

INVESTIGATION OF FACTORS AFFECTING BLACK-FOOTED FERRET LITTER SIZE

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ABSTRACT.—Understanding factors that influence recruitment can improve wildlife conservation. Endangered black-footed ferrets (*Mustela nigripes*) rely on prairie dogs (*Cynomys* spp.) for food and on prairie dog burrows for shelter. We hypothesized that younger female ferrets with greater densities of prairie dogs in their core use area and fewer adult ferrets in their respective prairie dog colony, would produce more kits due to age-dependent productivity, increased food resources, and decreased competition. We used generalized linear mixed-effects regression and Akaike's information criterion adjusted for sample size (AIC_c) to rank models relating adult female black-footed ferret litter size (range 1–7 kits, $n = 24$ litters) to female age, core area density of prairie dogs, and adult ferret densities from 3 sites in the USA, 2005–2008. We included year and site as random effects in all models. We observed great model uncertainty; the null model was most supported and received 44% of model weight (w). The next best-supported model included ferret density only ($\Delta AIC_c = 1.55$, $w = 0.20$). Ferret density may not have been great enough to negatively affect prey acquisition and litter sizes. Mean litter size did not vary among female ages, but inference was limited because only one individual was >3 years old ($\bar{x} = 2.13$ years, $SD = 0.99$). All adult females produced kits, suggesting that the observed minimum prairie dog density in ferret core use areas (12.3 individuals \cdot ha⁻¹) was above a threshold of minimal prey abundance for reproduction. Our findings support previous selections of reintroduction sites as those meeting minimum resource needs of individual ferrets for reproduction. Future selections of reintroduction sites may become more difficult if the number of areas with the minimum necessary prairie dog density decreases due to disease and reductions in habitat availability.

RESUMEN.—El comprender los factores que influyen en el reclutamiento puede mejorar la conservación de la vida silvestre. El hurón de pies negros (*Mustela nigripes*), que se encuentra en peligro de extinción, se alimenta de perritos de la pradera (*Cynomys* spp.) y utiliza sus madrigueras para protegerse. Proponemos la hipótesis de que los hurones hembra jóvenes con mayores densidades de perros de las praderas en su zona núcleo de actividad, y con menores hurones adultos en su respectiva colonia de perros de las praderas, producirán más crías debido a la productividad dependiente de la edad, a la disponibilidad de más alimento y a menor competencia. Utilizamos modelos lineales generalizados mixtos y el Criterio de Información de Akaike, que se adaptó al tamaño de la muestra (AIC_c), para clasificar los modelos que relacionan el tamaño de la camada de las hembras adultas (promedio: 1–7 crías, $n = 24$ lechos) con la edad de las hembras, la densidad en la población de perritos de la pradera en la zona núcleo, y las densidades de la población de hurones adultos de tres lugares de los Estados Unidos de América (EE. UU.), entre los años 2005 y 2008. En todos los modelos incluimos el año y el lugar como efectos aleatorios. Observamos que hay una gran incertidumbre en relación con los modelos; el modelo nulo fue el más apoyado y recibió el 44% de apoyo relativo (w). El siguiente mejor modelo sólo incluyó la densidad de la población de hurones ($\Delta AIC_c = 1.55$, $w = 0.20$). Es posible que la densidad de la población de hurones no haya sido lo suficientemente elevada como para afectar la obtención de presas y el tamaño de camadas de manera negativa. El tamaño medio de camada no presentó variaciones entre hembras de distintas edades, pero la inferencia fue limitada debido a que sólo un individuo de la especie era mayor de 3 años (promedio = 2.13 años, $SD = 0.99$). Todas las hembras adultas tuvieron crías, lo cual sugiere que la densidad mínima de 12.3/ha en la población de perritos de la pradera, que se observó en las áreas de influencia de los hurones, estaba por encima del umbral de abundancia mínima de presas para la reproducción. Nuestros hallazgos confirman la selección previa de sitios de reintroducción, que cumplen con las necesidades mínimas de recursos que los hurones necesitan para reproducirse. La futura selección de sitios de reintroducción puede resultar más difícil si la cantidad de áreas con la densidad mínima necesaria de población de perritos de la pradera disminuye debido a enfermedades y a menor disponibilidad de hábitat.

