Factors affecting Burrowing Owl occupancy of prairie dog colonies

RESEARCH ARTICLE

Factors affecting Burrowing Owl occupancy of prairie dog colonies

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ABSTRACT

Understanding patch dynamics can help scientists better understand metapopulations and the relationships of animals that share a habitat. The Burrowing Owl (*Athene cunicularia*) is a well-known associate of prairie dog colonies, thereby linking conservation measures that benefit these species. We used occupancy modeling to determine how colony attributes (e.g., size and edge effects) and the loss of prairie dog colonies to sylvatic plague affected the occupancy of those colonies by Burrowing Owls in north-central Montana. We surveyed presence–absence of Burrowing Owls during a 13-yr period (1995–2007) and analyzed the data using a robust-design occupancy model in Program MARK. The proportion of colonies occupied by Burrowing Owls ranged from 0.41 to 0.54 across years while the probability of detecting the owls ranged from 0.22 to 0.92. Contrary to our predictions, colony edge effects and plague epizootics showed only weak or no effects on Burrowing Owl occupancy. Prairie dog colony size had the greatest effect on Burrowing Owl occupancy patterns. Colonization of prairie dog colonies by owls generally increased with colony area, whereas owl extinction initially dropped and then increased as a function of increasing colony area. We found no direct link between Burrowing Owl occupancy of prairie dog colonies and plague history, but our results reaffirmed the importance of colony size. Collectively, this information will help inform future conservation efforts for Burrowing Owls that occupy prairie dog colonies.

Keywords: Athene cunicularia, black-tailed prairie dog, Burrowing Owl, *Cynomys ludovicianus*, occupancy, plague, robust design

Factores que afectan la ocupación por *Athene cunicularia* de colonias de perro de la pradera

RESUMEN

Comprender la dinámica de parches puede ayudar a los científicos a entender mejor las metapoblaciones y las relaciones de los animales que comparten el mismo hábitat. *Athene cunicularia* es una especie asociada a las colonias de perro de la pradera, lo que vincula las medidas de conservación que beneficien a estas especies. Empleamos modelos ocupaciones para determinar cómo los atributos de las colonias (e.g., tamaño y efectos de borde) y la pérdida de las colonias de perro de la pradera debido a plagas silvestres afectaron la ocupación de estas colonias por parte de *A. cunicularia* en el norte y centro de Montana. Realizamos muestreos de presencia-ausencia de *A. cunicularia* durante un período de 13 años (1995–2007) y analizamos los datos usando un diseño robusto de modelo de ocupación en el programa MARK. La proporción de colonias ocupadas por *A. cunicularia* varió desde 0.41 a 0.54 a lo largo de los años mientras que la probabilidad de detectar a los búhos varió desde 0.22 a 0.92. Contrariamente a lo que habíamos predicho, los efectos de borde de la colonia y la epizootia de la plaga mostraron un débil efecto o no tuvieron efecto sobre la ocupación de *A. cunicularia*. El tamaño de la colonia de perro de la pradera tuvo el mayor efecto sobre los patrones de ocupación de *A. cunicularia*. La colonización de las colonias de perro de la pradera por parte de los búhos generalmente aumentó con al área de la colonia mientras que la extinción de los búhos inicialmente cayó y luego aumentó como función del incremento del área de la colonia. No encontramos un vínculo directo entre la ocupación de *A. cunicularia* de colonias de perro de la pradera y la historia de la plaga, pero reafirmamos la importancia del tamaño de la colonia. En conjunto, esta información ayudará a guiar futuros esfuerzos de conservación de individuos de *A. cunicularia* que ocupan colonias de perro de la pradera.

