Dispersal, survival, and reproduction of wild-born, yearling swift foxes in a reintroduced population

D.E. Ausband and K.R. Foresman

Abstract: From 1998 to 2002, the Blackfeet Tribe and Defenders of Wildlife reintroduced 123 captive-reared swift foxes (*Vulpes velox* (Say, 1823)) to the Blackfeet Reservation in northern Montana. Because yearling swift foxes are colonizers of vacant habitats and are at the periphery of range expansion, we estimated 1st-year survival and explored aspects of dispersal to ascertain the contribution of wild-born juveniles to the reintroduction effort. First-year survival (post den emergence) of swift foxes averaged 0.38 and 0.36 for 2003–2004 and 2004–2005, respectively. Half of the females that survived to 1 June of their 1st year reproduced. Most dispersal (77%) and mortality (85%) occurred in autumn, with 80% of mortalities attributable to predation. Dispersal distance was not different among sexes and averaged 10.4 km. Understanding the contribution of yearling swift foxes — the colonizers — to reestablishing populations is important because several entities are currently reintroducing swift foxes and some states have expanding populations.

Résumé : De 1998 à 2002, la tribu des Pieds-noirs et les Defenders of Wildlife ont réintroduit 123 renards véloces (*Vulpes velox* (Say, 1823)) élevés en captivité sur le territoire de la réserve des Pieds-noirs dans le nord du Montana. Parce que les renards véloces d'un an sont ceux qui colonisent les habitats vacants et la périphérie de l'aire d'expansion, nous avons estimé la survie durant la 1re année et étudié certains aspects de la dispersion afin de mesurer la contribution des jeunes nés en nature attribuable à l'effort de réintroduction. La survie des renards véloces au cours de la première année (après l'émergence du terrier) était en moyenne de 0,38 et 0,36 respectivement en 2003–2004 et en 2004–2005. La moitié des femelles qui ont survécu jusqu'au 1er juin de leur 1re année se sont reproduites. La plus grande part de la dispersion (77 %) et de la mortalité (85 %) a lieu à l'automne et 80 % de la mortalité est due à la prédation. La distance de dispersion ne diffère pas en fonction des sexes et est en moyenne de 10,4 km. Il est important de comprendre la contribution des renards véloces d'un an — les colonisateurs — dans le rétablissement des populations, parce que plusieurs groupes sont actuellement en train de réintroduire les renards véloces et que les populations sont en croissance dans certains états.

[Traduit par la Rédaction]

Introduction

Swift foxes (*Vulpes velox* (Say, 1823)) were once common throughout the grasslands of Montana (Allardyce and Sovada 2003). Habitat loss, unregulated trapping, and poisoning, however, have led to the extirpation of swift foxes from the northern plains by the 1950s (Hoffmann et al. 1969; Carbyn et al. 1994; Allardyce and Sovada 2003; Herrero 2003). Beginning in 1998, the Blackfeet Tribe collaborated with Defenders of Wildlife to restore swift foxes to the Blackfeet Reservation in northern Montana. From 1998 to 2002, the Blackfeet Tribe successfully released 123 captive-reared swift foxes to tribal lands (Ausband and Foresman 2007). Ausband and Foresman (2007) used vital rates, population projections, and minimum abundance counts to determine that additional reintroductions were unnecessary.

As swift foxes colonize vacant habitat both on and off the Reservation, knowledge of the survival and dispersal ecology of yearlings — the colonizers — will be beneficial in predicting the current range and distribution of swift foxes in Montana. To our knowledge no published studies have reported dispersal distances or 1st-year survival of swift foxes from emergence to breeding. In addition, temporal aspects of dispersal are often of interest for wildlife managers. For example, do most juveniles disperse in autumn, and if so, is this the period when mortality is elevated for juveniles? Kamler et al. (2004) described some facets of juvenile dispersal, although the data were derived from populations in the southern extent of swift fox range and it is unclear if northern swift foxes from Montana differ. Furthermore, the population of swift foxes we studied originated from a captive-reared, reintroduced cohort of animals, and our results may be especially useful for managers in areas where reintroductions are being considered or where swift foxes are thought to be expanding their distribution. To ascertain their contribution to range expansion and restoration efforts, we estimated survival, dispersal, and reproductive ecology of wild-born, yearling, swift foxes.

