates of changes in area and levels

Table 1

Summary of changes in distribution of black-tailed prairie dog colonies in northwestern Chihuahua, Mexico, during the periods 1988–2000 and 2000–2005.

Colony complex attribute	Period	
	1988–2000	2000–2005
Initial area (ha) ^a	44,624	19,811
Area change (ha) ^a	–24,813	–8932
Area change (%) ^a	–55.6	–45.1
Annual area change (%) ^a	–6.5	–11.3
Area change excluding largest colony (ha) ^{a,b}	–736	67
Area change excluding largest colony (%) ^{a,b}	–67.3	7.8
Annual area change excluding largest colony (%) ^{a,b}	–8.9	1.5
Average annual area change per colony (%) ^c	–7.3	5.4
Number of extinct colonies	15	4
Number of reduced colonies	8	14
Number of stable colonies ^d	0	12
Number of expanded colonies	0	13
Number of fragmented colonies	4	7
Average number of resultant fragments ^e	4.5	3.7
% Area lost to agriculture (annual rate)	0.5	1.0
% Area lost to urban use (annual rate)	<0.1	<0.1

^a To make numbers comparable, data were calculated from a subsample of colonies whose status was known in 1988, 2000 and 2005; other estimates were calculated from period-specific focal colonies.

^b Colony El Cuervo, named after Ceballos et al. (1993) and Marcé (2001).

^c Excluding extinct colonies.

^d Colonies that changed <25%.

^e Only considering fragmented colonies.

of fragmentation for the entire system of colonies remain unknown. During the first period, 35% of focal colonies were reduced in area and 65% became extinct, but no colony was stable or extended; in addition, 50% of persisting colonies were fragmented (Table 1). During the second period, 33% of focal colonies were reduced, but 30% expanded, 28% remained stable and only 9% became extinct; furthermore, from the 91% of colonies that persisted, only 15% were fragmented (Table 1). Extinction of colonies during the first period occurred mostly at the northern portion of the complex (Fig. 1). Differences in colony change between periods were evident even when colony parameters were described as annualized rates (Table 1). On the other hand, analyses of focal colonies indicated that the area lost to agriculture and urbanization was about 6% by the end of each period (Table 1). Detailed information for individual colonies is provided by Avila-Flores (2009).

