Life on the edge: habitat fragmentation limits expansion of a restored carnivore

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Abstract

The successful recovery of imperiled species is dependent on knowledge of how demographic drivers mediate population growth and expansion. One of the largest species restoration projects has been the reintroduction of swift foxes *Vulpes velox* to southern Canada, where 947 foxes were released between 1983 and 1997. Swift foxes have since increased and expanded their range into northern Montana (USA), but have experienced a population decline and stall in recolonization over the past 10 years. The objective of this study was to estimate the survival and reproductive rates of swift foxes in northern Montana, which constitutes the southern edge of this population. In addition, we evaluated support for two different hypotheses of how environmental factors and several demographic factors influence survival. Although our length of monitoring was relatively short, we found that adult and juvenile annual survival rates were 54% and 74%, respectively, and fecundity was 0.85. We found the most support for the hypothesis that the percentage of native grassland at the 1-km scale influenced survival and found that survival increased, on average, 2.1% for every 5% increase in grassland. Compared to previous estimates of swift fox population growth immediately following the release, our data suggest the population is currently stable. The long-term successful recolonization and connectivity of swift fox populations in this region will likely be dependent on maintaining large tracts of contiguous grassland. Comparing the estimates of demographic rates among different points in space and time should help managers better understand the population dynamics and inform restoration strategies for recovering populations.

Introduction

Understanding how survival and reproduction influence population growth and expansion is critical for the management of reintroduced populations. Initially, the objective of a reintroduction program is to maintain a positive population growth rate during the establishment phase within a defined reintroduction area (US Fish and Wildlife Service, 1993; Seddon & Armstrong, 2016). As the population reaches carrying capacity and enters the persistence phase (Seddon & Armstrong, 2016), population growth slows and there is higher potential for animals to attempt to recolonize areas outside of the core reintroduction site (Jachowski *et al*., 2016). The process of recolonization itself typically occurs via one of two processes. First, a population may expand through contiguous suitable

habitat as gray wolves *Canis lupus* have in the Great Lakes region (Wydeven, Van Deelen & Heske, 2009) and African wild dogs *Lycaon pictus* in northern Kenya (Woodroffe, 2011). Second, recovery may occur in distinct core areas that require a species to overcome dispersal barriers for population connectivity and expansion, as is the case for the mountain lions in the Northern Great Plains (Gigliotti, Matchett & Jachowski, 2019) and wolves *C. lupus* in France and Switzerland (Valière *et al*., 2003). Therefore, studying individuals at the expansion front can illuminate the factors that enhance or inhibit range expansion, and identify which expansion process is occurring (Swenson, Sandegren & Söderberg, 1998; Jerina & Adamic, 2008; Urban *et al*., 2008).

The reintroduction of swift foxes to Canada is considered the largest canid reintroduction effort to date (Boitani, Asa

& Moehrenschlager, 2004). Nine hundred and forty-two foxes were released in southern Alberta and Saskatchewan between 1983 and 1997, after *c*. 45 years of extirpation (Moehrenschlager & Lloyd, 2016). Soon after, swift foxes were documented dispersing into northern Montana (USA), where swift foxes were previously extirpated, and the first documentation of reproduction in Montana occurred in 1997 (Zimmerman, 1998). Within 5 years (i.e. by 2001) the distribution of foxes had spread *c*. 50 km south into Montana (Moehrenschlager & Moehrenschlager, 2001); however, population expansion appears to have stalled since that time (Moehrenschlager & Moehrenschlager, 2018) and there is still a ~350 km gap in distribution to fox populations in south-eastern Montana (MTFWP, 2019). As a result, both the Swift fox Conservation Team (Dowd Stukel, 2011) and the Montana Swift Fox Conservation Strategy (MTFWP, 2019) have identified enhancing connectivity of this isolated population with southern populations as a primary objective. Therefore, studying the demographic rates of foxes at the expansion front of this population could provide information on factors influencing swift fox population dynamics and possible demographic and environmental factors that limit range expansion.

Multiple factors could influence swift fox survival and subsequent population expansion into suitable habitat. It is hypothesized that as an intermediate predator, swift foxes select for resources that minimize predation risk, mainly from coyotes *Canis latrans* (the top predator of swift foxes, Kitchen, Gese & Schauster, 1999; Olson & Lindzey, 2002), rather than select for resources that maximize access to prey (Thompson & Gese, 2007). In accordance with this hypothesis, swift foxes are thought to minimize predation risk by increasing their ability to visually detect their predators and decrease lethal encounters by avoiding prey-rich areas (Kamler *et al.*, 2003*a*; Russell, 2006; Thompson & Gese, 2007; Sasmal *et al.*, 2011; Butler *et al.*, 2020). There is less research on the influence of anthropogenic development, such as roads and natural gas development, on predation risk. Previous studies have found that swift foxes make use of roads and areas near roads and gas wells (Hines & Case, 1991; Sasmal *et al.*, 2011; Butler *et al.*, 2020), but previous studies have found that coyotes use roads as well (Grinder & Krausman, 2001; Hinton, Van Manen & Chamberlain, 2015; Murray & St. Clair, 2015). One hypothesis for why swift foxes select for areas closer to development is that these features provide a 'human shield' (Berger, 2007; Moll *et al.*, 2018), where human presence and activity associated with these features may cause coyotes to avoid these areas in rural landscapes typical of the Great Plains. Additional research is needed to determine whether these factors influence survival and how they may moderate range expansion.