Palabras clave: Athene cunicularia, *Cynomys ludovicianus*, diseño robusto, ocupación, perro de la pradera de cola negra, plaga

INTRODUCTION

Patch dynamics are an important component necessary for understanding metapopulations (Pulliam 1988). Rates of extinction and colonization interact to affect the total proportion of patches that are occupied by a species and are, thus, of interest to ecologists. Extinction and colonization probabilities are sometimes difficult to estimate (MacKenzie et al. 2003), especially when the focal species is hard to detect (and, hence, detection probability is <1.0; MacKenzie et al. 2002). Surveys rarely detect all the animals present in a patch, so detection probability is used to find the expected proportion of the animals present that are actually detected (Royle and Nichols 2003). Specific attributes of patches, such as their size or degree of isolation, often influence patch dynamics and suitability for a particular species (Hanski 1994, Franken and Hik 2004). Scientists also seek to better understand the effects that patch attributes have on patch dynamics, including colonization and extinction probabilities. These questions can be rigorously addressed to better understand the underlying processes of patch dynamics (MacKenzie et al. 2002).

Black-tailed prairie dogs (*Cynomys ludovicianus*) inhabit a relatively restricted range of level, arid, short-grass plains in North America (Hoogland 2006). Prairie dogs are sometimes considered a keystone species, whose loss could affect many other associated species (Kotliar et al. 2006). Prairie dogs play an important role in prairie ecosystems by modifying the vegetation community, aerating the soil, and excavating burrows that provide homes for other organisms and shelter for predators such as the Burrowing Owl (*Athene cunicularia*) and the black-footed ferret (*Mustela nigripes*) (Shefferly 1999, Hoogland 2006).

The Burrowing Owl is a ground-dwelling owl of grasslands and arid regions in the Americas and the Caribbean (Poulin et al. 2011). The species typically breeds on gently sloping areas, characterized by low, sparse vegetation (Poulin et al. 2011). The presence of potential nest burrows is a critical habitat requirement for the western subspecies of Burrowing Owl (*A. c. hypugaea*), which does not dig its own burrows (Poulin et al. 2011). These owls tend to select a burrow in an area with a high density of burrows, and nest densities are often greatest on the smallest colonies (Desmond and Savidge 1996). In Montana the average burrow density of prairie dog colonies is ~60 burrows ha^{-1} (Biggins et al. 2006), which is more than adequate to support breeding owls (Restani et al. 2001). Loss of prairie dog colonies due to agriculture and lethal prairie dog control limits the birds' access to nest burrows and has contributed to loss of Burrowing Owls in many parts of the western and southwestern United States (Desmond et al. 2000, Poulin et al. 2011). The species is also threatened indirectly by sylvatic plague, a disease that causes high mortality in prairie dogs and results in a loss of owl habitat. Sylvatic plague is a flea-borne disease that is caused by the bacterium *Yersinia pestis* (Barnes 1982, Gage et al. 1994). Infected fleas spread the disease to mammalian hosts such as prairie dogs, which often suffer >95% mortality (Barnes 1982). Plague quickly affects the number of prairie dogs on a colony (Collinge et al. 2005), but the consequences for owls are varied. The number and productivity of Burrowing Owls that live on those colonies were largely unaffected in one study (Restani 2003). However, a separate study found that the owls' diet was unchanged by plague outbreaks and that owls did not use colonies that were not reoccupied after plague epizootics (Conrey 2010). The same study hinted that Burrowing Owls might adapt and even benefit from plague and suggested that conservation of this species should emphasize the preservation of prairie dog colonies at the landscape level, rather than intensive plague management (Conrey 2010).

We assessed the metapopulation dynamics of Burrowing Owls breeding on plague-affected black-tailed prairie dog colonies in north-central Montana during a 13-yr period. We used a robust-design occupancy analysis to estimate (1) the proportion of colonies that were occupied by Burrowing Owls and (2) factors such as colony size and plague history that affected patch dynamics (extinction and colonization probabilities). Our primary interest was assessing the role of plague in owl occupancy patterns. A better understanding of the role of plague in owl population dynamics can help effectively manage prairie dog colonies for owls and other associated species.

