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Original Article

Age-specific Survival of Reintroduced Swift Fox in Badlands National Park and Surrounding Lands

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ABSTRACT In 2003, a reintroduction program was initiated at Badlands National Park (BNP), South Dakota, USA, with swift foxes (*Vulpes velox*) translocated from Colorado and Wyoming, USA, as part of a restoration effort to recover declining swift fox populations throughout its historical range. Estimates of age-specific survival are necessary to evaluate the potential for population growth of reintroduced populations. We used 7 years (2003–2009) of capture–recapture data of 243 pups, 29 yearlings, and 69 adult swift foxes at BNP and the surrounding area to construct Cormack–Jolly–Seber model estimates of apparent survival within a capture–mark–recapture framework using Program MARK. The best model for estimating recapture probabilities included no differences among age classes, greater recapture probabilities during early years of the monitoring effort than later years, and variation among spring, winter, and summer. Our top ranked survival model indicated pup survival differed from that of yearlings and adults and varied by month and year. The apparent annual survival probability of pups (0.47, SE = 0.10) in our study area was greater than the apparent annual survival probability of yearlings and adults (0.27, SE = 0.08). Our results indicate low survival probabilities for a reintroduced population of swift foxes in the BNP and surrounding areas. Management of reintroduced populations and future reintroductions of swift foxes should consider the effects of relative low annual survival on population demography.

KEY WORDS apparent survival, capture–recapture, Cormack–Jolly–Seber, Program Mark, swift fox, *Vulpes velox*.

The swift fox (*Vulpes velox*) was once abundant throughout the Great Plains of North America (Egoscue 1979). The species declined dramatically by the late 1800s (Zumbaugh and Choate 1985), with much of this decline attributed to conversion of native prairie to agriculture, associated decline in prey species, unregulated hunting and trapping, and predator-control programs aimed at larger carnivores (Kilgore 1969, Egoscue 1979, Carbyn et al. 1994, Allardyce and Sovada 2003). The present distribution of swift fox extends from northern Montana in the United States and southern Canada southward including southern Wyoming, South Dakota, eastern Colorado, Nebraska, western Kansas, the Oklahoma panhandle, eastern New Mexico, and northern Texas (Carbyn 1998, Swift Fox Conservation Team 2000, Zimmerman et al. 2003).

The first successful reintroduction program for swift fox began in 1983 by the Canadian Wildlife Service and cooperators, who focused their efforts largely on private lands in Alberta and Saskatchewan, Canada (Carbyn et al. 1994). Several reintroduction programs were then initiated to restore swift fox populations in unoccupied habitat within their historical range. These reintroductions included the Blackfeet Reservation in Montana from 1999 to 2002 (Ausband and Foresman 2007), Fort Peck Reservation in Montana, and 4 reintroductions in South Dakota—Bad River Ranches (Turner Endangered Species Fund), Lower Brule Sioux Tribal Land (Lower Brule Sioux Tribe Department of Wildlife, Fish and Recreation and the Maka Foundation), Badlands National Park (BNP; Schroeder 2007), and Pine Ridge Indian Reservation in 2009–2010 (Oglala Sioux Parks Recreation Authority).

Estimates of age-specific survival are useful when evaluating the potential for population growth of reintroduced fox populations (Wood 1958). Both yearling and adult foxes are important contributors to population growth as both age classes reproduce and rear pups (Wood 1958). Similarly, yearlings are important for population recovery and range expansion because of their dispersal capability (Harris and Trewhella 1988, Ausband and Moehrenschlager 2009); thereby, contributing to maintenance of genetic diversity via transfer of genes across the distribution of the species. Pup

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survival is an indicator of the reproductive success of yearlings and adults, key contributor to the potential for population change, and representative of prey availability because pups primarily depend on the ability of their parents to obtain food (Messier and Barrette 1982, Coonan et al. 2000, Wright 2006). Our objective was to assess the fate of reintroduced populations of swift fox through survival estimation of various age classes. Thus, we estimated age-specific apparent survival rates of swift fox for a reintroduced population that included BNP and surrounding region of southwestern South Dakota.