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D.E. Ausband.[1] Natural Science Building, Room 205, University of Montana, Missoula, MT 59812, USA.
K.R. Foresman. Division of Biological Sciences, 104 Health Sciences, University of Montana, Missoula, MT 59812, USA.

[1]Corresponding author (e-mail: david.ausband@mso.umt.edu).

Study area

This study occurred on the Blackfeet Indian Reservation, Glacier County, Montana. The Blackfeet Reservation is 600 000 ha of mostly grassland habitat lying on the eastern flank of the Rocky Mountains adjacent to Glacier National Park. Blackfeet lands are bordered on the north by Alberta, Canada, on the south by Birch Creek, to the west by Glacier National Park, and partially bordered on the east by Cut

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Bank Creek. Grazing predominates land use on the Reservation, with cropland comprising much of the remaining land area. All swift foxes were released on the 3200 ha tribal-owned AMS Ranch located along the Two Medicine River approximately 30 km southeast of Browning, Montana.

Two data loggers placed nonrandomly on fence posts at the release site recorded temperatures ranging from –40° C in January to 41° C in July. Yearly precipitation averaged 31.8 cm and elevation of the grasslands on the Reservation averaged 1200 m. Short-grass prairie vegetation including needle and thread grass (*Stipa comata* (Trin. & Rupr.) Barkworth), blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths), and thread-leaf sedges (*Carex filifolia* Nutt.) dominate much of the Reservation. Similar grassland habitat lies to the south and north of the Reservation.

Materials and methods

Swift fox captures

We livetrapped juvenile swift foxes in box-traps, 109 cm × 39 cm × 39 cm (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA), baited with wet cat food and either sardine oil or bullion placed on adjacent vegetation or a fence post to elevate scent and enhance capture rates. Box-traps were lined with wood and wire mesh to decrease the chance of injury to trapped animals (Moehrenschlager et al. 2003). Foxes were fitted with high-frequency radio collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) and injected with transponders (AVID ID Systems, Norco, California, USA) between their shoulder blades.

Juveniles (from 1 September to June each year) were trapped at natal dens in early September prior to dispersal by placing traps within 0.5 km of late-summer natal den sites. We set traps in the evening at 2200 and returned in the morning at 0600. We did not trap at temperatures below –20° C or above 32° C. Captured swift foxes were removed from the trap, placed in a sack, and weighed. One investigator then held and restrained the fox while the second investigator placed a sock over the animal's eyes and muzzle, attached a radio collar, implanted a transponder between the shoulder blades, determined sex, checked ears for tattoos (to determine if wild-born or captive-reared), and recorded tooth wear to estimate age. We assumed foxes with long, sharp, white canines and relatively little gray pelage along their backs to be juveniles and not adults. We closely examined the animal for any injuries that may have been sustained during the trapping process. Capture and handling of animals were approved under the Institutional Animal Care and Use Committee protocol No. 036-04KFDBS-043005.

Kit survival

Kits (from June to 30 August each year) were not permanently marked or radio-collared. Therefore, we estimated kit survival by counting the number of kits observed at a natal den upon emergence compared with the number of kits observed at the same den in late August during both 2004 and 2005. We used up to 10 repeated counts in both early and late summer to increase the accuracy of our visual estimation method. We did not include natal dens discovered after 1 July in our estimate of kit survival because of the potential that kits may have died before 1 July, would not be detected and counted, and would inflate survival estimates. We believe early summer counts to be accurate, or nearly so, because we never observed more kits at a den in August than we had counted in June.

Juvenile survival

We located radio-collared foxes at least weekly by vehicle using a magnetic, roof-mounted antenna for approach and an H-antenna for triangulation. Locations of swift foxes were recorded after sighting the radio-collared animal or by following the signal to the foxes' den. We also conducted telemetry flights as needed to locate missing animals.