The objectives of this study were to: (1) estimate sex- and stage-specific survival rates and fecundity rates of swift foxes at the edge of the population; (2) evaluate support for the predation risk and human shield hypotheses; (3) create a predictive model to assess viability of swift foxes in this region; and (4) evaluate sensitivity and elasticity of vital rates. Previous studies of swift fox survival and reproduction in the

Canada-Montana region occurred when the population was in the establishment and growth phase following reintroduction (Zimmerman, 1998; Moehrenschlager, List & Macdonald, 2007). Findings from our study will help identify if this swift fox population is in the establishment or persistent phase along the edge of their current range. If restoration managers seek to not only establish a restored population, but also facilitate population connectivity, demographic studies at the edge of a restoration area could help better identify and account for potential ecological traps or barriers to larger scale animal restoration.

Materials and methods

Study area

We conducted our study in the 17,991 km^2 area of northern Blaine, Phillips and Valley counties of north-eastern Montana from US route 2, north to the border with Canada. The dominant vegetation type in the study area was short and mixed-grass prairie interspersed with cultivated crop fields, predominately wheat fields, and areas covered by sagebrush *Artemisia* spp. Most of the roads were gravel or unimproved two tracks in pastures, with only a few paved roads in the study area. At the southern boundary of the study area, irrigated agricultural fields were common adjacent to the Milk River, which largely runs west to east along US route 2 (Fig. 1b). Most of the area was level or rolling terrain with some steep coulees along drainages, and elevation ranged from 629 to 1068 m. The average monthly temperature ranges from −1.8°C in the winter to 13.9°C in the summer and the average annual precipitation ranges from 190 to 520 mm (Zimmerman, 1998).

Capture and monitoring

To sample foxes across a range of conditions at the periphery of the population, we attempted to capture foxes within five focal sites across the entire study area (Fig. 1). We chose these five study sites in an attempt to capture swift foxes across a gradient of land use representing differing levels of cultivated crop field development intermixed within native grasslands. We captured foxes in lined box traps (Tomahawk Live Trap Co., Tomahawk, WI, USA; Moehrenschlager, Macdonald & Moehrenschlager, 2003), marked individuals in both ears with uniquely numbered ear tags (National Band and Tag Company, Newport, KY, USA) and fitted captured foxes with LiteTrack30 store on board Global Positioning System (GPS; Sirtrack, Havelock, New Zealand) collars that also emitted a VHF signal. We aged foxes based on tooth wear and color (Ausband & Foresman, 2007*a*) and classified foxes into two stages: juvenile or adult. We assumed that swift foxes were born in April as swift foxes in Canada breed in March and have a mean gestation period of 51 days (Moehrenschlager, 2000). We considered juveniles to only remain juveniles from October until March following their birth, and be adults thereafter. Handling procedures were approved by the Clemson University Institutional
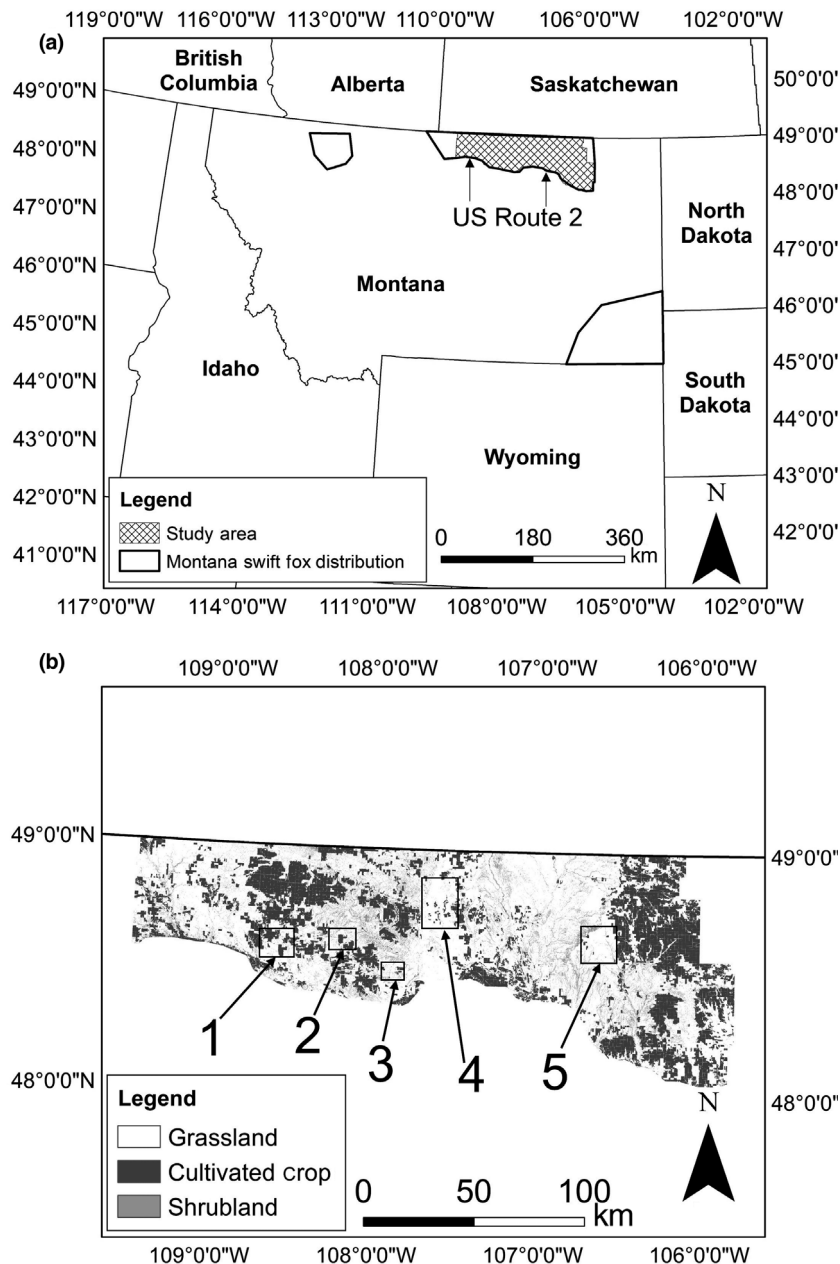
Figure 1 (a) Known distribution of swift foxes during this study (polygons) and study area (shaded area) within Montana where we estimated vital rates during 2016–2018; (b) focal sites within the study area where we trapped six swift foxes (1), four swift foxes (2), three swift foxes (3), 22 swift foxes (4) and 13 swift foxes (5) in 2016–2018.