Compared to species with greater abundances, threatened and endangered species are less likely to withstand declines in population size. This characteristic makes offspring

recruitment of increased importance in sustaining viable populations of these imperiled species (Comizzoli et al. 2009). Accordingly, some recovery plans for endangered species

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include captive breeding programs, which provide animals for reintroductions designed to increase recruitment into small populations (Hoffmann et al. 2011). Understanding what resources are needed for an individual to achieve reproductive success would improve evaluation of suitable reintroduction sites and thereby improve population viability analyses and recovery efforts. However, resource requirements for viable reproduction are often unknown. By identifying the free-ranging individuals best able to survive and reproduce and then investigating their behaviors and characteristics, biologists could determine resource needs of a species and focus management actions toward increasing resource abundance and improving population viability.

The black-footed ferret (*Mustela nigripes*) was thought by some to be extinct until a small population was found in 1964 in Mellette County, South Dakota, USA. The species was listed as federally endangered in the USA in 1967 (USFWS 2008). It was again considered extinct in 1979, but another wild population was found in 1981 in Meeteetse, Wyoming, USA (USFWS 2008). This population also declined, and the 18 remaining animals were captured for protection and breeding (Jachowski and Lockhart 2009). Fifteen animals from this captive population bred, thereby beginning a recovery program that has since produced thousands of offspring reintroduced to a total of 20 sites in western USA; Saskatchewan, Canada; and Janos, Mexico (Biggins et al. 2011, Hoffmann et al. 2011, USFWS 2013a). Self-sustaining populations at some sites are positive signs for species recovery, yet the species remains federally listed as endangered (USFWS 2013b).

Availability of prairie dogs (*Cynomys* spp.) is imperative to black-footed ferret survival and recruitment (Sheets et al. 1972, Campbell et al. 1987). Black-footed ferrets rely almost solely on prairie dogs as food, and ferrets use prairie dog burrows for shelter and as den sites to raise kits (Sheets et al. 1972, Campbell et al. 1987). This dependency results in sympatric distributions of ferrets and prairie dogs (Biggins et al. 2006b). However, each prairie dog colony is a unique habitat (Hoogland 1995, Livieri 2007, Jachowski et al. 2008), and local food abundance, constraints on resource use (e.g., competition), and biological condition of ferrets might influence litter size. Litter size is

one important aspect of recruitment that can be observed in the wild (O'Shea et al. 2010). Prey abundance affects population-level recruitment in black-footed ferret congeners (i.e., *Mustela* spp.; Erlinge 1974, Fitzgerald 1977), and might affect litter size in ferret populations. Biggins et al. (1993) suggested that a minimum of 272.5 prairie dogs were required annually to support a black-footed ferret family group (0.5 adult males, 1 adult female, and 3.3 kits), with some prairie dog mortality also attributed to other predators. However, prairie dog distributions in colonies are patchy and temporally dynamic (Jachowski et al. 2008). Though ferrets select areas of highest prairie dog density (Jachowski et al. 2011, Eads et al. 2011b), some ferrets live in areas with lower prairie dog densities (Biggins et al. 1993), which may reduce litter sizes.

Intrasexual territoriality is a common mechanism in mustelids that assists individuals in maximizing availability of space and prey and in reducing prey depression (i.e., heightened antipredator responses by prey; Powell 1994). However, if ferrets are abundant in a colony, females may expend more energy defending their territory and, consequently, less time hunting. This trade-off may be detrimental to reproduction because though it might increase prey availability, it might also decrease efficiency of food acquisition and subsequently decrease body condition (Amsler 2010). Knowing how ferret density influences ferret litter size might improve our understanding of the space needs of this species (Sergio and Newton 2003). For captive adult females older than one year, litter size decreased with increased female age, and the most productive individuals were ≤ 3 years old (Williams et al. 1991, Marinari and Kreeger 2006). Similarly, Hanson (1947) found that mink (*Neovison vison*) litter sizes were greatest for 2-year-old females and declined for females older than 2 years. Thus, age could be an important predictor of black-footed ferret kit production.