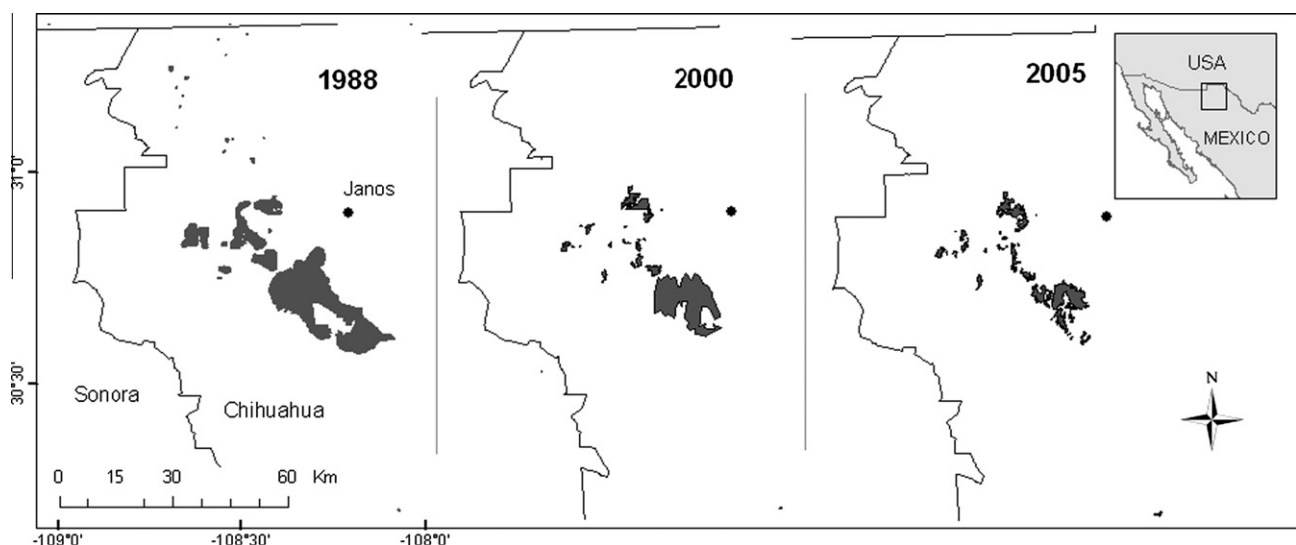


Fig. 1. Distribution of black-tailed prairie dog colonies in northwestern Chihuahua, Mexico, in years 1988, 2000 and 2005. Maps only show those colonies whose distributional history was completely traced from 1988 to 2005.

The most striking change in BTPD distribution was observed in colony El Cuervo, which was reduced from 31,497 ha in 1988 to 15,521 ha in 2000, and then to 6255 ha in 2005. El Cuervo colony remained as one colony until about 2000, but by 2005 it had been fragmented into 10 smaller colonies, and over half of the area had been lost. Interestingly, aside of the very large area lost in El Cuervo, in the second period there was a slight increase (8%) in prairie dog area (Table 1).

Although area changes in El Cuervo greatly contrast with area changes in other colonies, the causes of such great declines remain obscure. The only evident difference between extinct and persistent areas within El Cuervo is the proportion of grasslands and shrublands at the beginning of each period. At the beginning of the first period, extinct areas had approximately 89% grasslands and 6% shrublands, contrasting with persistent areas that had respectively 98% and 0.3%. During the second period, extinct areas had 87% grasslands and 3% shrublands, whereas persistent areas had respectively 97% and 2%. Therefore, El Cuervo areas with lower habitat suitability (reduced grassland cover) were apparently more likely to become extinct.

3.2. Extinction vs. persistence within colonies

Overall, initial habitat conditions in areas where BTPDs became extinct did not significantly differ from conditions in areas of the same colony where BTPDs persisted. At the beginning of both first (1988) and second (2000) periods, areas of extinction and persistence exhibited similar NDVI values (1988: $t = 1.53$, $df. = 7$, $P = 0.17$; 2000: $t = 1.89$, $df. = 37$, $P = 0.07$), as well as similar percent cover of grasslands (1988: $t = -0.72$, $df. = 7$, $P = 0.50$; 2000: $t = -0.17$, $df. = 37$, $P = 0.87$), shrublands (1988: $t = 0.94$, $df. = 7$, $P = 0.38$; 2000: $t = -0.70$, $df. = 37$, $P = 0.49$), and barren lands (1988: $t = -0.26$, $df. = 7$, $P = 0.80$; 2000: $t = -0.99$, $df. = 37$, $P = 0.33$). Only average NDVI values at the beginning of the second period were marginally different between areas of extinction and persistence, with extinction areas having slightly higher plant biomass levels than persistence areas. However, when observations were not paired by colony, areas of persistence had in average a higher cover of grasslands and a lower cover of shrublands at the beginning of the period 1988–2000, but no differences were detected for the period 2000–2005 (Table 2).

3.3. Extinction models

In general, areas where BTPDs became extinct had a lower cover of grasslands and a higher cover of shrublands at the beginning of each period (Table 2). This pattern was especially clear during the period 1988–2000 (Table 2). Extinction of entire colonies was better modelled for period 1988–2000 than for period 2000–2005. Whereas best extinction models of the first period explained >65% of deviance, no model of the second period explained >20% of deviance (Table 3). During the first period, the landscape model included only one explanatory variable (initial colony area) because inclusion of a second variable (initial number of colonies within 3 km) did not improve its explanatory power and made estimation of model parameters very unstable. Similarly, plant biomass models in both periods had NDVI as the only explanatory variable (cover area of barren lands was excluded). For the first period, the combined model produced the best fit of data followed by the landscape model. According to the best (combined) model, extinction was best explained by the negative effects of colony area (β -coefficient = -0.157 , $SE = 96.436$, $P = 0.999$), plant biomass (β -coefficient = -690.112 , SE and P not calculated), and grassland cover (β -coefficient = -10.408 , $SE = 2109.526$, $P = 0.996$). However, because parameters in such combined model had large standard errors and very high P -values, we produced an additional model

Table 2

Land cover features at the beginning of each period within spatial units of analysis used in this study. Areas of persistence and extinction are reported separately.