Animal Care and Use Committee (AUP2016-036) and Montana Department of Fish, Wildlife and Parks Scientific Collector's Permit (2016-107).

We programmed collars to attempt a GPS location every 2 h in October 2016–March 2017 and every 5 h in our second field season, October 2017–May 2018 (see Butler *et al.*, 2020 for more details). We attempted to locate collared foxes twice a week to monitor their survival status. When a mortality signal was detected, we attempted to determine the

cause of mortality by examining carcass puncture wounds, skeletal injuries and other evidence at the mortality site such as tracks of other animals and carcass location. We classified mortalities as coyote, other predation, vehicle or unknown.

During the study, we had issues with some collar batteries dying prematurely (Butler *et al.*, 2019). We expected collars to last at least 6 months, but several collars had batteries that died or lost their VHF antennas in the first 3 months. In an effort to re-sight collared individuals that had collar failure

and might still be alive, when we had not located a fox after a month, we deployed three baited, heat and motion-activated camera traps (TrophyCam, Bushnell, Overland Park, KS, USA) within a fox's known primary area of use or suspected area of use for 2 weeks. We determined these areas based on GPS data downloaded from the collars (Butler *et al.*, 2020), any locations determined from the VHF signal or proximity to the original trapping location if we did not have GPS or VHF locations. If we detected the fox, then we kept cameras active until the fox was no longer detected. If a collared fox was not detected after 2 weeks, then we moved cameras to a new location the individual historically frequented (i.e. secondary area) for an additional 2 weeks. We removed all cameras if the target fox was not located after 4 weeks. We were able to identify collared foxes by the number on their ear tags in the camera trap photographs.

Each spring, we searched clusters of GPS points to look for natal dens. When a den was located, we placed a camera trap 3–4 m away from the den. We considered the den a natal den if two swift foxes were observed near it and by the presence of one fox bringing back food to the den. If we determined that the den was not a natal den, then we searched other GPS clusters until we could locate a den that met our criteria. We also located dens by opportunistically observing uncollared swift foxes in the spring and summer. For these uncollared fox potential den sites, we immediately placed a camera trap at the den. We then considered the den to be a natal den using the same criteria as those located from collared individuals. Cameras were placed at least 3 m away from the den opening and programmed to take a burst of three pictures every time they were triggered, and cameras were kept at the same den sites until foxes moved to a new den site. We estimated litter size as the maximum number of pups counted in a single picture during our monitoring.

Data analysis

We estimated survival rates using the known-fate model in program R 3.5.3 (R Core Team, 2013) using the 'RMark' (version 2.2.7; Laake & Rexstad, 2008) and 'msm' (version 1.6.8; Jackson, 2011) packages. We summarized data into monthly (i.e., calendar month) encounter histories for individuals. If a fox was not observed during a month, then it was censored during that interval. We estimated the 12-month survival rates for adults and the 6-month survival rates for juveniles, as has been done in other swift fox studies (Sovada *et al.*, 1998; Kamler *et al.*, 2003*a*). To evaluate support for our hypothesis that swift fox survival was enhanced by selecting habitats at the third order (Johnson, 1980) that increased the probability of detecting predators as opposed to maximizing access to prey resources (Thompson & Gese, 2007), we evaluated the influence of the percentage of native grassland within a 1-km radius moving window (PG), topographic roughness (TRI) and normalized difference vegetation index (NDVI; see Butler *et al.*, 2020 for full description of how these variables were estimated) on swift fox survival. We predicted that the percentage of grassland would have a positive influence on survival because more