STUDY AREA

Our study area included the Badlands National Park region of southwestern South Dakota. The 1,846-km^2 study area included the north unit of BNP and surrounding area (Schroeder 2007). Twenty-three percent of the area was managed by the USDI National Park Service, 34% was managed by USDA Forest Service, and 43% was privately owned; <1% of the study area was used for row-crop agriculture (Schroeder 2007). The major industry in the region was cattle production; thus, the majority of the study area outside of BNP was grazed by cattle (Schroeder 2007). Within BNP, moderate- to low-intensity grazing by bison (*Bison bison*) occurred in 52% of the north unit; substantial grazing did not occur within the remainder of the north unit (Schroeder 2007).

Soils of the Badlands National Park area were comprised of midway clay loam and relatively infertile with a low water-holding capacity (Whisenant and Uresk 1989). Mean annual temperature and precipitation in this region of South Dakota were 10.1° C and 40 cm, respectively (Fahnestock and Detling 2002), with dramatic seasonal variation typical of the continental climate. Minimum and maximum temperature varied between −40° C and 47° C. Topography of the region was diverse and elevation ranged from 691 m to 989 m above-mean-sea-level (Russell 2006, Schroeder 2007). The area within BNP was typified by highly eroded cliffs and spires >100 m in height. Outside BNP, the terrain was less rugged and typified by rolling prairies and relatively flat areas (e.g., Conata Basin: Russell 2006, Schroeder 2007). Vegetation in the region was dominated by short- and mixed-grass prairie species including buffalo grass (*Bouteloua dactyloides*), western wheatgrass (*Pascopyrum smithii*), and prickly-pear cactus (*Opuntia polyacantha*); the region was mostly devoid of tree and brush species (Russell 2006, Schroeder 2007). The Cheyenne and White rivers formed the western and southern boundaries of the study area, respectively.

METHODS

We live-trapped swift foxes during 2003–2009. However, we did not trap foxes during April 2004; April, May, July, and December of 2006; January, February, April, and December of 2007; January, March, November, and December of 2008; and January, March, April, June, and August of 2009. We captured swift foxes (both translocated and wild born) with modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.3 cm × 25.4 cm × 30.5 cm (Sovada et al. 1998), which we set in the evening and checked the following morning. We manually restrained foxes, determined sex, and recorded general body condition. We weighed captured swift foxes with a spring scale (model 80210; Pesola® Macro-Line Spring scale, Baar, Switzerland, EU) and determined age using tooth wear (Wood 1958). We fitted captured foxes with very-high-frequency radiotransmitters (model M1830, <40 g; Advanced Telemetry Systems, Isanti, MN, USA) and injected transponders (AVID ID Systems, Norco, CA, USA) between their shoulder blades. We identified individuals using the transponders, each of which had a unique identification number that could be determined with a reader. Our animal handling methods followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Protocols 08-A039, A3958-01).

We collected capture–recapture data on swift foxes for 76 months from April 2003 until July 2009. We developed annual capture histories beginning in April to better reflect the biological year of swift foxes. We used 3 age classes among foxes for our study. Foxes 3−12 months of age were classified as pups, 1−2 years of age were classified as yearlings, and those ≥2 years of age were considered adults. In our study area, breeding of foxes occurred between late February through March, and young foxes left dens at approximately 3 months of age to explore natal home ranges (G.M. Schroeder, unpublished data). Thus, pups were exposed for capturing from 3 months of age onward to when they approached adult size and became eligible for collaring.

We used the age formulation of Cormack–Jolly–Seber capture–mark–recapture models (Cormack 1964, Jolly 1965, Seber 1970) in Program MARK (White and Burnham 1999) to model apparent survival (φ) and recapture (P) probabilities. Apparent survival combines the probabilities of survival and not permanently emigrating. We modeled probabilities for 3 groups: adults, yearlings, and pups. We followed a sequential approach to model selection, which was our pragmatic attempt to deal with models with large numbers of parameters (Franklin et al. 2004, Anthony et al. 2006, McGowan et al. 2011). We first determined the best model structure for the recapture parameter while keeping apparent survival as general as possible. Although not the primary focus of our analyses, we had *a priori* hypotheses for recapture probabilities. We tested whether recapture rates differed by age class, between early and late capture periods (capture−recapture efforts in the first 3 years [2003–2004, 2004–2005, and 2005–2006] were greater than the capture−recapture efforts in the last 3 years [2006–2007, 2007–2008, and 2008–2009]), and among months where trapping was conducted less frequently during April and May than June, July, August, September, and October. We rarely trapped during November, December, and January.

