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REPRODUCTION BY BLACK-TAILED PRAIRIE DOGS AND BLACK-FOOTED FERRETS: EFFECTS OF WEATHER AND FOOD AVAILABILITY

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ABSTRACT.—Food availability is one of the most important factors influencing reproduction in mammals. Reproductive success of some species can be negatively affected when body reserves are depleted during long periods of adverse weather conditions. We investigated the relationship of forage availability and weather variables on reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) and the effects of black-tailed prairie dog reproduction on reproduction by black-footed ferrets (*Mustela nigripes*), a prairie dog specialist predator. Prairie dogs draw on stored energy reserves to support reproduction (i.e., capital breeding), while ferrets likely rely on availability of prey during the reproductive period (i.e., income breeding). We expected that productivity of prairie dogs would positively correlate with precipitation during the previous summer and availability of spring forage and that harsh winter conditions would negatively affect reproduction. We also expected that productivity of ferrets would be positively correlated with productivity of prairie dogs because of the net increase in available prey during the ferret's litter-rearing season and because female ferrets might selectively prey on juvenile prairie dogs. At 2 sites in South Dakota during 2008–2010, reproduction by prairie dogs was most strongly influenced by precipitation received during the previous year and especially by winter severity. Harsh winter conditions resulted in a marked decline in reproduction during 2010. Although reproduction by ferrets varied little across years of our study, the success of long-term conservation and reintroduction strategies for the endangered black-footed ferret could be influenced by climate-driven changes in prairie dog reproduction.

RESUMEN.—La disponibilidad de alimento es uno de los factores más importantes que influye en la reproducción de los mamíferos. Sin embargo, el éxito reproductivo de algunas especies puede verse afectado negativamente cuando las reservas corporales se agotan durante períodos largos de condiciones climáticas adversas. Investigamos la relación entre la disponibilidad de forrajeo, variables climáticas, la reproducción de los perros de las praderas de cola negra (*Cynomys ludovicianus*), y la reproducción de los hurones de patas negras (*Mustela nigripes*), un depredador especialista de perros de la pradera. Los perros de la pradera utilizan sus reservas energéticas para su reproducción (o sea, reproducción por capital), mientras que los hurones, probablemente, se basan en la disponibilidad de presas durante el período reproductivo (o sea, reproducción por ingresos). Esperábamos que la productividad de los perros de la pradera se correlacionara positivamente con las precipitaciones durante el verano anterior y la disponibilidad de forrajeo en primavera, y que las condiciones invernales extremas afectaran negativamente la reproducción. También esperábamos que la productividad de los hurones se correlacionara positivamente con la productividad de los perros de las praderas debido a que el incremento neto de presas disponibles durante la temporada de cría de camadas de hurones, y porque los hurones hembra podrían cazar selectivamente a los perros de la pradera juveniles. En 2 sitios de Dakota del Sur, durante 2008–2010, la reproducción de perros de la pradera fue influenciada fuertemente por las precipitaciones ocurridas durante el año anterior y, especialmente, por la severidad del invierno. Las condiciones invernales tan duras dieron lugar a un descenso marcado en la reproducción durante el año 2010. A pesar de que la reproducción de los hurones varió a lo largo de los años de nuestro estudio, las estrategias de conservación y reintroducción a largo plazo del hurón de patas negras en peligro de extinción podrían estar influenciadas por los cambios en la reproducción de los perros de la pradera inducidos por el clima.

Food availability is one of the most important environmental factors influencing reproduction in mammals, and it acts both as a proximate and an ultimate cause of annual variation in reproductive output (Bronson 1989). Animals that support reproduction with energy stored from food consumed prior to the breeding season are considered capital breeders (Drent and Daan 1980, Houston et al. 2007), and individuals with larger energy reserves upon initiation of reproduction tend to have greater reproductive success (Prop and Black 1998). In contrast, income breeders immediately use energy from food to support reproduction (Drent and Daan 1980, Houston et al. 2007), and they generally exhibit weak

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correlations between body condition and reproductive success (Andersen et al. 2000, Boyd 2000). Across mammals, breeding strategies fall along a capital–income continuum, and many species exhibit a mixed strategy whereby animals rely on a combination of capital and income resources throughout their reproductive periods (Thomas 1988, Jönsson 1997, Drent 2006).

