Metapopulation Dynamics of Burrowing Owl (*Athene cunicularia*) in Western Nebraska

INTRODUCTION

Burrowing Owls (*Athene cunicularia*) are small, diurnal owls that breed from the southern portions of the Canadian prairie, throughout the Great Plains, and into Mexico. Burrowing Owl populations are thought to be declining across many portions of their range, but in some areas, including Nebraska, they are believed to be showing an increase. Burrowing Owls are listed as endangered in Canada and threatened in Mexico, and are a species of high conservation concern in nearly all states in which they occur. Nebraska listed Burrowing Owls as a Tier I (at-risk) species of conservation concern in their state wildlife action plan (Schneider et al. 2005).

Burrowing Owls nest primarily in burrows in prairie dog towns in areas characterized by sparse vegetation and bare ground (Haug and Oliphant 1987, Stockrahm 1995). They occasionally nest in burrows of other mammals, especially badgers (Haug and Oliphant 1990, Desmond and Savidge 1996). Burrowing Owls experience lower predation rates and have higher rates of nesting productivity in large, well-populated prairie dog towns (Butts 1982, Desmond and Savidge 1996, Toombs 1997). However, habitat destruction from agricultural production, sylvatic plague and eradication programs (e.g., focused use of chemical pesticides by producers to kill prairie dogs) has extirpated prairie dog populations from 90-98% of their former range (citation). When a prairie dog colony is lost to sylvatic plague or an eradication program, burrows rapidly deteriorate and dense vegetation encroaches on towns (Grant 1965, Butts 1973). Colonies become

unsuitable nesting habitat for Burrowing Owls in as little as one year after the loss of prairie dogs (Butts 1973).

Many studies have used Burrowing Owl occupancy and count data to study Burrowing Owl breeding productivity and habitat use. While understanding the ecological processes that dictate population dynamics within any given prairie dog town is important, it is equally important for the conservation of a species to understand the population dynamics among individual sites and over a large geographic area. We are unaware of any studies that have explored Burrowing Owl metapopulation dynamics and turnover rates over a large ecological scale.

Hanski (1994, also see Ettienne et al. 2004) introduced an approach for estimating metapopulation processes (rates of colonization and extinction) that determine site occupancy as a function of patch size and interpatch distance. This method, termed an Incidence Function Model (IFM), requires only snapshots of patch occupancy data on which to base estimates of extinction and colonization rates. This modeling technique has been implemented in several taxonomic groups including insects (Wahlberg et al. 2002, Thomas et al. 2002), mammals (Moilanen et al. 1998), and amphibians (Vos et al. 2000, Moilanen and Hanski 1998, Halley et al. 1996) and has been refined in a number of ways (Ettienne et al. 2004). Estimation techniques for IFM parameters have also improved (Moilanen 1999, Etienne et al. 2004), but the IFM remains based on the two assumptions of metapopulation theory: 1) larger patches will go extinct less frequently because they usually have larger local populations and are less affected by stochastic processes, and 2) more isolated patches are less likely to be colonized and will go extinct

more frequently because of a reduced rescue effect from neighboring patches (Hanski 1999)

Viewing prairie dog towns and other burrow complexes as discreet “patches” allows for implementation of the IFM to estimate extinction and colonization rates, while determining the significance of small and large burrow complexes to metapopulation viability. A major factor impacting Burrowing Owl populations is loss of habitat through prairie dog poisoning or plague events, both of which are often biased towards larger towns, and was observed during our surveys. Understanding how prairie dog control and plague events affect Burrowing Owl metapopulation processes will provide a clearer picture of population viability of Burrowing Owls in western Nebraska.

We sought to develop an IFM for the Nebraska panhandle in order to: 1) estimate relative colonization and extinction rates throughout the panhandle, 2) determine effects of patch size on Burrowing Owl occupancy, 3) determine the impact of prairie dog control on patch occupancy, and 4) develop predictions about the regional viability of Burrowing Owls in the Nebraska panhandle.

METHODS

Study Area

We studied Burrowing Owls breeding in the Nebraska panhandle (Figure 1). More than 90% of the land in this region is privately owned and used for row crop agriculture and ranching. Farming consists mainly of dryland and irrigated row-crops, including (but not limited to) small grains (wheat and millet) on dryland sites and corn, soy beans and sugar beets on irrigated sites. However, cattle ranching is the predominant practice where prairie dog towns occur. We surveyed 316 prairie dog towns/burrow complexes in the

panhandle at least once during the field season. Surveys encompassed 11 Nebraska panhandle counties: Banner, Box Butte, Cheyenne, Dawes, Deuel, Kimball, Keith, Morrill, Scotts Bluff, Sheridan, and Sioux (Figure 1). We surveyed fewer areas in Sioux and Sheridan Counties due to lack of roads and permission to access private lands.

