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Dynamics of Reintroduced Gunnison's Prairie Dogs

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Population Ecology

Population Dynamics of Reintroduced Gunnison's Prairie Dogs in the Southern Portion of their Range

ANA D. DAVIDSON,[1,2] *Department of Ecology & Evolution, Stony Brook, Stony Brook, NY 11794, USA; and Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

MICHAEL T. FRIGGENS, *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

KEVIN T. SHOEMAKER, *Department of Ecology & Evolution, Stony Brook, Stony Brook, NY 11794, USA*

CHARLES L. HAYES, *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA; and New Mexico Department of Game and Fish, Santa Fe, NM 87507, USA*

JON ERZ, *Sevilleta National Wildlife Refuge, Socorro, NM 87801, USA*

RICARDO DURAN, *School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA*

ABSTRACT Burrowing, herbivorous mammals play important roles as ecosystem engineers and keystone species of grassland ecosystems around the world, but populations of many species have declined dramatically because of myriad threats from human activities. Prairie dogs (*Cynomys* spp.) play important roles in shaping the central grasslands of North America, and have declined by about 98% across their range, with consequent losses in associated species and grassland habitat. This has prompted much interest in restoring their populations to protected areas. Managers lack a clear understanding of the long-term success of reintroductions, however, and how success may vary across different species of prairie dogs and their widespread geographic ranges. We reintroduced over 1,000 Gunnison's prairie dogs (*C. gunnisoni*) to a semi-arid grassland ecosystem in the southern portion of their range in central New Mexico, USA, and used standard capture–recapture methods to study their population dynamics over a period of 8 years. Mean adult survival was 27% over the course of the study, with precipitation identified as the primary driver of survival. Estimated survival was below 12% during severe drought periods and during the first few years following initial reintroduction, the latter likely because of high predation. Consequently, multiple releases of animals were required to prevent extirpation, and the long-term sustainability of this population remains questionable. Over the 8 years of our study, our site experienced 4 severe droughts during spring, the key period for prairie dog mating, pregnancy, and lactation. Production of offspring at the site was low, likely because of the dry and variable conditions that occurred. We show that prairie dog restoration in semi-arid grassland environments that are typical of the lower elevations and southern extent of their range may not succeed in producing viable colonies, and that dedicated management for multiple years is needed to counteract periods of slow or negative population growth. Our findings underscore the importance of maintaining and expanding existing colonies wherever possible in these more arid regions, and suggest that reintroductions should be treated as a secondary management strategy. Our work also reveals the high vulnerability of prairie dog population extinction due to drought, which has important implications for Gunnison's prairie dog conservation under a warming and drying climate.

KEY WORDS burrowing mammals, conservation, *Cynomys gunnisoni*, grassland, reintroduction, restoration, survival, translocations.

Social, burrowing, herbivorous mammals are a key functional group that shape grassland ecosystems around the world (Davidson et al. 2012). However, because of their large, engineering, and often keystone-level effects, many have been persecuted as pests and face a number of human threats (Miller et al. 2007, Delibes-Mateos et al. 2011, Davidson et al. 2012). Consequently, grassland ecosystems are often depauperate of these animals, especially in sufficient numbers to play their functional roles (Davidson et al. 2012). Their loss and the cascading effects of their decline on grasslands have inspired reintroductions of various species back into their native habitat (Dobson et al. 1997, Truett et al. 2001, Davidson et al. 2012).

Prairie dogs (*Cynomys* spp.) transform the central grasslands of North America through their burrowing and herbivory (Whicker and Detling 1988; Kotliar et al. 1999, 2006; Davidson and Lightfoot 2008; Davidson et al. 2012). By grazing and clipping vegetation they create a low mat of

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[1]*E-mail: davidson@iws.org*
[2]*Present address: Institute for Wildlife Studies, Arcata, CA 95521, USA*

dense forbs and grazing tolerant grasses, and dot the landscape with numerous mounds (Whicker and Detling 1988, Davidson et al. 2012). Their colonies represent unique islands of open grassland habitat that attract numerous animals, such as burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*), and predators that rely on prairie dogs as a primary food source, such as coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), raptors, and the highly endangered black-footed ferret (*Mustela nigripes*; Clark et al. 1982, Cartron et al. 2004, Davidson and Lightfoot 2007, Bayless and Beier 2011, and see refs. in Davidson et al. 2012). Although the magnitude of these impacts can vary by prairie dog species, colony density, or other site-specific factors, prairie dogs indeed play important ecological roles in grasslands across their range (Davidson et al. 2012).

Prairie dog populations have declined by about 98% over the last century (Hoogland 2006*a*). All 5 species of prairie dogs are considered either threatened or endangered, or have been petitioned for listing under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1970, 2008, 2009, 2010, 2011). Much of their decline is due to poisoning, introduced sylvatic plague, habitat loss, and shooting (Hoogland 2006*b*). Mass extermination programs began in the early 1900s by the United States government (U.S. Biological Survey), primarily to eliminate the purported competition of prairie dogs with livestock (Hoogland 2006*b*, Bergstrom et al. 2013). Such programs to lethally control their populations continue today, involving both public and private entities. The human-introduction of sylvatic plague from Eurasia has also devastated their populations (Cully and Williams 2001, Stapp et al. 2004, Cully et al. 2006), and is perhaps the biggest threat facing prairie dogs and associated species today (USFWS 2008, 2009, 2013).