METHODS

Study Area

From 1995 to 2007, we studied black-tailed prairie dogs and Burrowing Owls on a 3,000-km^2 area in southern Phillips County in north-central Montana. Within this study area, ~2,250 km^2 is in public ownership under the Bureau of Land Management (BLM, Malta field office) and the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge). This area was a mixed-grass prairie typified by flat-topped ridges dissected by shallow coulees and sagebrush flats (Dinsmore and Smith 2010). Within this area, we studied owls on black-tailed prairie dog colonies that were active (i.e. prairie dogs were present at least once during the study period) (Figure 1). We defined "colony" as a specific patch on the landscape that was occupied by prairie dogs during ≥1 year beginning in 1995 (Dinsmore and Smith 2010). Owls nest from mid-May to mid-July in this region and often return to the same nest burrows year after year; in a similar study, >50% of the birds returned to within 200 m of their previous burrows (Poulin et al. 2011). Inactive prairie dog

FIGURE 1. This Burrowing Owl rests atop an abandoned black-tailed prairie dog burrow on June 4, 2004, in Phillips County, Montana. Photograph by Stephen J. Dinsmore.

colonies (prairie dogs were absent) were monitored in subsequent years to check the status of their occupancy by prairie dogs. New prairie dog colonies were created almost yearly; we attempted to survey them for prairie dogs and owls soon after they were established. The study area and prairie dog survey methods are described in greater detail in Dinsmore and Smith (2010).

Prairie Dog Colony Characteristics

Spatial data for all active prairie dog colonies were obtained from BLM and USFWS staff and through our own efforts. We obtained two types of data from these two sources: (1) the area (in hectares) of each prairie dog colony and (2) Geographic Information System (GIS) coverage showing colony boundaries (Dinsmore and Smith 2010). To document plague history on the individual colonies, we relied solely on observational data from annual surveys of prairie dog colonies. We defined "plague event" as a reduction in prairie dog colony area of >90% in 1 yr. This definition should produce conservative study results on the influence of plague on owls, because our models include only large, obvious epizootics. Smaller epizootics may have been overlooked, but with our approach we cannot estimate whether or how often this occurred (Antolin et al. 2002).

Prairie dog colony area was annually measured using a global positioning device to delimit the boundaries of each colony. Colony edges are recognizable by changes in vegetation height (shorter on the colony) and can be confirmed by the presence of fresh diggings on burrows and fresh feces. A complete mapping of all of the colonies was done in 1998, 2000, 2002, 2004, and 2007 (Dinsmore and Smith 2010). For the other 8 yr, we obtained the measure of the colony areas in one of four ways, as described by Dinsmore and Smith (2010): (1) from an incomplete census of the colonies in the study area; (2) by extrapolating area from an estimated rate of change in a sample of one-third of all known active colonies in the study area; (3) by using the midpoint of colony area in adjacent years; or (4) from other additional sources (e.g., a plague event that eliminated a colony). Option 2 assumes that colony changes are correlated across years, and a correlation analysis of the 5 yr when all colonies were mapped showed that this was a valid assumption (Pearson correlation test, $r = 0.88$). In instances where we were unable to estimate colony area using one of those four ways, we set the colony area equal to the mean area of all colonies that year. By doing this, we effectively removed the colony from the calculation of area effects for that year. Using these approaches, 64% of colonies were directly mapped from complete mapping efforts, 31% were estimated by approach (2), 4% were estimated by approach (3), and 1% were estimated by approach (4).

For colonies that were mapped in the field, the colony mapping data were converted to shapefiles, and ArcGIS version 9.2 was used to calculate the area of each prairie dog colony. To calculate colony spatial features of interest (e.g., colony size or edge effects) with a 10-m-cell grid size, we used FRAGSTATS version 3.3 (McGarigal and Marks 1995). Because we lacked shapefiles for many years, we calculated the spatial characteristics only for colonies that were actually mapped in the field.

