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POPULATION VIABILITY ANALYSIS OF SWIFT FOX (*VULPES VELOX*) AT

THE BADLANDS NATIONAL PARK

BY

Indrani Sasmal

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Major in Wildlife Biology

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2011

POPULATION VIABILITY ANALYSIS OF SWIFT FOX (*VULPES VELOX*) AT

THE BADLANDS NATIONAL PARK

This dissertation is approved as a credible and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Jonathan A. Jenks   Date
Dissertation Advisor

                                                         Date

Head, Natural Resource
Management Department

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ABSTRACT

POPULATION VIABILITY ANALYSIS OF SWIFT FOX (*VULPES VELOX*) AT THE BADLANDS NATIONAL PARK

Indrani Sasmal

December 2011

The swift fox *(Vulpes velox)* was historically distributed in southwestern South Dakota including the region surrounding Badlands National Park (BNP). The species declined during the mid-1900s due to habitat fragmentation, non-target poisoning, and harvest. A remnant population occurred on USDA Forest Service lands in Fall River County, South Dakota. Following the successful reintroduction of the species in Canada (1983), a reintroduction program was initiated in BNP in the year 2003. Free-ranging swift fox from Colorado and Wyoming were translocated to BNP from 2003 to 2006. Despite these releases and observations of free-ranging swift fox occurring throughout western South Dakota, it was not known if a viable population occurred in western South Dakota. My study objectives were: (1) To determine the age-specific survival of the reintroduced swift fox population at BNP and surrounding area, (2) to determine the genetic diversity of the reintroduced population at BNP and (3) to determine habitat selection of female swift fox during the pup-rearing period (May – July), and finally, (4) to determine the viability of the reintroduced swift fox population at BNP and surrounding area. Monthly apparent survival probability of

pups, yearlings, and adults was 0.88 (95% CI: 0.86-0.90), 0.90 (95% CI: 0.88-0.92),

and 0.93 (95% CI: 0.91-0.94), respectively, in our study area. Accordingly, the

annual apparent survival probability of pups, yearlings, and adults in our study area

was 0.22, 0.29, and 0.39, respectively. We measured genetic diversity of the

reintroduced swift fox population at BNP and surrounding area, and in an area of

Colorado and Wyoming from where swift foxes were translocated to BNP, as well as

the local swift fox population neighbouring BNP in Fall River County, South Dakota,

using 12 microsatellite loci in Program Fstat version 2.9.3. We obtained mean gene

diversity values of 0.778 (SD=0.156) for the Colorado population, 0.753 (SD=0.165)

for the Wyoming population, 0.751 (SD=0.171) for the BNP population, and 0.730

(SD=0.166) for the Fall River population. We obtained an F_{st} value of 0.029 for the

BNP and Fall River fox population, and an F_{st} value of 0.014 for the Colorado and

Wyoming fox populations. We also obtained an F_{st} value of 0.020 for the Colorado

and Fall River populations as well as an F_{st} value of 0.0246 for the Wyoming and Fall

River populations. Analyses of location data from 13 radiomarked lactating female

foxes indicated disproportional use ($P<0.001$) of some habitats relative to their

availability within swift fox home ranges. Swift foxes used grassland ($\hat{w} = 1.01$),

sparse vegetation ($\hat{w} = 1.4$) and prairie dog towns ($\hat{w} = 1.18$) in proportion to their

availability, whereas they were less likely to use woodland ($\hat{w} = 0.00$), shrubland ($\hat{w} =$

0.14), pasture/agricultural-land ($\hat{w} = 0.25$) and development ($\hat{w} = 0.16$) relative to

availability. Swift foxes typically are located in habitats that provide greater

visibility, such as shortgrass prairie and areas with sparse vegetation; which allow

detection of approaching coyotes (*Canis latrans*: primary predator of swift foxes).

We used Progam VORTEX 9.99b to assess the viability of the reintroduced swift fox

population at BNP and surrounding area incorporating data on the pedigree of the

initial population. According to our findings, the reintroduced swift fox population at

BNP had a 100% chance of extinction in the next 10 years with a negative growth

rate under current conditions. The sensitivity analysis showed mortality rate to be the

major cause of probability of extinction. Even a slight increase in survival (33% for

pups and 45% for adults) would be capable of maintaining a stable population with a

positive growth rate. The probability of population extinction, mean population size,

and genetic diversity are crude estimations obtained from data on diverse interacting

processes that are too complex to be integrated intuitively. Thus, the outcomes of this

PVA should be considered an attempt to identify the factors affecting the persistence

of the reintroduced population rather than using it to estimate accurate extinction

probabilities and genetic changes to the population. To ensure viability of the

reintroduced population, the survival rate of the foxes should be increased by

increasing availability of suitable habitat, increasing prey availability, and keeping

predators under control. Moreover, the population should be monitored periodically

to assess demographic rates and genetic diversity.

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Age-Specific Survival of Reintroduced Swift Fox in Badlands National Park and

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ABSTRACT

Badlands National Park (BNP) and surrounding area are located within the historic distribution of swift fox (*Vulpes velox*). The swift fox population in western South Dakota declined dramatically by the late 1800s and much of the decline was attributed to conversion of native prairie to agriculture and associated decline in prey species, unregulated hunting and trapping, and predator control programs aimed at larger carnivores. A total of 114 swift foxes were reintroduced at BNP from 2003 to 2006 as part of a swift fox restoration effort to recover the declining fox population throughout its historic range. Age-specific survival is an important demographic parameter used to measure the viability of reintroduced populations. We used 7 years (2003-2009) of capture-recapture data on swift fox at BNP and the surrounding area to construct Cormack-Jolly-Seber (CJS) model estimates of survival within a capture-mark-recapture (CMR) framework using Program MARK. We estimated monthly as well as annual apparent survival (φ) probabilities of pup, yearling, and adult swift foxes using capture histories of 243 pups, 29 yearlings, and 69 adults. Monthly apparent survival probability of pups, yearlings, and adults was 0.88, 0.90, and 0.93, respectively, in our study area. Annual apparent survival probability of pups, yearlings, and adults was 0.22, 0.29, and 0.39, respectively. Comparatively low annual apparent survival probabilities of age classes in our study area demands further study of the genetic and demographic aspects of the reintroduced population for assessing viability of the population.

INTRODUCTION

Swift foxes (*Vulpes velox*) were once abundant throughout the Great Plains of North

America (Egoscue 1979). The species declined dramatically by the late 1800s

(Zumbaugh and Choate 1985) and much of this decline was attributed to conversion of

native prairie to agriculture and 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 foxes includes a fragmented population extending from southern Wyoming

through eastern Colorado, western Kansas, eastern New Mexico, Oklahoma panhandle,

northern Texas, South Dakota and Nebraska, Canada, and Northern Montana (Carbyn

1998, Swift Fox Conservation Team 2000, Zimmerman et al. 2003).

The first successful reintroduction program for swift foxes began in 1983. The

Canadian Wildlife Service and cooperators began a swift fox reintroduction, focusing

their efforts largely on private lands in Alberta and Saskatchewan, Canada (Carbyn et al.

1994). Following the first reintroduction program in Canada, several reintroduction

programs had been initiated in an effort to restore swift fox populations to unoccupied,

yet suitable habitat within their historic range. These reintroductions include the

Blackfeet Reservation in Montana from 1999-2002 (Ausband and Foresman 2007), Fort

Peck Reservation in Montana, and four 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 in 2009-2010 the Pine

Ridge Indian Reservation (Oglala Sioux Parks Recreation Authority).

Estimates of age-specific survival are necessary to evaluate the potential for

population growth of reintroduced populations. Survival of age groups of swift fox, such

as pups, yearlings, and adults, contribute towards the sustainability of the species. Adults

are an important contributor towards population growth as they reproduce and rear pups.

Similarly, pups/yearlings are important because they are good dispersers, thereby

contributing to maintenance of genetic diversity via transfer of genes across the

distribution of the species. Pup survival is an indicator of the success of yearlings and

adults in rearing pups and thereby, increases the potential for population growth. Thus,

the fate of reintroduced populations can be assessed through survival estimation of

various age classes of swift fox populations. Our objective was to estimate age-specific

apparent survival probabilities of swift fox for the reintroduced population that included

the BNP region of southwestern South Dakota.

STUDY AREA

Badlands National Park is located in southwestern South Dakota (Fig.1). The 1,846-km²

study area included the north unit of BNP and surrounding area (Schroeder 2007).

Twenty three percent of the area was managed by the National Park Service, 34% by

United States Forest Service, and 43% was privately owned (Fig. 2); <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 in

the remaining 48% of the north unit (Schroeder 2007).

Soils of the Badlands National Park area are composed of midway clay loam and

are relatively infertile with a low water holding capacity (Whisenant and Uresk 1989).

Mean annual temperature and precipitation in this region of South Dakota was 10.1° C

and 40 cm, respectively (Fahnestock and Detling 2002) with dramatic seasonal variation,

which is typical of the continental climate. Minimum and maximum temperature varied

between −40° C to 47° C. Topography of the region was diverse and elevation ranged

from 691 to 989 m above mean sea level (Russell 2006; Schroeder 2007). The area

within BNP was typified by highly eroded cliffs and spires over 100 m in height. Outside

BNP, the terrain was less rugged and typified by rolling prairies and a relatively flat area

(e.g., Conata Basin: Russel 2006; Schroeder 2007). Vegetation in the region was

dominated by mixed grass prairie species including buffalograss (*Buchloe dactyloides*),

western wheatgrass (*Pascopyrum smithii*), and prickly-pear cactus (*Opuntia

polyacantha*); the region was mostly void 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 generally trapped foxes throughout the year from 2003 to 2009. However, we did not

carry out any trapping of foxes during the following months: April 2004; April, May,

July, and December of 2006; January, February, April, and December of 2007; January,

March, November, and December of 2008; January, March, April, June, and August of

2009. From 2003 to 2006, 114 swift foxes were translocated from Colorado and

Wyoming to Badlands National Park. We translocated 15 male and 15 female foxes from

Colorado in the year 2003; 13 male and 16 female foxes from Colorado again in the year

2004; 14 male and 16 female foxes again in the year 2005 from Colorado; 10 male and

16 female foxes in the year 2006 from Wyoming. We captured swift foxes with modified

wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of

dimensions 81.3 cm $\times$ 25.4 cm $\times$ 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, Rebmattli 19, CH-6340

Baar, Switzerland, EU) and determined age of captured foxes using tooth wear. We

fitted captured foxes with Very High Frequency (VHF) radiocollars (model M1830, <40

g; Advanced Telemetry Systems, Isanti, MN, USA) and injected them with transponders

(AVID ID Systems, Norco, California, USA) between their shoulder blades. We

captured both translocated as well as wild born foxes in the same procedure. We were

able to identify each individual fox with the help of transponders, each of which had a

unique ID number that could be determined with the help of 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 (Approval number 08-A039, A3958-01).

We collected capture – recapture data on swift foxes from September 2003 until October 2009. Foxes were considered pups from 3 months to 12 months of age, yearlings from 1year to 2 years of age, and adults beyond 2 years of age. 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 their parent's home range. Thus, pups were exposed for capturing from 3 months of age onwards when they approached adult size but not weight and were eligible for collaring. We used the Cormack–Jolly–Seber (CJS) capture-mark-recapture (CMR) 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 probability of survival and the probability of not permanently emigrating. We modeled probabilities for 3 groups; adults, yearlings, and pups and one covariate, gender of foxes. Individual capture histories were prepared using classifications of estimated age and trapping occasions. Our objective was to estimate the age-specific apparent survival of swift foxes; as such, our first model had constant survival and recapture in each age class but different survival and recapture in different age classes [φ(age)p(age)]. We then incorporated the effect of a gender covariate in our preliminary model to determine if the additional covariate improved model fit. We used an information-theoretical measure of model parsimony, Akaike's information criterion (AIC) (Akaike 1973; Burnham & Anderson 2002) to compare models. We used overlap of confidence intervals of apparent survival estimates

for age classes to determine significance among estimates. We raised the monthly apparent survival of foxes to the 12th power to estimate the annual apparent survival of foxes of different age group. We also compared confidence intervals of the apparent survival by gender to ascertain if males and females differed relative to estimates of apparent survival.