For capital breeders, body reserves can provide an energetic buffer against challenging environmental or nutritional conditions that might occur during winter and early spring (Fauchald et al. 2004), but harsh winter weather can influence rates of reserve depletion (Stewart et al. 2005, Parker et al. 2009). Adverse winter conditions can negatively influence the nutritional status of female ungulates in north temperate regions (Adams 2005, Garroway and Broders 2005), resulting in smaller offspring at birth (Adams 2005, Couturier et al. 2009), delayed parturition, reduced postnatal growth and development (Rachlow and Bowyer 1991, Adams 2003), and reduced survival of neonates (Adams et al. 1995, Hamel et al. 2010). Reproductive success of smaller mammals also can be influenced by severe winter conditions. For example, prolonged snow cover decreased litter size and frequency of reproduction in yellow-bellied marmots (*Marmota flaviventris;* Van Vuren and Armitage 1991). Similarly, reproduction by Columbian (*Spermophilus columbianus*) and Belding's (*S. beldingi*) ground squirrels was negatively affected by late-winter and early spring snowstorms (Morton and Sherman 1978, Neuhaus et al. 1999). Indeed, frequency and duration of severe winter conditions can be important drivers of population dynamics in many mammal species (Gaillard et al. 2000, Patterson and Power 2002).

Prairie dogs (*Cynomys* spp.) are colonial ground squirrels that rely on energy reserves gained during the autumn for reproduction during the subsequent spring. One of the most important factors affecting their annual reproductive success is the body mass of adult females (Hoogland 2001). Body mass of adult female prairie dogs is closely associated with the quantity and quality of available forage (Wright-Smith 1978, Garrett et al. 1982, Rayor 1985, Travis and Slobodchikoff 1993, Hoogland 1995, Cully 1997). Body mass of female black-tailed prairie dogs (*C. ludovicianus*) during autumn was positively correlated with body mass during the next breeding season, and heavier females had higher reproductive success (Hoogland 1995). Annual reproductive success often is estimated by the number of juveniles that emerge from natal burrows (Hoogland 1995). Litter sizes of black-tailed prairie dogs counted in utero were positively correlated with precipitation received during the previous summer (Knowles 1987), which also suggests that forage availability during the previous growing season influenced reproductive success. These relationships suggest that on the capital–income breeding continuum, prairie dogs appear to be most closely associated with capital breeders. However, if prairie dogs use a mixed strategy, which is typical of most species that rely on capital resources during reproduction (Mainguy and Thomas 1985, Meijer and Drent 1999, Bowen et al. 2001, Gauthier et al. 2003, Fletcher et al. 2013), then availability of forage during lactation may also influence reproductive success.

Black-footed ferrets (*Mustela nigripes*) prey primarily on prairie dogs and are probably like other small mustelids, which store little body fat and show little seasonal variation in accumulation of fat (Sheets et al. 1972, Campbell et al. 1987, Buskirk and Harlow 1989, Harlow 1994). Limited fat reserves likely provide a benefit in maintaining the long, slim body shape required for hunting burrowing prey (Brown and Lasiewski 1972). Consequently, on the capital–income continuum, ferrets are likely income breeders, meaning that availability of prey during the reproductive period likely influences reproductive success. Young prairie dogs are especially important prey items to many predators including black-footed ferrets (Clark 1976, Hoogland 1981, Halpin 1983, Loughry 1987, Brickner et al. 2014). Recent research has suggested that adult female ferrets likely focus predation on juvenile prairie dogs while raising young (Brickner et al. 2014), which suggests a functional link between the reproductive success of ferrets and prairie dogs.