Our goal was to assess effects of prairie dog density in ferret core areas, effects of ferret density, and effects of ferret age on individual litter sizes. Use of multiple metrics allowed comparison of the relative importance of each metric to variation in litter size. We hypothesized that younger female ferrets with greater core area density of prairie dogs and lesser ferret density in their respective prairie dog

colony would have larger litters due to greater age-related productivity, greater food resources, and less competition.

METHODS

Data were collected from 3 black-tailed prairie dog (*Cynomys ludovicianus*) colonies at Locke subcomplex (445 ha) on the UL Bend National Wildlife Refuge (NWR), Montana, during 2006 and from 2 colonies in Conata Basin, South Dakota, including North Exclosure (227 ha) during 2005–2006 and South Exclosure (452 ha) during 2007–2008 (452 ha) (Jachowski et al. 2008, 2010, 2011, Eads et al. 2011a, 2011b). The UL Bend NWR comprises 22,682 ha within Charles M. Russell NWR that consist of sagebrush (*Artemisia* spp.) grassland transitioning through ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*) forest to river-bottom forests of Great Plains cottonwood (*Populus deltoides monilifera*) and sandbar willow (*Salix exigua*). Vegetation in Conata Basin, a 29,000-ha mixed-grass prairie, is dominated by western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), and buffalograss (*Buchloe dactyloides*), with cottonwood trees dispersed among seasonal water drainages that align many of the prairie dog colonies, including our study colonies (Poessel et al. 2011).

We used data from 24 black-footed ferret litters, including numbers of kits per litter, UTM locations of individual ferrets, and UTM locations of prairie dog burrow openings to model relationships between these potential explanatory variables and ferret litter size. Data comprised 3 ferrets (3 litters) in the UL Bend, Montana, colonies; 6 ferrets (8 litters) in the North Exclosure colony (Jachowski et al. 2011) in Conata Basin, South Dakota; and 11 ferrets (13 litters) in the South Exclosure colony in Conata Basin, South Dakota (Eads et al. 2011b). Ferrets were located by spotlighting for eyeshine from a vehicle along a predetermined route (Eads et al. 2012). Ferrets were identified by unique dye coloration on the nape of the neck or implanted passive integrated transponders read with an AVID[®] Microchip I.D. Systems (AVID, Norco, CA, USA) automated reader loop antenna placed around the openings of burrows occupied by ferrets (Biggins et al. 2006a). A relocation of each ferret was attempted on nearly consecutive nights from

June to October each year (Eads et al. 2012). Ferret locations were recorded using a hand-held GPS accurate to ≤ 15 m (Eads et al. 2011b).

After birth, black-footed ferret kits remain with their mother until about early September (Paunovich and Forrest 1987, Forrest et al. 1988). During June–August, we occasionally observed an adult female above ground with her kits, either carrying each kit in succession to a new burrow or leading the kits in a line to a new burrow. If we observed a female ferret above ground with kits, we initiated a focal observation to count kits (although a few counts were derived from video footage; Jachowski 2007). We accumulated >2 kit counts for each adult female, and the maximum kit count served as our index of minimum kit production. Minimum counts provide a relative index of kit production by different female ferrets, and such counts have been used in several studies (e.g., Forrest et al. 1985, 1988, Grenier et al. 2009).

Prairie dog burrows were surveyed during July–September 2005 in the UL Bend and North Exclosure colonies and during 2007 in the South Exclosure colony (Jachowski et al. 2008, Eads et al. 2011b). Open burrows were classified as active or inactive by determining presence of black-tailed prairie dogs or recent sign from these rodents (e.g., digging or fresh feces; Biggins et al. 1993, Dullum 2001). Burrow locations were recorded using an ATV-mounted GPS (Matchett 1994, Jachowski et al. 2008).