Loss of prairie dogs has resulted in declines in species associated with the habitats they create, including the burrowing owl and mountain plover, and those dependent or heavily reliant upon prairie dogs as prey, including black-footed ferrets and ferruginous hawks (*Buteo regalis*) (Kotliar et al. 2006, Davidson et al. 2012). Additionally, grasslands have been invaded by shrubs in areas where black-tailed prairie dogs (*C. ludovicianus*) have been poisoned in the southern distribution of their range, demonstrating their role in maintaining grasslands and the ecosystem services they provide to humans (Weltzin et al. 1997, Ceballos et al. 2010).

Reintroductions of prairie dogs have been occurring over the last 2 decades, and are often designed to remove the animals from areas where they are in conflict with human activities to protected areas (e.g., Truett et al. 2001, Bly-Honness et al. 2004, Dullum et al. 2005, Shier 2006, Nelson and Theimer 2012). Considerable research has been conducted to determine successful methodologies for reestablishing prairie dogs, which involves releasing them into pre-existing burrows or constructed artificial burrow systems (Long et al. 2006). Most of the work published on prairie dog reintroductions has been on black-tailed prairie dogs (e.g., Truett et al. 2001, Bly-Honness et al. 2004, Roe and Roe 2004, Long et al. 2006, Shier 2006) and Utah prairie dogs (*C. parvidens*; Turner 1979, Player and Urness 1982, Coffeen and Pederson 1989, Curtis 2012), with a couple of studies on Gunnison's prairie dogs (*C. gunnisoni*; Davidson et al. 1999, Nelson and Theimer 2012). Given significant behavioral differences among the species and the wide range of grassland habitats they occur in (Hoogland 1995, 1999), reintroduction outcomes are likely to vary. Despite the numerous reintroduction efforts occurring across their range, few published studies have reported on the long-term success of reintroductions, and how success varies in the context of climate dynamics, environmental factors, and across different parts of their geographic range (Facka et al. 2010). Such information is especially needed in the context of climate change, with climate in the southern portion of their range projected to experience continued warmer temperatures, rapid drying, and inhibited recovery from drought conditions (Seager et al. 2007, Gutzler and Robbins 2011).

The purpose of our research was to evaluate the population dynamics of reintroduced Gunnison's prairie dogs in the southern portion of their range over a period of 8 years, to inform wildlife managers concerned with the conservation and management of prairie dogs. We asked 3 key questions: 1) What were their population abundance and survival rates following reintroduction? 2) Was precipitation an important predictor of their survival? 3) Did predation or other environmental stressors have a significant impact on their survival? We were interested in understanding these questions in the context of their initial reintroduction as well as over time.

STUDY AREA

We reintroduced Gunnison's prairie dogs to the Sevilleta National Wildlife Refuge (NWR), the site of the Sevilleta Long Term Ecological Research (LTER) Program, located in Socorro County, New Mexico. The Sevilleta NWR is a restricted-access unit of the National Wildlife Refuge system. It is not grazed by cattle, and is available for research and education purposes, making it an ideal site for prairie dog reintroductions. The 92,000-ha refuge previously supported colonies of Gunnison's prairie dogs prior to extermination during the 1960s (J. Ford; retired Animal Control Officer, Wildlife Services, U.S. Department of Agriculture, personal communication; Fig. 1). Of all potential reestablishment localities at the Sevilleta NWR, we chose the site with the most extensive southern shortgrass steppe habitat on the refuge, located in the western foothills of the Los Piños Mountains (latitude 34°20′32.9″, longitude 106°37′40.9″, elevation 1,650 m; Fig. 1). This site was dominated by short-stature blue grama (*Bouteloua gracilis*), a mixture of black grama (*B. eriopoda*) and James' galleta (*Pleuraphis jamesii*) grasses, various annual and perennial forbs, and some small shrubs such as Mormon tea (*Ephedra torreyana*) and cacti (*Opuntia clavata*, *O. imbricata*). The mean annual precipitation at the Sevilleta NWR is 244 mm (SD 66.4 mm), much of which comes during the summer rainy season (Jun–Sep; mean 141.1, SD 49.5 mm; Moore