We estimated survival of radio-collared juveniles using a staggered-entry Kaplan–Meier formula (Pollock et al. 1989). This staggered-entry procedure allowed for animals to be entered into the survival analysis as we captured them at different times throughout the study. Since no swift fox died within 2 weeks of capture, we did not include a handling acclimation period and used all available data (Winterstein et al. 2001). Preliminary analyses suggested that survival rates differed at different times of the year for juveniles. Because survival was lower during autumn than during winter or spring, we calculated juvenile survival from 1 September to December, then from January to 1 June, and used the product to obtain a 9-month survival rate. Because we did not have kit survival estimates from 2003 and kit survival was not different between years, we used the product of kit survival (from June to 30 August 2004) and juvenile survival (from September 2003 to June 2004) to estimate 1st-year survival for 2003–2004 and 2004–2005.

We defined juvenile dispersal distance as the straight-line distance from where a fox was captured in early September to where it was located on 1 June of the following year or to where it died. We did not classify a juvenile as having dispersed if this distance was <2.0 km (Schauster et al. 2002).

A swift fox was considered to have been killed by a coyote (*Canis latrans* Say, 1823) if there were puncture wounds on the skull and the carcass had not been fed upon. Coyote tracks at the site further corroborated kill classification. In addition, a fox was considered to have been killed by a raptor if feathers were present at the kill site, the carcass had been fed upon extensively, skin and fur were peeled back, tufts of fur were scattered about, the fox had been eviscerated, and there were no puncture wounds on the skull. Aside from incidental observations, we made no attempt to quantify predator abundance in our study area and no specific predator control was used to possibly enhance swift fox population establishment.

Statistical analyses

We arcsine-transformed survival rates and used *z* tests to examine differences in survival between years for kits and juveniles (Moore 2000; Ramsey and Schafer 2002). We used χ^2 analyses to test for differences in juvenile survival by season (De Veaux et al. 2005). We also used the arcsine-transformed data and a *z* test to examine differences in survival between juveniles that stayed within their natal range and juveniles that dispersed from their natal range. We log-transformed dispersal distances and used Student's *t* test to ascertain differences in average dispersal distance be-

Fig. 1. Number of juvenile swift fox (*Vulpes velox*) mortalities and dispersers by month from 2003 to 2005 on the Blackfeet Indian Reservation, Montana.

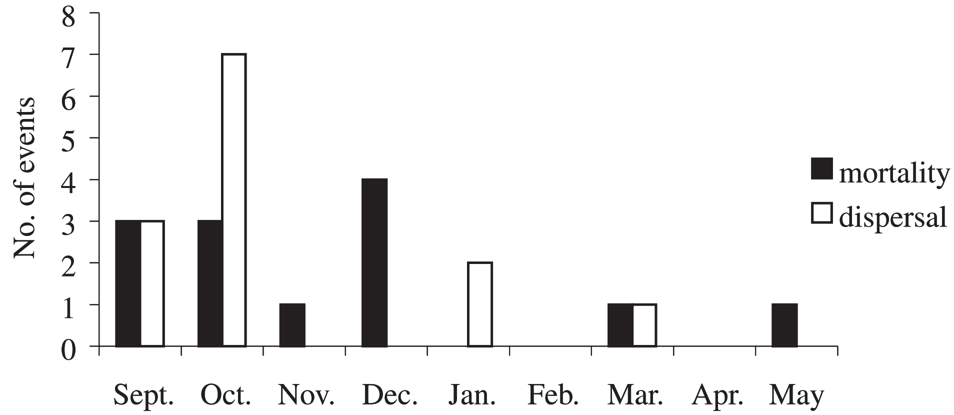


Table 1. Juvenile swift fox (*Vulpes velox*) survival estimates during autumn and winter–spring on the Blackfeet Indian Reservation, Montana.