contiguous grasslands minimize the influence of tall cultivated crop fields, which increases predator detection. We predicted that TRI would have a negative impact on survival because swift foxes have a larger viewshed in more level terrain (Russell, 2006). We predicted that NDVI would have a negative impact on survival because the areas of high vegetation growth are likely to be selected for by coyotes due to higher prey availability (Thompson & Gese, 2007). To evaluate support for our human shield hypothesis, we assessed the influence of distance to nonpaved roads (NonPaved) and distance to natural gas wells (DistWell) on swift fox survival. Specifically, we predicted that increasing distance from nonpaved roads and natural gas wells would have a negative effect on survival due to stronger avoidance by coyotes to these features (Kamler *et al.*, 2003*b*). We intended to extract these environmental variables from within the home range of each individual fox. However, due to GPS collar failure, we were unable to download GPS data from 10 individuals. For seven of these individuals, encounter histories were entirely from the VHF signal detection alone, and three of the encounter histories came from camera re-sights. Therefore, instead of excluding these individuals from the analysis, we decided to extract environmental data from a 3.66 km buffer, which is equal to the average home range size of foxes in our study area (Butler *et al.*, 2020), around the initial trap location of all foxes. In addition to environmental variables, we also hypothesized that survival could be influenced by two demographic variables, sex and stage. Previous research has found that survival rates can differ between males and females during the dispersal season (August–December) or annually (Ausband & Foresman, 2007*b*), but most often they are similar (Matlack, Gipson & Kaufman, 2000; Olson & Lindzey, 2002; Schauster, Gese & Kitchen, 2002). Therefore, we predicted that there would not be an effect of sex. A previous study found that juvenile swift foxes have a higher survival rate than adults (Kamler *et al.*, 2003*a*), but more frequently, studies have found that adults have a higher survival rate than juveniles (Sovada *et al.*, 1998; Schauster *et al.*, 2002; Ausband & Foresman, 2007*b*). Therefore, we predicted that adults would have higher survival rates than juveniles. Lastly, we included year as a variable to account for a potential difference in survival due to differences in monitoring between the two field seasons.

We evaluated support for each *a priori* monthly survival model we developed (Table 1) using Akaike's information criterion adjusted for sample size (AIC$_c$; Burnham & Anderson, 2002). Due to our small sample size and model convergence issues when trying to fit models with multiple predictor variables, we only evaluated univariate models (Table 1). We selected top model(s) by first considering all models within two ΔAIC$_c$ values of the top model. Because each model was univariate, we used a two-step approach to determine which model from this top candidate set to interpret and estimate survival from. First, we compared the relative support for each remaining model by comparing AIC$_c$ weights (Burnham & Anderson, 2002). Second, we calculated 85% confidence intervals (CI: Arnold, 2010) and

considered the variable to be informative if CIs did not overlap zero. For those remaining models, we then estimated the 12-month adult and 6-month juvenile survival rates based on the top model(s).

To estimate the population growth rate [the change in population size from the current time step to the next (λ)] and assess population viability, we created a pre-birth-pulse female-based stochastic Lefkovitch matrix model consisting of three stages: pup (0–5 months old), juvenile (6–12 months) and adult (>1-year-old):

$$A = \begin{bmatrix} 0 & 0 & F_{\text{adult}} \\ S_{\text{pup}} & 0 & 0 \\ 0 & S_{\text{juvenile}} & S_{\text{adult}} \end{bmatrix},$$

where F represents fecundity and S represents survival. We projected the population at a yearly interval t using the equation:

$$N_{(t+1)} = A \times N_{(t)},$$

where $N_{(t)}$ is the abundance vector for each stage at time t and A is the projection matrix.

We parameterized our matrix with demographic rates determined from the above methods, with the exception of pup survival which we gathered from the literature. We assumed litters born during our study had a 1:1 sex ratio (Sovada *et al.*, 2003; Sasmal *et al.*, 2016). Therefore, to estimate annual female fecundity (the number of female offspring produced per female) we divided the total number of pups observed for each den in half and averaged that value across the dens monitored. We used estimates of pup survival from another reintroduced population of swift foxes in Montana, which was *c*. 385 km west of our study area (Ausband & Foresman, 2007*b*). To determine the composition of our initial abundance vector, we used population estimates from an international census conducted in winter 2014–2015

that largely overlapped with our study area (Moehrenschlager & Moehrenschlager, 2018). This census estimated that there were 346.9 ± 79.5 foxes within our study area, and we used 174 female foxes as our starting abundance as several past studies have found *c*. 1:1 sex ratio (Olson & Lindzey, 2002; Kamler *et al.*, 2004; Ausband & Foresman, 2007*b*; Sasmal *et al.*, 2016). We assumed a 1:1 ratio of adults to juveniles and our starting vector was composed of 0 pups, 87 female juveniles and 87 female adults. We did not include any pups as we assumed our model represented the population during the winter when all pups had already transitioned to juveniles. To incorporate demographic stochasticity, for each simulation we varied the survival values based on the normal distribution between the low and high 95% CIs.