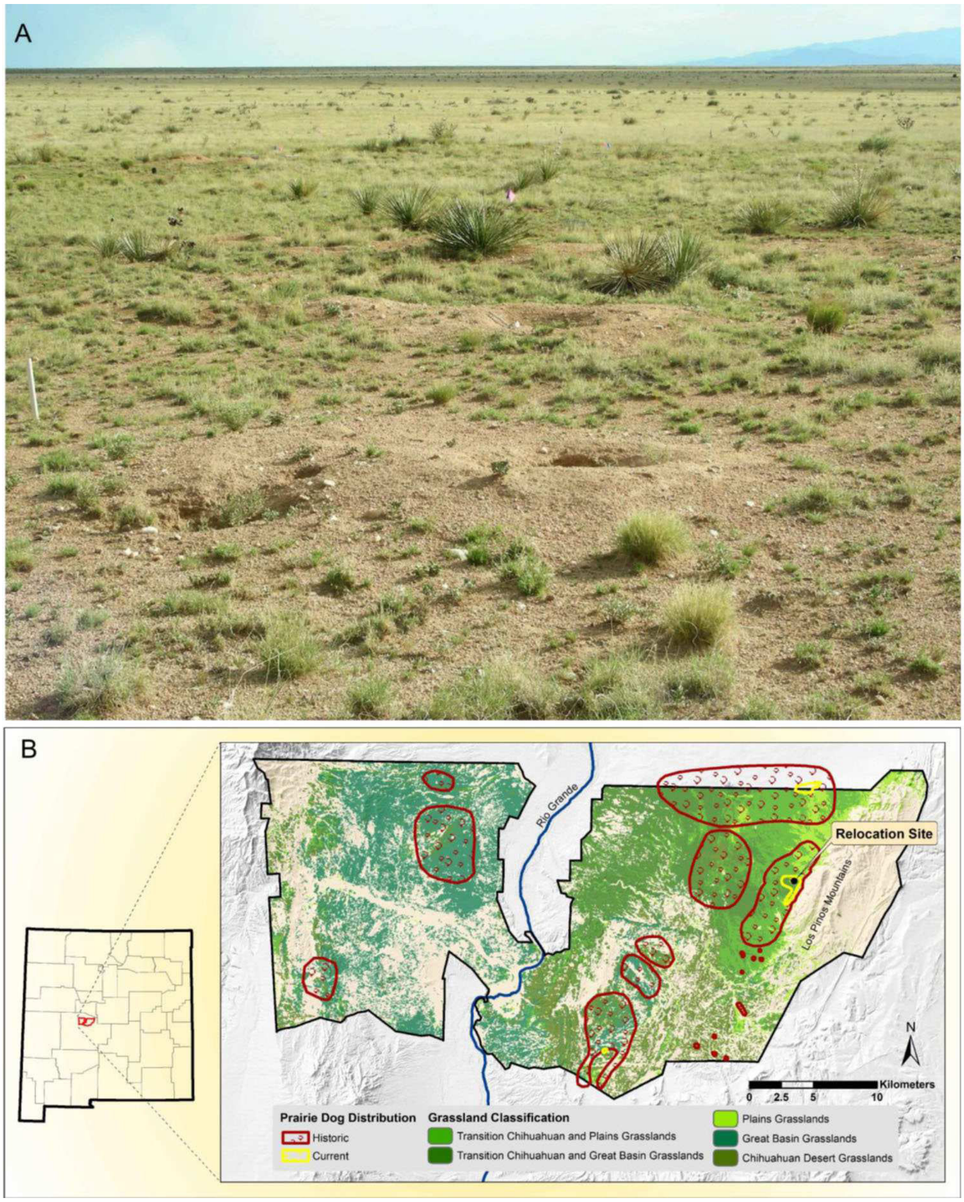

Figure 1. Reintroduction study site at the Sevilleta National Wildlife Refuge (NWR), Socorro County, New Mexico, USA. (A) Photo of study site, taken in 2009. (B) Historical and current distribution of Gunnison's prairie dogs (*Cynomys gunnisoni*) on the Sevilleta NWR. Supervised vegetation classification created from Thematic Mapper satellite imagery (Muldavin et al. 1998).

2013). Precipitation during the winter-spring period (Oct–May) is especially highly variable from year to year in this system (mean: 103.2 mm, SD 56.4), with droughts (<50 mm) during this period being frequent (Moore 2013).

METHODS

Field Methods

We established 3 1-ha plots for reintroductions; we fitted each plot with 33 artificial burrows that we used repeatedly for prairie dog releases over the course of the study. Release plots were between 200 m and 400 m from one another, so that newly released animals would remain at the study plots during the short-term, but prairie dogs could naturally expand toward neighboring plots over time. Artificial burrows consisted of 40-L nursery pots turned upside down, fitted with wire mesh floors, hay and 2 1.5-m corrugated plastic tubing tunnels extending out of holes cut on opposite sides of the pot (Fig. 2A). We placed this apparatus approximately 1 m deep in a 2-m long × 0.5-m wide trench dug with a backhoe (Fig. 2B). The plastic tunnels extended laterally in the trench and angled gently toward the surface to provide 2 entrances at each burrow (Fig. 2B, C, and D).

We captured prairie dogs released on the study plots from nearby urban and rural areas in and around Santa Fe (approx. 200 km from the Sevilleta NWR) and Albuquerque, New Mexico (approx. 105 km away) in 2005, 2007, 2008, and 2009. Methods used in this project were approved by the University of New Mexico's Institutional Animal Care and Use Committee (Protocol 12-100768-MCC). All

Figure 2. Reintroduction of Gunnison's prairie dogs at the Sevilleta National Wildlife Refuge. (A) Construction of an underground artificial burrow showing nest box and tubing, (B) artificial nest box filled with hay, (C) aboveground acclimation cage with feed, (D) reintroduced prairie dogs in acclimation cages, and (E) a reintroduced prairie dog in 2012.

reintroduced animals were of the putative *C. g. zuniensis* subspecies that occurs in the lower elevation grasslands, and were from the prairie population of Gunnison's prairie dogs (A. P. Martin and L. C. Sackett, University of Colorado at Boulder, unpublished report for Colorado Division of Wildlife [CDOW]; USFWS 2013). The prairie population (*C.g. zuniensis*) is the native subspecies at the Sevilleta NWR (A. P. Martin and L. C. Sackett, unpublished CDOW report; USFWS 2013).

We captured prairie dogs using flushing and trapping methods, and followed similar protocols to those discussed in Long et al. (2006). We housed captured individuals in a humane setting certified by the Prairie Dog Coalition, a part of The Humane Society of the United States. We kept individuals in holding with their apparent family groups (hereafter, clans) and fed them daily for a period of at least 1 week to optimize health upon release (Shier 2006; but also see Bly-Honness et al. 2004, Long et al. 2006, and Curtis 2012). We dusted all animals with flea powder (© DeltaDust, Bayer CropScience LP, Research Triangle Park, NC) to prevent transporting potentially plague-infected fleas to the release site (Long et al. 2006). Capture efforts began in early June, only after young of the year had emerged. For most of the captured individuals, we obtained data on weight and sex and applied numbered ear tags.