	Unit of analysis			
	Polygons		Entire colonies	
	Persistent	Extinct	Persistent	Extinct
<i>1988–2000</i>				
NDVI	0.1	0.1	0.1	0.0
% Grassland	80.1	61.3	87.4	47.8
% Shrubland	15.8	33.0	8.2	46.0
% Barren lands	3.3	5.2	3.2	6.2
% Change agriculture (active) ^a	0.1	0.3	1.0	0.0
% Change agriculture (inactive) ^a	0.2	2.2	6.3	0.0
% Change urban lands ^a	0.0	0.0	0.0	0.0
<i>2000–2005</i>				
NDVI	0.0	0.0	0.0	0.0
% Grassland	80.5	80.2	81.3	73.8
% Shrubland	12.4	11.9	12.3	17.0
% Barren lands	0.1	0.2	0.2	0.0
% Change agriculture (active) ^a	0.0	-0.5	-0.1	-4.3
% Change agriculture (inactive) ^a	9.1	9.1	9.0	10.2
% Change urban lands ^a	1.7	1.7	1.8	0.0

^a Percent change in relation to initial area of spatial unit.

combining the two variables (colony area and NDVI) that separately produced the highest model fit (each explained >40% of deviance). This landscape-plant biomass model produced a similar fit as the combined model ($\Delta AIC_c = 3.05$; Table 3) and showed that extinction of entire colonies was negatively related to both colony area (β -coefficient = -0.029 , $SE = 0.023$, $P = 0.201$) and average NDVI (β -coefficient = -56.283 , $SE = 34.155$, $P = 0.099$). In sum, these results suggest that small colonies occupying areas with low plant biomass were more likely to become extinct by the end of the period 1988–2000. It was particularly true for areas with low cover of grasslands.

Extinction of entire colonies was poorly modelled for the period 2000–2005, as demonstrated by the low values of model performance estimates (Table 3). The low number of colonies that became extinct during this period (4 out of 43) is probably the cause of poor model performance. However, extinction of colonies was best explained by plant biomass as indicated by the very high AIC weight of this model (Table 3). In contrast to 1988–2000, extinction of colonies between 2000 and 2005 was positively related to average NDVI (β -coefficient = 52.522 , $SE = 26.528$, $P = 0.048$). This model suggests that colonies with high plant biomass in 2000 (a year with close-to-average precipitation) were more likely to become extinct by 2005.

4. Discussion

This study documents a severe reduction of BTPD colonies in northwestern Chihuahua, Mexico, between 1988 and 2005. Although the 56% decline reported in this study for the first period does not exactly match the 64% decline by 2000 reported by Marcé (2001) (different subsets of colonies were used in calculations), it is clear that BTPD colonies exhibited a pronounced decline in area in Mexico during that period. This pattern is consistent with reductions in population numbers and other ecological changes reported for the area (Ceballos et al., 2010; List, 1997; Manzano-Fischer, 1996). While the overall trend of decline continued because the largest colony became smaller and more fragmented, the rest of the colonies, which together represent a smaller area than El Cuervo, either remained stable or increased after 2000. Although the magnitude of the decline of BTPD colonies observed by the end of the 20th century may have been overestimated because less precise mapping techniques were used in 1988, scattered information

Table 3

Relative performance of logistic models built to explain extinction of black-tailed prairie dog colonies during periods 1988–2000 and 2000–2005. Abbreviations of variables are: CA = colony area; NC3 = number of colonies within 3 km; NDVI = Normalized Difference Vegetation Index; GL and SL = percent cover of grasslands and shrublands, respectively; AA, IA and UA = percent change in cover of active agricultural, inactive agricultural, and urban lands, respectively.