We determined λ for the population by calculating the mean for 1000 simulations projected out to 100 years in program R. Lastly, we performed sensitivity and elasticity analysis using the package 'popbio' (version 2.7; Stubben & Milligan, 2007) to determine the importance of each life-history stage and demographic rate following the methods of Caswell (1989). Low sensitivity values indicate that a change in that rate, survival or fecundity, has a small influence on the population growth rate whereas a high value indicates that a change in the rate has a large influence on the population growth rate. In this case, sensitivity values cannot be compared between survival and fecundity rates because they are measured on difference scales. A low elasticity value indicates that a proportional change in one rate, survival and fecundity, has a small influence on the population growth rate and a large proportional change has a large influence. In this instance, elasticities can be compared because they are based on a proportional rate.

Results

We captured and collared 46 swift foxes in north-eastern Montana during October–December in 2016 and 2017 (Table S1). We collected survival data between October–April 2016–2017 and October 2017–May 2018. While most re-sightings were based on VHF telemetry (29 of 46 collared foxes), five additional encounters were recorded using camera traps for individuals we had monitored for several months via telemetry but had not been able to locate due to collar malfunction. In addition, camera traps provided a single re-sighting encounter for three collared individuals that we had not been able to locate since their capture due to collar malfunction. In total our analysis was based on encounter histories for 32 individual collared swift foxes (10 adult males, eight juvenile males, nine adult females and five juvenile females) and foxes were monitored for an average of 5 months (range: 2–8 months). We documented eight mortalities during the study including five due to coyote predation, one hit by a car, one by fur trapping and one unknown cause.

We monitored two dens of radio-collared foxes and two additional dens of uncollared foxes in May–July 2017, and three dens of radio-collared foxes and three dens of uncollared foxes in May–July 2018. Litter counts ranged from

Table 1 Model selection results for swift fox survival known-fate survival models in north-eastern Montana, 2016–2018

Model	k	AICc	ΔAIC$_c$	w_i
S(~PG)	2	54.2	0.00	0.26
S(~TRI)	2	55.2	1.01	0.16
S(~1)	1	55.3	1.10	0.15
S(~NDVI)	2	56.2	2.05	0.09
S(~Year)	2	56.4	2.20	0.09
S(~Stage)	2	56.5	2.37	0.08
S(~Sex)	2	56.9	2.73	0.07
S(~NonPaved)	2	57.2	2.98	0.06
S(~DistWell)	2	57.3	3.17	0.05

k, number of parameters; AICc, AICc value for each model; ΔAICc, difference in AIC value between top model and other model; w_i, Akaike weights; S, survival; PG, percentage of native grassland within a 1 km radius moving window; TRI, topographic roughness; NDVI, normalized difference vegetation index; NonPaved, distance to nonpaved roads; DistWell, distance to natural gas well; Year, year captured; Stage, stage class; Sex, sex class.

two to four pups. Five dens where we did observe signs of parental care by two adult foxes did not produce any pups, one produced two pups, one produced three pups and three produced four pups (Table 4). In 2017, the female fecundity rate was 1.5 and in 2018 it was 0.42 with a combined overall average fecundity rate of 0.85 female pups per female.

Our model selection analysis of survival indicated a relatively high amount of model uncertainty (Table 1), with percent grassland being the top-ranked model and two other models within 2 ΔAIC values of the top model (TRI index and the null). The percentage of grassland model had almost twice as much model weight as the other two model in our confidence set (Table 1). Percentage of grassland had a positive influence on survival ($\beta = 0.57$) and monthly survival increased, on average, 2.1% for every 5% increase in the percentage grassland (Fig. 2). The average percentage of grassland for the entire study area was 62% and the estimated monthly survival rate at that percentage of grassland was 95%. When we extrapolated this survival rate to 6 and 12 months, the average annual adult survival rate during our study was 0.54 (95% CI = 0.30, 0.84) and the average juvenile survival rate was 0.74 (95% CI = 0.56, 0.92). The second-ranked model (based on AIC weights), TRI index, had 85% CI that overlapped zero (−0.16, 1.72). Therefore, we considered there to be only weak evidence to support a positive effect of roughness. Our third ranked model was the null model, suggesting constant survival across all foxes in this study. Based on the null model, we estimated monthly survival to be 94%, then we extrapolated this survival rate to the average annual adult survival rate of 0.48 (95% CI = 0.23, 0.73), and the average juvenile survival rate was 0.69 (95% CI = 0.49, 0.89).

We parameterized our population matrix using the estimates of adult and juvenile survivorship based on the top predictive model that included percentage grassland (Table 2) and we used the average pup survival rate of 0.73 (95% CI = 0.55, 0.89) from Ausband & Foresman (2007b):

$$A = \begin{bmatrix} 0 & 0 & 0.85 \\ 0.55 - 0.89 & 0 & 0 \\ 0 & 0.52 - 0.96 & 0.30 - 0.84 \end{bmatrix}.$$

Based on 1000 simulations, we estimated the average λ to be 1.002 (95% CI = 0.996, 1.008). We chose to only forecast the population out 50 years into the future due to the potential for wide variation in population performance year to year. We found that the population size remained stable over 50 years (Fig. 3). Adult survival was the most sensitive and elastic vital rate (Table 2).