RESULTS:

We captured, marked, released, and subsequently recaptured 321 individual foxes over 7 years beginning September 2003 through October 2009. Of the 341 individuals, there were 243 pups, 29 yearlings, and 69 adults (Table 1). Using the model of constant survival and recapture probabilities among each age class but different survival and recapture probabilities among different age classes [φ(age)p(age)], monthly apparent survival of pups, yearlings, and adults was 0.88 (SE=0.012, 95% CI=0.855–0.901), 0.90 (SE=0.012, 95% CI=0.876–0.922), and 0.93 (SE=0.007, 95% CI=0.909–0.938), respectively (Table 2). The annual apparent survival of pups, yearlings, and adults was estimated to be 0.22, 0.29, and 0.39, respectively, in our study area. The 95% CI of the monthly apparent survival of pups (0.8–0.9) differed from that of yearlings and adults. Yet, there was no difference between the survival of yearlings (0.9–0.92) and adults (0.9–0.94).

DISCUSSION

We calculated apparent survival of swift foxes using the CMR method. Apparent

survival estimation includes dispersal and our survival estimation is comparable to other

studies that used telemetry data due to the long-term study period (7 years). The

estimated apparent survival rate for age classes of swift foxes in our study area (~30%)

was lower than previously documented survival estimates of swift foxes (Covell 1992,

Sovada et al. 1998, Sharps and Whitcher 1984, Kamler et al. 2003, Olson and Lindzey

2002, Ausband and Foresman 2007, Moehrenschalger et al. 2006). Reported annual

survival of swift foxes in Colorado was 53% (Covell 1992), that in western Kansas was

54% (Sovada et al. 1998), and in South Dakota, survival rate was 50% (Sharps and

Whitcher 1984). An estimated 52% to 60% survival rate for swift foxes was reported in

the fragmented landscape of Texas (Kamler et al. 2003) whereas a 40% to 69% survival

rate of swift foxes was reported in southeastern Wyoming (Olson and Lindzey 2002).

Ausband and Foresman (2007) reported 36% to 38% of survival for the first year of foxes

in a reintroduced population on the Blackfeet Reservation in northern Montana, whereas

the estimated survival probability of first year foxes in our reintroduced population was

29%. The annual survival probability of foxes after 12 months of age was estimated to be

45% in the Canada/Montana reintroduced population (Moehrenschlager et al. 2006). The

reintroduction in BNP started in 2003, whereas the reintroduction in Canada took place in

1983 (Carbyn 1998). Generally more time and risk are associated with establishing

territories for translocated foxes, which might affect the survival rate of foxes in a

reintroduced population. Therefore, the survival rate of the reintroduced fox population

in Canada, which has established itself with time, was greater than that of the more recent

BNP reintroduced population, which might as well be true for the Montana reintroduced

population that took place in 2002 (Ausband and Foresman 2007). Time also could be

the reason behind the comparatively lower survival rate of the reintroduced population at

BNP than other established and stable populations of swift fox in Colorado, Kansas,

Wyoming, and Texas.

Adult swift fox survival in our study area (39%) was higher than survival of foxes

in all other age classes. Survival of adults is important as fecundity in adults is generally

higher than that for yearlings. In short-lived species, like swift foxes, fecundity is a

critically important factor in population growth. Average number of pups observed in

our study area was nearly 6 per pair of adult foxes. As pup survival in our study area was

low (22%), high fecundity is necessary to increase population growth rate. Both pups

and yearlings are good dispersers, which is essential for maintaining genetic diversity

across the landscape. The habitat in our study area comprised sparsely vegetated spires

and rugged terrain of the badlands, which may not be suitable for foxes (Sasmal et al.

2011, Chapter 3). Because of low amount of suitable habitat within BNP, the swift fox

population in the park might have reached stability by saturating suitable habitats

available in the park. Thus, foxes released within the park boundary would have a

tendency to migrate out of the park to the surrounding area comprised of suitable habitats

like prairie dog towns, sparse vegetation, and grasslands (Sasmal et al. 2011, Chapter 3).

This migratory tendency of foxes might be responsible for the low survival rates of both

adults and yearlings as migration tendency also increases the chances of their exposure to predation (Kamler et al. 2004) and anthropogenic-induced mortality (Russell 2006).

Kamler et al. (2003) stated that swift fox are more habitat specific than other North American canids. Specialized habitat selection by female swift fox during the pup-rearing season also has been documented at BNP and surrounding areas (Sasmal et al. 2011, Chapter 3). Habitat plays an important role in the survival of a species as survival is enhanced by the presence of suitable habitat. The Blackfeet Reservation in Northern Montana was mainly dominated by cropland areas where the survival rate was 36% to 38% (Ausband and Foresman 2007). The swift fox survival rate was 52% to 60% at the study site in Texas, which was mainly dominated by agricultural fields, nonnative grasslands, and Conservation Reserve Program grasslands (Kamler 2003). Swift fox habitat in southeastern Wyoming was characterized as a transition between sagebrush (*Artemisia* sp.) steppe and short-grass prairie where the survival rate was 40% to 60% (Olson and Lindzey 2002). In contrast, swift fox habitat in western Kansas was comprised of highly fragmented cropland with contiguous native grassland and the survival rate there was 54% (Sovada 1998). Our study area was mainly comprised of unsuitable rugged terrain of the badlands, along with limited amount of mixed grass prairies and prairie dog towns with low vegetation height, which may be the reason behind lower survival rate of foxes (22% to 39%).

Environmental stress or conditions that could affect the survival of a species could be accounted for in a long-term study to estimate survival. An above average year of rainfall might affect the vegetation height of the study area which in turn might affect the

survival of the species due to loss of suitable habitat (Sasmal et al. 2011, Chapter 3). Our

survival estimates for age classes of swift fox were based on a study period of 7 years,

which could be considered long term relative to the age of foxes and the probability that

environmental stressors would affect survival of the foxes. Generally, survival rates for

species serve as important demographic parameters to assess the viability of a population.

Yet, survival rate alone is not sufficient to predict the future persistence of a population.

Information on genetic diversity and habitat suitability also is necessary for population

viability analysis. Therefore, further study on the genetic diversity and habitat selection

is in need for determining population viability of the reintroduced swift fox population at

BNP in southwestern South Dakota.

MANAGEMENT IMPLICATIONS

Our study provides support for low survival probabilities of swift foxes in the

reintroduced population at BNP and surrounding areas. These findings imply that other

demographic factors like suitable habitat, food availability, and low predator populations

should be evaluated to increase the survival rate of the reintroduced population and to

eliminate potential negative effects on this population. Managers should periodically

reevaluate survival to ensure long-term viability of this threatened population of swift

foxes. Future monitoring will allow assessment of the need for additional supplement via

new individuals from other similar habitats to augment the population.

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Table 1. Number of male and female swift foxes of different age groups among the 243
individuals that were captured from 2003 to 2009 at the Badlands National Park, South
Dakota, USA.

	Males	Females
Pups	111	132
Yearlings	12	17
Adults	32	37

Table 2. Parameter Estimates of apparent monthly survival of swift fox at different age class along with standard error and 95% confidence interval at the Badlands National Park, South Dakota, USA.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
Pup survival	0.879	0.012	0.855	0.901
Yearling survival	0.901	0.012	0.876	0.922
Adult survival	0.925	0.007	0.909	0.938

Figure 1. Badlands National Park located in southwestern South Dakota, USA.
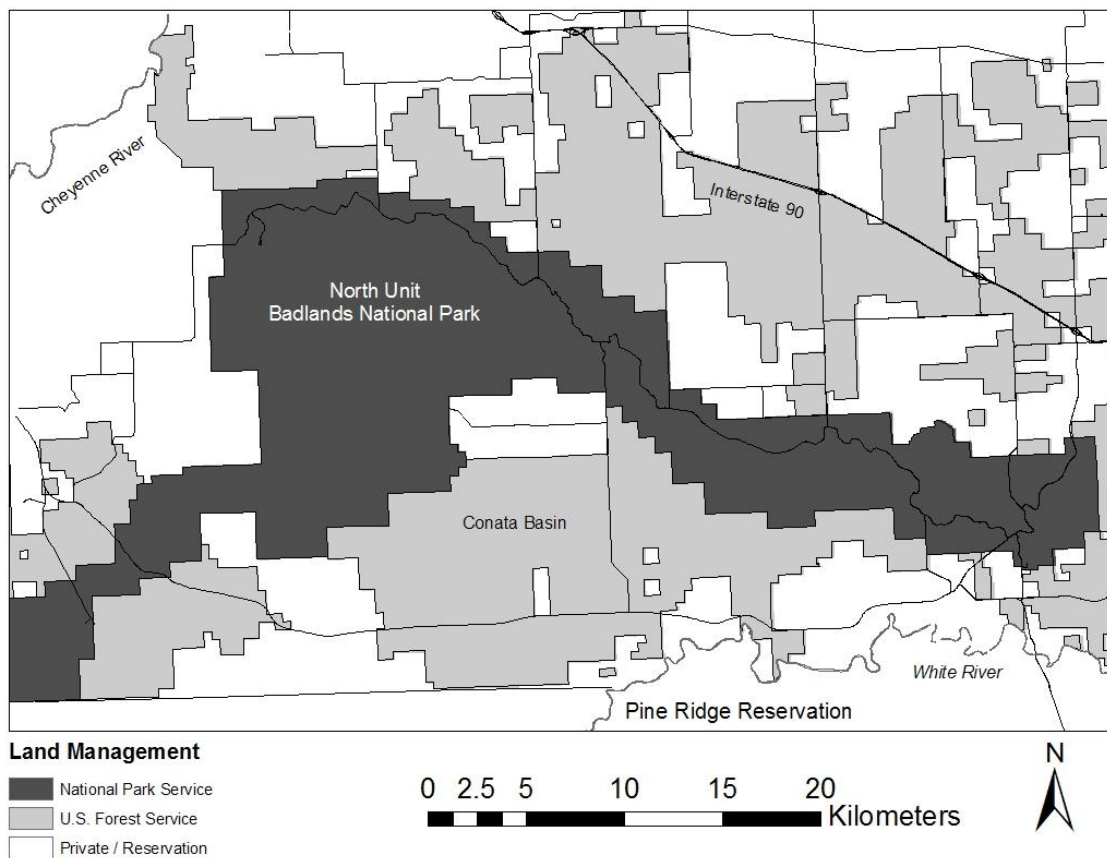
Figure 2. Study area map delineating land management jurisdiction, rivers, and primary roads. Study area was located in southwestern South Dakota, USA.

Chapter 2

Genetic Diversity in Reintroduced Swift Fox Population

Summary

1. We measured genetic diversity in a reintroduced swift fox population at Badlands National Park and its surrounding area, in an area of Colorado and Wyoming from where swift foxes were translocated to the BNP, as well as the local swift fox population neighbouring BNP in Fall River County, South Dakota, using 12 microsatellite loci. We used program FSTAT version 2.9.3 to evaluate Hardy-Weinberg (HW) equilibrium, linkage disequilibrium, genetic diversity, number of alleles per locus, allelic richness, and genetic differentiation among the populations for the 12 loci used for analyses.

2. We obtained genotypes of 252 wild born foxes, 108 released foxes from the BNP, and 40 individual foxes from the neighbouring Fall River area of South Dakota. Released foxes were translocated from Colorado in 2003, 2004, and 2005, whereas those foxes released in the year 2006 were translocated from Wyoming. We genotyped 28 foxes released in the year 2003, 28 foxes released in the year 2004, 26 foxes released in the year 2005, and 26 foxes released in 2006.

3. We obtained mean gene diversity values of 0.778 (SD=0.156) for the Colorado population, 0.753 (SD=0.165) for the Wyoming population, 0.751 (SD=0.171) for the BNP population, and 0.730 (SD=0.166) for the Fall River population. We obtained an F_{st} value of 0.029 for the BNP and Fall River fox population, and an F_{st} value of 0.014 for the Colorado and Wyoming fox populations. We also obtained an F_{st} value of 0.020 for the Colorado and Fall River populations as well as an F_{st} value of 0.0246 for the Wyoming and Fall River populations.

4. The BNP reintroduced fox population has a high genetic diversity as compared to its source population in Colorado and Wyoming and also good connectivity with the neighbouring population i.e., Fall River population. It can be inferred from the genetic data that the reintroduction of foxes to BNP has been successful, although further analysis is required to confirm short- and long-term viability of this population.