We transported prairie dogs to the release site in pet carriers and an air-conditioned van, and followed release procedures similar to those described by Long et al. (2006). All releases began early in the morning to minimize heat stress while animals awaited release into artificial burrows. We transported pet carriers filled with hay to the burrows by hand. One burrow entrance was fitted with an aboveground acclimation cage consisting of 1-cm wire mesh (0.5 m × 0.5 m × 0.25 m). Each acclimation cage had a hole in the floor center to fit over the artificial burrow entrance. We supplied the cage with hay, black-oil sunflower seeds, and carrot slices before fixing it over the burrow entrance with rebar stakes and wire to keep the cage door propped open (Fig. 2C and D). Depending on size and sex of the prairie dogs, we released up to 8 individuals from the same clan into the other burrow entrance before we covered it with the same cage configuration. If a clan was larger than 8 individuals, we placed one half of the group in one artificial burrow and the other in an adjacent burrow. We removed animals from the pet carrier by hand and carefully transferred them to the burrow entrances. We released all captured animals to our study site. The ratios of age classes varied depending on the season we captured them (i.e., spring vs. summer). Often we placed adult males in separate artificial burrows, adjacent to clan-member females and pups.

Acclimation cages remained over burrow entrances for 2 to 5 days, allowing individuals to explore the surface visually, communicate with nearby captive individuals (or previously released free-ranging prairie dogs), eat, and acclimate before removal of the cages. We fed newly released animals daily while cages were in place, twice weekly thereafter for 1 month, and once per week or less depending on forage conditions (i.e., if vegetation was green or not) for the rest of the summer. Once released, prairie dogs dug their own natural burrow systems, often continuing to use the artificial burrow as well.

Population assessment during the course of the study consisted of 2 methods: live capture–recapture trapping and burrow-mound counts. Trapping occurred during the spring (late Mar), early summer (late Jun), and late summer (late Aug), but we did not conduct all 3 trapping periods every year (see Fig. 3). We used 100 welded wire mesh treadle-type live traps (19 cm × 19 cm × 48 cm or larger) with double doors at each 1-ha plot, with 2 traps placed at each numbered, flagged, and mapped station near active burrows. We wired traps open and pre-baited them for 2 days prior to trapping events, set and baited them at dawn each day of a trapping event, and left them open during the morning until ambient temperature reached 25°C. Each trapping period consisted of 3 consecutive trap days, for a total of 3,600 trap days. We labeled captured individuals with the trap station number and carried them to a shaded processing location off-plot. We transferred individuals from the trap to a canvas cone where they could be processed (Hoogland 1995), and recorded their trap station and ear-tag numbers.

We conducted mound surveys during late summer (Sep) with a handheld sub-meter global positioning system (GPS) unit (Trimble GeoXT, Sunnyvale, CA). Technicians walked the entire 15-ha study area (see Fig. 4), mapping all active burrow-mounds encountered. We considered burrow-mounds to be active if we found clear evidence of recent digging and scat. We created annual maps of overall mound distribution in ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA; Fig. 4). We obtained monthly precipitation data from a Sevilleta LTER meteorological station located 0.5 km from the study site, which was fitted with a tipping bucket rain gauge (Moore 2013).

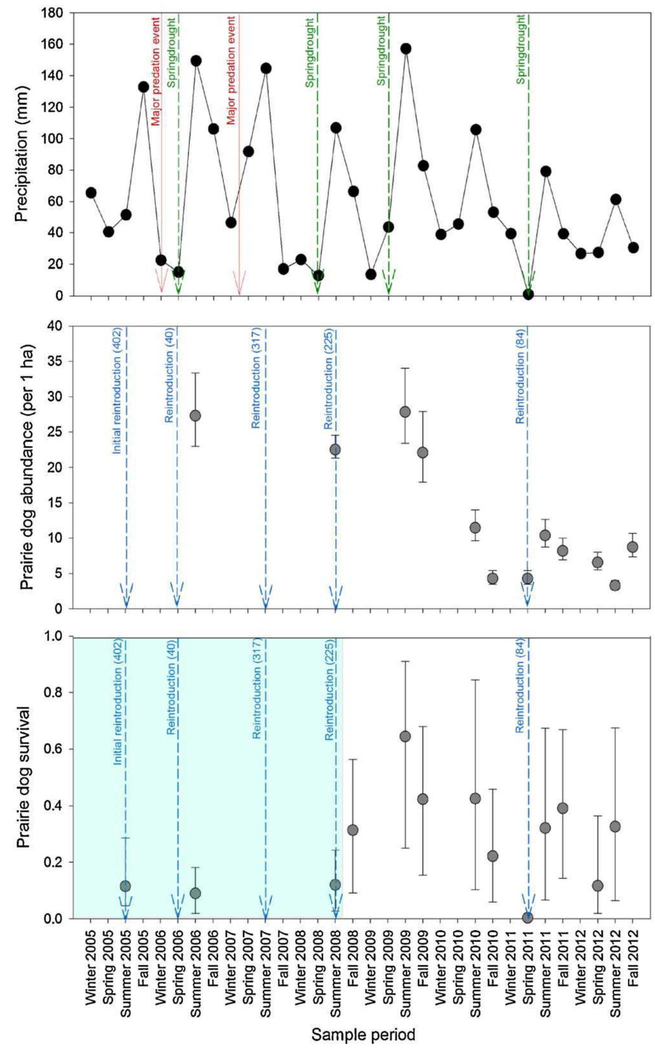

Figure 3. Environmental variables and prairie dog population dynamics from 2005–2012 at the Sevilleta National Wildlife Refuge in New Mexico. (A) Total precipitation during each of the 4 seasons over time, with periods of extensive predation and spring droughts noted. Mean (B) abundance and (C) annualized survival rates of prairie dogs (±SE) plotted for each primary sampling period across the 1-ha study plots, with reintroduction events indicated and the main period of initial establishment highlighted in light blue. For each reintroduction event, the total number of prairie dogs released across the 3 1-ha plots is provided in parentheses.