Field Methods

We surveyed Burrowing Owls at prairie dog colonies and small burrow complexes of other mammals. At each complex we chose a location that offered the best view of all burrows; for extremely large colonies we used multiple points that provided non-overlapping views. We surveyed for owls in late June and throughout July, a period when juvenile owls were able to be observed at nesting sites. We conducted surveys between sunrise and 1000 or 1700 and sunset, when owls were usually present and readily visible outside burrows.

During each visit we conducted two independent three-minute point count surveys, during which both adults and chicks were counted using a high-power spotting scope. We conducted the first count prior to broadcasting a Burrowing Owl territorial or alarm call for 1 minute. We conducted the second count immediately after broadcasting the call. We did not conduct surveys if it was raining or if wind speeds exceeded 32 km_hr^{-1}. In years prior to 2005 we conducted surveys at each site once per year, but beginning in 2005 we visited each survey site multiple times during the survey period (1-3 times in 2005 and 2006 and 2 times in 2007). We used data from repeated visits to estimate detection probabilities for both adult and juvenile owls (see Post van der Burg 2008 for full details of how we estimated detection probabilities).

Analytical Methods

We digitized burrow complexes using ArcView 3.2 (ESRI 2000) and high-resolution aerial photos taken across the study area in 2004. If a road bisected a burrow complex, we treated the burrow complex as one large complex instead two smaller complexes in proximity to one another. Using the XTools feature of ArcView 3.2, we estimated the area of each burrow complex. We designated a 1m radius of breeding habitat area surrounding the nesting burrow for all burrows made by other mammals which could not be digitized. Designating an area for these small burrows allowed us to use them in the development of our IFM. We calculated a centroid point for each burrow complex. The IFM was created with occupancy data from 2006 and 2007 because those years had similar sample sizes and sites in common (n = 275 sites in common, n = 246 prairie dog towns) . We entered centroid UTMs, burrow areas, and 2006 and 2007 occupancy data into the program SPOMSIM V1.0b (Moilanen 1999, 2004). We further divided burrow complexes into Networks, or groups of patches that are likely to have similar ecologies (e.g. – climate, persecution pressures, etc.). Networks were divided by counties (Patch Network 1-11), and whether each complex was a prairie dog town or other mammal burrow complex (Patch Network (1-2). We conducted all IFM analyses in the program SPOMSIM.

Adult and juvenile Burrowing Owls have different detection probabilities (0.56 and 0.46 respectively; Post van der Burg 2008). We accounted for this difference in detectability for adults and juveniles in our modeling. Detectability was better for adults, so we used the 2007 adult occupancy data (n = 2 visits) and the following equation:

$$\mathbf{d2 = 1 - (1-d)^2}$$

to obtain an adult detectability estimate; where d2 is the detection probability after two surveys and d is the single-visit detection probability. We then subtracted d2 from 1 to get our probability of not detecting owls that were present (0.2), which was incorporated into the IFM for all analyses.

We estimated the following parameters in the IFM: dispersal rate, connectivity among patches, colonization probability and extinction probability. We estimated dispersal rate using the equation:

$$\mathbf{k() = exp\ (-\mathit{A} \cdot D\mathit{ij})}$$

where Dij is the distance between patches i and j and the dispersal function parameter *A* controls the shape of the relationship between dispersal and distance, where larger *A* values correspond to lower dispersal. We estimated connectivity using the equation:

$$\mathbf{Si(t) = sum\ [\ pj(t) \cdot k() \cdot Ai^{\mathit{b}}\ ]}$$

where connectivity (*b;* Si(t) = connectivity of patch i at time t) is a function of the number of patches around a given patch, the distance to each patch, the dispersal function, and the area of each patch (Ai), which determines the potential contribution of colonists for that patch. We estimated colonization probability (*y*) using the equation:

$$\mathbf{Ci(t) = Si(t)^2 / (\mathit{y}^2 + Si(t)^2)}$$

where the colonization function gives a saturating rate of colonization with increasing connectivity, and the parameter *y* controls the rate at which colonization increases with increasing connectivity. Therefore, if connectivity is constant, a larger *y* means slower colonization saturation. We estimated extinction probability using the equation:

$$\mathbf{Ei = min\ (1\ ,\ \mathit{u} / Ai^{\mathit{x}}\ )}$$

where the IFM extinction function is a simple function of patch area, where parameter *x* controls the rate at which extinction declines with increasing area, and the parameter *u* is related to the extinction rate in the smallest patch that is capable of supporting a population. Therefore, larger values of *x* give faster drops in extinction rate with increasing area.