Surveys for Owls

Each active prairie dog colony was surveyed for owls ≥ 3 times $year^{-1}$, once or more in each of three sampling periods (May 20–June 10, June 11–30, and July 1–20) that spanned the primary owl nesting season. Many (>50% of total) inactive colonies were also surveyed for owls, in case recolonization had occurred. During an owl survey, the observer traversed the colony in a vehicle and recorded whether adult owls were present or absent. The occupancy data that we used in our analysis assume demographic closure (no births, deaths, immigration, or emigration) during the owl nesting season (Conrey 2010).

Occupancy Modeling

We used the robust-design occupancy model (MacKenzie et al. 2003) in Program MARK (White and Burnham 1999) to investigate owl occupancy of prairie dog colonies. This model estimates the annual values of four parameters, three of which are directly related to the patch dynamics of interest. It estimates the proportion of prairie dog colonies

occupied by owls (Ψ); conditional probabilities for the rate of colonization of prairie dog colonies by owls (γ) and for the rate of extinction of prairie dog colonies by owls (ε); and the probability (p) of detecting 1 or more owls on a prairie dog colony given that owls were present. Thus, γ is the probability that a colony not occupied by owls in one year will become occupied in the next year, and ε is the probability that a colony occupied by owls in one year will become unoccupied in the next year. Together these two parameters can be used to describe patch dynamics of owls residing on large complexes of prairie dog colonies. Our model set included two parameterizations for this model: one that estimates Ψ1 (occupancy in the first year only), γ, and ε; and a second that estimates all Ψ values and ε. Both parameterizations were necessary to model year-specific covariates on each of these parameters (Ψ, γ, and ε). We allowed detection probability (p) to vary between and within years; within years, we allowed the first sampling period (p1) to differ from the remaining two sampling periods, because owls might be more visible early in the nesting season (Poulin et al. 2011).

A Priori Predictions

We developed a list of biological factors to explain how plague, colony size, and colony shape influence the occupancy of black-tailed prairie dog colonies by owls during the nesting season. Here, we identify primary sources of variation in occupancy and state our hypothesis regarding each.

(1) **Plague history.** The first known plague epizootic in Phillips County was in 1992, and several smaller epizootics have occurred since then (Collinge et al. 2005, Dinsmore and Smith 2010, S. J. Dinsmore et al. personal observation). We predicted that a colony with a history of plague was less likely to be colonized by owls and that extinction probability would be high for the years after plague affected a colony. This could occur because of (1) a decline in colony area, (3) a decrease in the number of suitable nesting burrows, (4) an increase in predation (e.g., by badgers [*Taxidia taxus*]; Kotliar et al. 2006), or (5) unknown plague effects that would make the colonies unsuitable for the owls. We further predicted that plague could cause either an immediate loss of owls after the epizootic (if, for example, the presence of prairie dogs results in greater food resources for owls) or an immediate loss of owls followed by a slow recolonization of the colony. Finally, we predicted that as the time (in years) after plague affected a colony increased, (1) the extinction probability would decrease and (2) the colonization probability, given that the colony was recolonized by prairie dogs, would increase. To test this, we included four sets of covariates for each colony in our models. The first set accounted for the presence or absence of plague on a colony for each of the 13 yr (1995–2007) (e.g.,

0000000010000 for a colony that was decimated by plague in 2003). The remaining three covariates accounted for the time since the plague epizootic occurred (e.g., 0000000043210 for a colony that was decimated by plague in 2003). Note that the nonzero numbers in this set are dummy variables and do not force any directionality in the plague effect. We modeled these chronic effects by looking at 2-, 3-, and 4-yr time lags since a plague epizootic occurred on a colony. We hypothesized that both extinction (ε) and colonization (γ) can likely be explained by long-term chronic effects of plague. Plague history was intended to account for the effects of plague that were not directly accounted for in the annual measures of colony size. This portion of the analysis is nearly identical with that of the Mountain Plover (*Charadrius montanus*) study of Dinsmore and Smith (2010).