Discussion

Our study suggests that swift foxes at the edge of their range in north-eastern Montana have relatively low survivorship compared to previous studies of this population that were conducted during the establishment phase post-reintroduction or establishment. Adult survival during our 2-year study was lower than two previous estimates from the Canada-Montana

population that were calculated during the growth phase of the population following reintroduction that occurred >20 years previous (Zimmerman, 1998; Moehrenschlager, 2000), and that of a recently established population of foxes on the Blackfeet Reservation in western Montana (Table 3; Ausband & Foresman, 2007b). Observing lower survival outside of the core reintroduction area post-reintroduction is similar to the results of Devineau *et al.* (2010), who found that Canada lynx *Lynx canadensis* that moved outside of the core reintroduction area in Colorado had lower survival than those inside it. We might expect this to occur because release areas are often chosen to maximize the long-term survival and reproduction of the restored population (Moehrenschlager & Lloyd, 2016).

Our study indicates that the population of swift foxes in north-eastern Montana is currently stable, but likely not producing enough individuals to successfully expand southward into unoccupied habitat that is suitable based on previous habitat assessments (Alexander *et al.*, 2016; Butler, 2019). In source-sink theory, source populations occur in areas where reproduction is greater than mortality, and there is a surplus of juveniles in the population that disperse to other areas (Pulliam, 1988). From a species restoration or recovery perspective, in order for a population to expand its range, the current population needs to produce a sufficient number of 'surplus' dispersing individuals (Lubina & Levin, 1988). Moehrenschlager (2000) found 64% of swift fox juveniles remained in their natal range into the winter, and all the juvenile foxes we were able to monitor into spring remained in the area where we caught them (Butler *et al.*, 2020), which may have led to their relatively high survival rates (Table 3). Thus, the stable growth rate we observed suggests that the population is likely not acting as a source population for the region; and could explain why despite there being suitable habitat in the gap between populations (Alexander *et al.*, 2016; Butler, 2019), areas south of our study area remain unoccupied.

In accordance with our predation risk hypothesis, survival was best explained by the amount of grassland within a fox's area of use (Table 1), which was also the strongest predictor of resource use by swift foxes in the region (Butler *et al.*, 2020). Previous studies have also shown that swift foxes prefer short- and mixed-grass prairies over other cover types because grasslands increase the ability to visually detect predators, provide swift foxes with denning opportunities and enhance population connectivity (Kitchen *et al.*, 1999; Russell, 2006; Thompson & Gese, 2007; Sasmal *et al.*, 2011; Schwalm, 2012). We found that survival increased as the amount of grassland inside the home range increased, indicating that survival decreases near and in crop fields, despite these areas supporting higher prey densities (Kaufman & Kaufman, 1989; Kaufman, Kaufman & Clark, 2000; Stanley, 2010). Survival might have increased in grassland-dominated areas because swift foxes were better able to avoid coyotes and red foxes there. In our study area, grasslands have been converted to and fragmented by cultivated crop fields, which is predicted to continue into the future (Lipsey *et al.*, 2015), and red foxes and coyotes have
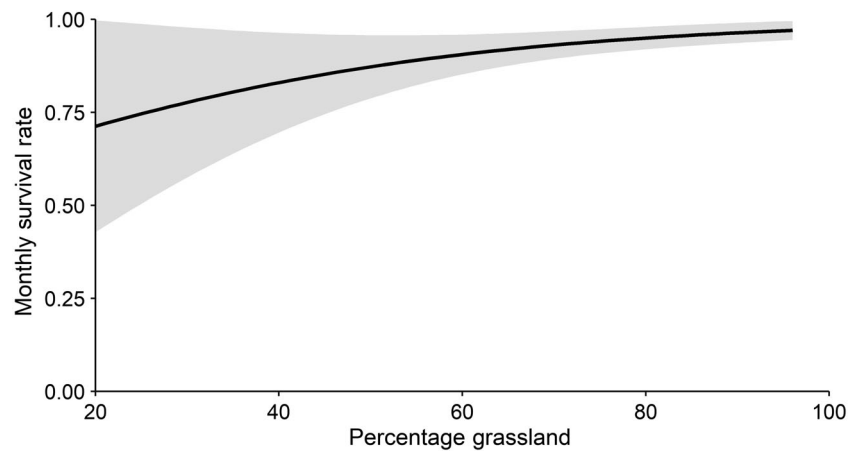
Figure 2 Predictive plot showing the effects of percent grassland on monthly survival rates of swift foxes in north-eastern Montana during 2016–2018. The gray region represents the 95% confidence interval of the population at each percentage of grassland.