We used locations of openings to prairie dog burrows to estimate colony boundaries in ArcMap 9.3.1 (Environmental Systems Resource Institute, Redlands, CA) by placing a 20-m buffer around all burrow openings, merging them into one polygon, and using a negative buffer to reduce the polygon margin by 20 m (Eads et al. 2011b). We used ferret locations ($n \geq 30$) to estimate individual 95% fixed-kernel utilization distribution (UD) home ranges (Millsbaugh et al. 2006) by using plug-in bandwidth selection (Gitzen et al. 2006) and the Kde folder (Beardah and Baxter 1995) in MATLAB (The MathWorks Incorporated, Natick, MA). We used area independent methods (AIM; Seaman and Powell 1990) to determine each ferret's core area of use. Area-independent methods delineate areas of use that differ most from random space use, thus delineating areas of concentrated space use in home ranges.

TABLE 1. Data collected from 24 black-footed ferret (*Mustela nigripes*) litters in UL Bend, Montana (3 litters), and Conata Basin, South Dakota (North Exclosure, 8 litters; South Exclosure, 13 litters), USA, 2005–2008.

Variable and colony	Mean	SD	Range
Core area prairie dog density	46.87/ha	15.74	12.31–67.38
UL Bend	16.22	6.19	12.31–23.35
North Exclosure	49.50	10.73	26.38–57.99
South Exclosure	52.33	11.38	31.88–67.38
Density of adult ferrets in colony	0.027/ha	0.0055	0.014–0.032
UL Bend	0.014	—	—
North Exclosure	0.031	—	—
South Exclosure	0.028	—	—
Age of adult female ferrets	2 years	0.99	1–5
UL Bend	2	1.00	1–3
North Exclosure	2	0.93	1–3
South Exclosure	2	1.09	1–5
Litter size	3.17 kits	1.24	1–7
UL Bend	2.33	1.15	1–3
North Exclosure	3.00	1.07	1–4
South Exclosure	3.46	1.33	2–7

Such methods may be preferred to choosing an arbitrary UD percentage (e.g., 50%). We then clipped AIM core areas at prairie dog colony edges, because ferrets spend little time away from these colonies (Biggins et al. 2006b). We used density of active prairie dog burrow openings (burrows \cdot ha⁻¹) in each clipped core area to estimate core area densities of black-tailed prairie dogs (prairie dogs \cdot ha⁻¹) for each ferret by using the following equation: Prairie dog density = (0.179 \times Active burrow density)/0.566 (Biggins et al. 1993).

We used generalized linear mixed effects regression (function *glmer* in R; Comprehensive R Archive Network 2010) to measure the relationship of adult female ferret age (years), density of adult ferrets in each colony (ferrets \cdot ha⁻¹), and core area prairie dog density (prairie dogs \cdot ha⁻¹) with maximum number of kits observed with each adult female ferret in a single year. Additionally, we used year of observation and site as random variables in all models to account for autocorrelation within years and sites. Adult ferret density in each colony was calculated by Eads et al. (2011b) and Jachowski et al. (2011) by dividing number of adult ferrets detected in a colony by area of that colony. In general, we fit an *a priori* candidate set of 8 models, including all 7 combinations of predictor variables and a null model (with only a fixed predictor of 1 and random variables of site and year). We used Akaike's information criterion adjusted for sample size (AIC_c; Burnham and Anderson, 2002) and model weights (*w*) to rank models (package MuMIN in R). We calculated relative importance values

(RI; Burnham and Anderson 2002) and 90% confidence intervals (CI) for each predictor variable to show overall contribution of each variable to model weights. We used pseudo-R² values (Gelman and Hill 2007) to determine the goodness of fit of each model by using deviance ($-2 \times$ Log Likelihood) values: pseudo-R² = 1 – (deviance of fitted model/ deviance of null model).

RESULTS

Variation in litter size and predictor variables was observed (Table 1); however, there was considerable model uncertainty. The null model was most supported (AIC_c = 18.20, *w* = 0.44) and the second most supported model included ferret density only (Δ AIC_c = 1.55, *w* = 0.20; Table 2). Pseudo-R² values indicated poor overall model fit (range 0.000–0.181; Table 2). We failed to detect relationships between litter size and ferret age, ferret density in the colony, or core area prairie dog densities, as 90% CIs of model parameters included zero (Table 3). Using relative importance values, ferret density was the most supported predictor variable (RI = 0.32; Fig. 1), followed by age and core area prairie dog density.