Initially, the only manually-adjusted parameter was dispersal (*A*). We gave an initial estimate of 0.00005 for *A* in all models to allow the model to run, but we estimated *A* along with the other parameters based on our observed occupancy patterns. Estimating an *A* value for a highly mobile taxonomic group like birds is problematic. Birds can move great distances and are potentially less affected by the matrix habitat than animals that are required to migrate across unsuitable habitat to reach suitable habitat. Therefore, the question for estimating *A* was how far a bird would move to find suitable habitat if it arrived at its breeding area and found it to be unsuitable.

We initially estimated parameters without incorporating regional stochasticity (e.g. probability of a sylvatic plague outbreak, varying climatic conditions) into the model, and used the Original Incidence Function Model (OIFM) based on Hanski (1994). Our first two parameter estimates for each model used a false zero probability = 0.2, a wide initialization range, 2x effort level, one turnover event per year, and the non-linear regression (NLR) estimation method. We used the NLR estimates as the initial estimates for our final model that used the same settings, but utilized the Markov Chain Monte Carlo (MCMC) estimation method developed for the IFM by Moilanen (1999). Parameter estimates at this point were considered best approximations. We then used

these MCMC-derived parameter estimates to simulate population viability using 100 replications of the first 100 years.

We used the IFM to estimate extinction and colonization rates and metapopulation viability for 5 different metapopulation scenarios. Specifically, we ran 1) a model with all patches (full model); 2) a model without the largest 1/3 of the prairie dog towns (large model); 3) a model without the "other" burrow complexes and the smallest 1/3 of the prairie dog towns (small model); 4) a model with 50% of the sites randomly removed (50% model); and 5) a model with 80% of the sites randomly removed (20% model). These models were designed to address the current viability of the metapopulation, as well as to discern impacts that varying patch size and increased interpatch distance (patches going extinct due to human impacts of plague events) had on regional metapopulation viability.

When a model was said to be "without" a certain type or percentage of prairie dog towns, this was not accomplished by removing the patch from the modeling, but instead by giving both occupancy states for 2006 and 2007 a 0 instead of a 1. While removing patches from the analysis would increase interpatch distance, the estimates would still be based on the occupancy of the remaining patches and would estimate the parameters independent of any perceived loss of habitat.

We estimated a second set of parameters using the same method and settings, except that regional stochasticity was incorporated in the estimation process. Regional stochasticity was incorporated at a 0.5 level (stochastic event every 2 years). We assumed that regional stochasticity was likely to occur throughout the panhandle, so we did not incorporate any stochasticity into the model based on patch location (Network 1)

or patch type (Network 2). Parameter estimates with regional stochasticity incorporated were also simulated with the same settings and subsequent simulation for all five models o approximate regional population persistence.

RESULTS

Estimates of Burrowing Owl site occupancy (uncorrected for detection probability) were relatively high in most years, ranging from a low of 50% in 2007 to a high of 69% in 2002 (Table 1). Of the 95 sites first surveyed in 2001, we observed owls on over 50% of the sites in at least 5 of the years, and observed owls on 17% (n = 16) sites in all 7 years (Table 2). However, our uncorrected data suggested that our average extinction rate was ~5% greater than our average colonization rate over the same time period (Table 1). Our uncorrected extinction rate ranged from a low of 10% between 2003 and 2004 to a high of 21% between 2006 and 2007. The uncorrected colonization rate ranged from a low of 6% between 2006 and 2007, to a high of 20% between 2001 and 2002.