Introduction

Swift foxes (*Vulpes velox*) were once abundant throughout the Great Plains of North America (Egoscue 1979). The species declined dramatically by the late 1800s (Zumbaugh and Choate 1985) and much of this decline was attributed to conversion of native prairie to agriculture and 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 foxes includes a fragmented population extending from southern Wyoming through eastern Colorado, western Kansas, eastern New Mexico, the Oklahoma panhandle, northern Texas, South Dakota, Nebraska, Canada, and northern Montana (Carbyn 1998; Swift Fox Conservation Team 2000; Zimmerman et al. 2003).

The first successful reintroduction program for swift foxes began in 1983. The Canadian Wildlife Service and cooperators began a swift fox reintroduction, focusing their efforts largely on private lands in Alberta and Saskatchewan, Canada (Carbyn et al. 1994). Following the first reintroduction program in Canada, several reintroduction programs

had been initiated in an effort to restore swift fox populations to unoccupied, yet suitable,

habitat within their historic range. These reintroductions include the Blackfeet

Reservation in Montana from 1999-2002 (Ausband and Foresman 2007), Fort Peck

Reservation in Montana, and four 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 in 2009-2010 the Pine Ridge Indian

Reservation (Oglala Sioux Parks Recreation Authority).

Genetic diversity is a fundamental source of biodiversity and is defined as any

measure that quantifies the magnitude of genetic variability within a population (Hughes

et al. 2008). It also provides the raw material for evolution (Fisher 1930). Allelic

diversity, allelic richness, and heterozygosity are a few means of measuring the genetic

diversity within a population. Allelic diversity incorporates information about the

average number and relative frequency of alleles per locus and is an index of molecular

genetic diversity (e.g. Shanon-Wiener diversity) (Hughes et al. 2008). Allelic diversity is

generally measured with the help of molecular markers at putative neutral loci (Hughes et

al. 2008). Allelic richness is measured by the average number of alleles per locus

(Hughes et al. 2008). Heterozygosity on the other hand is the measure of genetic

variation which is based upon the proportion of individuals in a population that are

heterozygous, i.e., having different alleles at a locus (Allendorf et al. 2008). Populations

that lose genetic diversity are more prone towards becoming extinct in comparision to

those that maintain higher levels of genetic diversity (Koons 2010). Thus, genetic

diversity is a measurement of the intrinsic viability of a population which should be assessed to evaluate the viability of reintroduced swift fox population at the BNP

Isolated populations tend to lose genetic variation at a faster rate than connected populations due to the absence of genetic exchange among populations through migration (Ouborg 2009). Thus, connectedness of populations with other populations is indicative of genetic diversity maintenance and as such helps in assessing the viability of the population. Connectedness between two subpopulations can be measured with the help of the inbreeding coefficient F_{ST}, the concept of which was developed by Sewall Wright (1931, 1951). F_{ST} is a measure of genetic divergence among subpopulations (Allendorf and Luikart 2008). The value of F_{ST} ranges between one and zero, where one indicates complete panmixia or randomly mating populations and zero indicates complete isolation between two populations. To ensure long term viability of the reintroduced swift fox population at the BNP and surrounding area it is important to evaluate the connectedness of the reintroduced population with other neighboring populations.

Use of DNA microstellite loci cloned from the dog genome and used for closely related kit fox (*Vulpes macrotis*) (Ostrander et al. 1993; Fredholm and Wintero 1995; Francisco et al. 1996; Ralls et al. 2001) and primers developed for the swift fox genome by Cullingham et al. (2007) provided insights into swift fox population genetics. Because microsatellites are hypervariable single locus genetic markers, they can be analysed from miniscule tissue samples using polymerase chain reaction (PCR) (Forbes and Boyd 1996). Microsatellites are valuable for population genetic studies because numerous alleles are often segregating in a population at these loci (e.g., Schlotterer et al.

1991; Ellegren 1992; Bowcock et al. 1994; Taylor et al. 1994; Morin et al. 1994; Paetkau

& Strobeck 1994; Paetkau et al. 1995; Forbes and Boyd 1996). Microsatellite loci have

been used previously by Kitchen et al. (2006), for understanding multiple breeding

strategies in the swift fox, as well as for assessing the genetic and spatial structure within

a swift fox population (Kitchen et al. 2005). Also Cullingham et al. (2010) used

microsatellite loci for swift fox fecal DNA profiling, and Harrison et al. (2002) used

microsatellite loci for a swift fox population survey in New Mexico. However, no study

has been conducted to measure the genetic diversity and connectedness between fox

populations after a reintroduction. Our objective was to measure the genetic diversity

and connectedness of the reintroduced population of foxes at the BNP and its surrounding

area, thereby assessing the viability of the population.

Methods:

STUDY SITE

Badlands National Park (BNP) is located in southwestern South Dakota. The 1,846-km²

study area included the north unit of BNP and surrounding area (Schroeder 2007).

Twenty three percent of the area was managed by the National Park Service, 34% by

United States 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 in the remaining 48% of the north unit (Schroeder 2007).

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

Fall River County is located in the south west corner of South Dakota. The topography of the area varies from gently rolling to deeper canyons with the presence of minor eroded badlands (Moravek 1990). Average winter and summer temperatures are about -3°C and 22°C, respectively, with an annual precipitation of 41.81 cm (Kalvels 1982). The area consisted of stony and loamy soil on mountain and uplands; uplands

were further characterized by silty, loamy, sandy, and clayey soil, whereas flood plains of the area were characterized by loamy and silty soil (Kalvels 1982). The county was dominated by mixed grasses among which western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), prairie Junegrass (*Koeleria cristata*), and cactus (*Opuntia spp.*) were common. Small reservoirs were scattered usually in a density of several per section throughout the area. The Fall River area was further characterized by gently rolling hills, with several moderately deep draws near the center and with little woody vegetation (Moravek 1990).

SAMPLE COLLECTION AND DNA ISOLATION

Swift foxes were captured with modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.3 cm $\times$ 25.4 cm $\times$ 30.5 cm (Sovada et al. 1998), which were set in the evening and checked the following morning. Blood samples were collected from foxes caught in box traps and stored using FTA classic cards (Whatman Inc., NJ, USA). DNA was extracted from blood samples using a blood Qiagen protocol (Qiagen Inc. Valencia, CA, USA). Three FTA punches of 3 mm diameter were used to extract DNA from FTA cards.

MICROSATELLITE ANALYSIS

Swift fox microsatellites (Saiki, Scharfm& Faloona 1985; Kitchen et al. 2005) (n = 14) were amplified by multiplex polymerase chain reaction (PCR). Fourteen microsatellite loci were used to assess genetic diversity of swift foxes. Among these microsatellites, 9 primer pairs that successfully amplified microsatellites in the dog and kit fox (Ostrander

et al. 1993; Fredholm and Wintero 1995; Francisco et al. 1996; Ralls et al. 2001) were

optimized by the Waits Laboratory in Idaho, Moscow, USA for swift fox samples.

Another 5 microsatellite primer pairs developed for the swift fox genome by Cullingham

et al. (2007) were redesigned by the Waits Laboratory in Idaho, Moscow, USA for

multiplex PCR. The following microsatellites were genotyped for this study: CXX20,

CXX173, CXX109, CXX263, CXX403, CXX2062, CXX377, FH2054, CPH3, VVE2-

111, VVE5-33, VVE2-110, VVE-M19, and VVE3-131. DNA was amplified in 3

multiplex reactions: 1) CPH3/CXX173/CXX20/CXX377/CXX403/FH2054, 2)

CXX109/CXX2062/CXX263/VVE2-111/VVE5-33, and 3) VVE2-110/VVE-

M19/VVE3-131. Forward primers were flourescently labeled with 6-FAM, VIC, NED,

or PET (Applied Biosystem, Carlsbad, California, USA), while reverse primers were

unlabelled (Integrated DNA Technology, Coralville, Iowa, USA). Microsatellite loci

were chosen to be part of a particular multiplex reaction based upon amplicon size and

flourescent label (Table 3). A Qiagen Mutiplex Kit (Qiagen Inc. Valencia, CA, USA)

was used to amplify microsatellites (Table 3). Touchdown PCR was performed for each

multiplex reaction and slightly different touchdown protocols were used for the 3

different multiplex reactions (Table 4).

     Flourescently labeled PCR products were mixed with an internal size standard

(GeneScan[TM] 600 LIZ[®], Applied Biosystem) and Hi-Di[TM] Formamide (Applied

Biosystem), and loaded onto an ABI PRISM[®] 3130 genetic analyzer for fragment

analysis. Genotyper software (Applied Biosystem, Carlsbad, California, USA) was used

for genotyping microsatellites. The PCR product for mutiplex 1 was diluted in a 1:5 ratio

i.e., 2µl of product with 8µl of sterilized water, and for multiplex 3 the PCR product was diluted in a 1:10 ratio i.e., 2µl of product with 18µl of water. No dilution of PCR product was done for multiplex 2 amplicons. The diluted PCR product was then combined with 10µl of Hi-Di/LIZ mixture and the solution was denatured at 94°C for 5 minutes followed by 4°C until used in the analyzer. For each sample, 0.55µl of LIZ was mixed with 10µl of Hi-Di to prepare the LIZ/Hi-Di mixture. We reamplified blood samples from 80 individuals and observed the error rate per single locus genotype out of the 400 samples. Accuracy of genotypes assigned in Genotyper were manually confirmed. We estimated error rate by calculating the number of errors divided by the number of amplifications.

 STATISTICAL METHODS

Program FSTAT version 2.9.3 (Goudet 2001) was used to evaluate Hardy-Weinberg (HW) equilibrium, linkage disequilibrium, genetic diversity, number of alleles per locus, allelic richness, and genetic differentiation among populations for the 12 loci used for analyses. F_{is} (Wright 1931) measures the departure from Hardy-Weinberg proportions within local subpopulations and will be positive if there is a deficit of heterozygotes and negative if there is an excess of heterozygotes. FSTAT (Goudet 2001) uses F_{is} to test for HW equilibrium, where it generates two tables of P-values both high and low for a two tailed test. The FSTAT test (Goudet 2001) reports Bonferroni corrected nominal level (5%) P-values as well as the actual P-value for testing for Hardy-Weinberg equilibrium. FSTAT (Goudet 2001) also reports the Bonferroni adjusted P-value at the 5% nominal level and the actual P-value to estimate linkage disequilibrium among all pairs of loci.

Gene diversity is a measure of allelic diversity (Nei 1973) that, unlike heterozygosity, can be calculated when a population is not mating randomly. Nei's method for measuring heterozygosity or gene diversity "is applicable to any population without regard of the number of alleles per locus, the pattern of evolutionary forces such as mutation, selection, and migration, and the reproductive method of the organism used" (Nei 1973). Genetic differentiation between two populations was measured with pairwise F_{st} tests in the program FSTAT (Goudet, 2001), which calculates the mutilocus Weir and Cockerham (1984) estimator of F_{st} (theta) between all pairs of samples.

Released foxes were translocated from Colorado in the year 2003, 2004, and 2005, whereas foxes released in the year 2006 were translocated from Wyoming. We grouped released individuals into two subpopulations for data analysis: the Colorado and the Wyoming subpopulations. Program SYSTAT 10 (Wilkinson 1990) was used to perform paired t-tests to compare the genetic diversities of different populations and also to compute the means and standard deviatons of the genetic diversity parameters for different populations. The approximate distances between the Colorado and Wyoming fox populations was 136 km, that between Colorado and Fall River was 319km, and distance between Wyoming and Fall River fox populations were 216 km. We considered 4 populations of foxes depending on their place of origin for data analysis: the Colorado population, the Wyoming population, the BNP population, and the Fall River population (Figure 3).

Results

We isolated DNA from 433 individual foxes comprising both released and wild born

foxes at the BNP as well as foxes from the Fall River area. We removed 33 samples

from our analysis due to unsuccessful amplification of those samples despite repeated

attempts. Thus, 7.6% of our samples were omitted from the analysis. We used the

genotypic data from the remainder of the samples ($n = 400$) for gene diversity analyses.