DISCUSSION

The independent variables under the range of conditions evaluated were poor predictors of black-footed ferret litter size. Density of prairie dogs in ferret core use areas was hypothesized to have a positive effect on litter

TABLE 2. Model-fitting results for prediction of litter size in black-footed ferrets (*Mustela nigripes*) in UL Bend, Montana, and Conata Basin, South Dakota, USA, 2005–2008.

Model ^a	K	AIC _c	ΔAIC _c	w	Pseudo R ²
Null	3	18.20	0.00	0.44	—
Ferrets	4	19.75	1.55	0.20	0.124
Age	4	20.83	2.63	0.12	0.025
CorePD	4	21.10	2.90	0.10	0.000
CorePD + Ferrets	5	22.34	4.14	0.06	0.181
Age + Ferrets	5	22.66	4.46	0.05	0.152
Age + CorePD	5	24.05	5.85	0.02	0.026
Age + CorePD + Ferrets	6	25.74	7.54	0.01	0.200

^aModels shown in rank order from most to least supported by AIC_c. Model components include adult female ferret age in years (Age), density of adult black-footed ferrets (individuals per ha) in each colony (Ferrets), and density of black-tailed prairie dogs (individuals per ha) in each ferret core use area, determined using the area independent method (CorePD).

TABLE 3. Linear model variables for predicting litter size of black-footed ferrets (*Mustela nigripes*) in UL Bend, Montana, and Conata Basin, South Dakota, USA, 2005–2008.

Variable ^a	Estimate ^b	90% CI ^b	Relative importance
Ferrets	29.53	−12.45–71.51	0.32
Age	0.06	−0.13–0.25	0.20
CorePD	0.00	−0.02–0.01	0.19

^aVariables ranked from most to least predictive according to relative importance as calculated by the sum of Akaike model weights. Variables include adult female ferret age in years (Age), density of adult black-footed ferrets (individuals per ha) in each colony (Ferrets), and density of black-tailed prairie dogs (individuals per ha) in each ferret core use area, determined using the area independent method (CorePD; see Seaman and Powell 1990).

^bEstimates and CI from model-averaging using all models including that variable.

size because black-footed ferrets prey almost exclusively on prairie dogs (Sheets et al. 1972, Campbell et al. 1987) and prairie dog abundance is expected to influence ferret reproduction (Biggins et al. 1993, 2006c). It has been proposed that increased food abundance leads to greater individual recruitment (Wauters and Lens 1995). However, we failed to detect a relationship between prairie dog densities in ferret core areas and ferret litter size (Fig. 1). This might reflect an abundance of prairie dogs at our study sites that exceeded minimum requirements by female ferrets. All adult female ferrets in these populations were observed with at least one kit, suggesting that prairie dog abundance at our study sites provided each female ferret the food resources necessary to reproduce and support birth and development of at least one offspring.

We hypothesized that younger female ferrets would produce larger litters than older females, but there was little variation in litter size among ages. However, only one ferret was >3 years old (litter size = 4 kits), which prevented observation of potential differences in

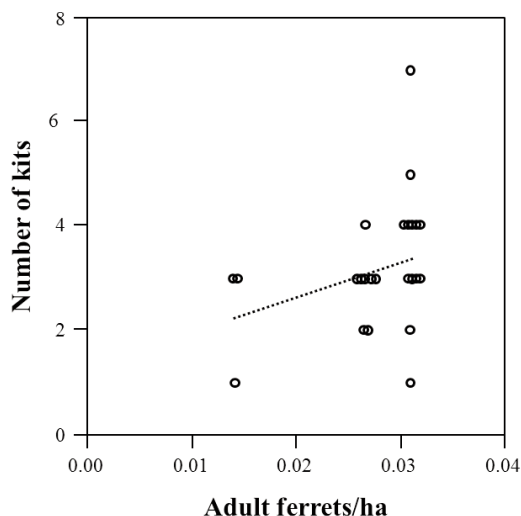


Fig. 1. Linear relationship between density of adult ferrets in each of 3 colonies (see Table 1) and numbers of kits observed with female ferrets for 24 ferret litters in UL Bend, Montana (3 litters), and Conata Basin, South Dakota (North Enclosure, 8 litters; South Enclosure, 13 litters), USA, 2005–2008. Data points are scattered along the x-axis; clusters of data points are for the same density of adult ferrets.

litter size between more productive-aged animals (≤ 3 years old) and those older than 3 years (Williams et al. 1991). Grenier et al. (2007) reported that only 25% of adult ferrets were >2 years old in a Wyoming population. Because most wild adult female ferrets are <4 years old (Forrest et al. 1988, Grenier et al. 2007), it will likely be difficult to detect an effect of age on litter size.