Understanding the effects of seasonal weather patterns on reproductive success of prairie dogs is important to the long-term conservation of prairie dogs and associated species, especially under changing climate conditions. Prairie dogs serve as ecosystem engineers and often are recognized as a keystone species in the grassland ecosystems of

North America (Miller et. al 1994, 2000, Kotliar et al. 1999, Davidson et al. 2012). Black-footed ferrets are extreme specialists that depend on prairie dogs for food and also use prairie dog burrows for shelter (Sheets et al. 1972, Campbell et al. 1987, Biggins 2006). A better understanding of factors that influence reproductive success of both prairie dogs and ferrets will assist managers in evaluating potential recovery strategies and reintroduction sites for black-footed ferrets, which are federally endangered mammals (USFWS 2013). Furthermore, knowledge about how weather influences the dynamics of the prairie dog and black-footed ferret system can facilitate integration of changing climate regimes into conservation strategies for both species.

We investigated relationships between seasonal forage availability, weather variables, reproduction of prairie dogs, and reproduction of ferrets. First, we hypothesized that productivity of prairie dogs would positively correlate with precipitation during the previous summer (Knowles 1987), as well as with availability of spring forage during the current year, and that harsh winter conditions would negatively affect reproduction. We used estimates of each of these variables at 2 study sites to model relationships between predictors and an index of prairie dog reproduction. Second, we hypothesized that productivity of ferrets would be positively correlated with productivity of prairie dogs because of the net increase in available prey during the ferret's litter-rearing season and because female ferrets might selectively prey on juvenile prairie dogs. We used 2 indices of ferret reproduction at one of our study sites to qualitatively examine this relationship.

METHODS

Study Area

We conducted our study on 2 native prairie grasslands, the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, located approximately 250 km apart in central and southwestern South Dakota, USA, respectively. At the Lower Brule Indian Reservation, our research was conducted on the Fort Hale Bottom prairie dog complex (Zone 14N, 469857 E, 4868645 N, NAD 83; hereafter, Lower Brule), located in a fragmented mixed-grass prairie dominated by western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), buffalograss (*Bouteloua dactyloides*), and needle-and-thread (*Hesperostipa comata*). The area is primarily used for livestock grazing, but production agriculture also is common. Black-footed ferrets were reintroduced to this site beginning in 2006 (USFWS 2013).

Our research at the Buffalo Gap National Grasslands occurred on the Heck Table prairie dog complex (Zone 13N, 699205 E, 4843996 N, NAD 83; hereafter, Buffalo Gap). The site is a mixed-grass prairie dominated by western wheatgrass, buffalograss, blue grama (*Bouteloua gracilis*), and plains pricklypear cactus (*Opuntia polyacantha*); and it is nearly devoid of tree and shrub species (Schroeder 2007, Livieri and Anderson 2012). Primary uses for the area are cattle grazing and recreation (Livieri and Anderson 2012). Ferrets were reintroduced to this site beginning in 1999 (Biggins et al. 2011).

Prairie Dog Reproduction

We captured and marked prairie dogs to develop a relative index of the ratio of juvenile : adult prairie dogs to characterize annual reproductive success. We conducted trapping within randomly selected 0.5-ha trapping plots during June–July 2008 and June 2009 at both study sites and also during June 2010 at the Lower Brule site. At Lower Brule, we established 4 trapping plots on each of the 7 prairie dog colonies that ranged in size from 9.3 to 207.7 ha ($\bar{x}$ = 58.1 ha), which resulted in sampling 1%–22% of the area of each colony. At Buffalo Gap, we established trapping plots on 2 prairie dog colonies, and the number of plots was proportional to the size of the prairie dog colony; we sampled 3% of each colony, with 16 plots on the larger colony (284.6 ha) and 12 plots on the smaller one (213.5 ha). Each plot contained 61 wire cage traps (Tomahawk Livetrap Company, Tomahawk, WI; Tru-Catch Traps, Belle Fourche, SD) baited with grain and molasses pellets and spaced 10 m apart in a 7 × 7 design. In areas with high densities of burrow openings, 12 additional traps were placed to minimize trap saturation. We prebaited plots 3 days prior to trapping, and we set and checked traps twice each day for 4 consecutive days and checked them once on the fifth day for a total of 9 trapping sessions. We marked prairie dogs on initial capture with hair dye in 2008, by clipping a toenail in 2009, and by clipping a toenail and applying individually numbered ear tags in 2010. To develop a relative index of reproductive success, we averaged the number of juvenile and adult prairie dogs captured on trapping plots within each prairie dog colony and expressed these calculations as a ratio.