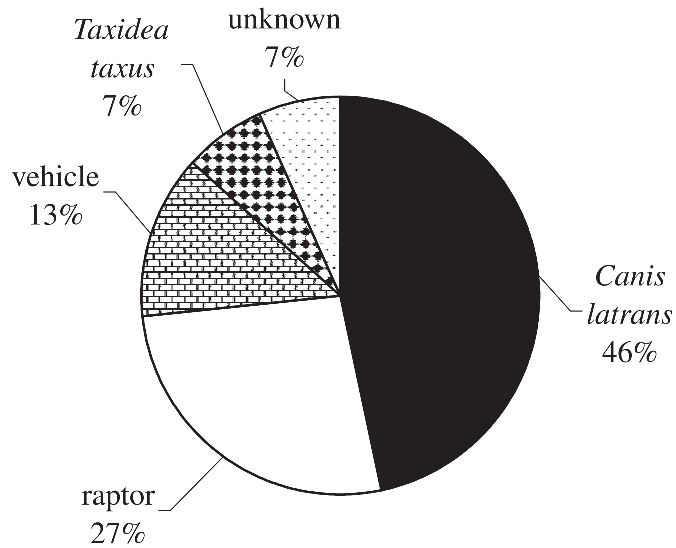
	September–December	January–June
Juveniles 2003–2004	0.67	0.83
Juveniles 2004–2005	0.62	0.77

tween 2003–2004 and 2004–2005 (Ramsey and Schafer 2002). We considered results significant if $P < 0.05$.

Results

Kit survival averaged 0.69 (95% CI = 0.55–0.83) and 0.77 (95% CI = 0.65–0.89) for 2004 and 2005, respectively, and did not differ between years ($z = -1.07$, $P = 0.14$). We radio-collared 13 and 22 wild-born, juvenile (16 females, 19 males) swift foxes at 17 natal dens in 2003 and 2004, respectively. Juvenile survival was lower in autumn (September–December) during both years ($\chi^2 = 10.9$, $P = 0.01$) (Table 1), but did not differ between years ($z = 0.49$, $P = 0.31$). We did not find any evidence that survival differed among sibling groups. Juvenile survival from September to 1 June averaged 0.56 (95% CI = 0.32–0.80) for 2003–2004 and 0.47 (95% CI = 0.32–0.62) for 2004–2005. Sample sizes were not large enough in 2003–2004 to meaningfully analyze survival by sex. However, in 2004–2005, juvenile female survival (0.70, 95% CI = 46–94) was significantly higher ($z = 2.10$, $P = 0.02$) than juvenile male survival (0.30, 95% CI = 14–46). The product of kit and juvenile survival provided an average 1st-year survival of 0.38 (95% CI = 0.27–0.49) and 0.36 (95% CI = 0.27–0.45) for 2003–2004 and 2004–2005, respectively. Survival for juveniles that stayed within their natal range averaged 0.36 (95% CI = 0.21–0.51), whereas 0.59 (95% CI = 0.41, 0.77) of juveniles that dispersed survived to become adults the following June ($z = -1.46$, $P = 0.07$). We did not observe differences in sex of juveniles that stayed within their natal range (8 females, 6 males). One of 2 juvenile females that survived to 1 June of their 1st year reproduced in 2004 and 3 of 6 juvenile females reproduced in 2005. The juvenile female in 2004 had a litter of 4 kits and litter sizes averaged 3.3 for the 3 juvenile females that reproduced in

Fig. 2. Cause of juvenile swift fox mortalities from 2003 to 2005 on the Blackfeet Indian Reservation, Montana ($n = 15$).



2005. In addition, 2 of 3 juvenile males that survived to 1 June of their 1st year found mates and reproduced in 2004, whereas none of 3 juvenile males that survived their 1st year found mates or reproduced in 2005.

We were not able to obtain exact dispersal dates for all radio-collared juveniles; however, for animals with reliable dispersal dates, most (77%, $n = 13$) dispersed in September and October. Most (85%, $n = 13$) juvenile mortalities were recorded in autumn (September–December) as well (Fig. 1). Predation accounted for 12 of 15 (80%) juvenile mortalities, while vehicles caused 2 of 15 mortalilties, and we were unable to determine the cause of death for 1 juvenile (Fig. 2). We did not observe differences in mortality by sex (7 females, 8 males).

Dispersal distance did not differ between years ($t = 1.55$, $P = 0.14$) and averaged 10.4 km (SE = 2.0 km) for both years combined. Male dispersal distance (11.0 km, SE = 2.7 km) was similar to female dispersal distance (9.8 km, SE = 3.0 km). Five of 13 animals with reliable dispersal dates exhibited 2 distinct bouts of dispersal. After moving >2.0 km from their natal range, 1 juvenile dispersed farther in November, 1 in December, 2 in February, and 1 in

March. The average distance of this second dispersal event was 23.4 km (SE = 4.2 km) for the 5 juveniles combined.