Investigating the variation in factors that may influence species reproduction could help us understand mechanisms of natural selection and phenotypic persistence. Such investigations

can also provide insight into how humans can conserve threatened and endangered species (Caro and Sherman 2011). However, we have demonstrated that variation in some resource-use metrics may not always relate to variation in animal fitness. Poor overall model fits suggest that our models lacked one or more predictor variables necessary to explain variation in litter size, or that variation in our predictor variables was insufficient to detect relationships with litter size. Though we had a relatively large sample size for a study on endangered black-footed ferrets, we still may have lacked the power to determine factors that influence variation in litter size. Further, only 3 of the litters were from the UL Bend population in Montana, whereas the rest were in the similar Conata Basin sites. This sampling condition possibly limited variability in our predictor variables to a narrower range than the full range of natural conditions.

Although support was weak, we detected a positive effect of ferret density on litter size, which effect contrasts our original hypothesis. The slight trend of greater ferret density correlating with greater litter size (Fig. 1) counters our prediction of increased competition leading to reduced litter size. This trend may also be an artifact of productive habitats being able to support ferrets that can produce more kits. However, variability in ferret density may have also been limited because ferret density was measured at the colony level and was therefore used only at the 3 levels of the study sites. Additionally, ferret densities at the 2 Conata exclosures were similar (Table 1), and small sample size ($n = 3$) from the UL Bend colony may have inhibited a lower ferret density from showing a stronger effect in our models.

We offer 4 recommendations for future studies that relate resource use to fitness. First, we encourage use of multiple indices or estimates of fitness (e.g., survival, breeding success, and lifetime and annual offspring production). Testing associations between these metrics may help improve investigations and assumptions of biological outcomes (Ayers et al. 2013). Second, investigations of variation in animal fitness should use multiple predictor variables to determine which variables are most influential on biological outcomes (Ayers et al. 2013). Third, we encourage investigations at multiple spatial scales to identify the scale most

pertinent to the species of interest (Gaillard et al. 2010). Fourth, studies should include sites with variability in resource abundance and heterogeneity to better relate fitness of the focal species to the range of habitat conditions experienced by that species (Aldridge and Boyce 2008). For example, the minimum threshold of prairie dog density needed to support individual black-footed ferrets, or ferret families, should be determined using field data to improve selection of reintroduction sites and recommendations for conservation efforts (Biggins et al. 2006c).

Knowledge of factors that limit reproduction would enhance conservation of threatened and endangered species like the black-footed ferret (Maxwell and Jamieson 1997, Andrabi and Maxwell 2007). Though we were unable to detect a significant relationship between prey density and litter size, our results do support selecting black-footed ferret reintroduction sites that contain black-tailed prairie dog densities of at least 12 individuals \cdot ha⁻¹ in ferret core areas (Biggins et al. 1993, 2006c). Though Biggins et al. (1993) modeled necessary prairie dog densities based on a 75-ha area of use by adult females, our results provide additional information on potential prairie dog densities necessary for kit production. Additionally, association of individual-level (i.e., ferret-level) prairie dog density with litter size at any spatial scale has not been published to our knowledge. However, additional characteristics of future reintroduction sites should be considered. For example, precipitation influences the abundance of aboveground vegetation, which seemingly influences prairie dog recruitment, thereby moderating prey availability to ferrets (Biggins et al. 2006c). In addition, diseases are important, particularly plague, a zoonosis caused by the primarily flea-borne bacterium *Yersinia pestis*. Plague can decimate populations of prairie dogs and ferrets (Biggins et al. 2011). Ensuring sufficient prairie dog abundance and understanding causes of juvenile ferret mortality will improve our ability to facilitate recovery of the endangered black-footed ferret.

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