After determining the model structure for the recapture probabilities, we then modeled apparent survival. We

Table 1. Number of wild born or released male (M) and female (F) swift foxes for 3 different age groups along with year of first capture among the 340 individuals used to construct the capture history for survival analysis from 2003 to 2009 at Badlands National Park, South Dakota, USA.

	2004		2005		2006		2007		2008		2009		
Age group	M	F	M	F	M	F	M	F	M	F	M	F	Total
Wild born													
Pups	8	10	2	1	17	17	29	34	27	31	14	18	208
Yearlings	0	1	6	7	0	0	2	0	0	0	0	0	16
Adult	3	2	0	0	2	3	1	6	1	0	0	0	18
Total	11	13	8	8	19	20	32	40	28	31	14	18	242

	2003		2004		2005		2006		
Age group	M	F	M	F	M	F	M	F	Total
Released									
Pups	0	4	2	1	5	5	7	11	35
Yearlings	0	0	1	1	3	7	0	1	13
Adult	15	11	3	6	5	4	2	4	50
Total	15	15	6	8	13	16	9	16	98

hypothesized that apparent survival varied by age, seasonally (winter [Oct through Feb], spring [Mar through May], and summer), gender, and between released and wild-born foxes. Additionally, we determined whether apparent survival varied for the month by year interaction.

We used Akaike's Information Criterion for small sample size (AIC_c; Akaike 1973) to select the most parsimonious model and considered models differing by ≤ 2 ΔAIC_c units from the selected model as potential alternatives (Burnham and Anderson 2002, Arnold 2010). There is no formal goodness-of-fit test for age-structured Cormack–Jolly–Seber models, so we evaluated model robustness by artificially inflating $\hat{c}$ (i.e., a model term representing over dispersion) from 1.0 to 3.0 (i.e., no dispersion to extreme dispersion; Devries et al. 2003, Barber-Meyer et al. 2008, Grovenburg et al. 2011). We used Akaike weights (w_i) as an indication of support for each model. We used the delta method (Seber 1982, Powell 2007) to estimate variance of annual apparent survival probabilities as the product of monthly estimates and their standard errors.

RESULTS

We captured 15 male and 15 female foxes from Colorado in 2003; 13 male and 16 female foxes from Colorado in 2004; 13 male and 16 female foxes in 2005 from Colorado; and 10 male and 16 female foxes in 2006 from Wyoming for translocation to BNP. We captured, marked, released, and subsequently recaptured 340 individual foxes over 7 years beginning September 2003 through October 2009 at BNP. Of the 340 individuals, there were 243 pups (132 M and 111 F), 29 yearlings (12 M and 17 F), and 68 adults (32 M and 36 F; Table 1). We obtained capture histories of 242 wild-born foxes and 98 released foxes at BNP (Table 1). We documented 149 mortalities of foxes in our study area during our study period of which 32 (21.5%) were coyote (*Canis latrans*) killed, 42 (28.2%) were due to vehicle collision, and 1 was snared (i.e., non-target trapped). We could not determine the cause-specific mortality for 74 (49.6%) foxes.

The best model for recapture probabilities was characterized by no difference among age classes, but was characterized by differences among years and seasons (Table 2). Specifically, recapture probabilities were greater in the early years (2003–2004, 2004–2005, 2005–2006) compared with the later years (2006–2007, 2007–2008, 2008–2009), and recapture probabilities were intermediate in April-May, lowest in November-January, and greatest in the "Remainder" (Jun–Oct, Feb–Mar periods of the year; Fig. 1). Other models we evaluated were not competitive with this model (i.e., $\Delta AIC_c > 44$ for all other models; Table 2).