Because ferret presence can influence numbers of prairie dogs on colonies, we classified colonies by whether or not they were occupied by female ferrets with litters during the summer or autumn seasons (Biggins et al. 2012). Female ferrets raising litters have elevated energetic requirements, resulting in higher rates of predation on prairie dogs (Biggins et al. 1993); consequently, females with litters should have a greater effect on the attributes of prairie dog populations than females without litters or male ferrets. We did not attempt to estimate ferret densities. Unoccupied colonies were those where female ferrets with litters were not detected.

Black-Footed Ferret Reproduction

We developed 2 indices to characterize the annual reproductive success of ferrets at the Lower Brule study site. We estimated litter size by recording the number of juvenile offspring observed with adult female ferrets during summer and autumn spotlight surveys (Biggins et al. 2006). We also estimated the ratio of juvenile : adult females captured and marked during spotlight surveys conducted during September and October of each year. Nighttime spotlight surveys were conducted from a vehicle with a roof-mounted spotlight, and prairie dog colonies were searched for the reflective eye-shine of ferrets (Biggins et al. 2006). We captured ferrets by using wire cage traps (91.5 × 10 × 10 cm) placed into burrow entrances. In a mobile laboratory setting, each captured individual was anesthetized with isoflurane and implanted with a passive integrated transponder (PIT; AVID® Microchip I.D. Systems, Folsom, LA). We recorded the sex and age class (juvenile or adult) of each ferret; adults were distinguished from juveniles by measuring the width of the upper canine teeth and by examining tooth coloration (Santymire et al. 2012). All procedures were approved by the University of Idaho Animal Care and Use Committee (Protocol #2008-26) and are consistent with guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

Weather Variables

We obtained weather data (temperature, average daily wind speed, snow depth, and precipitation) from the nearest automated weather stations to each study site (South Dakota Office of Climatology 2013). We calculated a prairie dog winter severity index (PDWSI) for each study site following an approach employed in other studies (e.g., Brinkman et al. 2005, Grovenburg et al. 2011) which uses the number of days with a maximum wind chill index of less than or equal to −12.0 °C and the number of days with ≥13.0 cm of snow on the ground. The wind chill index was calculated using the average daily wind speed and maximum daily temperature and was used instead of ambient temperature because wind can result in a substantial increase in heat loss (Bakken 1981) and reduced aboveground activity of prairie dogs (Severson and Plumb 1998). We calculated winter severity scores from 1 November to 15 March by assigning one point for each day the wind chill index or snow depth exceeded thresholds and 2 points for each day when both conditions exceeded thresholds. We categorized these values as mild (PDWSI < 40), moderate (PDWSI = 40–80), and severe (PDWSI > 80) and treated these as ordinal variables in our analyses.

We obtained precipitation data during the previous year's growing season for each study site. In northeastern Montana, in utero litter sizes of prairie dogs were correlated with the amount of precipitation received during June–September of the previous year (Knowles 1987). Because our study sites are located at more southerly latitudes where the growing season is longer, we used total precipitation that occurred during May–October of the previous year in our analyses (South Dakota Office of Climatology 2013).

Forage Availability

To evaluate the influence of food on the reproductive success of prairie dogs, we estimated an index of available forage on prairie dog colonies during the current year's growing season. We visually stratified colonies by plant community (forb or grass) and grouped colonies by general soil association units (USDA 2006) to account for variability in vegetative productivity associated with these variables. A total of 24, 1-m^2 plots per study site were randomly located within prairie

TABLE 1. Set of 11 *a priori* candidate models explaining reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008–2010.