Data Analysis

We used Bayesian open-population models to estimate seasonal abundance and survival rates. We used Pollock's robust design (Pollock 1982, Kendall et al. 1997), under which we assumed the study population was closed to mortality and temporary emigration within seasons. We modeled survival (φ) as a logit-linear function of mean monthly precipitation. We modeled temporal process variation in survival as a random intercept that varied across primary sampling periods. The overall survival process can be expressed according to Equation (1):

$$logit\{(Q_t)^{\frac{1}{p}}\} = \beta_0 + \beta_1 \cdot \mathrm{precip}_t + \beta_2 \cdot q_t \qquad (1)$$

where φ_t represents the annualized survival rate in the interval between primary sampling periods t and $t+1$, p represents the length of this sampling interval, β_0 is an intercept term representing the upper limit to annual survival under mean precipitation conditions, β_1 represents the logit-linear fixed effect of precipitation on survival, precip_t represents the mean monthly precipitation during the focal time frame (primary sampling period t to $t+1$) standardized with a mean of 0 and standard deviation of 1, β_2 represents the (logit) reduction in survival associated with the lower limit, and q_t represents the degree to which survival rate in sampling period t matched the lower limit.

Following the standard robust design model, we estimated 2 temporary emigration parameters (γ_1 and γ_2) representing the probability of remaining outside the sampled area and the probability of leaving the sampled area, respectively. Because sampling efforts were highly standardized (3 1-ha trap grids),

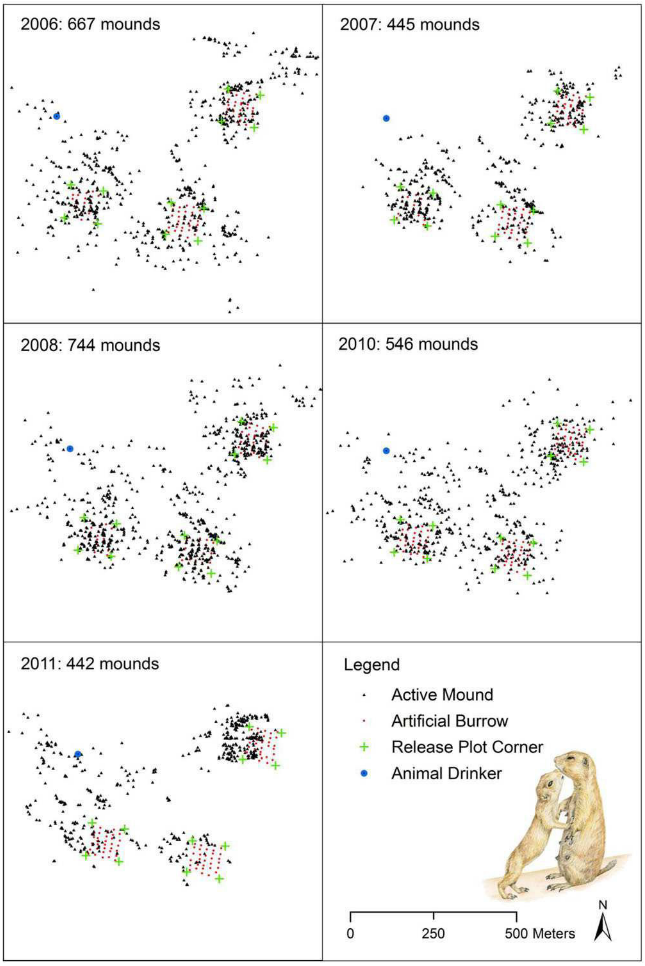

Figure 4. Maps depicting location and number of active prairie dog mounds within the 15-ha study site, and the 3 1-ha release plots with artificial burrows at the Sevilleta National Wildlife Refuge from 2006 to 2011.

we modeled probabilities of capture (*p*) as constant per secondary sampling period (trap day). We estimated seasonal prairie dog density within the sampled areas using a Horvitz–Thompson estimator (McDonald and Amstrup 2001). We did not assess age or sex as predictor variables because of inconsistent field data collection of these variables.

We estimated parameters with Markov-Chain Monte Carlo (MCMC) methods using WinBUGS 1.4 (Lunn et al. 2000), which was called from the R environment via the R2WinBUGS package (Sturtz et al. 2005, R Development Core Team 2012). We assigned uninformative uniform prior probability distributions to all free parameters. We ran 3 independent Markov chains, discarding the first 25,000 MCMC samples as a burn-in and storing every fifth sample of the remaining 25,000 MCMC iterations for further analysis. We tested for convergence of the Markov chains to the stationary posterior distribution with the Gelman–Rubin diagnostic (Bolker 2008). We summarized posterior distributions for all parameters with the mean of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (Bolker 2008). Scripts for running this analysis (R and WinBUGS) are provided in Supporting Information.