(2) **Prairie dog colony size.** Numbers of owls are positively correlated with prairie dog colony size in many parts of their range (Desmond and Savidge 1996). Owls in larger colonies are more likely to return to the same nesting sites, experience lower rates of nest predation, and have higher rates of nesting success than owls in smaller colonies (Dechant et al. 2002). In small prairie dog colonies, there is a smaller nearest-neighbor distance between owl nesting burrows, which results in more abandoned owl nests (Dechant et al. 2002). For this reason, we considered that larger colonies were more likely to be colonized and less likely to be vacated by owls than were small colonies; larger colonies also probably had more habitat and owls. We modeled this as a linear (T) and quadratic (TT) effect across years on both extinction (ε) and colonization (γ) rates. A linear trend is plausible for many reasons, and we included a quadratic trend to account for possible threshold patterns in these rates. Colony size could also have an effect on detection probability because owls are known to have clumped nest distributions in large (>35 ha) prairie dog colonies (Orth and Kennedy 2001), which might make them easier to detect.

(3) **Colony edge effect.** We hypothesized that owl presence might increase as the amount of edge in a colony increased because owls sometimes concentrate their nests at the edges of prairie dog colonies (Butts 1973, Desmond et al. 1995, Toombs 1997, Conrey 2010). To model colony edge effects, we computed two simple shape indices for each colony. We calculated a simple patch shape index (PSI) and the perimeter-to-area ratio (PARA) for each colony. Both metrics resulted in year-specific covariates for each colony except in 4 yr (1997, 2003, 2005, and 2006) when we had little or no spatial data (Dinsmore and Smith 2010). The shape index takes on values ≥1; a value of 1 indicates a patch that is maximally compact (e.g., a circle); patch irregularity increases with higher values (McGarigal and Marks 1995).

The robust-design occupancy model in Program MARK does not currently have a goodness-of-fit test, so we were unable to rigorously test for a lack of independence in the data (overdispersion).

Model Selection and Parameter Estimation

We evaluated competing models to explain dynamics of owl occupancy of prairie dog colonies using an Akaike's Information Criterion (AIC) framework, corrected for small sample sizes (AIC$_c$; Akaike 1973, Burnham and Anderson 2002). Models in the set were ranked in relation to the model with the lowest AIC$_c$ value. We interpreted models as having generally strong support (ΔAIC$_c$ < 2) to little or no support (ΔAIC$_c$ > 10) (Burnham and Anderson 2002). Instead of presenting parameter estimates from a single "best" model, we model-averaged parameter estimates across the entire model set (Burnham and Anderson 2002). We also used model-averaged regression coefficients (betas) to predict the effects of colony area on the colonization and extinction rates of prairie dog colonies occupied by owls.

RESULTS

Colony size ranged from 0 to 246 ha in our sample of 81 colonies over the 13-yr study; mean ($\pm$ SD) across all colonies and years was 27.9 $\pm$ 31.99 ha. The proportions of colonies in 25-ha size bins were 61% (0–25 ha), 22% (25–50 ha), 9% (50–75 ha), 4% (75–100 ha), 2% (100–125 ha), 1% (125–150 ha), and 1% (>150 ha). The number of colonies where owls were present ranged from 0 to 44 (mean $\pm$ SD = 16.5 $\pm$ 11.2) across the 39 sampling periods (3 in each of the 13 yr). Owl numbers on a colony were generally low, ranging from 0 to 21 (mean $\pm$ SD = 2.9 $\pm$ 2.5); 60% of occupied colonies had 1 or 2 owls.