Discussion

Our study provides additional knowledge about 1st-year swift fox ecology. For example, no published studies have estimated 1st-year survival or average dispersal distance in a population of reintroduced swift foxes. Kit survival averaged 0.13 (Covell 1992) and 1st-year survival averaged 0.05 (O.J. Rongstad, unpublished report) for a swift fox population in southeast Colorado. Clearly, our 1st-year survival estimates (0.38 in 2003–2004 and 0.36 in 2004–2005) are higher. Juvenile (September–June) survival (0.56 in 2003–2004 and 0.47 in 2004–2005) was comparable with, or higher than, estimates from Texas (Kamler et al. 2003) and western Kansas (Sovada et al. 1998) when survival rates are projected to a 9-month interval. Lower survival in autumn compared with that in winter appears to be correlated to the time at which most juveniles disperse (Fig. 1). Juvenile survival and 1st-year survival may have been higher in our study area because the habitat was recently uninhabited by swift foxes and dispersing juveniles could more readily find suitable vacant territories.

Similar to other studies, predation accounted for a large proportion of radio-collared juvenile deaths, with coyotes being the largest single contributor (Sovada et al. 1998; Kamler et al. 2003, 2004). However, we did not find a study with similar proportions of mortality that were attributable to raptors. It is unlikely that we misidentified scavenging as predation because field necropsies were conducted soon after death and most raptors observed on the Reservation do not typically eat carrion (Elphick et al. 2001). Furthermore, much of the Reservation is fenced and used for cattle grazing. We speculate an abundance of ideal raptor perches in the form of fence posts may have facilitated predation on swift fox.

Kamler et al. (2004) reported that significantly more juvenile males dispersed than females, contrary to our findings. Furthermore, we found no significant difference in average dispersal distance of male and female swift foxes. We believe that this may be because this population is recolonizing a relatively vacant habitat, thereby affecting the distribution of potential mates on the landscape. Although the difference was not statistically significant, we were surprised to find juveniles that exhibited philopatry had a 23% lower survival rate than those that dispersed from their natal range. Upon further examination, we believe that this difference is attributable to high mortality in early fall while juveniles are still within their natal range, but may be traveling alone, farther from the den site, and are in essence, in unfamiliar territory with little knowledge of the locations of escape holes.

Differences in juvenile survival (from 1 Septemer to June) by sex in 2004–2005 were difficult to assess largely because the survival estimates were based on 1 year of observations, but also because we did not estimate kit survival (from June to 30 August) by sex as we chose not to handle kits to limit natal den disturbance.

We found similar autumn trends in juvenile dispersal as Covell (1992) and Kamler et al. (2004). However, Kamler et al. (2004) found that juveniles also dispersed in January–Februrary. Although we did not find a similar trend in initial dispersal occurring in January–February, we did observe five juveniles that exhibited subsequent dispersal bouts for relatively long distances after the autumn season. For example, a fox would travel >2.0 km outside its natal range, and then, sometimes 4–5 months later, would disperse again farther from the location it first occupied after the initial dispersal. Our estimates of juvenile swift fox dispersal (10.4 km) are similar to the total distance moved (11.9 km) reported for swift foxes in Colorado (Schauster et al. 2002) and the dispersal distance of San Joaquin kit foxes (*Vulpes macrotis mutica* Merriam, 1902) in California (7.8 km) (Koopman et al. 2000).

Understanding the contribution of yearling swift foxes — the colonizers — to range expansion and distribution is important, as several entities are currently reintroducing swift foxes into their former range and some states have expanding populations (Stuart and Wilson 2006). Furthermore, our reintroduction used only captive-reared and mostly (89%) juvenile swift foxes. Ausband and Foresman (2007) demonstrated that the population is growing, is consistently reproducing in the wild, and has expanded its range along the Rocky Mountain Front in Montana as a result of these reintroduction efforts. Based on their ability to survive, disperse, and subsequently reproduce, we believe that yearlings are an important component of range expansion and can play a vital role in the restoration of swift fox populations.

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