RESULTS

Reintroductions and Population Trends

We reintroduced 1,028 Gunnison's prairie dogs to the Sevilleta NWR from 2005 through 2011, with the majority (944) of them being released during the first 4 years of the study, from 2005 to 2008 (Fig. 3). We released 402 animals across each of the 3 1-ha plots during the first year (summer 2005), and an additional 40 animals in spring 2006. Our mark-recapture efforts resulted in 819 captures of 609 unique individuals. One year following the initial reintroduction, in summer of 2006, the population was estimated at 27.3 (95% credible interval: 27.0–33.3) individuals per ha. But, by summer 2007, the prairie dog population had declined dramatically, based on the widespread decline in activity reflected in lack of fresh fecal pellets, burrow excavation, and digging. Because the population had crashed in 2007, we did not trap that summer and instead released another 542 animals in 2007 and 2008 (Fig. 3). Following these additional releases, the estimated population bounced back to 22.1 (17.9–27.9) to 27.8 (23.4–34) animals per ha in 2008 and 2009. From 2009 to 2012, we monitored the natural population dynamics of the prairie dog colonies without further reintroductions or supplemental feed, with the exception of 1 release of 84 animals and associated supplemental feed on 1 plot in spring 2011. From 2010 to 2012, the population hovered around an estimated 3.3 (2.8–4.0) to 11.5 (9.7–14.0) individuals per ha. Notably, we did not capture pups in traps during the entire study, but we did observe limited numbers in 2008 and 2010–2012, suggesting low overall offspring production.

The number of active prairie dog burrow-mounds, which we counted in September each year, reflected the expansion and contraction of the colony over the course of the study, going from 667 in 2006, contracting to 445 in 2007, expanding after the additional releases in 2007 and 2008 to 744 mounds in 2008, and declining again to 546 in 2010 and 442 by 2011 (Fig. 4). Most of the active mounds in 2011 were located off the 1-ha plots, except those on the north treatment plot that received additional animals that year. Many were centered on the wildlife drinker, a water well for Sevilleta NWR wildlife (see blue dot, Fig. 4). Notably, we observed prairie dogs drinking from the drinker and establishing mounds nearby (Fig. 4).

Survival and Environmental Stressors

Mean annualized adult survival over the course of the study was 17%. Survival rates during the first few years following initial establishment were particularly low (ranging between 9% and 12% between summer 2005 and summer 2008; Fig. 3C). Thereafter, annualized survival rate peaked at 64% in summer 2009, and subsequently ranged from 22% to 43%, with the exception of low survival estimates for prairie dogs captured in both spring 2011 and 2012 (0.4% and 12%, respectively; Fig. 3C). Geometric mean annual survival rate after the initial establishment period was 26%.

Mean monthly precipitation had a significant (i.e., 95% credible interval for this coefficient did not contain 0), positive effect on survival (Table 1 and Fig. 5). The first

Table 1. Raw parameter estimates from the mark-recapture model used to estimate demographic rates for a reintroduced prairie dog population at the Sevilleta National Wildlife Refuge, New Mexico. Note that we computed abundance as a derived parameter and is therefore not included here.

Parameter	Mean	Lower limit 95% CI[a]	Upper limit 95% CI[a]
B_0 upper limit to seasonal survival (intercept, logit)	−0.562	−1.579	0.562
q, global probability of low survival[b]	0.469	0.117	0.831
B_1, effect of precipitation on survival (logit)	1.386	0.643	2.249
B_2, reduction in survival at lower limit (logit)	−2.039	−2.926	−1.012
p, mean capture probability	0.275	0.206	0.35
γ_1, probability of remaining outside sampled region	0.356	0.034	0.74
γ_2, probability of leaving sampled region	0.388	0.167	0.582

[a] Lower and upper limits represent Bayesian credible intervals (CI), computed as the 2.5 and 97.5 percentiles of the posterior distribution.
[b] We computed q_t terms (controlling the degree to which each season's survival rate matched the lower limit vs. upper limit) from the Markov-Chain Monte Carlo results as a derived parameter, and the results were as follows: 0.85 (summer 2005), 0.98 (summer 2006), 0.99 (summer 2008), 0.27 (fall 2008), 0.15 (summer 2009), 0.1 (fall 2009), 0.58 (summer 2010), 0.04 (fall 2010), 0.61 (spring 2011), 0.42 (summer 2011), 0.05 (fall 2011), 0.61 (spring 2011), and 0.36 (summer 2012).

spring following release (2006) was characterized by severe drought, and the additional releases in 2007 and 2008 were again followed by severe spring droughts in 2008 and 2009 (Fig. 3A). Spring 2011 exhibited the lowest survival rate over the study, and coincided with another severe spring drought (Fig. 3A).

Based on informal field observations, time periods associated with low annualized survival coincided with extensive evidence of predation (i.e., predator scat, digs, and burrow excavations). We observed this predator activity especially during the first and second winter periods following the initial release (winter 2005–2006 and 2006–2007), during which newly released prairie dogs were hibernating (Fig. 3A). To manage predator impact in the field, we trapped and relocated 2 badgers and a kit fox (*Vulpes macrotis*) in 2006, and, in 2007, we captured and relocated a family of kit foxes, 2 adults and 4 sub-adults, whose den was surrounded by an abundance of scat laden with prairie dog fur and bones. Throughout the study, we continued to observe some evidence of predation, especially in the form of badger digs; raptors, prairie rattlesnakes (*Crotalus viridis*), kit foxes, coyotes, and badgers all occupied the area within and around the study site. Nonetheless, after the first few years (2005–2008) following the initial reintroduction effort, our model suggests that precipitation was the primary driver of observed variation in survival rates (Table 1).