We obtained genotypes of 252 wild born, 108 released foxes from BNP, and 40 foxes

from the Fall River area. We genotyped 28 foxes released in 2003, 28 released in 2004,

26 foxes released in 2005, and 26 foxes released in 2006. We obtained genotypes of wild

born foxes from 2004 to 2009 as follows: 14 in 2004, 24 in 2005, 41 in 2006, 77 in 2007,

53 in 2008, and 40 in 2009.

Two of the primer pairs (CXX173 and CXX109) did not amplify DNA and thus,

we eliminated them from our analyses. We found that all the 12 loci used for data

analysis were in Hardy-Weinberg (HW) equilibrium after Bonferroni corrections as per

the p-value of the F_{is} computed by program FSTAT. We did not find any linkage

disequilibrium between any pair of loci in any of the populations. We obtained a mean

gene diversity value of 0.778 (SD=0.156) for the Colorado population, 0.753 (SD=0.165)

for the Wyoming population, 0.751 (SD=0.171) for the BNP population, and 0.730

(SD=0.166) for the Fall River population (Table 5). We obtained the maximum number

of allleles (31) at locus VVE-M19 for the BNP population (Table 5). We also obtained

the highest mean allelic richness of 11.154 (SD=7.97) for the BNP population (Table 5).

We did not document differences in genetic diversity between any of the populations. We also did not document differences in allelic richness among any of the populations except between the Wyoming and the BNP population (Table 6). We obtained an F_{st} value of 0.029 for the BNP and Fall River swift fox populations and an F_{st} value of 0.014 for the Colorado and Wyoming fox populations. We also obtained an F_{st} value ranging from 0.020 to 0.0246 between the Fall River population and the Colorado and Wyoming population (Table 7).

Discussion:

The close genetic similarity of the BNP swift fox population with the Colorado and the Wyoming populations (~0.7) can be explained by the fact that the Colorado and Wyoming fox populations served as the source for the BNP fox population restoration. Similarity between the genetic diversity of the Colorado and Wyoming fox populations indicates that gene flow has been taking place through migration of foxes between these two populations. Exchange of genetic material through immigration and emigration of foxes between the Colorado and Wyoming populations also is evident from the low F_{st} value (0.014). The low F_{st} value for the Fall River and Colorado fox populations (F_{st}=0.020) and Fall River and Wyoming (F_{st}=0.025) fox populations as well as similarity between genetic diversity among these populations indicates gene flow thorugh migration of fox individuals among these populations. In addition, the F_{st} value for the Fall River and the BNP fox populations also was low (0.029), which indicates connectedness. Considering that 6 years (2003 to 2009) might not provide enough time for dispersal to

occur, the low F_{st} value between Fall River and BNP fox populations might be due to the relatively short distance between Fall River and source populations (Colorado and Wyoming), which suggests that genetic exchange has been occurring between these populations. The Fall River population has been considered a remnant population, which was believed to be on the edge of extinction with only about 60 individuals (Uresk et al. 2003). The reason behind the Fall River population not becoming extinct may be due to the connectedness and therefore, gene flow between this population and a neighbouring population in Wyoming. Connectedness between multiple populations is important to rescue rare populations from becoming extinct as well as for the persistent viability of the overall population (Koons 2010).

The swift fox populations in Colorado, Wyoming, and Fall River County, South Dakota could be considered as stable populations as these populations have been extant from the prehistoric time period despite declining and disappearing swift fox populations from other historic sites inhabited by foxes. Heterozygosity obeserved by Harrison et al. (2002) in the extant swift fox population of New Mexico was nearly 0.7, and heterozygosity in the reintroduced swift fox population of Saskatchewan and Alberta in Canada also was aprroximately 0.7 (Cullingham 2010). Our study populations also have a high genetic diversity in comparision to other canid species such as wolves (*Canis lupus*, 0.605; Forbes and Boyd 1996), and coyotes (*Canis latrans*, 0.75; Williams et al. 2003), and its close relative the kit fox (*Vulpes macrotis mutica*, 0.4; Schwartz 2005). The BNP reintroduced fox population has a high genetic diversity as compared to its source population of Colorado and Wyoming and also good connectivity with the

neighbouring population i.e., Fall River population. Maintenance of high genetic

diversity and good connectedness also indicates avoidance of inbreeding. Inbreeding

may cause decreased fitness and lower the potential for evolutionary adaptation (Ouborg

2009).

A population tends to lose genetic variability when an effectively small number of

individuals are used as founders for the population (Wright 1931; Nei et al. 1975).

Generally, the loss of genetic variability takes place due to the loss of rare alleles, which

become especially susceptible to loss during a bottleneck (Allendorf and Luikart 2008).

Reduction of genetic diversity can happen due to genetic drift and is independent of the

number of alleles present (Allendorf and Luikart 2008). Thus, it is important to ascertain

if genetic variability is reduced in newly established populations. No reduction of genetic

diversity or allelic richness took place in the newly established BNP fox population in

comparision to the Colorado or Wyoming founder populations, which is indicative of a

successful reintroduction. Finally the viability analysis of the reintroduced fox

population at BNP will be helpful to assess the success of the reintroduction.

It can be inferred from the genetic data that the reintroduction of foxes at the BNP

has so far been successful, although future viability analysis is required to confirm this

result. A periodic monitoring of genetic variability of the BNP reintroduced population is

required to evaluate the status of the population. Also, connectivity maintainence with

other neighbouring fox populations for gene flow between subpopulations is required to

assure the future viability of the BNP reintroduced fox population.

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Table 3. The PCR concentration and volume of each primer along with their size range and flourescent label. Amount of Qiagen mastermix, Q-soultion, and DNA for each multiplex reaction was constant but the amount of water differed depending upon the primer volume to make a total reaction volume of 8 µL. Different primers were used in different multiplex reactions to obtain the genotype of captured swift fox individuals (2003-2009) for determining the genetic diversity of swift fox at the Badlands National Park, South Dakota, USA.

Primers	Volume (µl)	PCR concentration (µM)	Multiplex	Dye lable	size range	Qiagen Mastermix (2x)	Q-solution (5x)	DNA (µL)
CPH3 F & R (10µM)	0.1	0.15	1	6FAM	150-160	3.5	0.7	2
CXX403 F & R (10µM)	0.19	0.30	1	VIC	263-281			
FH2054 F & R (10uM)	0.058	0.15	1	NED	167-191			
CXX20 F & R (10µM)	0.093	0.23	1	VIC	114-144			
CXX377 F & R (10µM)	0.058	0.11	1	VIC	165-193			
VVE2-111 F & R (20µM)	0.08	0.23	2	NED	107-142	3.5	0.7	2
VVE5-33 F & R (20µM)	0.25	0.71	2	NED	188-250			
CXX2062 F & R (10µM)	0.25	0.36	2	6FAM	135-160			
CXX263 F & R (10µM)	0.05	0.07	2	6FAM	94-142			
VVE3-131 F&R (10µM)	0.07	0.10	3	PET	153-185	3.5	0.7	2
VVE-M19 F&R (10µM)	0.05	0.07	3	VIC	227-356			
VVE2-110 F&R (10µM)	0.2	0.29	3	6FAM	231-346			

Table 4. Protocol used for running different multiplex PCRs in thermocycler to amplify swift fox DNA.

	Multiplex 1		
	Initial denaturation	95°C	15 min
Touchdown	Number of cycles :	**20(strong samples*[1]) 14 (weak samples*[2])**	
	Denaturation :	94°c	30 sec
	Annealing:	**55°c - 0.3°C**	90 sec
	Elongation :	72°C	1 min
Cycling	Number of cycles :	**20**	
	Denaturation :	94°c	30 sec
	Annealing:	**51°c**	90 sec
	Elongation :	72°C	1 min
	Final elongation	60ºC	30 min
	Multiplex 2 and 3		
	Initial denaturation	95°C	15 min
Touchdown	Number of cycles :	**12**	
	Denaturation :	94°c	30 sec
	Annealing:	**53°c - 0.5°C**	90 sec
	Elongation :	72°C	1 min
Cycling	Number of cycles :	**20(strong samples*[1]) 25/30 (weak samples*[2])**	
	Denaturation :	94°c	30 sec
	Annealing:	**47°c**	90 sec
	Elongation :	72°C	1 min
	Final elongation	60ºC	30 min

*[1] samples that contain more DNA; *[2] samples that contain less DNA

Table 5: The minimum, maximum, mean, and standard deviation values of genetic

diversity, number of alleles, and allelic richness of fox populations studied at Colorado,

Wyoming, BNP, and Fall River area.

Genetic Diversity				
	Colorado	Wyoming	BNP	Fall River
Minimum (locus)	0.322 (CXX403)	0.347 (CXX403)	0.303 (CXX403)	0.335 (CXX403)
Maximum (locus)	0.906 (VVE5-33)	0.907 (VVE-M19)	0.922 (VVE2-110)	0.898 (CXX20)
Mean	0.778	0.753	0.751	0.73
SD	0.156	0.165	0.171	0.166
Number of alleles				
	Colorado	Wyoming	BNP	Fall River
Minimum (locus)	5 (CXX263 &VVE3-131)	4 (VVE3-131)	5 (CXX263)	5 (CXX263)
Maximum (locus)	23 (VVE2-110)	15 (VVE-M19)	31 (VVE-M19)	12 (CXX20)
Mean	10.083	7.5	11.167	7.917
SD	6.007	3.398	7.998	2.353
Allelic Richness				
	Colorado	Wyoming	BNP	Fall River
Minimum (locus)	4.892 (VVE3-131)	4 (VVE3-131)	5 (CXX263)	5 (CXX263)
Maximum (locus)	16.858 (VVE2-110)	14.805 (VVE-M19)	30.88 (VVE-M19)	12 (CXX20)
Mean	8.551	7.455	11.154	7.917
SD	4.193	3.345	7.97	2.353

Table 6: Comparison of genetic diversity and allelic richness between different populations. Paired t test was used for the comparison at 95% level of significance.

	Genetic Diversity					
	Colorado Vs Wyoming	Colorado Vs Fall River	Colorado Vs BNP	Wyoming Vs Fall River	Wyoming Vs BNP	Fall River Vs BNP
p-value	0.267	0.141	0.134	0.554	0.898	0.0555
t- test	1.168	1.587	1.617	0.61	0.131	0.608
	Allelic Richness					
	Colorado Vs Wyoming	Colorado Vs Fall River	Colorado Vs BNP	Wyoming Vs Fall River	Wyoming Vs BNP	Fall River Vs BNP
p-value	0.063	0.492	0.068	0.496	0.028*	0.131
t- test	2.069	0.711	2.021	0.705	2.528	1.631

* Significantly different

Table 7. The calculated pairwaise F_{st} values between different swift fox populations.