Parameter values used to estimate colonization (*y*) and extinction rates (*u* and *x*) varied considerably between the different IFM scenarios (Table 3), and simulations for all models revealed that local extinction and colonization events occurred frequently, but were more constant in areas with large concentrations of burrow complexes. For all models that did not incorporate regional stochasticity in the estimation process, local colonization and extinction events offset each other in most portions of the panhandle, which resulted in a relatively stable number of occupied patches (Figures 2, 3, and 4). However, as a greater amount of habitat was removed from the model, it appeared that extinctions began to outweigh colonizations and our simulations showed a declining trend over the next 100 years (Figures 2, 3, and 4). In contrast to our uncorrected

estimates, our full model results indicated that local colonizations are currently more than offsetting extinctions (increasing number of occupied patches within the metapopulation in Figure 2), highlighting the importance of correcting model data for imperfect detectability.

Based on our IFM simulations, “patch size” did not appear to have a significant effect on patch occupancy or regional metapopulation persistence. The resulting simulations for both the “large” and “small” models both with and without regional stochasticity were similar in shape to that of the full model (Figure 2), and therefore from here on we treat these 3 models similarly.

Removing 50% and 80% of known potential prairie dog towns from our study area greatly decreased the proportion of patches occupied by Burrowing Owls (Figures 3 and 4). This manipulation also increased the extinction probability and made the metapopulation more susceptible to stochastic processes such as sylvatic plague events (Figures 3 and 4). Two factors played into this increased extinction probability: a significant loss of breeding habitat, and a significant increase in interpatch distance that had to be compensated for by the dispersal parameter estimate (Table 3). Simulations for IFM parameter estimates for all three models without regional stochasticity had 100% survival of all annual simulation runs (though the 20% model averaged less than 15% patch occupancy). This suggested regional metapoplation viability over the next 100 years despite declining patch occupancy probabilities and a loss of up to 80% of breeding habitat (Figures 2, 3, and 4). However, when regional stochastic processes were incorporated into the modeling process, a significant number of the replicates for the 50%

model went extinct, and the metapopulation viability of the 20% model bordered on total extinction over the next 100 years (Figures 2, 3, and 4).

DISCUSSION

We surveyed more than 300 burrow complexes from 2001-2007. While this is a large number of survey sites, it probably underestimates the number of prairie dog towns in several counties, including Sioux County, in which visible access to sites was limited by the small number of roads in the county. Our owl counts indicated that occupancy on surveyed sites was relatively high. Furthermore, because detection probability was <1, more surveyed sites were likely to have been occupied than we observed.

Although our count data suggested that some degree of patch turnover was occurring every year, 17% of patches were occupied by owls in every year. This suggests that while local extinction and colonization events are occurring (~27% of sites on average), a large number of patches were frequently occupied and helped to maintain a stable population in the face of turnover and stochastic events (Figures 2, 3, and 4).

Based on our observations during counts and our IFM parameter estimates, patch size did not appear to be important to the occupancy and regional persistence of Burrowing Owls in western Nebraska. We routinely observed large numbers of chicks produced from nests in single burrows or other mammals, so it may be possible that these could be highly productive sites. It is also possible that these single burrows might experience lower predation compared to smaller prairie dog towns, solely because of the inconspicuous nature of these burrows on the landscape. Although single burrows appeared to become unsuitable after a year or two, it is possible that single burrows throughout the Nebraska panhandle can serve as refugia. However, our study suggested

that single burrows and small prairie dog towns had minimal effect on the overall regional metapopulation viability in its current state.

Relatively large prairie dog towns were also not essential to regional metapopulation persistence. What appeared to be most essential to metapopulation persistence in our analysis were the large number of patches available, and the relatively high occupancy rate of those patches. Although large prairie dog towns were productive Burrowing Owl sites, they are also the most likely to be persecuted by landowners, and therefore may be less dependable for providing suitable breeding habitat on a yearly basis. However, we observed several large prairie dog towns go extinct because of plague events during our study, followed by a subsequent recolonization of prairie dogs after multiple years without. In some of these cases, the prairie dog town still had suitable breeding habitat for owls even in the absence of prairie dogs. This suggests that as long as prairie dogs are present in the system and poisoned and plagued sites are able to be recolonized, only mechanical destruction of prairie dog towns can remove potential habitat from the landscape.

The number of prairie dog towns in the metapopulation did appear to be important to persistence of Burrowing Owls, based on our simulations. With the advent of Rozol and other prairie dog eradication chemicals and programs, the possibility exists for the coordinated widespread persecution and loss of prairie dog towns in western Nebraska. While our results indicate a recently stable metapopulation, the loss of huge numbers of acres of prairie dog towns could be detrimental to Burrowing Owl viability in western Nebraska.