Model	Variables[a]
1	Null (intercept only)
2	Previous year rain
3	Previous year rain + ferret presence
4	Previous year rain + winter severity
5	Spring forage
6	Spring forage + ferret presence
7	Spring forage + previous year rain
8	Winter severity
9	Winter severity + ferret presence
10	Winter severity + previous year rain + spring forage
11	Winter severity + spring forage

[a]Variables for models: previous year rain (total rainfall from 1 May to 31 October), winter severity (the number of days with a maximum wind chill index of less than or equal to −12.0 °C and the number of days with ≥13.0 cm of snow on the ground from 1 November to 15 March), ferret presence (prairie dog colonies with (1) or without (0) a maternal ferret), and spring forage (average biomass [$g \cdot m^{-2}$] available to prairie dogs May–June based on vegetation collected within plots).

dog colonies and distributed across strata in proportion to the area of colonies within each stratum at each study site. Exclosures were placed around the plots in mid-May of each year; and after approximately 5 weeks, vegetation within the exclosures was clipped at the ground surface, dried at 40 °C for 24 h, and weighed to estimate biomass of potential forage. Exclosures were approximately 30 cm high and constructed of expanded metal (4 sides and top cover), which prevented all herbivores (e.g., prairie dogs, livestock) from grazing in plots.

Statistical Analyses

We modeled factors that potentially influence reproductive success of prairie dogs by using a mixed linear model that included a repeated measure on colony (PROC MIXED in SAS 9.3; SAS Institute Inc., Cary, North Carolina). We constructed a set of 11 *a priori* candidate models (Table 1) representing multiple hypotheses and evaluated them using an information theoretic approach, with models ranked via Akaike's information criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). Models within $\Delta AIC_c \leq 2$ of the best model were considered competing models. We calculated Akaike weights (w_i), the probability that the *i*th model is the best approximating model among all candidate models, and determined the 95% confidence set of models (Burnham and Anderson 2002). For models within the 95% confidence set, we calculated the relative importance weights for each parameter.

RESULTS

Prairie dog reproduction varied across years in a similar pattern at both study sites. Reproduction was markedly higher at both sites in 2009 than in 2008 and was lowest at the Lower Brule site during 2010. At Lower Brule, the relative index of juveniles to adults captured per colony ($n = 7$) averaged 0.56 juveniles : adults (range 0.30–0.86) in 2008, 0.97 (range 0.32–1.20) in 2009, and 0.20 (range 0.05–0.42) in 2010 (Table 2). At Buffalo Gap, the index on the 2 colonies that we monitored was 0.56 juveniles : adults (range 0.39–0.66) in 2008 and 0.81 (range 0.73–0.84) in 2009 (Table 2).

Estimates of available forage on prairie dog colonies varied markedly across years at the Lower Brule site, but less so at the Buffalo Gap study site. Dry weight biomass of potential forage at Lower Brule averaged 70.9 $g \cdot m^{-2}$ across 3 soil strata (range 56.8–96.4 $g \cdot m^{-2}$) during 2008, which was 1.5 times greater than the 2009 estimate and 2 times higher than the 2010 estimate (Table 2). In contrast, available forage estimates were more similar between years at the Buffalo Gap study site ($\bar{x}$ = 56.8 $g \cdot m^{-2}$ across 2 soil strata in 2008 and 44.5 $g \cdot m^{-2}$ in 2009).

Precipitation received during the previous year varied moderately among years, but values in all years were above long-term seasonal averages for both study sites. The Lower Brule site received 40.0, 49.0, and 42.4 cm of precipitation during May–October in 2007, 2008, and 2009 (Table 2), respectively, which was slightly above the long-term (1971–2006) average of 36.8 cm (South Dakota Office of Climatology 2013). A similar pattern of precipitation occurred at the Buffalo Gap site during our study. An estimated 33.7 and 48.7 cm of precipitation occurred during May–October of 2007 and 2008 (Table 2), respectively, and the long-term average was 31.7 cm (South Dakota Office of Climatology 2013). In contrast to summer–fall precipitation, winter conditions varied considerably between study sites. At Lower Brule, winters were mild, moderate, and severe in 2007–2008, 2008–2009, and 2009–2010, respectively; but winter conditions at Buffalo Gap were classified as mild during both years of our study (Table 2).