	Colorado	Wyoming	BNP	Fall River
Colorado	-	0.014	-	0.020
Wyoming	0.014	-	-	0.025
BNP	-	-	-	0.029
Fall River	0.020	0.025	0.029	-
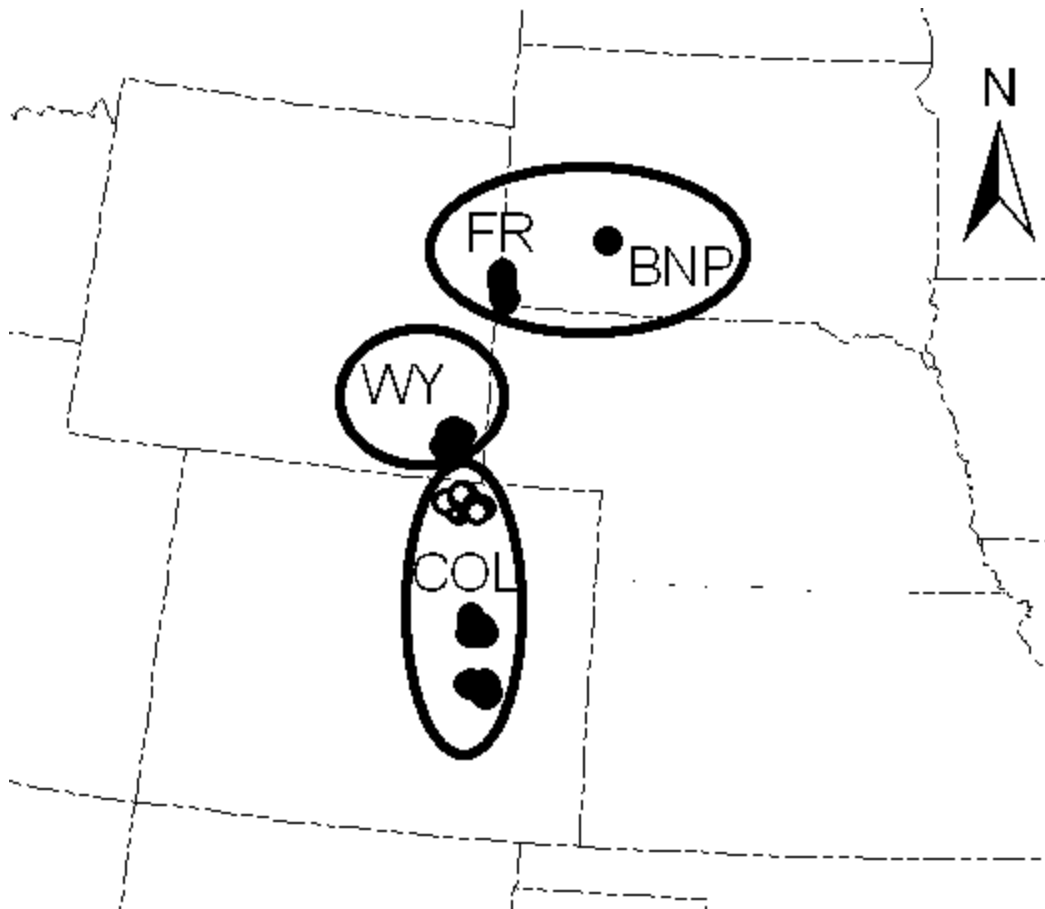
Figure 3. Map showing the location of foxes that were captured from Colorado,

Wyoming, Fall River Area, and Badlands National Park, USA, for genetic diversity

analysis. FR: Fall River Area; BNP: Badlands National Park; WY: Wyoming; COL:

Colorado.

Chapter 3

Habitat Selection by Female Swift Foxes (*Vulpes Velox*) During the Pup-Rearing

Season

ABSTRACT

The swift fox (*Vulpes velox*) was historically distributed in western South Dakota

including the region surrounding Badlands National Park (BNP). The species declined

during the mid-1800s, largely due to habitat loss and poisoning targeted at wolves (*Canis

lupis*) and coyotes (*C. latrans*). Only a small population of swift foxes near Ardmore,

South Dakota persisted. In 2003, an introduction program was initiated at BNP with

swift foxes translocated from Colorado and Wyoming. We report on habitat use by

female swift foxes during the pup-rearing season (May–July) in 2009. Analyses of

location data from 13 radiomarked female foxes indicated disproportional use ($P<0.001$)

of some habitats relative to their availability within swift fox home ranges. Swift foxes

used grassland ($\hat{w} = 1.01$), sparse vegetation ($\hat{w} = 1.4$) and prairie dog towns ($\hat{w} = 1.18$) in

proportion to their availability, whereas they were less likely to use woodland ($\hat{w} = 0.00$),

shrubland ($\hat{w} = 0.14$), pasture/agricultural-land ($\hat{w} = 0.25$) and development ($\hat{w} = 0.16$)

relative to availability. Swift foxes typically are located in habitats that provide greater

visibility, such as shortgrass prairie and areas with sparse vegetation; which allow

detection of approaching coyotes (i.e., primary predator of swift foxes).

INTRODUCTION

Swift foxes (*Vulpes velox*) inhabit shortgrass and mixed-grass prairies of the Great Plains of North America (Egoscue 1979). Historically, this small (~ 2 kg) fox occurred in parts of North Dakota, South Dakota, Montana, Nebraska, Wyoming, Colorado, Kansas, Oklahoma, New Mexico, and Texas, and the southern prairie region of Alberta, Manitoba, and Saskatchewan (Hall and Kelson 1959, Hall 1981, Samuel and Nelson 1982, Scott-Brown et al. 1987, Sovada and Scheick 1999). Swift foxes were once abundant throughout much of their range buthad declined dramatically by the late 1800s (Zumbaugh and Choate 1985). Decline in swift fox abundance was attributed to conversion of native prairie to agriculture and associated declines 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). Swift fox population declines were most severe in the southern and northern periphery of the species' range (Allardyce and Sovada 2003).

The present distribution of swift foxes includes a fragmented population extending from southern Wyoming through eastern Colorado, western Kansas, eastern New Mexico, Oklahoma panhandle, northern Texas, South Dakota and Nebraska, Canada, and Northern Montana (Swift Fox Conservation Team 2000, Carbyn 1998, Zimmerman et al. 2003). A reintroduction program was initiated in Badlands National Park and the surrounding area in South Dakota.From 2003 to 2006, 114 swift foxes were translocated from Colorado and Wyoming to Badlands National Park.

Little is known about habitat selection of female swift foxes in western South Dakota. Hence, the objective of our study was to evaluate habitat selection of female swift foxes during the pup-rearing season in western South Dakota. Swift fox breeding begins within the months of March to April in the study area. Previous studies (Russell2006, G. M. Schroeder, Badlands National Park, unpublished data) indicated that swift fox selected habitats of short structure allowing long-distance visibility and areas nearer to prairie dog towns, roads and water bodies. These habitat features likely increased potential for the capture of prey and improved the ability of swift fox to detect approaching coyotes (*Canis latrans*); the primary cause of swift fox mortality (Allardyce and Sovada 2003). Based on previous results, we hypothesized that during the pup-rearing period; female swift foxes would select habitat types with high visibility and located near to prairie dog towns, which would provide constant and readily available food.

STUDY AREA

Badlands National Park (BNP) is located in southwestern South Dakota . The 1,846-km² study area included the north unit of BNP and surrounding area (Schroeder 2007). Twenty three percent of the area was managed by the National Park Service, 34% by United States 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 in the remaining 48% of the north unit (Schroeder 2007).

Mean annual temperature and precipitation in this region of South Dakota was 10.1°C and 40 cm, respectively (Fahnestock and Detling 2002) with dramatic seasonal variation, which is typical of the continental climate. Minimum and maximum temperature varied between −40°C to 47°C. Topography of the region was diverse and elevation ranged from 691 to 989 m above mean sea level (Russell 2006). The area within BNP was typified by highly eroded cliffs and spires over 100 m in height. Outside BNP, the terrain was less rugged and typified by rolling prairies and a relatively flat area (e.g., Conata Basin; Russel 2006). Vegetation in the region was dominated by mixed grass prairie species including buffalograss (*Buchloe dactyloides*), western wheatgrass (*Pascopyrum smithii*), and prickly-pear cactus (*Opuntia polyacantha*); the region was mostly void of tree and brush species (Russell 2006). The Cheyenne and White rivers formed the western and southern boundaries of the study area, respectively.

METHODS

We captured swift foxes, early May 2009, 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, weighed, and recorded general body condition. We weighed captured swift foxes witha spring scale (model 80210; Pesola®Macro-Line Spring scale, Rebmattli 19, CH-6340 Baar,

Switzerland, EU) and determined age of captured foxes with tooth sectioning (Wood

1958). We noted lactation of captured female foxes by presence of swollen nipples and

matted hair as evidence of suckling and later confirmed presence of pups by checking den

sites for evidence or observations of pups. We fitted lactating females with Very High

Frequency (VHF) radiocollars (model M1830, <40 g; Advanced Telemetry Systems,

Isanti, MN, USA).Our animal handling methods followed guidelines approved by the

American Society of Mammalogists (Gannon et al. 2007) and were approved by the

Institutional Animal Care and Use Committee at South Dakota State University

(Approval number: 08-A039).

Because swift foxes are nocturnal, we monitored radiocollared foxes twice per

night from dusk to dawn. We started monitoring foxes each day at approximately 2030

hours and completed monitoring at 0500 hours. We collected two locations per night for

each fox at an interval of approximately 3 to 4 hours. To maintain temporal

independence, we avoided collecting locations at the same time on two successive days

for any individual. We collected telemetry locations by using a null-peak vehicle

mounted antennae system, equipped with an electronic digital compass and GPS unit

(Brinkman et al. 2002). We calibrated telemetry systems with transmitters in known

locations (Cox et al. 2002). We obtained estimates of swift fox locations using 3–4

bearings collected within a 10 minute period (Kitchen et al. 2005; White and Garrot

1990). We used LOCATE III (Nams 2006) to estimate locations using a minimum of

three azimuths for all fox locations. We excluded location estimates from home range

analyses with 95% error ellipses $\geq$20 ha (Brinkman et al. 2005). We used $\geq$50 locations

to estimate home ranges of individual foxes. Mean number of locations used to calculate home ranges was 64 (SE= 1.4, range51–68) and we used only foraging locations for current analyses. We imported location estimates into ArcView (ESRI, Inc., Redlands, CA, USA) and used the Home Range Extension (HRE; Rodgers and Carr 1998) to calculate 95% home ranges during the pup-rearing season (May–July). Because estimated fox locations were clustered, we used the adaptive kernel method for home range calculation. We conducted Geographic Information Systems (GIS) analyses with ArcGIS 9.1 (ESRI, Redlands, CA, USA) and usedNAD83, UTM Zone13N for all GIS data collection and analysis.

We determined percentages of each habitat type available within individual fox home ranges from the USGS-NPS vegetation mapping of BNP (Loh et al. 1999). For resource selection analyses, habitat categories included grassland, shrubland, pasture/agricultural land, development, sparse vegetation, prairie dog towns, and woodlands. Grassland included the western wheatgrass grassland alliance, introduced grassland, blue grama (*Bouteloua gracilis*) grassland, little bluestem (*Schizachyrium scoparium*)-grama grassland-threadleaf sedge (*Carex filifolia*) grassland, 3-leaved sumac (*Rhus trilobata*)/threadleaf sedge shrub grassland, soap weed yucca (*Yucca glauca*)/prairie sand reed (*Calamovilfa longifolia*)/shrub grassland; shrubland included western snowberry (*Symphoricarpos occidentalis*) shrubland, chokecherry (*Prunus virginiana*)-American plum (*P. americana*) shrubland, silver buffaloberry (*Shepherdia argentea*) shrubland, silver sagebrush (*Artemisia cana*)/western wheatgrass shrubland, sand sagebrush (*Artemisia filifolia*)/prairie sand reed shrubland, sandbar willow (*Salix*

interior) temporarily flooded shrubland; woodland comprised of eastern cottonwood (*Populus deltoides*)/sandar willow woodlands, green ash (*Fraxinus pennsylvanica*)-American elm (*Ulmus Americana*)/chokecherry woodlands, Rocky Mountain juniper (*Juniperus scopulorum*)/ little seed rice grass (*Piptatherum micranthum*) woodland; pasture/agricultural land included cropland-pasture and other agricultural land; development comprised of strip mines, quarries and gravel pits, mixed urban/built-up land, sandy-area beaches; sparse vegetation comprised of only Badlands sparse vegetation complex whereas prairie dog towns included only prairie dog town complexes. Row crop agricultural practices occur around BNP, which included alfalfa, winter wheat, and spring wheat, corn, soybean, millet, and oats. Planting and harvesting seasons varied according to the different types of row crops such as winter wheat (planted in the fall and harvested the subsequent summer) to corn(planted in spring and harvested in fall) to alfalfa (harvested one or more times from spring through fall).

We assessed habitat selection by comparing use and availability of habitat types at the individual home range level (Manly et al. 2002). Use was defined as animal locations in a particular habitat and availability was defined as the percentage of each habitat available at the individual home range level. We calculated selection ratios and chi-square values to estimate the overall deviation from random use of habitat types with program R version 2.8.1 (R Development Core Team 2009) and the adehabitat library (Calenge 2006). Selection ratios ($\hat{w}$) indicated habitat selection if they differed from 1 and were computed for each habitat type and each animal as the ratio of the used proportion to the available proportion (Calange and Dufour 2006).Selection for or against

a habitat category was indicated if the confidence interval for $\hat{w}$ did not contain 1.