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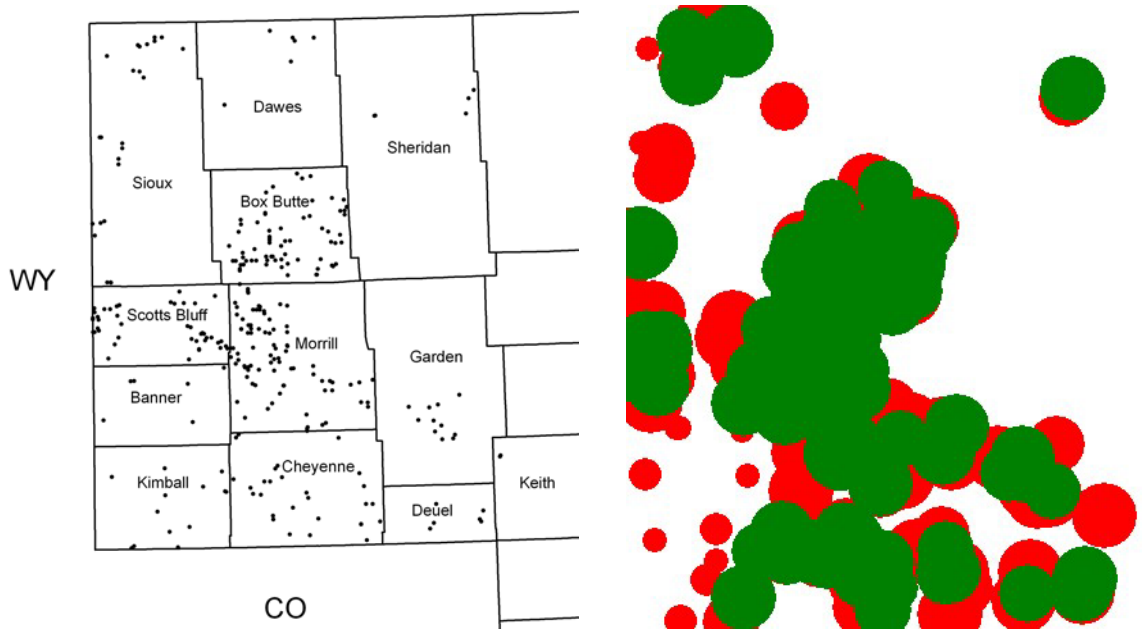

Figure 1. Distribution of sites within study area, and input of distribution into SPOMSIM for 2006 and 2007 field seasons, where occupied patches are indicated with a green dot and unoccupied patches with a red dot, and size of the dot is relative to the size of the patch.