Modeling Results

Our analyses included a set of 26 models and revealed that colony size had the greatest influence on the dynamics of prairie dog colony occupancy by owls (Table 1). In all of the competitive models (ΔAIC$_c$ $\leq$ 5), detection probability (p) varied by survey period within year; the presence of owls was easier to detect in the first survey period (p = 0.67, range: 0.31 to 0.92; coefficient of variation [CV]: 0.03–0.23) and then slightly harder to detect in each of the two subsequent survey periods (p = 0.58, range: 0.22–0.87; CV: 0.04–0.28). Plague history was present on the proportion of colonies occupied in 4 of the 13 competitive models but was not a strong predictor of ϵ, γ, or p. The extinction probability (ϵ) showed a strong quadratic effect of colony size (extinction probability declined nonlinearly as a function of colony size), whereas the colonization probability (γ) showed a weaker quadratic effect of colony size (Table 1). Midsized colonies had lower extinction

probabilities than small or large colonies. The greatest difference in extinction and colonization probabilities occurred in medium-sized colonies (50–100 ha) (Figure 2). The model-averaged coefficients ($\pm$ SE) for the area effects on extinction probability were β_{Area} = -0.031 $\pm$ 0.011 (95% confidence interval [CI]: -0.053 to -0.001) and β_{Area^2} = 0.000210 $\pm$ 0.000065; 95% CI: 0.000080 to 0.000335). There was considerable uncertainty in what was affecting colony occupancy (Ψ) by owls, in contrast to clearer patterns for extinction and colonization probabilities. Plague history, linear and quadratic time trends across years, and area effects were all present in competitive models of the proportion of colonies occupied, but the coefficients for each effect were nonsignificant (95% CIs included zero). The model-averaged proportion of colonies occupied (Ψ) showed a nearly linear increase across years and increased from 0.41 in 1995 to 0.54 in 2007. None of the edge variables was an important predictor of owl dynamics on prairie dog colonies.

DISCUSSION

Metapopulation theory suggests that patch attributes should influence whether and how a species occupies a particular site (Hanski 1994), and this was partly confirmed in our study of Burrowing Owl use of prairie dog colonies in Montana. Of the factors we investigated, colony size seemed to be the most important predictor of owl dynamics on these colonies. We found no strong evidence that plague played a role in owl occupancy of colonies or in the rates at which owls colonized or vacated those colonies, nor did colony edge attributes explain occupancy patterns. Understanding the factors that affect owl occupancy is critical and can allow for more informed conservation measures, not only for declining birds like the Burrowing Owl but possibly for other species that rely on prairie dog colonies for habitat.

We made several important assumptions about our data collection and analysis that may have affected our findings. One assumption is that our observations to determine plague events were accurate. The almost complete disappearance of a colony within a 1- to 2-wk period cannot be reasonably interpreted as anything but plague, but it is possible that observational data overlook small outbreaks. Second, our measures of prairie dog colony area did not take into account other factors such as prairie dog density, burrow density, vegetation cover, and slope of the land, each of which may be important to Burrowing Owls (Poulin et al. 2011). Our inferences thus assume that all colonies were equal with respect to these factors. Lastly, our study contains only presence–absence data. A more detailed analysis of owl occupancy that incorporates owl abundance (e.g., the approach of Royle and Nichols 2003, Royle 2004) or density might produce slightly different

TABLE 1. Model selection results for prairie dog colonies occupied by Burrowing Owls in southern Phillips County, Montana, 1995–2007. Models are ranked by ascending Akaike's Information Criterion corrected for small samples (ΔAIC_c). We also report AIC_c model weights (w_i) and the number of parameters (k). Model parameters included proportion of colonies occupied by Burrowing Owls (Ψ), the probability of extinction (ε) and colonization (γ) of prairie dog colonies by owls, and the detection probability of owls (p).