Model (variables)	K	Deviance	AIC _c	ΔAIC _c	w _i	Pseudo-R ²
<i>1988–2000</i>						
Landscape (CA) ^a	2	10.9	15.5	5.3	0.05	0.632
Plant biomass (NDVI) ^a	2	17.8	22.4	12.1	0.00	0.403
Landscape-plant biomass (CA + NDVI)	3	6.0	13.3	3.1	0.17	0.798
Habitat suitability (GL + SL) ^b	3	20.9	28.1	17.9	0.00	0.299
Habitat loss (AA + IA + UA)	4	19.6	30.4	20.2	0.00	0.342
Combined (CA + NDVI + GL)	4	0.0	10.2	0.0	0.77	1.000
<i>2000–2005</i>						
Landscape (CA + NC3)	3	24.8	31.4	4.9	0.07	0.061
Plant biomass (NDVI) ^a	2	22.2	26.5	0.0	0.77	0.159
Habitat suitability (GL + SL) ^b	3	26.2	32.9	6.3	0.03	0.008
Habitat loss (AA + IA + UA)	4	23.0	32.1	5.6	0.05	0.130
Combined (CA + NDVI + AA)	4	21.8	30.9	4.4	0.09	0.174

^a Univariable models.

^b Colinearity present ($r > 0.7$).

provided by local people and extinction of entire colonies confirms the occurrence of a large distributional decline before 2000 (List, 1997; Marcé, 2001).

The relatively high degree of fragmentation observed in BTPD colonies at the study area, particularly during the period 1988–2000, could be a logical consequence of the generalized population decline that confined individuals to increasingly smaller areas. However, because fragmentation tends to produce smaller and more isolated colonies that are more likely to become extinct, this process may have a negative feedback on BTPD distribution (Lomolino and Smith, 2001; Magle and Crooks, 2009). Once fragmentation of colonies reaches some critical level, it may accelerate BTPD population declines by increasing the probability of extinction of local populations. In the case of BTPDs, isolation effects are enhanced after fragmentation takes place because the absence of foraging activities in empty areas facilitates the development of shrublands (Ceballos et al., 2010; Weltzin et al., 1997) and tall grasses which preclude re-colonization.

Results of this study support the hypothesis that fragmentation of colonies has facilitated the extinction of BTPDs in local areas of northwestern Mexico (Marcé, 2001). In a preliminary analysis, Avila-Flores (2009) reports that colony sites initially surrounded by a low proportion of colony area and a high proportion of hostile habitat were more likely to become extinct by the end of both study periods. At a larger scale, the initial colony size was the most important variable predicting extinction of entire colonies during the period 1988–2000, smaller colonies being more likely to become extinct than larger ones. The fact that most colony extinctions during that period occurred in the northern portion of the colony complex, where grassland patches are scarce and shrublands are dominant, suggests that isolation effects were enhanced by inhospitable surrounding areas. During the period 2000–2005, while there was a very large reduction in prairie dog colony area, extinction of colonies was so rare that not a single variable properly explained extinction events. These findings are consistent with extinction patterns observed in Oklahoma for the periods 1967–1989 and 1989–1997 (Lomolino et al., 2003; Lomolino and Smith, 2001) and with patch occupancy dynamics in an urban landscape of Colorado (Magle and Crooks, 2009), which supports the idea that BTPD populations are sensitive to reduced colony size and to increased isolation (although increased isolation could indeed reduce the extinction probability of colonies in areas affected by plague; Lomolino et al., 2003). However, although size and isolation effects may explain the occurrence of many extinction events, they do not provide information about the factors that originally caused fragmentation of colonies. Furthermore, these landscape effects do

not explain why few colonies became extinct during the period 2000–2005, when small and isolated colonies were more common.