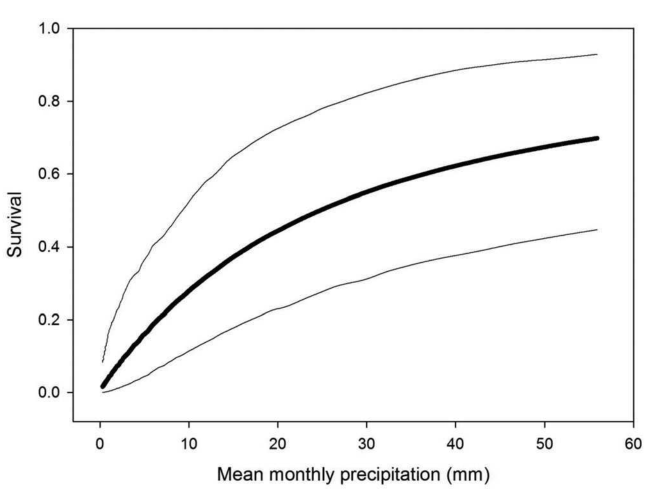

Figure 5. Relationship between mean monthly precipitation (mm) and annual survival of reintroduced adult Gunnison's prairie dogs at the Sevilleta National Wildlife Refuge modeled as a linear function with a logit link. Mean survival rate is depicted as a heavy dark line, and solid light lines encompass the 95% credible interval.

DISCUSSION

Our research demonstrates that reintroducing Gunnison's prairie dogs into the southern, semi-arid parts of their geographic range, where weather is highly variable and spring droughts are frequent, requires intensive management over a period of multiple years. Such efforts are needed to help colonies become established and prevent their extirpation, because in this variable, dry climate, populations of prairie dogs are vulnerable to extinction. Spring droughts, during March through June, are especially problematic because this is during the energetically-demanding periods of mating, pregnancy, and lactation (Rayor 1988, Clutton-Brock, 1989, Hoogland 2003). These findings are similar to those found for black-tailed prairie dog colonies reintroduced into desert grasslands (Facka et al. 2010).

Prairie dog densities at our site ranged from 3 to 11 animals/ha, when the population was not being augmented with additional releases. These densities are similar to the reported typical densities for Gunnison's prairie dogs of <7 animals/ha, including from an arid site in Arizona at 8.6 animals/ha (Hoogland 1995, 1999). Natural densities of Gunnison's prairie dogs vary greatly across the different habitats where they occur, however, and reported densities from montane habitats have been as high as 50–70 animals/ha (Longhurst 1944, Rayor 1985*a*, Cully et al. 1997). Indeed, maximum prairie dog densities at our site were less than half of the estimated adult and juvenile Gunnison's prairie dog densities from 2 ongoing studies within montane habitats of northern New Mexico (C. L. Hayes, University of New Mexico, unpublished data; J. L. Hoogland, The University of Maryland, unpublished data). Notably, our approach of releasing 100 animals to each 1-ha plot resulted in artificially high densities at the start of our study, which leveled-out over time to more natural densities for our system. Future release strategies might consider reintroducing animals at more natural, but still high, densities across a larger landscape that more closely mimics a natural colony setting.

Survival rates at our study site were low, with estimated mean survival after the initial establishment period at about 26%. In naturally occurring Gunnison's prairie dog colonies, adult survival rates typically range from about 30% to 50% (Rayor 1985*b*, Cully et al. 1997, Hoogland 2001). Survival rates reported for reintroduced prairie dogs during the first few months following reintroduction have generally been high (40–80%; Bly-Honness et al. 2004, Dullum et al. 2005, Long et al. 2006), but longer term estimates (i.e., 1 or more years after reintroduction) of annual survival have varied from about 10% to 70% (Truett et al. 2001, Long et al. 2006, Facka et al. 2010, Nelson and Theimer 2012), underscoring the importance of long-term monitoring.

Survival was especially low (9–12%) during the first few years following initial reintroduction (Fig. 3C). This was probably due in large part to predation; we observed extensive predator activity across the study site during this period (Fig. 3A). This is not surprising, as animals were released at densities above carrying capacity, all were naïve to the environment at the Sevilleta NWR, and many had come from urban or exurban areas where they may never have encountered natural predators. Heavy predation is common during the first several years following prairie dog reintroductions that use artificial burrow systems, because prairie dogs have not yet constructed complex, deep burrows that help protect them from predation (Long et al. 2006, Shier 2006). This is especially true for hibernating species of prairie dogs, including Gunnison's, and is likely why marginal survival rates (when factoring out the precipitation effect) were lowest during the first few years following initial reintroduction and during the winter sampling periods of our study (Fig. 3C). Although many prairie dogs released during the first year may not survive, these animals are key to laying the groundwork of underground burrow systems. Impacts of predation may therefore be offset by establishing large numbers of prairie dogs across as large of an area as possible, and augmenting the populations in subsequent years, depending on the population status. These additional animals help replace those lost to predation and help develop the more complex burrow structure necessary to protect against predation.

All individuals captured during our study appeared in good health condition, but we only captured adults. Based on the apparent low offspring recruitment, we suspect that the population was not productive enough to offset population death rates, and population extirpation was likely circumvented only by subsequent release events. Food resource availability has a large effect on prairie dog offspring production (Garrett et al. 1982, Rayor 1985*b*, Hoogland 2006*a*, Yeaton and Flores-Flores 2006), and production and survival of offspring have been found to be near 0 in reintroduced black-tail colonies declining because of drought in the Chihuahuan Desert (Facka et al. 2010; A. D. Davidson, Institute for Wildlife Studies, unpublished data). Comparatively, reintroductions of black-tailed prairie dogs in more mesic sites in New Mexico and South Dakota show high survival of juveniles (approx. 37–60%) 1 year post-release (Long et al. 2006). These studies, along with ours, illustrate the importance of environment in reintroduction success, which likely transcends inherent behavioral differences among prairie dog species.