We had 3 competing models for estimating swift fox survival (Table 3). Our top-ranked model indicated survival differed among pups, yearlings, and adults, with differences in survival by month and year. Our other 2 top models included either gender or whether the animals were released or wild born. However, these models had essentially the same deviance as our top model, with the addition of the 1 parameter and the 95% confidence interval for the coefficient for both gender and released or wild born overlapped zero.

Table 2. Ranking of 8 *a priori* models based on Akaike's Information Criterion results for determining the probability of recapture model structure for Cormack–Jolly–Seber models of apparent annual survival of swift foxes captured from 2003 to 2009 in Badlands National Park, South Dakota, USA. AIC_c—small sample unbiased Akaike Information Criterion, ΔAIC_c—differences in scores between each model and the best model, w_i—model weight, K—number of parameters in the model.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(year-early or year-late + A–M or N–D–J^d or remainder)	3,249.69	0.00	1.00	72	2,955.52
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(year-early or year-late + month)	3,293.72	44.03	0.00	81	2,913.95
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(year-early or year-late + N–D–J^e or remainder)	3,296.42	46.73	0.00	71	3,010.42
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(month)	3,567.93	318.24	0.00	80	3,198.90
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(pup or yearling = adult + month)	3,580.30	330.61	0.00	81	3,200.53
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(pup or yearling or adult + month)	3,591.35	341.66	0.00	82	3,200.48
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(.)	3,786.18	536.50	0.00	69	3,515.86
$\varphi^a(g \times t^c/g \times t^c/g \times t^c)$ p^b(pup or yearling or adult)	3,799.57	549.88	0.00	71	3,513.57

[a] Survival probability.
[b] Recapture probability.
[c] Group × time.
[d] Apr–May or Nov–Dec–Jan.
[e] Nov–Dec–Jan.