Disappearance of BTPDs from certain areas occurs because individuals die or move in response to changing environmental conditions, and it may be a slow or fast process depending on the nature of changes. Information from the literature (e.g. Hoogland, 1995, 2006; Miller et al., 2007; Proctor et al., 2006) and field observations suggest that disappearance of BTPDs from particular areas may be caused by direct killings (e.g. poisoning, shooting, road-kills), natural catastrophes (e.g. flooding), epizootic diseases (e.g. plague), loss of suitable habitat (e.g. agriculture, shrub-encroachment), or food shortage (overgrazing, drought). Because there is no historical record of unusual large-scale catastrophes or any epizootic disease (Cully et al., 2006; G. Suzán pers. comm.) in the study area, these two factors appear less likely than others to have caused the population decline. None of the remaining factors, however, can be excluded from this list of potential drivers. Ceballos et al. (1993), List (1997), and Marcé (2001), relying upon informal interviews with local people and detailed observations in a small portion of the complex, concluded that poisoning in private ranches, expansion of agriculture and shrub encroachment were the primary causes of the BTPD collapse in northwestern Chihuahua between 1988 and 2000. Poisoning was particularly responsible for much of the colony area losses observed before 2000 in one of the largest ranches of the region (Rancho El Uno), as evidenced by the many empty poison tubes found at colony areas (Ceballos et al., 1993; Marcé, 2001). However, because poisoning activities have been neither consistent nor extensive in the study area (they have been restricted to those private ranches where poisoning campaigns can be afforded), it is unlikely that it caused the generalized decline observed in BTPD populations. Similarly, results of this study failed to demonstrate that habitat loss due to agriculture and urbanization were the leading causes behind most BTPD declines.

Because suitable habitat for BTPDs is characterized by open areas with short vegetation and low cover of shrubs (Avila-Flores et al., 2010), functional habitat loss can be described as the expansion of tall herbaceous vegetation and shrubs into short-vegetation areas. The role that this type of habitat loss played in BTPD declines is difficult to evaluate because unsuitable vegetation develops in areas where BTPDs are scarce or where they have already disappeared (then the question of what caused population declines remains open). However, we found some evidence that the probability of extinction increased in areas that initially exhibited low habitat suitability. Under close-to-average rain regimes (after year 2000), BTPDs that occupied more productive areas were more likely to become extinct by the end of the study. Furthermore,

initial habitat suitability was the only factor that could explain extinction of BTPDs in the largest colony of the complex, both before and after 2000. Within that colony, areas where BTPDs persisted had higher cover of open grasslands compared to areas of extinction. These results suggest that some colonies suffered a gradual process of extinction, where tall vegetation and shrubs slowly invaded areas probably occupied by low-density BTPD populations.

The fact that all colonies were greatly reduced (and most became extinct) during the first but not during the second period suggests that BTPD populations were exposed to a large-scale mortality agent between 1988 and 2000. Indeed most mortality probably occurred between 1988 and 1996, as the declining process was slower after 1996, at least at the centre of the complex (List, 1997; Marcé, 2001). The coincidence of the greatest decline with a severe period of drought occurring between 1994 and 2000, particularly during the winter and spring (Stahle et al., 2009), suggests that the reduced plant production during the reproductive season may have had strong effects on BTPD populations. The virtual absence of reproduction in 2006 following an unusually dry winter exemplifies the potential impact of drought on BTPD populations (Avila-Flores, 2009). Similarly, reductions in BTPD monthly survival, adult body weight, and population size in southern New Mexico were associated to occurrence of drought (Facka et al., 2010). Because drought has severe negative effects on short- and long-term plant productivity (Haddad et al., 2002), as has been shown for our study area (Ceballos et al., 2010), BTPDs must have been exposed to an unusually extreme, large-scale food and water shortage during that period. In the scenario of most severe drought, populations living in areas with the least plant biomass would be the most affected by food shortages. In support of this prediction, we found that initial plant biomass was one of the best predictors of extinction of colonies during the period 1988–2000, colonies in low-biomass areas being the most likely to become extinct. However, the reversed trend was observed during 2000–2005, when probability of extinction was positively associated with plant biomass (for a detailed discussion on the dual role of plant biomass on BTPD populations, see Avila-Flores, 2009). Extreme reductions in plant productivity during that period were enhanced by livestock overgrazing, which for decades has been a common practice in the study area (Ceballos et al., 2005). However, it is unlikely that food shortage due to overgrazing alone was the driving force behind most BTPD declines because its distribution and magnitude are not homogenous across the region. Furthermore, overgrazing by cattle has occurred in the region even during periods of colony stability or expansion (e.g. after 2000, except for the largest colony).