TABLE 2. Reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) and factors used to model prairie dog reproduction on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008–2010. Numbers of adults, juveniles, and juvenile : adult ratios are the mean values (SE) of individuals captured within 1-ha live-trapping plots at each study site. Forage biomass is an estimate of forage available (SE) on prairie dog colonies at each site during May–June based on vegetation collected within plots. Previous year rain is the total rainfall received from 1 May to 31 October. Winter severity is the number of days of severe weather categorized as mild (1), moderate (2), or severe (3).

	Lower Brule			Buffalo Gap	
	2008	2009	2010	2008	2009
Adults	15.6 (1.5)	21.5 (1.9)	20.0 (2.0)	3.8 (0.7)	8.6 (1.1)
Juveniles	8.7 (1.4)	20.9 (3.1)	3.9 (0.8)	2.1 (0.5)	7.0 (0.9)
Juvenile : adult ratio	0.56 (0.07)	0.97 (0.11)	0.20 (0.05)	0.56 (0.16)	0.81 (0.26)
Forage biomass ($g \cdot m^{-2}$)	70.9 (9.4)	47.5 (7.0)	35.0 (5.3)	56.8 (6.0)	44.5 (6.9)
Previous year rain (cm)	40.0	49.0	42.4	33.7	48.7
Winter severity (days)	12 (1)	55 (2)	137 (3)	16 (1)	12 (1)

TABLE 3. Ninety-five percent confidence set of candidate models of factors influencing reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008–2010.

Model[a]	AIC_c	ΔAIC_c	w_i	$\sum w_i$	w_{best}/w_i
Winter severity + previous year rain	16.7	0	0.61	0.61	—
Winter severity	19.8	3.1	0.13	0.74	4.7
Null	19.9	3.2	0.12	0.86	5.0
Winter severity + ferret presence	20.8	4.1	0.08	0.94	7.8
Previous year rain	22.6	5.9	0.03	0.97	19.1

[a]The Akaike information criterion adjusted for small sample size (AIC_c), ΔAIC_c, Akaike weights (w_i), sum of Akaike weights ($\sum w_i$), and evidence ratios (w_{best}/w_i) are reported for each model. Variables for models: previous year rain (total rainfall from 1 May to 31 October), winter severity (the number of days with a maximum wind chill index of less than or equal to −12.0 °C and the number of days with ≥13.0 cm of snow on the ground from 1 November to 15 March), and ferret presence (prairie dog colonies with [1] or without [0] a maternal ferret).

Prairie dog reproduction was most strongly influenced by precipitation levels during the previous year and by winter severity during our study. The top-ranked model included both of these variables, had 61% of the Akaike weight (w_i), and was 4.7 times more likely (w_{best}/w_i) to be the best explanation for variation in prairie dog reproduction than the next best supported model (Table 3). The second model, which contained the variable for winter severity only, had a $\Delta AIC_c \geq 3.1$ and thus was not considered a competing model. Additionally, all 5 models in the 95% candidate set (except the null model) included either precipitation received during the previous year or winter severity. One model in the candidate set also included the variable for presence of ferrets, and none included the variable for forage availability, suggesting that these 2 parameters had less influence on prairie dog reproduction during our study.

Prairie dog reproduction was negatively affected by severe winter conditions and positively affected by precipitation received during the previous summer–fall growing season, and both of these parameter estimates were significant (Table 4). The relative importance value for winter severity ($R_i = 0.82$) was higher than the value for previous year's rain ($R_i = 0.64$), suggesting that harsh winter conditions had a greater effect on reproduction by prairie dogs during our study than the influence of rainfall during the previous growing season. The inclusion of the null model with a ΔAIC_c of 3.2 in our 95% candidate set, however, suggests that the effects of the significant variables in the top model (previous year's rain and winter severity) were likely modest, given our ability to detect an effect. At Lower Brule, the previous year's rain increased 23% from 2008 to 2009, and the index of reproduction by prairie dogs increased by 73% between those years. During the same years at Buffalo Gap, precipitation increased 45%, and the index of reproduction by prairie dogs similarly increased by 45%. Winter conditions were characterized as mild and moderate during this period at Lower Brule and mild during both of these years at Buffalo Gap. In contrast, reproduction by prairie dogs at Lower Brule in 2010

TABLE 4. Parameter estimates for the best-supported model evaluating reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008–2010.