Table 2 Average vital rate values (S, survival; F, female fecundity) with 95% lower confidence interval (LCI) and upper confidence interval (UCI) used to parameterize projection matrix and sensitivity and elasticity values for swift foxes in north-eastern Montana, 2016–2018. Sensitivity and elasticity values were calculated from average rates

Parameter	Value (LCI, UCI)	Sensitivity	Elasticity	Source
S_{pup}	0.73 (0.55, 0.89)	0.33	0.24	Ausband & Foresman (2007b)
$S_{juvenile}$	0.74 (0.56, 0.92)	0.32	0.24	This study
S_{adult}	0.54 (0.30, 0.84)	0.52	0.28	This study
F_{adult}	0.85 (NA, NA)	0.28	0.24	This study

been shown to be associated with these cover types (Kamler & Ballard, 2002; Kamler *et al.*, 2005). In other systems, red foxes *Vulpes vulpes* have been found to out compete smaller foxes such as kit foxes (Clark *et al.*, 2005) and arctic foxes *Vulpes lagopus* (Tannerfeldt, Elmhagen & Angerbjörn, 2002). While there is no study documenting the effects of red foxes on swift foxes, and we did not have data to do so, we hypothesize that red foxes may have a negative impact on swift foxes as well, through interference and exploitative competition. The importance of contiguous grassland was further supported in a concurrent study where we were able to document potential dispersal movements by two adult foxes that moved 25 km south toward the Milk River, but then moved back to their area of origin (Butler, 2019). This suggests that agricultural development along the Milk River at the southern extent of our population might be a barrier to recolonization both behaviorally in terms of movement, as well as demographically in terms of reduced survival. In addition, genetic studies of the reintroduced population indicate that extensive croplands may be a barrier to dispersal movement, so much so that it can cause geographic and

genetic structure (Cullingham & Moehrenschlager, 2013; Schwalm, Waits & Ballard, 2014). However, it should be noted that most of the swift foxes we monitored were in grassland-dominated areas. Future research should focus on finer-scale monitoring of swift foxes to determine the fine-scale attributes of grasslands that influence survival (sage brush distribution, grass height, etc.), as well as cropland-dominated areas to better the seasonal attributes of crop fields (e.g. conditions pre- or post-harvest) that could influence survival (Matlack *et al.*, 2000).

Consistent with other studies of North American foxes, coyote predation was the primary cause of mortality of swift foxes (Sargeant, Allen & Hastings, 1987; Sovada *et al.*, 1998; Kitchen *et al.*, 1999; Cypher *et al.*, 2000; Farias *et al.*, 2005). We did not find support for the human shield hypothesis as distance to unpaved road and distance to natural gas wells were the least supported models. This could have been because human development and population levels were not high enough to provide a 'shielding effect' or because of wide-ranging behavior. In our study area, swift foxes had some of the largest home ranges recorded for the species (Moehrenschlager *et al.*, 2007; Butler *et al.*, 2020) which may have been due to low prey abundance. Two winters of extreme snowfall and a summer of record low precipitation (NWS Glasglow MT, 2018, 2019) occurred during our study, which might have further increased movement to meet foraging needs and exposed swift foxes to increased predation risk. Further, we must note that caution must be taken when interpreting our survival estimates as we extrapolated survival across almost double the time that we collected survival data. Given that several studies have found swift fox survival to be lower in the spring and summer compared to fall and winter (Covell, 1992; Sovada *et al.*, 1998; Moehrenschlager & Macdonald, 2003), it is possible that coyote predation is highest during these periods and our survival estimate may be biased higher than the actual annual survival.
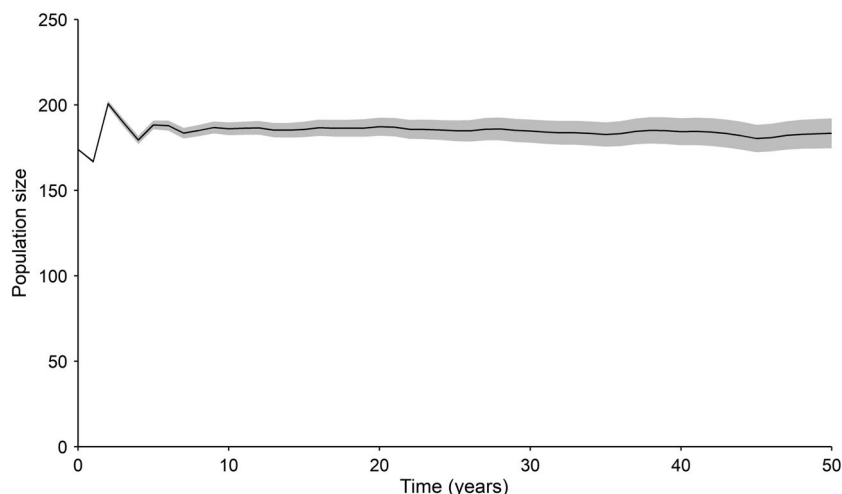
Figure 3 Population projection of the swift fox population in north-eastern Montana based on a stage-based matrix incorporating demographic stochasticity. Gray region is the 95% confidence interval of the population size at each year.