Because patches of suitable habitat are probably smaller, scarcer and of lower quality at the southern edge of BTPD distribution (Avila-Flores et al., 2010; Proctor et al., 2006), populations living at these latitudes could be more affected by climatically driven habitat changes. As plant productivity in desert grasslands is the lowest among all North American grasslands (Sims et al., 1978), extreme reductions in the rain regime are expected to have substantial negative impacts in southern BTPD populations. Indeed, it is likely that BTPD populations have historically experienced recurrent episodes of expansion and decline in response to fluctuations in climate (Forrest, 2005). Climate shifts occurring in southwestern North America also seem to be partially responsible for shrub encroachment (Brown et al., 1997; Gao and Reynolds, 2003), a widely documented process that is also promoted by anthropogenic factors such as grazing by cattle, fire suppression, and elimination of keystone rodents (Brown et al., 1997; Brown and Archer, 1999; Curtin et al., 1999; Gao and Reynolds, 2003; Van Auken, 2000; Weltzin et al., 1997; Yanoff and Muldavin, 2008). The dominance of shrublands in vast areas around small and remote BTPD colonies suggests that shrub encroachment has

been taking place in the study area for many years. The fact that BTPDs were present in south-eastern Chihuahua (400 km south-east of current geographic limits) perhaps no more than 10,000 years ago (and as far as central Mexico sometime within the Late Pleistocene; Goodwin, 1995), indicates that the southern limit of its geographic range has gradually been moving northward. It is likely that this range reduction has been associated with climate shifts, considering that drought events (some of them much longer and more severe) have periodically occurred in the Great Plains at least over the last 8000 years (Clark et al., 2002; Woodhouse and Overpeck, 1998). If this is true, BTPD colonies from northwestern Mexico could indeed represent relict populations that deserve special attention (but see Truett et al., *in press*).

5. Conservation and management implications

Results of this study suggest that BTPD populations in northwestern Mexico, especially the smaller and more isolated ones, are highly susceptible to extreme reductions in plant productivity. This vulnerability becomes critical in the scenario of global warming, as more severe drought events in arid regions are consistently predicted by general circulation models (Stahle et al., 2009; Wetherald and Manabe, 1995). Because grassland ecosystems are sensitive to all drivers of global warming, this biome is expected to suffer one of the greatest biodiversity changes within the next 100 years (Sala et al., 2000). Therefore, environmental authorities and other decision makers in Mexico should pay special attention in BTPD populations during the most severe periods of drought. The predicted negative impact of extreme drought on survival and reproduction of BTPDs could be mitigated by adjusting the cattle stocking rates to the rainfall/plant productivity; this action, at the same time, would reduce economic losses of ranchers because less livestock mortality would occur, and the grassland would recover more rapidly after the drought episode. In colony areas where shrubs are slowly replacing the shorter perennial grasslands, land managers can develop programs of controlled fires, as well as mechanical and chemical control of mesquite and other woody plants. Agriculture expansion needs to be controlled, because while not the main cause of prairie dog colony loss, it is an additional pressure, which also represents a barrier for prairie dog movements. The expansion of colonies observed outside from El Cuervo during the second period is encouraging, as it represents an opportunity to maintain and restore connectivity within the complex, which would also contribute to maintain genetic variability and to reduce the additional risk of colony extinction by inbreeding or genetic drift (Castellanos-Morales, 2009). Regional management and conservation programs should ensure effective long-term protection of large BTPD colonies (preferably supporting the highest densities) at the centre of the complex, which are more likely to persist and become source populations for re-colonization of the area. Recognizing the importance of BTPDs and their ecosystem, the Mexican government decreed a half a million ha reserve to protect the Janos region (Ceballos et al., 2010; List et al., 2010). This is a first effort for the long-term conservation of one of the largest remnants of what used to be one of the most widespread ecosystems in North America.

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