Variable[a]	$\hat{\beta}$ (SE)	95% CI
Previous year rain	0.0454 (0.0125)	0.019 to 0.072
Winter severity	−0.227 (0.0663)	−0.370 to −0.085

[a]Variables for models: previous year rain (total rainfall from 1 May to 31 October) and winter severity (the number of days with a maximum wind chill index of less than or equal to −12.0 °C and the number of days with ≥13.0 cm of snow on the ground from 1 November to 15 March).

(the year of the severe winter) was 79% and 64% lower than in 2009 and 2008, respectively.

We observed no qualitative decrease in the relative reproductive success of ferrets following low prairie dog reproduction at the Lower Brule site. Observed litter size of ferrets averaged 3.7 (n = 7), 3.3 (n = 6), and 3.7 (n = 7) in 2008, 2009, and 2010, respectively; and during those years, with similar effort, we captured and marked 2.4, 2.5, and 3.0 juvenile ferrets per adult female. These data suggest that a consistent number of juvenile ferrets were born annually during this period despite marked differences among years in reproduction by prairie dogs.

DISCUSSION

During our study, weather conditions were the primary factors that affected prairie dog reproduction. Our results support previous research indicating that precipitation received during the previous year is a significant factor affecting *in utero* litter sizes of prairie dogs (Knowles 1987). Although other research has suggested that persistent snow cover and cold temperatures can delay breeding in prairie dogs (Knowles 1987), we could find no other reports of substantial negative effects of harsh winter weather on prairie dog reproduction. Our research suggests that prairie dogs, like other capital breeders, can be markedly affected by variation in weather patterns across multiple seasons. This finding could be important for long-term persistence of populations, given changing precipitation and winter climatic conditions that are expected within the species' range (Melillo et al. 2014).

Our results also suggest that during mild and moderate winters, precipitation received during the previous summer and fall strongly influences reproduction by prairie dogs. During our study, precipitation at both study sites was at or above average for all years. During a study by Knowles (1987), precipitation ranged from drought conditions to record high rainfalls, and prairie dog productivity in that study was correlated with those extremes. Abundant rainfall received at our study sites should have provided adequate food resources to support high prairie dog productivity during all years of our study. Although precipitation received during the previous year might have the greatest influence on prairie dog reproduction during most years, the effects of severe winter conditions during our study appeared to trump the positive effects of abundant precipitation. We hypothesize that winter conditions likely have a threshold effect rather than an additive effect on the reproduction of prairie dogs, since the negative effects of winter conditions were not evident in our study until conditions were severe.

Prairie dogs in our study area are typically active year-round, but during one winter of our study they experienced severe cold and snowy weather that persisted for much of the winter season including early portions of the breeding season. Although we did not measure aboveground activity of prairie dogs during our study, we noted a distinct lack of such activity for 3–4 months during the winter of 2009–2010. Until recently, black-tailed prairie dogs were not thought to hibernate during the winter (King 1955, Bakko 1977, Bakko et al. 1988, Hoogland 1995). However, evidence has recently been published indicating that black-tailed prairie dogs exhibit a range of winter thermoregulation behavior. They can enter short, shallow bouts of facultative torpor induced by environmental conditions (Lehmer et al. 2001, 2003, Lehmer and Biggins 2005), as well as longer periods indicative of hibernation during severe drought conditions (Lehmer et al. 2006). Black-tailed prairie dogs that experience harsh winter conditions at the northernmost extent of the species' range are thought to hibernate during winter, and they do exhibit varied depths of torpor across years and among colonies, suggesting that annual and local variation in climate or microclimate influences torpor patterns (Gummer 2005). Based on the distinct lack of aboveground activity during an extended period of severe winter conditions, we believe that prairie dogs in our study area entered a prolonged torpor or hibernation.