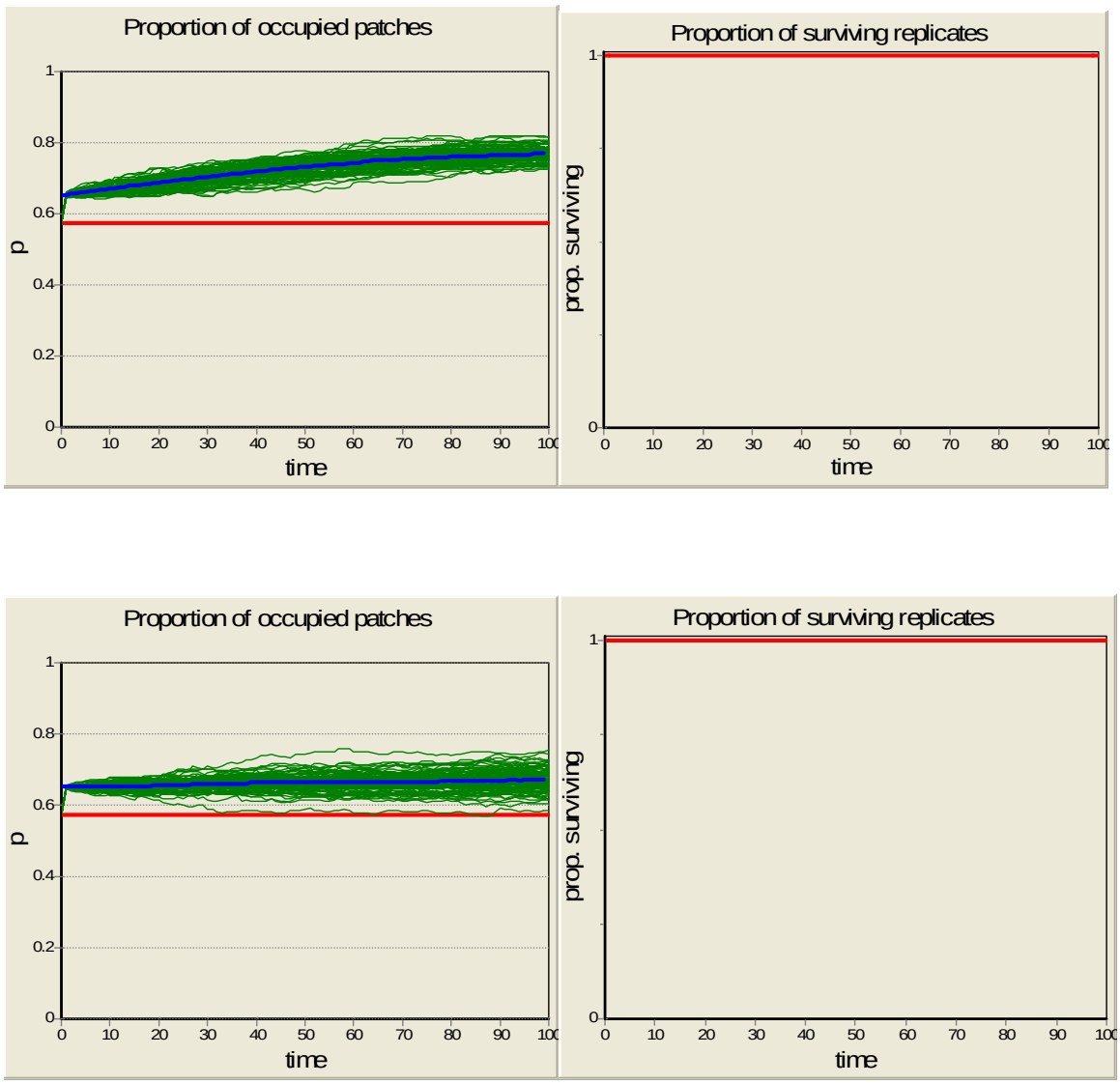

Figure 2. Simulation results for the next 100 years illustrating the proportion of occupied patches and number of surviving replicates (annual simulations) of each full simulation run using parameters estimated with the Markov Chain Monte Carlo estimator for the current complement of patches and occupancy states in western Nebraska. Results are from simulations that did not incorporate regional stochasticity (above) and that did incorporate regional stochasicity (below). The blue line represents the average result for all 100 simulations.