Selection for the habitat category was indicated if the lower limit of $\hat{w}$ was >1, whereas

selection against the habitat category was indicated if the upper limit of $\hat{w}$ was <1. Use in

proportion to availability (neutral selection) was indicated if the confidence interval for $\hat{w}$

contained the value 1 (Manly et al. 2002). Eigenanalysis of selection ratios was

performed to explain variation in selection of habitat type among animals (Calange and

Dufour 2006). If all animals selected the same habitat types, then use of the first axis of

the analysis explained most of the variation in habitat selection, whereas the method

returns several axes if there is variability in habitat selection among monitored animals

(Calange and Dufour 2006).

We generated equal numbers of random locations within the buffered Minimum

Convex Polygon area of all fox locations, which we used to delineate the boundaries for

habitat analysis. We performed logistic regression analysis with SYSTAT 11 (Wilkinson

1990) to fit an appropriate model to evaluate the influence of presence of prairie dog

towns, water bodies, and roads on fox locations. We measured distances of fox and

random locations to prairie dog towns, water bodies, and roads. We coded random

locations as 0 and fox locations as 1 to run binary logistic regression for model

evaluation. We calculated mean distance of actual fox locations and random locations

from prairie dog towns, water bodies, and roads. We performed a paired *t*-test to

compare whether distance from prairie dog towns, water bodies, and roads differed

between swift fox and random locations at the 90% level of significance (alpha of

$P \leq 0.10$). We determined vegetation height by sliding a 15-cm disc down a Robel pole

(Robel et al. 1970) until it contacted any portion of a plant (Kennedy et al. 2001). We

collected vegetation height at fox locations twice per week for comparison of habitat use

by foxes for different vegetation heights. We collected vegetation heights at fox

locations within 3 days of obtaining a VHF location estimate.

RESULTS

From May to July in 2009, we monitored 14 female swift foxes and recorded 842

locations. Of the 14 female foxes, 4 were captured and radio-marked in 2009 and 10

were marked in previous years (2004 to 2008). We verified pup rearing for all 14 female

foxes by observing pups at dens. The average 95% home range of female swift foxes

during the pup-rearing season was 8.83 km^2 (SE = 1.32, 95% CI=5.96–11.71).

Some habitats within the 95% home-range estimates were not used by individual

swift foxes in proportion to availability (χ^2_1 = 73.43, P< 0.001, Table 8). During the pup-

rearing season, female foxes used grassland, sparse-vegetation, and prairie dog towns in

proportion to availability, whereas they avoided woodlands, shrublands, development,

and pasture/agricultural land (Table 9). Resource selection was assessed from data

collected from 13 swift foxes as the home range of one individual was located outside the

vegetation mapping area that we used for habitat analyses. Eigenanalysis of selection

ratios was used to explain the variability in the data (Fig. 4a, 4b). Sparsely vegetated

habitat and prairie dog town habitat explained ~71% of the variability in individual

animal habitat selection during the pup-rearing season. The first axis, which represented

sparse vegetation, explained 42% of the variability, whereas the second axis, which

represented prairie dog towns, explained 29% of the variability. Addition of the third

axis, which represented grassland vegetation, increased information explained to 88%.

Average distance of fox locations from prairie dog towns was 0.90 km (95%

CI=0.80–1.00); from water bodies was 0.69 km (95% CI=0.62–0.77), and from roads was

2.2 km (95% CI=2.08–2.32). Average distance of random locations from prairie dog

towns was 0.81 km (95% CI = 0.76–0.87); from water bodies was 0.61 km (95% CI =

0.54–0.67); and from roads was 2.36 km (95% CI = 2.24–2.48). We were unable to

develop a logistic regression that fit the distance data for fox and random locations.

However, paired t-tests conducted between distances of fox locations and random

locations to prairie dog towns (P=0.003), water (P=0.087), and roads (P=0.067) indicated

that swift foxes were closer to roads but farther from prairie dog towns and water sources

than random distances. Average vegetation height of habitats used by foxes was 15.9cm

(95% CI= 15.50–16.40). Lactating female foxes used ($\chi_1^2 = 638.46$, $P < 0.001$) locations

with low vegetation height (71.8%) more than locations having medium (26.5%) and

high (1.7%) vegetation heights.

DISCUSSION

Unfortunately, we were only able to collect data on female swift foxes during one

pup-rearing period, which limits inferences from our study. Nevertheless, few data have

been collected on habitat selection of swift foxes that have recolonized the northern

portion of the historic distribution of the species via restoration efforts. Furthermore, our

study was focused on a sample ($n = 14$) of females actively provisioning pups while

using a variety of habitats. At the time of our study, this sample represented 27% of actively reproducing female swift foxes known to inhabit the area under study. Therefore, we believe our results provide a robust assessment of habitat selection during the pup-rearing period for female swift foxes occupying the Northern Great Plains.

Habitat selection can be referred to as a hierarchical process of behavioral responses that result in the disproportionate use of habitats, and that influence survival and fitness of individuals (Jones 2001). Our study indicated that during the pup-rearing season (May–July), female swift fox avoided woodlands, shrublands, development, and pasture/agricultural land habitat types. Habitats are heterogeneous with 'rich' habitats, providing high survival and reproductive fitness to the organism, and 'poor' habitats, providing low survival and reproductive fitness (Rice and Owsley 2005). The definition of 'rich' habitat for swift fox is characterized by sparse vegetation of low height that provides greater visibility (Olson 2000, Harrison and Schmitt 2003, Russell 2006, Thomson and Gese 2007). Our results support previous research indicating that foxes select sparse vegetation. Swift foxes are opportunistic foragers (Sovada et al. 2001) and feed on a variety of food resources (Harrison 2003), which may influence the variation in resource selection observed by female swift foxes during the pup-rearing season. The eigenanalysis indicated that all 3 axes were necessary to explain the resource selection of swift fox. Although most of the individuals used sparse vegetation, prairie dog towns, and grassland vegetation types, some individuals also used pasture/agricultural land, shrubland, woodland, and development to a small extent. Among the individuals studied

for habitat selection, those with limited access to "rich" habitats, like grassland, sparse vegetation, and prairie dog towns, frequented pasture/agricultural land, shrubland, woodland, and development.

The swift fox is restricted to areas west of the tallgrass prairies in central North America (Egoscue 1979, Scott-Brown et al. 1987). Swift fox select open vegetation with greater visibility to avoid predation from carnivores of larger body size (Thomson and Gese 2007), such as red fox (*Vulpes vulpes*) and coyotes, which have been reported as a major cause of fox mortality (Kamler and Ballard 2002, Karki et al. 2007). Also, swift fox avoidance of habitat with tall vegetation was evident from our results that most locations were in low vegetation. In New Mexico, swift fox visited scent stations less than expected when grass height was >30 cm (Harrison and Schmitt 2003). Kamler (2003) reported that mean shoulder height of adult swift fox ranged from 29 to 30 cm. Thus, if the vegetation height is greater than a swift fox's shoulder height, visibility would be reduced. Low visibility increases vulnerability to coyote depredation (Kamler 2003).

Female swift foxes used locations that were farther away from prairie dog towns and water but closer to roads during the pup-rearing season than would be expected based on random points. These results are in accordance with previous research (Russell 2006) that indicated foxes selected locations closer to roads likely due to increased prey availability and decreased coyote predation (Almasi-Klausz and Carbyn 1999). Foxes do not depend on prairie dogs solely for their prey; however, use of prairie dog town habitat equivalent to availability indicate that prairie dogs provide increased access to both live

prey and carrion during this critical period in the life history of the species (Nicholson et

al. 2006). Russell (2006) documented a frequency of occurrence of 41.2% for prairie

dogs in feces of swift foxes during summer 2005 in western South Dakota, which was at

least twice the frequency of occurrence documented in spring seasons. Other factors that

could affect swift fox use of prairie dog town habitat include the presence of golden

eagles (*Aquila chrysaetos*) and coyotes.

During pup-rearing season from May to July 2009, average home range size of

female swift foxes within the Badlands ecosystem was 8.8 km^2. The smallest home-

range for a female swift fox in our study was 1.4 km^2, whereas the largest home-range

was 17.4 km^2. Variation in home-range size may be due to difference in age of

individual foxes and habitat type within the home-range of individual foxes. For

example, the fox with the smallest home range was approximately 5 years old and

inhabited an area that was comparatively closer to prairie dog towns (1.67 km) and water

bodies (0.09 km) but was farther from roads (4.84 km) than that of other foxes.

Conversely, the fox with the largest home range was approximately 2-years-old, was

farther away from prairie dog towns (2.48 km) but was closer to roads (0.17 km) than

other foxes. Consequently, older foxes might possess enough experience to select

suitable habitat with easy access to prey. Also, older foxes might be more dominant over

the younger individuals forcing them to possess lower quality habitat within their home

ranges. Our sample size of age groups of female swift foxes did not allow statistical

analysis that would provide support for this hypothesis. However, age structure of swift

fox populations may be linked to population viability in regions with high road densities and fragmented suitable foraging habitat.

MANAGEMENT IMPLICATIONS

Habitat selection of female swift foxes that were rearing pups in and around Badlands National Park indicated that swift fox avoided habitats with tall vegetation such as agricultural land/pasture, shrublands, and woodlands and human-caused disturbances. Success of female swift fox in rearing pups plays a vital role in both long- and short-term viability of populations and is strongly related to habitat quality and availability, population demographics, and the genetic fitness of individuals. Managers can maintain suitable habitats for swift fox populations by manipulating the height of vegetation via grazing and/or mechanical methods like prescribed fire. Moreover, suitable habitats for swift fox during the pup-rearing season can be maintained by converting unfavorable vegetation types which were avoided by swift foxes like pasture/agricultural land, woodland, shrubland, and developed areas, into native grassland. Also, maintaining prairie dog towns will enhance suitable habitats for swift foxes during the pup-rearing season.

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Table 8. Percent availability and use of habitat typesfor lactating female swift fox during the pup-rearing season (May–July 2009) at Badlands National Park and surrounding areas, South Dakota.

Habitat	Available (%)	Use (%)
Grassland	70.8	75.0
Woodland	0.2	0.0
Shrubland	3.4	0.4
Pasture/agricultural land	3.4	0.9
Development	0.2	0.2
Sparse Vegetation	9.4	9.4
PD Towns[*]	12.6	14.6

[*] Prairie dog towns

Table 9. Estimated selection ratios, standard errors, and confidence intervals of selection for habitats of female swift foxes ($n = 13$) in Badlands National Park and surrounding areas during the pup-rearing season (May–July) of 2009 using design III (Manly et al. 2002) with known proportion of available resource units.

Habitat	Design III			
	Selection Index	SE	CI	
	($\hat{w}$)		Lower	Upper
Grassland	1.010	0.046	0.899	1.122
Woodland	0.000	0.000	0.000	0.000
Shrubland	0.139[-]	0.075	0.000[a]	0.322
Pasture[b]	0.254[-]	0.202	0.000[a]	0.750
Development	0.157[-]	0.215	0.000[a]	0.684
Sparse Vegetation	1.426	0.298	0.697	2.156
PD Town	1.181	0.253	0.560	1.802

[a]For shrubland, pasture, and development negative lower limit was changed to 0.000; [b]Pasture includes agricultural land; [-]Indicates that the selection index ($\hat{w}$) is significantly different from 1 and the habitat is used less than expected from available.