Our study site had one of the highest abundances of prairie dogs within the Sevilleta NWR in the 1960s, prior to when they were exterminated and before the establishment of the Sevilleta NWR (J. Ford, personal communication). Gunnison's prairie dog colonies also currently occur naturally in the area surrounding the Sevilleta NWR, within kilometers of our study site. So, our study site is well within both the historical and current geographic range of Gunnison's prairie dogs. But, because this location is on the southern edge of their range, in a region that is becoming increasingly arid with climate change (Gutzler 2013), reintroductions in this region will likely require more intensive management to establish populations successfully, compared to locations with more plentiful food resources or where climatic conditions are less marginal (Truett et al. 2006, Facka et al. 2010).

Our findings beg the question whether or not managers should invest in reintroducing prairie dogs into the southern, semi-arid parts of their native range, given the high frequency of drought in this system and associated low survival. Our findings also raise the question of whether or not reintroduction efforts are viable in this region over the long-term, considering the climate in the area is warming. The American Southwest has warmed significantly already over the last several decades, including at the Sevilleta NWR (Gutzler 2013, Moore 2013). Temperature has steadily risen, which has already caused increasingly arid conditions and this trend is projected to continue (Seager et al. 2007, Gutzler 2013, Moore 2013). The answer to these questions remains to be determined, and requires long-term studies similar to ours (see also Facka et al. 2010). Nevertheless, reintroductions in these drier areas clearly need long-term management and dedication to be successful and avoid population extinctions.

Further, although prairie dogs in these lower elevation or southern parts of their range face the constraints of drought, those in more mesic environments farther north, and especially at higher elevations, experience greater frequency of sylvatic plague epizootics (Snäll et al. 2008; USFWS 2008, 2013; Johnson et al. 2011). The increased likelihood of plague outbreaks in the montane range of Gunnison's prairie dogs was the primary reason for originally designating these populations as warranting protection under the United States Endangered Species Act (ESA) in 2008, whereas prairie populations were not deemed in need of such conservation status (USFWS 2008). So although recently reintroduced Gunnison's prairie dogs thrive and rapidly expand in places such as Vermejo Park Ranch (VPR) in the montane habitat of northern New Mexico (Truett et al. 2006), unlike prairie dogs at the Sevilleta NWR, managers at VPR must dust the prairie dog burrows with insecticide (to kill fleas that carry plague) annually to prevent plague epizootics (D. Long, Turner Endangered Species Fund, personal communication). If prairie dog colonies are not dusted at such frequency in montane habitats, they often experience increased losses from sylvatic plague (Hoogland et al. 2004; D. Long, personal communication). So, both habitat types have their own set of management challenges. Note that we never dusted for plague on our Sevilleta NWR colonies. We do not suspect plague as the cause of population declines we observed because the declines did not follow the rapid die-off pattern typical of plague epizootics, and our model indicated the declines could be explained by drought during most years.

Our work not only provides the results of a long-term reintroduction experiment from a site in the semi-arid grasslands of central New Mexico, it also elucidates the population dynamics of Gunnison's prairie dogs, in the more arid portion of their range, which represents the prairie population (USFWS 2013). Populations in the prairie portion of the range, however, have not been considered at risk. The USFWS recently re-evaluated the conservation status of Gunnison's prairie dogs, to consider whether or not both recognized subspecies (generally corresponding to previous delineations of montane and prairie populations) warrant listing under the ESA (USFWS 2013). The USFWS concluded that neither population warrants protection under the ESA because of new information from population surveys and the ability to locally control plague outbreaks in highly managed situations (USFWS 2013). However, we provide new information showing clearly that prairie dogs in the lower elevation and southern part of their range are threatened by drought, which occurs with high frequency in this region. Our findings also are consistent with long-term prairie dog (*Cynomys* spp.) population declines observed elsewhere in the American Southwest and northern Mexico, related to drought (Ceballos et al. 2010; A. D. Davidson, unpublished data). Such stresses by climate are only predicted to increase with continued climate warming (Seager et al. 2007, Gutzler 2013). Consequently, we conclude that Gunnison's prairie dogs are highly threatened by drought within the southern, prairie portion of their range, compounding impacts from plague and other threats.

MANAGEMENT IMPLICATIONS

Reintroduction efforts should aim to establish large numbers of prairie dogs over extensive areas of grassland habitat in order for prairie dogs to play their functional role (Jachowski et al. 2011, Davidson et al. 2012). Small or low-density colonies may be insufficient to support associated species or ecosystem function of prairie dog colonies (Lomolino and Smith 2003, Proctor et al. 2006, Davidson et al. 2012, Miller and Reading 2012). Our results demonstrate that relocation in the more arid parts of their range may not successfully mitigate the loss of prairie dog colonies and ecosystem function that could otherwise be achieved through in situ conservation. Although prairie dog reintroductions are an important component of grassland conservation, they are intensive, costly, and ultimately small-scale. Our findings emphasize the importance of maintaining and expanding naturally occurring prairie dog colonies wherever possible, especially in the drier parts of their range, and implementing conservation incentives where needed to achieve these goals (Andelt 2006, Davidson et al. 2012).

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