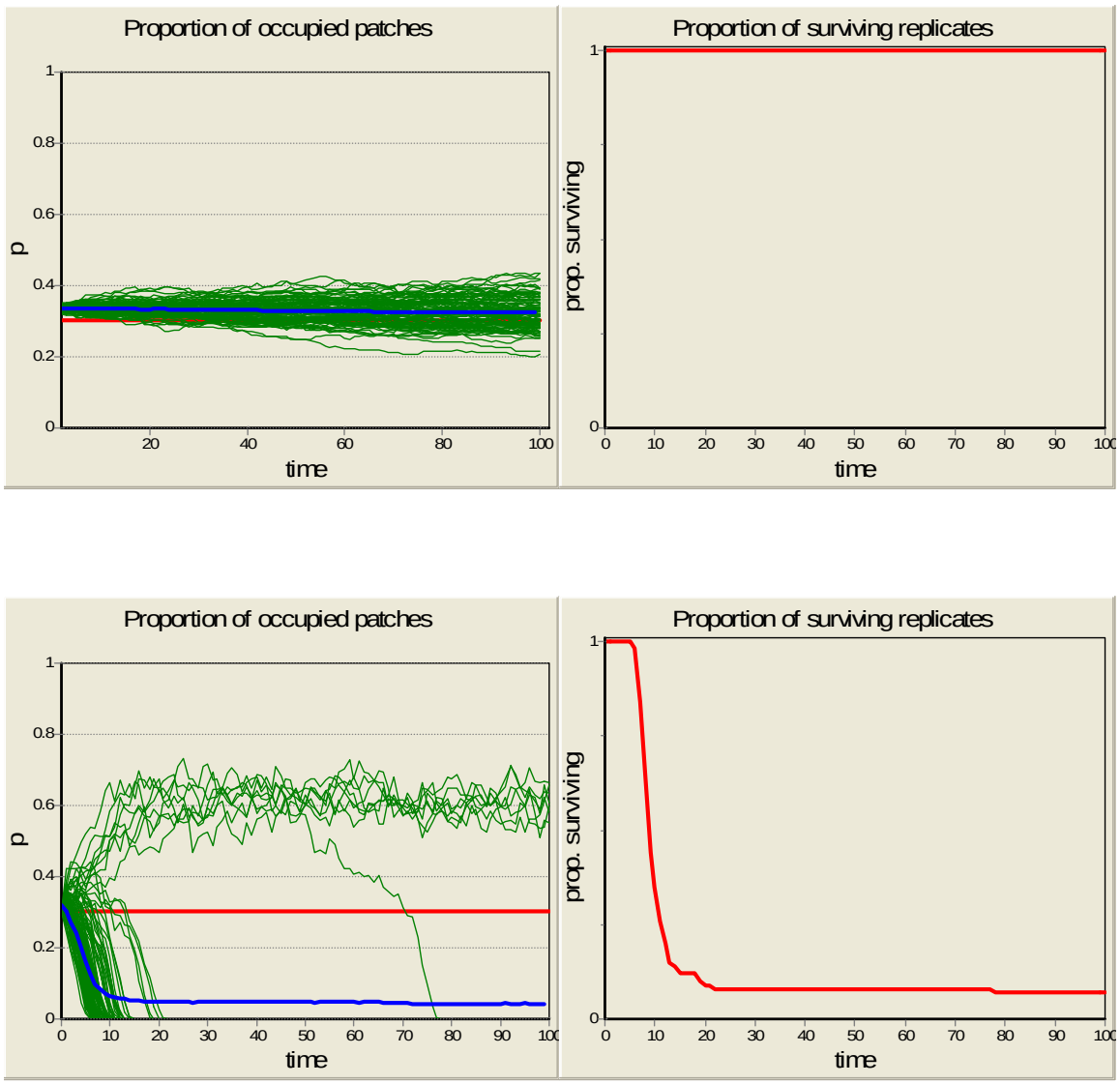

Figure 3. Simulation results for the next 100 years illustrating the proportion of occupied patches and number of surviving replicates (annual simulations) of each full simulation run using parameters estimated with the Markov Chain Monte Carlo estimator when 50% of the current patches' occupancy states are given an unoccupied status in western Nebraska. Results are from simulations that did not incorporate regional stochasticity (above) and that did incorporate regional stochasicity (below). The blue line represents the average result for all 100 simulations.