Figure 4. Results of the eigenanalysis of home-range level (design III; Manly et al. 2002) selection ratios conducted to highlight habitat type selection by 13 lactating female swift fox on seven habitat types in Badlands National Park in South Dakota, USA, May–July2009. (a) Habitat type loadings on the first 2 factorial axes. (b) Animal scores on the first factorial plane. Vectors represent individual swift fox. PD = Prairie dog towns, P = Pasture/Agricultural land, S = Shrubland, G = Grassland, SV = Sparse Vegetation, W = Woodlands, D = Development.
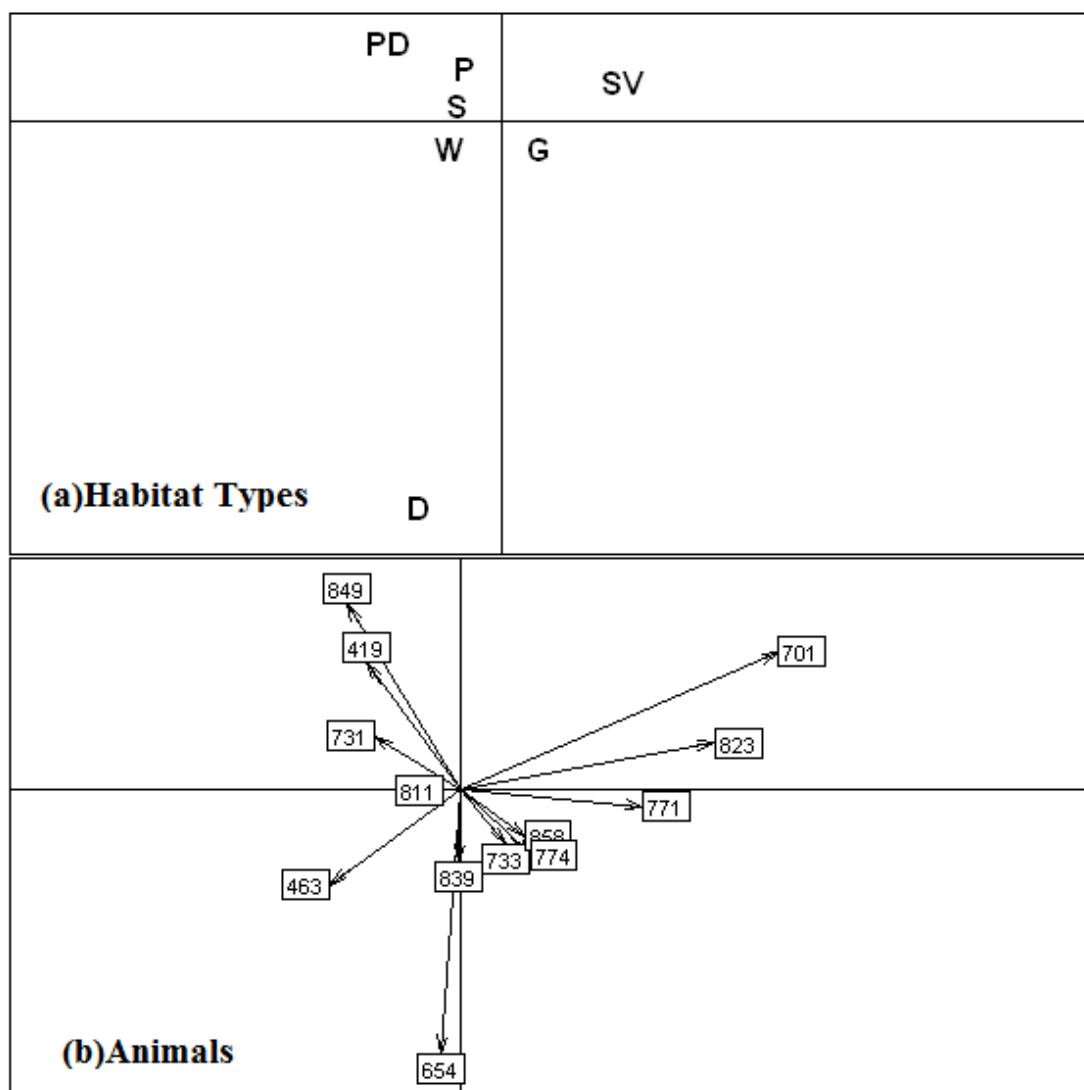
Chapter 4

Population Viability Analysis of Reintroduced Swift Fox Population at the Badlands

National Park, South Dakota, USA

Abstract:

We used Progam VORTEX 9.99b to assess the viability of the reintroduced swift fox

population at Badlands National Park (BNP) and surrounding area incorporating data on

the pedigree of the initial population. We used 1000 iterations to evaluate population

viability in terms of probability of extinction (PE), mean growth rate (r), mean expected

heterozygosity (GD; genetic diversity), and mean inbreeding coefficient (F; 1-observed

heterozygosity) for 100 years. We simulated a baseline model evaluating the

demographic parameters using the average values observed in the BNP swift fox

population, 2003 to 2009. We performed a sensitivity analysis by simulating the baseline

model under 7 different scenarios to identify key factors for evaluating the population

dynamics of the reintroduced swift fox population at BNP. According to our findings,

the reintroduced swift fox population at the BNP had a 100% chance of extinction in the

next 10 years with a negative growth rate under current conditions. The sensitivity

analysis showed mortality rate to be the major cause of probability of extinction. Even a

slight increase in survival (33% for pups and 45% for adults) would be capable of

maintaining a stable population with a positive growth rate. The probability of

population extinction, mean population size, and genetic diversity are crude estimations

obtained from data on diverse interacting processes that are too complex to be integrated

intuitively. Thus, the outcomes of this PVA should be considered an attempt to identify

the factors affecting the persistence of the reintroduced population rather than using it to

estimate accurate extinction probabilities and genetic changes to the population. To

ensure viability of the reintroduced population, the survival rate of the foxes should be

increased by increasing availability of suitable habitat, increasing prey availability, and keeping predators under control. Moreover, the population should be monitored periodically to assess demographic rates and genetic diversity.

Introduction

An intentional release of animals to the wild to establish, reestablish, or augment a population is termed as translocation, many of which may consist of more than one release (Griffith et al., 1989). Translocations can be considered successful if translocated populations become self sustaining. Successful translocation has so far been a rare event (Griffith et al. 1989, Wolf et al. 1996), where less than 25% of all the translocations achieved success (Fischer and Lindenmayer 2000). Also, more than 90% of carnivore translocations have failed (Yalden 1993). If the deterministic factors that caused the extinction of a population still persist, then the reestablishment of the translocated population also will remain under threat (Shaffer 1987). Thus, it is important to understand the extinction process and thereby identify the requirements for species (Shaffer 1990). The moment the translocated population becomes self sustaining i.e., the population becomes able to maintain its vigor and its potential for evolutionary adaptation, that population is considered viable (Soulé 1987). Franklin (1980) proposed that viable populations must maintain an effective population size of 50 individuals in the short term and an effective size of 500 in the long term. Soule et al. (1986) also

suggested that a population should maintain 90% heterozygosity (heterozygosity maintained from original founders) for 200 years to be considered viable.

Small populations are vulnerable to demographic, environmental, and genetic stochasticity (Mills et al. 2005). Demographic stochasticity is a phenomenon where the birth rate, death rate, and sex ratio of a population might cause random fluctuation even if the probabilities of birth and death remain constant (Lacy 1993). Environmental variation includes fluctuations like sudden prevalance of enzootic disease, variability of nest sites or other required microhabitats, abundance of prey and predators, either randomely or cyclically, over time, which might cause fluctuation in the probabilities of birth and death (Lacy 1993). Genetic drift is the phenomenon of fluctuation in allele frequencies due to random sampling of genes in each generation (Allendorf and Luikart 2008). Genetic variation in individuals as well as populations is lost due to genetic drift which might negatively impact demographic rates and increase susceptiblity to environmental perturbations and catastrophes (Lacy 1993). Most reintroduced populations are small in size and thus, demographic and genetic aspects of the reintroduced population should be studied for measuring the viability of the population for its proper management and conservation.

Population viability analysis (PVA) is a process that entails evaluation of data and models for the purpose of anticipating the likelihood that a population will persist for some arbitrarily chosen time into the future (Boyce 1992; Shaffer 1981; Shaffer 1987). PVA can be used for evaluating the risk of various management scenarios, to identify the

demographic and genetic parameters to which the populations are more sensitive, and to indicate research focus to provide information necessary for management of the population (Bustamante 1996). According to Lacy (1993), "computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting, deterministic, and random processes."

Swift foxes (*Vulpes velox*) were once abundant throughout the Great Plains of North America (Egoscue 1979). The species declined dramatically by the late 1800s (Zumbaugh and Choate 1985) and much of this decline was attributed to conversion of native prairie to agriculture and 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 foxes includes a fragmented population extending from southern Wyoming through eastern Colorado, western Kansas, eastern New Mexico, Oklahoma panhandle, northern Texas, South Dakota and Nebraska, Canada, and Northern Montana (Carbyn 1998, Swift Fox Conservation Team 2000, Zimmerman et al. 2003).

The first successful reintroduction program for swift foxes began in 1983. The Canadian Wildlife Service and cooperators began a swift fox reintroduction, focusing their efforts largely on private lands in Alberta and Saskatchewan, Canada (Carbyn et al. 1994). Following the first reintroduction program in Canada, several reintroduction programs had been initiated in an effort to restore swift fox populations to unoccupied, yet suitable, habitat within their historic range. These reintroductions include the

Blackfeet Reservation in Montana from 1999-2002 (Ausband and Foresman 2007), Fort

Peck Reservation in Montana, and four 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 in 2009-2010 the Pine

Ridge Indian Reservation (Oglala Sioux Parks Recreation Authority).

The objective of our study was to evaluate the population viability of the

reintroduced swift fox population at BNP and its surrounding area by examining the

current demographic and genetic parameters of the population; also to identify factors

that might affect the viability of the population by altering scenarios thereby indicating

urgently needed research that would provide proper management implications. Our

results can provide important recommendations for the proper management of the

reintroduced population as well as for any other reintroduced populations or future

reintroductions.

Materials and methods

Study area

Badlands National Park (BNP) is located in southwestern South Dakota. The 1,846-km²

study area included the north unit of BNP and surrounding area (Schroeder 2007).

Twenty three percent of the area was managed by the National Park Service, 34% by

United States 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 (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 in the remaining 48% of the north unit (Schroeder 2007).

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

PVA simulations

We used Progam VORTEX 9.99b (Lacy et al. 2005) to assess the viability of the reintroduced swift fox population at BNP and surrounding area incorporating data on the pedigree of the initial population. The VORTEX computer program uses Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife population to simulate model (Lacy 1993). The program simulated the population through a stepwise series of events like mate selection, reproduction, mortality, increment of age by one year, truncation to the carrying capacity, etc. VORTEX generated pseudo-random number to determine the occurrence of probabilistic events such as reproduction, litter size, sex determination and death to model demographic stochasticity (Lacy 1993). VORTEX modelled genetic drift by simulating the transmission of alleles at a hypothetical locus (Lacy 1993).

We collected data on the reproductive system and age-specific survival (Table 10) as well as genetic variability of the reintroduced swift fox population at BNP for 7 years (2003 – 2009). We used Program MARK to estimate the age-specific survival of the swift fox population at BNP and surrounding area (Chapter 1). Initial population size for swift fox at BNP was determined from the survey report of BNP biologists in the year 2009. We considered that foxes born from 2004 to 2009 at BNP represented the BNP fox population. We estimated the allele frequencies of the BNP fox population using Program FSTAT (Chapter 2) and used that allele frequency when running simulations.

We used demographic parameters for the simulation of the baseline scenario

(Table 10) using average values observed in the BNP fox population for 2003-2009. We

defined the reproductive system of the population as monogamous because we observed

single pairs of foxes in all the dens during breeding season (Egoscue 1979; Kamler

2002). We used a value of 10% of the mean as environmental variation for percentage

adult females breeding, and also as a standard deviation value for the mean number of

progeny (Haig et al. 1993). Because we calculated carrying capacity based on suitable

habitat availability, we assumed that standard deviation in carrying capacity due to

environmental effect could be high for which we standardized the standard deviation in

carrying capacity as 10. We used 1000 iterations for 100 years where we considered 365

days to be the duration of each year for running all simulations. We defined extinction as

only one sex remaining in the population. We evaluated population viability in terms of

probability of extinction (PE), mean growth rate (r), mean expected heterozygosity (GD;

genetic diversity), and mean inbreeding coefficient (F; 1-observed heterozygosity) over

100 years.

Carrying Capacity Estimation

We calculated the carrying capacity based on the available suitable habitat and average

home range size of swift fox (Ryan and Jamieson 1998). We used habitat selection as an

indicator of carrying capacity (Hobbs and Hanley 1990). Female swift foxes in our study

area used grassland, sparse vegetation, and prairie dog (*Cynomys ludovicianus*) towns in

proportion to availability and avoided shrubland, woodland, and agricultural land/pasture

and development during the pup-rearing season (Sasmal et al. 2011, chapter 3). Nicholson (2006) also found that foxes in general use prairie dog habitat in proportion to availability. Stephens and Anderson (2005) found that swift fox avoided agricultural land and development. Thus, we only considered grassland, sparse vegetation, and prairie dog towns as suitable habitat for swift foxes and calculated carrying capacity based on the total area of available suitable habitat at BNP and immediate surrounding area. We estimated swift fox home range by calculating the average of three home range values obtained from three different studies: the average home range sizes of foxes in Wyoming (Pechacek et al. 2000) and Colorado (Kitchen et al. 1999) from where the foxes were translocated to BNP, and the average home range size of female swift foxes during the pup-rearing season at BNP (Sasmal et al. 2011, chapter-3). We then divided the available suitable habitat area for swift foxes with the average home range size of foxes to estimate the approximate carrying capacity of our study area. We used data from the USGS-NPS vegetation mapping program for BNP (Loh et al. 1999) to estimate carrying capacity.