Model [a]	ΔAIC_c [b]	w_i	k
Ψ (T) ε (Area^2) p (year + p1 different)	0.00	0.19	19
Ψ (.) ε (Area^2) γ (Area^2) p (year + p1 different)	0.06	0.19	21
Ψ (.) ε (Area^2) γ (Area) p (year + p1 different)	0.43	0.15	20
Ψ (.) ε (Area^2) γ (.) p (year + p1 different)	1.14	0.12	19
Ψ (TT) ε (Area^2) p (year + p1 different)	2.09	0.07	20
Ψ (Area^2) ε (Area^2) p (year + p1 different)	2.74	0.05	20
Ψ (3PL) ε (Area^2) p (year + p1 different)	3.51	0.03	19
Ψ (2PL) ε (Area^2) p (year + p1 different)	3.66	0.03	19
Ψ (Area) ε (Area^2) p (year + p1 different)	3.76	0.03	19
Ψ (4PL) ε (Area^2) p (year + p1 different)	3.97	0.03	19
$\Psi 1$ (.) ε (Area) γ (.) p (year + p1 different)	3.98	0.03	18
Ψ (PL) ε (Area^2) p (year + p1 different)	4.06	0.03	19
$\Psi 1$ (.) ε (T) γ (T) p (year + p1 different)	4.61	0.02	19

[a] Only models with $\Delta AIC_c <5$ are shown. Models with Ψ provide year-specific estimates of occupancy, whereas a model with $\Psi 1$ estimates only occupancy in the first year. Model effects included linear (T) and quadratic (TT) effects across years, a colony area effect, a quadratic effect on area (area^2), 1- to 4-year plague effects (PL, 2PL, 3PL, 4PL), no effect (.), and a model in which detection probability in the first survey period (p1) within each breeding season differed from the others.
[b] The best model had an AIC_c value of 1,792.22.

results about what affects the occupancy of prairie dog colonies by these birds.

Burrowing Owl Dynamics on Prairie Dog Colonies

During the breeding season, owls occupy suitable prairie dog colonies that contain burrows for nesting (Poulin et al. 2011). We found that both extinction and colonization probabilities were affected by the size of a prairie dog colony, which is consistent with the results of other studies. But colony size is only one of several colony attributes selected by the owls. They favor colonies that have a high density of burrows (Poulin et al. 2011), which changes with the size of the colony, making it difficult to infer a relationship between colony size and prairie dog density. We noted a greater difference between the colonization and extinction probabilities in midsized colonies than in the smallest and largest colonies; only in the largest colonies ($\geq$200 ha) was the probability of extinction greater than the probability of colonization. The disappearance of owls from large colonies may be due to declining burrow density on these colonies (Desmond and Savidge 1996) or is perhaps a response to recreational shooting of prairie dogs that usually occurs on the largest colonies (Vosburgh and Irby 1998, Woodard 2002). Regardless of the cause, owl numbers in general were low on colonies where we worked (<3 owls colony^{-1}, on average). The pattern of extinction we found in owls mirrors the pattern that the smallest and largest prairie dog colonies are also most vulnerable to extinction (Stapp et al. 2004).

During the 13 yr of our study, the proportion of colonies occupied by owls increased linearly by ~32%. This increase might be indicative of a long-term recovery by owls from the initial effects of plague that occurred in the early 1990s, although we have no pre-1990 monitoring data for owls. The area occupied by prairie dogs gradually increased during our study, a pattern that is matched by increases in owl occupancy of the same prairie dog colonies. Our occupancy data do not assess the owl population per se,
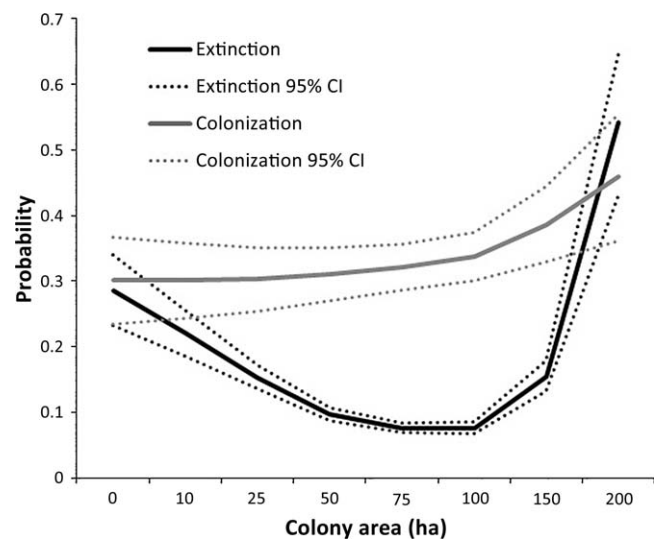