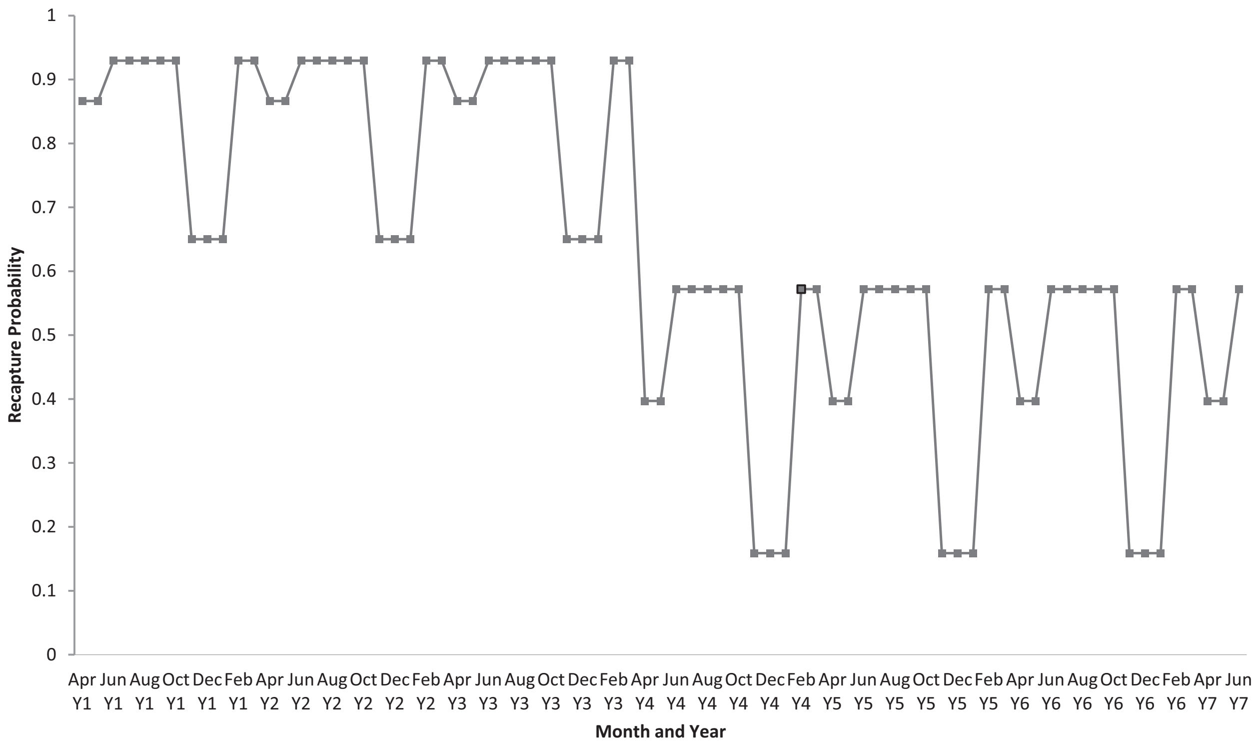

Figure 1. Recapture probabilities (combined over age classes) by month and year for swift foxes in Badlands National Park, South Dakota, USA, from 2003 to 2009. Recapture probabilities were greater in the early years compared to later years; recapture probabilities were intermediate in April–May, lowest in November–January, and greatest in the "Remainder" (Jun–Oct, Feb–Mar) time of the year. The *X*-axis represents month of a year starting with April of 2003 and ending in June of 2009 where Y1 = 2003, Y2 = 2004, Y3 = 2005, Y4 = 2006, Y5 = 2007, Y6 = 2008, and Y7 = 2009.

Table 3. Ranking based on Akaike's Information Criterion results of 20 *a priori* Cormack–Jolly–Seber models of apparent annual survival of swift foxes captured from 2003 to 2009 in Badlands National Park, South Dakota, USA. AIC_c—small sample unbiased Akaike Information Criterion, ΔAIC_c—differences in scores between each model and the best model, w_i—model weight, *K*—number of parameters in the model.

Model	AIC_c	ΔAIC_c	w_i	*K*	Deviance
φ[a](pup or yearling = adult + year + month) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,249.89	0.00	0.67	23	3,194.61
φ[a](pup or yearling = adult + year + month + gender) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,252.67	2.78	0.17	24	3,194.50
φ[a](pup or yearling = adult + year + month + released) *p*[b](year-early or year-late + A–M[c]/N–D–J[d] or remainder)	3,252.76	2.87	0.16	24	3,194.59
φ[a](pup or yearling = adult + month) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,367.18	117.30	0.00	17	3,328.29
φ[a](pup or yearling or adult + month) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,369.33	119.44	0.00	18	3,327.82
φ[a](month) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,375.16	125.27	0.00	16	3,338.84
φ[a](pup or yearling = adult + O–N–D–J–F[e] or remainder) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,376.27	126.38	0.00	7	3,361.44
φ[a](pup or yearling = adult + O–N–D–J–F[e] or M–A–M[f] or remainder) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,377.98	128.09	0.00	8	3,360.90
φ[a](pup or yearling = adult) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,390.79	140.91	0.00	6	3,3787.18
φ[a](pup or yearling or adult) *p*[b](year-early or year-late + A–M[c] or N–D–J[d] or remainder)	3,392.99	143.10	0.00	7	3,378.16

[a] Survival probability.
[b] Recapture probability.
[c] Apr–May.
[d] Nov–Dec–Jan.
[e] Oct–Nov–Dec–Jan–Feb.
[f] Mar–Apr–May.

We considered these parameters spurious (Burnham and Anderson 2002). All other models had $\Delta AIC_c > 100$ and, thus, were not competitive.

Our estimated apparent annual survival probability of pups (0.47, SE = 0.10) was nearly double the apparent annual survival probability of yearlings and adults (0.27, SE = 0.08) for 2003 to 2009 (Table 4). Apparent survival was greatest in the fourth year of study for both pups (0.75, SE = 0.05), and yearlings and adults (0.57, SE = 0.66); whereas, we observed lowest apparent survival estimates in both the first (pups = 0.20; adult or yearlings = 0.05) and last (pups = 0.16; ad or yearlings = 0.04) years of study for all 3 age groups of foxes. The survival trend was increasing in the first 4 years, after which it decreased for the last 2 years.