Sensitivity analysis

A variety of deterministic as well as stochastic factors act on a population simultaneously to determine the fate of a population. Thus, to determine the relative impact of factors that can affect the viability of a population we created different future scenarios reflecting levels of higher mortality due to intraguild predation, lower carrying capacity due to loss of suitable habitat or lower prey availability, and inbreeding depression. We simulated 7

different scenarios (Table 10) to identify key factors for determining population

dynamics of the reintroduced swift fox at BNP. We assumed that inbreeding was not

occurring during the study interval because nearly all the males and females were

participating in the breeding process indicating that there were enough reproductively

active animals available to avoid inbreeding. Also there have been no inbreeding

reported in swift foxes and closely related kit foxes so far (Moehrenschlager 2006). As

such, when running the baseline scenario we did not include inbreeding depression.

However, we included inbreeding depression in one of the scenarios as a sensitivity

analysis to assess the consequences of inbreeding under present conditions. We

considered the default value of 3.14 lethal equivalents provided as a default within

Program VORTEX when running the simulation under an inbreeding depression

scenario. Swift foxes at BNP were observed to select habitats with short vegetation

height (Russell 2006; Sasmal et al. 2011, chapter-3). Higher precipitation in any year

might cause the vegetaion height to increase thereby converting suitable to unsuitable

habitats for foxes. Also, a disease epizootic (e.g., plague; *Yersina pestis*) might cause a

decrease in prey species such as prairie dogs thereby reducing prey availability and

habitat suitability. Because we considered that carrying capacity was dependent on the

availability of suitable habitat, loss of suitable habitat would therefore affect carrying

capacity. Thus, we ran the simulation considering a reduction in carrying capacity due to

moderate (25%) or a high (50%) degree of habitat loss. Another key factor that plays an

important role in the viability of a population is mortality rate. Mortality rate can

fluctuate depending on many factors like increase/decrease in intraguild predation,

fluctuating prey availability, or habitat loss. Thus, we considered running a simulation to assess the effect of a decreased mortality rate of 10%, and 20%, less of the baseline scenario mortality rate respectively on population trend since the current mortality rate was already low. We then assessed population trend by combining the effects of both decreased carrying capacity and increased survival simultaneously.

Results

 In the year 2009, 117 swift fox pups and 51 swift fox litters were observed at BNP and its surrounding area. In general, a pair of swift foxes was observed to be associated with a litter at the study site. Thus, the approximate initial population size of swift foxes in the year 2009 at the study site was estimated to be 219, which comprised 102 adult foxes (51*2) and 117 pups. A total of 7,483.6 km^2 of BNP was comprised of grassland, sparse vegetation, and prairie dog towns. The average home range size of swift foxes was estimated to be 9.37 km^2 (Colorado: 7.6 km^2 [Kitchen et al. 1999], Wyoming: 11.7 km^2 [Pechacek 2000], BNP: 8.8 km^2 [Sasmal et al. 2011, chapter-3]). Remaining suitable habitat at BNP after a 25% loss of suitable habitat was estimated to be 5,612.7 km^2, whereas the remaining suitable habitat area after a 50% loss of suitable habitat was estimated to be 3,741.8 km^2. To run the sensitivity analysis under an increased survival scenario, mortality was decreased by 10 % and 20% for both pups and adult foxes. Also, we performed sensitivity analysis by running the simulation under 77 % of mortality for

pups in place of 88% mortality (current conditions), and 55% mortality of adults in place of 66% mortality.

The reintroduced swift fox population at the BNP was at risk of extinction within 10 years of time under current conditions due to a negative growth rate of -0.47. After decreasing the mortality by 10% (79% mortality for pups and 59% for adults) the population still remained under the threat of extinction within 41 years. However, a 20 % decrease in mortality (70% for pups and 54% for adults) resulted in zero percent probability of extinction for the population in the next 100 years with a positive growth rate of 0.23 (Table 11). The reintroduced population reached a stable condition without any probability of extinction in the next 100 years when mortality rate was set at 77% for pups and 55% for adults under current conditions. The fluctuation in carrying capacity did not affect either the probability of extinction of the population or the growth rate of the population under the moderate survival scenario (Table 11).

Discussion

Population Viability Analysis is a process that synthesizes information about a population for the purpose of developing the best possible model of persistence (Boyce 1992). It is important to assess the viability of a reintroduced population not only to evaluate the success of the reintroduction but also to identify the key factors affecting viability. We assessed the success of the swift fox reintroduction program at BNP and its surrounding

area using population modeling in Program VORTEX. Every model has its limitations as it solely depends on the data that has been used for validation of the model. Our population modeling of the reintroduced swift fox population resulted in an extinction probability of 100% and negative growth rate of -0.47, which indicated that the success of the reintroduction could not be guaranteed as a viable population has not been maintained at BNP and its surrounding area.

We concentrated on the demographic and genetic aspects of the reintroduced swift fox population at BNP for modeling the dynamics of the population. Because catastrophes (e.g., wild fires, floods) are rare events at BNP and are not considered an important cause of swift fox population decline, we did not incorporate catastrophes in our assessment of population viability. Although catastrophes are rare events in this system, they might negatively effect the population directly via mortality or indirectly through habitat destruction. We standardized the effect of environmental variance (EV), which in realistic levels might be greater and could become the cause of population extinction even under positive growth rate (Lande 2002). We also did not consider the effects of density dependence on the population, either positive population responses to low-density or negative responses (e.g. Allee effects), or more complex relationships (Lacy 1993). Thus, outcomes of this PVA should be considered as an attempt to identify the factors affecting the persistence of the reintroduced population rather than to estimate accurate extinction probabilities and genetic change in the population.

Decline in swift fox abundance in most of its native habitats was attributed to conversion of native prairie to agriculture and associated declines 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). Hunting and trapping was prohibited in our study area and also, suitable habitat availability was increased due to short grass prairie restoration as well as increased prey species, such as prairie dog availability. In spite of all the efforts in maintaining swift fox habitats at BNP as well as those aimed at increasing prey availability, the survival probability remained low. In our study area, decreased number of coyotes also was reported by park biologists (Badlands National Park) due to spread of sarcoptic mange epizootics caused by a mite *Sarcoptes scabiei* (Chronert et al. 2007). Because predation from coyotes (*Canis latrans*) has been reported as a major cause of fox mortality (Kamler and Ballard 2002; Karki et al. 2007), decline in coyotes supposedly aided in increased survival of swift fox in our study area. Increased mortality rate was observed to be the major cause behind the extinction probability as it is directly related to persistence. Increased mortality rate also effectively decreased the growth rate of the population. All these variables indicated that even a stable population can be threatened by extinction by the increase in mortality rate, which can be caused due to habitat loss, decrease in prey availability due to spread of disease like plague, or increased predation.

Though decrease in carrying capacity did not pose a significant effect on probability of extinction, it should be considered for long-term viability of a population. Carrying capacity of a population is directly related to availability of suitable habitats,

which ensure long-term viability. The major cause of swift fox population decline was identified to be loss of suitable habitat (Allardyce and Sovada 2003). Moreover, availability of suitable habitat might help the declining population with high mortality to stabilize and/or increase by releasing the population from the pressure of predation from competition with other canid species by providing opportunity for population expansion. Decreased carrying capacity also affected the genetic diversity and inbreeding coefficient of the population to a greater extent.

Ensuring long-term viability of a population is one of the major goals of a translocation process. Demographic and environmental factors mainly address short-term viability of a population whereas genetic factors are considered to ensure long-term viability (Haig et al. 1991). A population tends to lose genetic variability when an effectively small number of individuals are used as founders for the population (Wright 1931; Nei et al. 1975). Loss of genetic variability takes place due to the loss of rare alleles, which become especially susceptible during a bottleneck (Allendorf and Luikart 2008). Reduction of genetic diversity can happen due to genetic drift and is independent of the number of alleles present (Allendorf and Luikart 2008). Thus, it is important to ascertain if genetic variability is reduced in newly established populations. Few examples of PVA to date have considered genetic change in reintroduction despite its importance in population viability (Ogden et al. 2005; Grueber and Jamieson 2008). Loss of genetic diversity was not evident in our simulation of the population that persisted under the present conditions. However, effective loss of genetic diversity has been identified in cases of increased mortality (Vrijenhoek 1994). Inbreeding has not

been identified as a problem under present conditions but may pose a threat under increased mortality and decreased carrying capacity via change in mortality rate (Stockley et al. 1993).

The probability of population extinction, mean population size, and amount of genetic diversity are crude estimations obtained from data on diverse interacting processes that are too complex to be integrated intuitively (Lacy 1993). PVA is a computer simulation model that focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest and thus, can only be as good as the data and assumptions used to develop the model (Lindenmayer et al. 1993). Therefore, PVA is only capable of forecasting the likely effects of those factors incorporated into the model (Lacy 1993). Considering the factors assessed from field data collected for 7 years (2003-2009) and incorporated into the PVA model, the reintroduced population of swift fox at BNP and surrounding area produced a short- term viable population. However, future monitoring is critical to ensure long-term viability of the population.

Conclusion

Ecological processes are complex, dynamic, as well as stochastic and thus, do not guarantee a stable state. Even a number of initially successful reintroductions were determined to be declining at later stages (Seddon 1999). Thus, managers of

reintroduced populations should monitor them periodically for vital rates and genetic diversity. Different management tactics should be adopted to develop a better understanding of the system. Because mortality was identified as a key factor in maintaining a viable population, managers should attempt to keep mortality under control (less than 77% for pups and 55% for adults). The main factors affecting mortality should be identified to limit their impact. Loss of habitat has played an important role in the extirpation of the swift fox population at BNP. Therefore, proper care should be taken for the maintenance of a suitable habitat. Periodic supplementation should be done to prevent inbreeding depression in the absence of gene transfer through immigration. Care should be taken to maintain connectivity with other neighboring populations to ensure genetic diversity maintenance.

Acknowledgements

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Table 10. Summary of initial values for VORTEX for simulation of the translocated swift

fox population at the Badlands National Park, South Dakota, USA.

Parameter values for all scenarios

Initial population size	219
Age of first reproduction for females	1
Age of first reproduction for males	1
Maximum age of reproduction	6
Maximum number of progeny/year	7
Sex ratio at birth (% males)	50
Adult males in the breeding pool (%)	100
Adult females breeding (%)	100
Mean number of progeny per female/year	5.5

Parameter values that varied in different scenarios

Mortality Rates (%)

Baseline (B)		Low Survival (LS)		Moderate Survival (MS)	
Males and Females		Males and Females		Males and Females	
Age 0-1	88(1 SD)	Age 0-1	79 (1 SD)	Age 0-1	70 (1 SD)
Adults	66 (1 SD)	Adults	59 (1 SD)	Adults	54 (1 SD)

Carrying Capacity (K)

Baseline (B)	Moderate (MK)	Less (LK)
799	599	399

Table 11. Scenario results from stochastic simulations in program VORTEX over 100

years and 1000 iterations for understanding reintroduced swift fox population at Badlands

National Park, South Dakota, USA.

Scenario	P(E)	r	GD	F
Baseline	1	-0.47	-	-
Moderate survival	0	0.23	0.95	0.05
Low survival	1	-0.09	-	-
Mortality with 77% and 55% (LS)	0	0.06	0.94	0.06
Moderate survival-MK	0	0.23	0.93	0.07
Moderate survival-LK	0	0.22	0.9	0.1
LS-MK	0	0.05	0.93	0.07
LS-LK	0	0.05	0.9	0.1

P(E): Probability of extinction
r: Mean Growth rate
GD: Gene Diversity (Expected Heterozygosity)
F: Inbreeding Coefficient
MK: Moderate Carrying Capacity
LK: Low Carrying Capacity