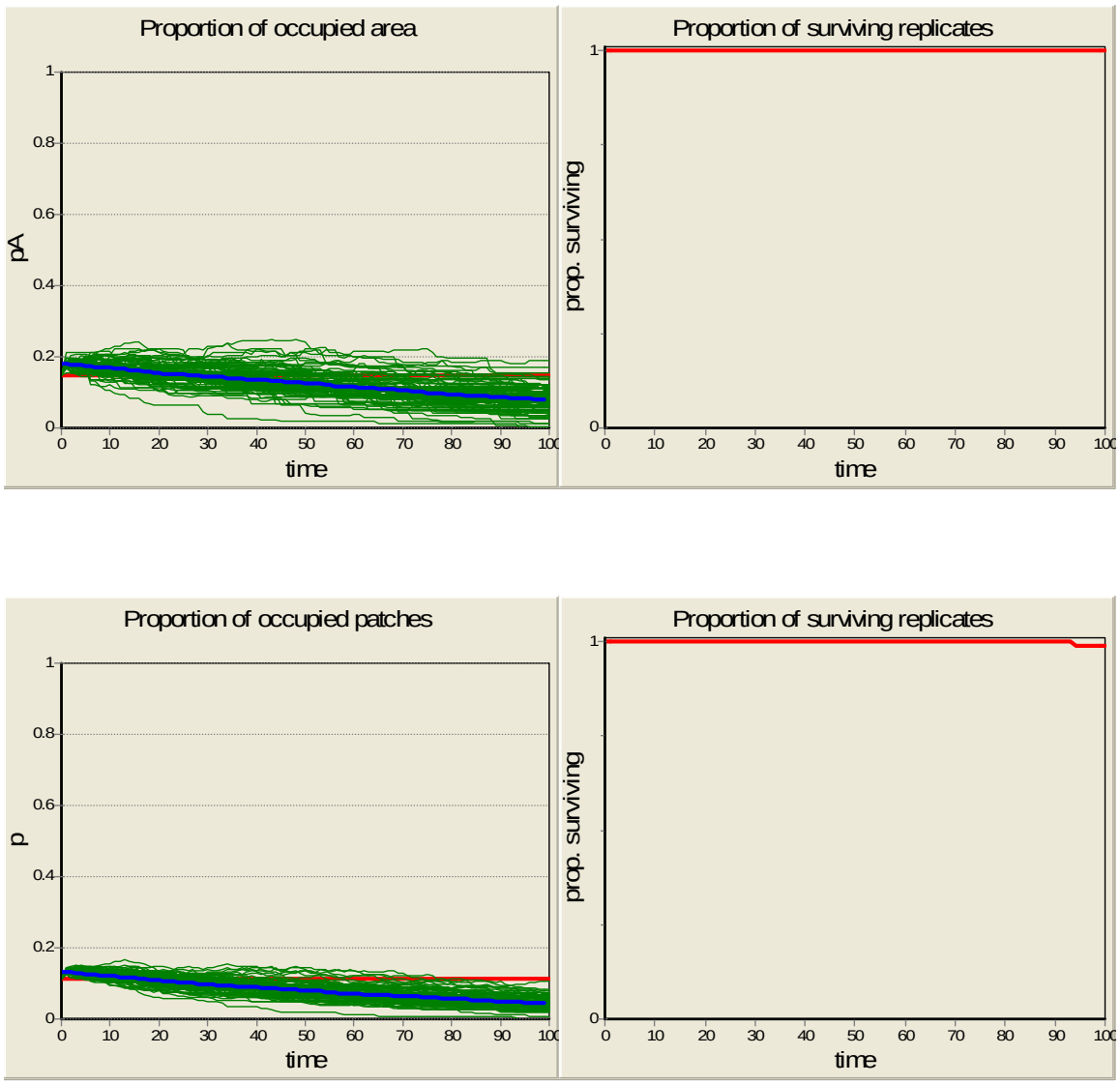

Figure 4. Simulation results for the next 100 years illustrating the proportion of occupied patches and number of surviving replicates (annual simulations) of each full simulation run using parameters estimated with the Markov Chain Monte Carlo estimator when 80% of the current patches' occupancy states are given an unoccupied status in western Nebraska. Results are from simulations that did not incorporate regional stochasticity (above) and that did incorporate regional stochasicity (below). The blue line represents the average result for all 100 simulations.

Table 1. Raw occupancy and turnover data (uncorrected for imperfect detection probability) for Burrowing Owl sites surveyed in western Nebraska, 2001-2007.

Year	# Patches	# Occupied (uncorrected)	# Extinctions (uncorrected)	# Colonizations (uncorrected)	# Turnover Events (uncorrected)
2001	95	62	na	na	na
2002	144	100	13	19	32
2003	197	119	28	12	40
2004	202	124	20	20	40
2005	167	121	22	15	37
2006	277	179	30	21	51
2007	281	142	60	18	78
Average		64%	16%	11%	27%

Table 2. Sum of the number of individual occupied patches (not corrected for imperfect detection probability) of the original 95 burrow complexes surveyed in 2001, where Burrowing Owls were encountered in subsequent years.

Years Occupied	Number of Patches
0	6
1	6
2	10
3	8
4	15
5	19
6	15
7	16
Total	95

Table 3. Markov Chain Monte Carlo parameter estimates (*A* = dispersal parameter, *b* = connectivity parameter, *y* = colonization probability parameter, and *u* and *x* = extinction probability parameters) for each of the IFM's developed for the Burrowing Owl metapopulation in western Nebraska, 2006-07.

Model	**Error**	***A***	***b***	***y***	***u***	***x***
Full Patch Model	100.39	1.82E-06	0.761	2.520E+10	3.7080E-06	1.054
Full Patch Model (Stochasticity)	139.1	4.97E-06	0.2519	1.255E+07	8.0070E-06	2.1624
50% Patch Model	102.48	8.764E-09	0.0441	4.611E+06	3.5669E+00	0.8954
50% Patch Model (Stochasticity)	300.12	2.074E-09	0.00308	1.375E+02	2.2539E+01	0.002671
20% Patch Model	60.383	2.55E-11	0.4482	1.522E+09	2.6650E+07	2.7416
20% Patch Model (Stochasticity)	165.7	2.956E-09	0.033	1.596E+06	5.6843E+02	1.669