While capturing prairie dogs in June 2010, we noted that many females were not lactating (i.e., had no visible teats), and those that were experienced delayed molting (many females were nearly hairless) and poor body condition (e.g., conspicuous rib and pelvic bones). These observations are noteworthy because when animals enter torpor, periodic arousals occur during which body temperatures return to normal, and this can be energetically costly (Wang 1979). Animals that store fat to survive prolonged periods of torpor or hibernation are limited in the number of arousals that occur (Thomas et al. 1990), and they risk exhausting fat reserves if the number of arousal periods are excessive (Jonasson and Willis 2011, 2012). The high prevalence of nonlactating females in our populations suggested that many females were in poor condition and either did not breed or did so and reabsorbed embryos, which has been documented previously in prairie dogs (Foreman 1962, Knowles 1987). Furthermore, individual body condition can affect molting (Hollister 1916, Hoogland 1995) such that individuals in poorer body condition molt later than those in better condition. Hoogland (1995) reported that lactating females typically have the poorest body condition and latest molting dates compared to other prairie dogs. Our observations suggest that prairie dogs during our study might have entered some level of torpor or hibernation during harsh winter conditions, which negatively affected body condition and subsequent reproduction.

The lack of a strong effect of spring forage on prairie dog reproduction lends support to the assertion that prairie dogs are capital breeders that rely on resources acquired prior to the breeding season to support reproduction. It is also plausible that adequate rainfall might have resulted in adequate forage such that forage was not a limiting factor for reproduction during our study. Regardless, this variable had less of an influence on reproduction than either previous year's rain or winter severity. More research is needed to better understand the importance of forage availability during the lactation and weaning periods on recruitment of prairie dogs into the breeding population.

Although there has been considerable debate about the effects of black-footed ferret predation on population dynamics of prairie dogs (Henderson et al. 1969, Hillman and Linder 1973, Biggins et al. 2012), the presence of maternal ferrets on prairie dog colonies did not strongly influence prairie dog reproduction during our study. We followed the approach of Biggins et al. (2012) and used a binary variable to indicate colonies that were occupied by a maternal ferret. A more robust analysis would evaluate the influence of ferret density; however, accurate estimates of ferret densities are difficult to obtain because of their semifossorial and elusive nature. Thus our assessment of the effect of ferrets should be interpreted with caution.

Indices of the relative reproductive success of ferrets varied little across all years of our study at Lower Brule, despite a 77% decrease in reproduction of prairie dogs in 2010 from the previous year. We expected that ferret reproduction would correlate with fluctuations in prairie dog reproduction because of changes in prey availability during the litter-rearing phase of ferret reproduction, an effect that has been reported for other specialist mustelids (King 1983, King et al. 2003). Furthermore, our prediction would have been bolstered if female ferrets selectively preyed on juvenile prairie dogs. Predators typically prey upon young, old, or sick individuals (Errington 1946, Slobodkin 1968, Curio 1976, Morse 1980); and a juvenile prairie dog is likely easier for a female ferret to kill than an adult prairie dog, which weighs about 2 times more than a female ferret (Anderson et al. 1986, Hoogland 1995). Recent investigations into the diet of ferrets using stable isotopes indicated that female ferrets selected smaller prey than males did, which suggests females might selectively prey on juvenile prairie dogs over adult prairie dogs (Brickner et al. 2014). Although our qualitative data did not support our prediction, a quantitative comparison of the age structure of prairie dogs within populations and ferret kills would provide a critical test of this hypothesis.

Regional conservation strategies are increasingly including provisions for system responses to changing climate patterns (e.g., Browne and Humburg 2010, Schrag 2011). Our results suggest that these considerations should be incorporated into conservation planning for the prairie dog–ferret system. Changing climatic conditions could adversely affect prairie dogs in the northern Great Plains due to severe periodic reductions in forage availability caused by an increased frequency of drought (Schrag 2011, Melillo et al. 2014). Hotter and drier summers coupled with severe winter weather could reduce viability of prairie dogs in some areas; and because black-footed ferrets are inextricably linked to prairie dogs, long-term conservation for this endangered mammal also might be affected. Understanding and anticipating such changes could help guide conservation planning for prairie grassland ecosystems and, specifically, selection of future reintroduction sites for black-footed ferrets.

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