Table 3 Geographic location, survival rates (%) of all individuals, adult or juvenile swift foxes, number of foxes tracked in the study and study length of swift foxes in North America. Average values exclude this study

Study area	All individuals	Resident adult survival rate	Juvenile survival rate	Number of foxes	Study length (years)	Citation
Alberta/Saskatchewan, Canada		46	40[a]	73	3	Moehrenschlager *et al.* (2007)
Montana, US	46			11	2	Zimmerman (1998)
Montana, US		54	74[b]	32	2	This Study
Montana, US		67	52[c]	73	2	Ausband & Foresman (2007b)
South Dakota, US		27	27[a]	98	6	Sasmal *et al.* (2016)
Wyoming, US		58		56	3	Olson & Lindzey (2002)
Colorado, US	65			133	2	Schauster *et al.* (2002)
Colorado, US		45	13[d]	23	1.5	Andersen *et al.* (2003)
Kansas, US		45	33[b]	65	0.92	Sovada *et al.* (1998)
Texas, US		53	60[b]	46	2.5	Kamler *et al.* (2003)
New Mexico, US		53		27	2.67	Harrison (2003)
Average	56	49	38	61	2.7	

[a] 12-month estimate.

[b] 6-month estimate.

[c] 9-month estimate.

[d] 11-month estimate.

Lack of population growth in our study population could also be due to reduced reproductive output. Our elasticity analyses indicated fecundity only had a slightly smaller influence on population growth than adult survival (Table 3). While the average litter size of females in our study was similar to those of other studies (Table 4), the number of females that produced pups that survived to come above-ground was lower than in other studies. Although our sample size was small, we believe that the cause of the low number of females reproducing might be due to low prey abundance. In a review of the factors affecting kit fox and swift fox demographics, White & Garrott (1997) found that reproductive rate was positively influenced by leoprid abundance and precipitation levels. Moreover, the lower reproductive rate during the second field season of our study followed a year

of exceptionally low precipitation (NWS Glasglow MT, 2018, 2019), which has been found to influence small mammal abundance and kit fox reproduction (White & Garrott, 1999; Cypher *et al.*, 2000). Future research should investigate how seasonal and inter-annual variability in prey availability at a landscape scale influence population expansion or contraction at the edge of swift fox range.

Our study on the status of swift foxes in north-eastern Montana provides a snapshot of the dynamics of this population, but similar to other small canids, population fluctuations could be highly stochastic depending on environmental conditions. Previous long-term studies of the arctic fox and kit fox have found that these species exhibit large fluctuations in abundance, survival and reproduction (Angerbjörn *et al.*, 1994; Angerbjorn, Tannerfedlt & Erlinge, 1999; White &

Table 4 Geographic location, percent of tracked females reproducing, average litter size, number of social units (male-female or trios) monitored and study length of swift foxes in North America. Average values exclude this study

Study area	Females with pups	Average litter size	Social units	Study length (years)	Citation
Alberta/Saskatchewan, Canada	85	3.8	29	3	Moehrenschlager (2000)
Montana, US		5.0	3	2	Zimmerman (1998)
Montana, US	50	3.4	10	2	This Study
Montana, US	67	4.0	27	2	Ausband & Foresman (2007*b*)
Wyoming, US	79	4.6	25	3	Olson & Lindzey (2002)
Colorado, US	60	2.3	42	2	Schauster *et al.* (2002)
Colorado, US	63	3.4	5	1.5	Andersen *et al.* (2003)
Kansas, US	53	3.1	11	0.92	Sovada *et al.* (1998)
New Mexico, US		2.3	4	2.67	Kamler *et al.* (2003)
Average	68	3.6	18	2.1	

Garrott, 1999; Cypher *et al.*, 2000). In a 15-year study of San Joaquin kit foxes, Cypher *et al.* (2000) found that they can experience rapid booms and busts in population size, density and growth rate due to changes in the current and previous year's rodent abundance and precipitation from the previous three years. Precipitation has also been found to be important in determining the abundance prairie rodents, which can similarly undergo large annual changes in population abundance (Heisler, Somers & Poulin, 2014). Therefore, while we currently estimate that this population of swift foxes is stable, we hypothesize that its behavior might be-similar to that of arctic and kit foxes, and we should assume that demographic rates will fluctuate due to stochastic environmental events. It would be beneficial to evaluate how long-term fluctuations in precipitation and prey populations could explain observed variation in swift fox demography.

This study highlights the utility of studying demographic rates across space and time to not only improve our understanding of reintroduction success and population establishment (Converse & Armstrong, 2016), but also to identifying barriers to broader species expansion and recolonization of historically occupied habitats. Although our sample sizes were relatively small, we had the ability to compare current swift fox demographic rates against those immediately post release (Moehrenschlager & MacDonald, 2003), which helped to illuminate what recovery phase the population was likely to be in. In addition, by studying the population at the edge, relative to where the initial reintroductions occurred and subsequent gap between reintroduction areas, we were able to determine that the population was likely not recolonizing additional former range due to demographic processes linked to habitat fragmentation. Managers looking to better understand the recovery dynamics of a specie's should gather demographic information at multiple points post-restoration, particularly at the edge of the species range, so that comparisons can be made to guide recolonization and connectivity strategies for restored populations.

Acknowledgements

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Characteristics of swift foxes captured in Montana during 2016–2018 including fox ID, stage, sex, trapping site number (referenced to Fig. 1b), if the individual was used in the current analysis, the date the individual was collared and last located, the best guess of the fate of the individual, the number of encounters derived from the camera traps used in the survival analysis, and additional notes.