FIGURE 2. Model-averaged estimates of the probability of extinction (ε) and colonization (γ) of prairie dog colonies by Burrowing Owls as a function of colony area, southern Phillips County, Montana, 1995–2007.

which may still be below pre-1990 levels. The importance of prairie dog colonies to owls in the Great Plains is well known (Desmond et al. 1995, Desmond and Savidge 1996), and our study in Montana further confirms the importance of midsized colonies to nesting Burrowing Owls (see review by Lantz et al. 2007).

Impacts of Plague

We found no compelling evidence that plague indirectly affects the probability that nesting owls occupy black-tailed prairie dog colonies in Montana. Plague had a weak positive effect (the 95% CIs included zero) on the proportion of colonies occupied by owls in 3 of our top 10 models but was not an influence on either colonization or extinction probability (Table 1). This finding contradicts our hypothesis that plague plays a role in owl occupancy of prairie dog colonies; other studies have found varying responses by owls to plague epizootics (Restani 2003, Conrey 2010).

Implications for Owl Conservation

The Burrowing Owl is currently federally protected by the Migratory Bird Treaty Act in the United States and Mexico, is listed as an endangered species in Canada, and is a species of concern in Montana (Klute et al. 2003). Their numbers have dropped significantly in Canada, especially in Alberta and Saskatchewan, just north of Montana (Klute et al. 2003). In the United States, numbers of Burrowing Owls have decreased by an estimated 0.5% year^{-1} (Sheffield 1997). Black-tailed prairie dogs, which provide important nesting habitat in the Great Plains, have also experienced steep population declines and a reduction in their former range (Hoogland 2006, Kotliar et al. 1999). It is estimated that there has been a 98% decline in prairie dog populations due to a combination of sylvatic plague and habitat loss (Sheffield 1997, Kotliar et al. 1999). Therefore, any decline in prairie dogs could result in a similar decline in owls. In a Nebraska study, the declines in local owl populations were correlated with crashes in prairie dog populations following the poisoning of prairie dogs (Desmond et al. 2000). The loss of prairie dogs to other processes, such as plague, could also cause declines in owls; thus, any such processes are a concern.

Protection of burrowing mammals such as prairie dogs is an important management strategy for the conservation of Burrowing Owls (Wellicome and Holroyd 2001, Poulin et al. 2011). Conrey (2010) suggested that it is better to preserve prairie dog habitat and connectivity rather than intensively manage against plague to conserve Burrowing Owls. This is supported by the results of our study: Colony size, but not plague history, was an important predictor of owl occupancy dynamics on prairie dog colonies. Conservation of Burrowing Owls and prairie dogs is important because both species serve as sentinels for the overall health of grassland ecosystems in North America (Holroyd et al. 2001). Conservation efforts for the owl should continue to focus on protecting prairie dogs and their habitat connectivity, which might be helped by restricting recreational shooting, restocking efforts, or directly managing the risk of plague through insecticide treatments that kill host fleas (Karhu and Anderson 2000). Protecting prairie dogs from plague may also be beneficial to owls but is less important than outright protection of prairie dogs. We concur with Conrey (2010) that owl conservation should emphasize the landscape-scale preservation of prairie dog colonies and their connectivity.

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