DISCUSSION

Reintroduction (or translocation) of species to areas from which they have become extirpated has increasingly been used in attempts to restore populations of endangered, threatened, or imperiled native wildlife (Sarrazin and Barbault 1996, Ostermann et al. 2001, Seddon et al. 2007). Translocation of foxes were carried out for the first 4 years (2003–2006) of our study period (2003–2009), which might explain the greater recapture probabilities in the early years of our study because the population was comprised of some individuals, new to the study area, that were struggling to establish territories, find mates, and procure food.

The pup-rearing period on our study site was from May to August followed by a dispersal period from September to October. Primary demand of foxes during the pup-rearing season is procurement of food (Strand et al. 2000) for which we documented the greatest recapture probability of foxes likely because trap bait provided an easily accessible food source. Moreover, dispersal tendency of individuals might have increased their recapture probability (Kamler et al. 2004). Pups in our study area were generally born between April–May, which might have restricted swift fox activity and movement (Kitchen et al. 2005) in our study area as was evidenced from the intermediate recapture probability during that period of time. November to January marked the pairing season of swift foxes in our study area during which individuals invested all their efforts and time for mate search (Kitchen et al. 2005); the lowest recapture probability for our study was documented during this period.

Table 4. Apparent annual survival estimates of pup, yearling, and adult swift foxes from 2003 to 2009 at Badlands National Park, South Dakota, USA.

	Pups		Adult and yearlings	
Year	Survival	SE	Survival	SE
2003–2004	0.20	0.07	0.05	0.03
2004–2005	0.62	0.08	0.39	0.08
2005–2006	0.48	0.07	0.24	0.05
2006–2007	0.75	0.05	0.57	0.07
2007–2008	0.59	0.06	0.35	0.05
2008–2009	0.16	0.05	0.04	0.01

Annual survival of adult swift foxes was similar to that of yearlings, but lower than survival of pups. In short-lived species, such as swift foxes, fecundity of adults is a critical factor in population growth. The average number of pups observed in our study area was nearly 5.5/pair of adult foxes (G.M. Schroeder, unpublished data). High fecundity in our study area probably compensated for the lower survival rates in adults and yearlings because high fecundity is necessary to increase population growth rate. Our estimate of survival rate of reintroduced foxes at BNP was lowest during the year following release, which might be the result of translocation stress (Armstrong and Seddon 2008). However, our study area was comprised of sparsely vegetated spires and generally rugged terrain of the badlands, which may have limited habitat for foxes (Sasmal et al. 2011). If habitat within BNP was limited, the swift fox population might have reached stability by saturating available habitats. Thus, foxes released within the park boundary would have a tendency to disperse out of the park to the surrounding area comprised of habitats such as black-tailed prairie dog (*Cynomys ludovicianus*) towns, sparse vegetation, and grasslands (Sasmal et al. 2011). This dispersal tendency of foxes might be responsible for the reduced survival rates of adults and yearlings in the last 2 years of our study because dispersal tendency also increases the chances of their exposure to predation and anthropogenic-induced mortality (Kamler et al. 2004, Russell 2006).

Environmental stress or conditions that affect survival of a species can be accounted for in a long-term study to estimate survival. Generally, survival rates for species serve as important demographic parameters to assess the viability of populations. Yet, survival rate alone is not sufficient to predict the future persistence of a population. Information on genetic diversity of reintroduced foxes at BNP and the surrounding area suggest that the reintroduced population has high genetic diversity comparable to source populations in Colorado and Wyoming (Sasmal et al. 2013). Viability of a population is not only dependent on deterministic processes, but also is influenced by stochastic processes, so long-term viability should be assessed through continual monitoring. The reintroduced swift fox population at Badlands National Park could result in restoring the population of this South Dakota threatened species.

MANAGEMENT IMPLICATIONS

Our study provides support for low survival probabilities of swift foxes in the reintroduced population at BNP and surrounding areas. Management of reintroduced populations and future reintroductions of swift foxes should consider the effects of relative low annual survival on population demography. These findings imply that to increase the survival rate of swift foxes managers should maintain habitat by manipulating the height of vegetation via grazing and/or mechanical methods like prescribed fire, and maintaining native grassland as well as prairie dog towns.

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