SWIFT FOX SURVIVAL AND PRODUCTION IN SOUTHEASTERN WYOMING

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We estimated annual survival rates of swift foxes (Vulpes velox) and documented number of young per pair in a transition zone between shortgrass prairie and sagebrush steppe plant communities in southeastern Wyoming during 1996–2000. Annual adult survival ranged from 40% to 69%, with predation by coyotes (Canis latrans) the primary cause of deaths. Two foxes died of canine distemper virus. Annual survival rates did not differ among years (P > 0.12). Nineteen of 24 (79%) swift fox pairs were observed with young over 3 years. Mean minimum litter size was 4.6 based on these 19 litters and 6 others not associated with our radiocollared foxes. Adult survival was similar and litter size slightly larger than observed elsewhere in the species range, suggesting that viable swift fox populations can be supported by sagebrush steppe and shortgrass prairie transition habitat.

Key words: canine distemper virus, litter size, sagebrush steppe, survival rates, swift fox, Vulpes velox, Wyoming

Swift foxes (Vulpes velox) were historically distributed from south-central Canada to central Texas and from the eastern edge of the Great Plains west to the Rocky Mountains (Egoscue 1979). Although extirpated or reduced in numbers over much of their historic range (Clark and Stromberg 1987; Egoscue 1979; Kilgore 1969; Soper 1964) their distribution has changed little in Wyoming (Lindberg 1986) where the western periphery of their historic range occurs. The western periphery of this historic range in Wyoming is located near or within a transition zone between sagebrush (Artemisia) shrub steppe and grassland communities (Knight 1994). Habitat in this portion of the species range contains a substantial shrub component, which is generally absent in the short and mixed grass prairies that are considered typical swift fox habitat in other areas (Clark and Stromberg 1987; Cutter 1958; Egoscue 1979; Kilgore 1969).

The swift fox was proposed for listing as endangered in 1992, and the United States Fish and Wildlife Service concluded that its listing was “warranted but precluded” in 1995 (Federal Register 1995). It was recently removed, however, from the warranted list and is not being considered for listing now (Federal Register 2001). Understanding population characteristics of potentially threatened or endangered species is critical to their recovery. Better knowledge of swift fox survival rates, causes of death, and production are needed to support conservation and recovery efforts, particularly in peripheral parts of their range where they are seldom studied. Estimates of swift fox natality and survival in this zone of transition between sagebrush steppe and shortgrass prairie will help managers estimate the potential for persistence of swift fox populations in these nontypical habitats.

Swift foxes produce 1 litter per year and are able to breed in their 1st year, with litter sizes typically ranging from 3 to 6 young
(Egoscue 1979). Although swift foxes may produce up to 7 young in a single litter (Egoscue 1979), average litter sizes reported in wild populations are much lower. Parturition occurs from March to May (Kilgore 1969; Pruss 1994) and is likely influenced by latitude (Hillman and Sharps 1978).

Primary cause of swift fox and kit fox (Vulpes macrotis) deaths is predation by coyotes (Canis latrans—Brechtel et al. 1993; Covell 1992; Ralls and White 1995; O. J. Rongstad et al., in litt.; Sovada et al. 1998; Spiegel and Disney 1996). Other causes of death include predation by large raptors and badgers (Taxidea taxus) and collision with vehicles. Little is known of swift fox susceptibility to disease, and fox deaths caused by disease have not been confirmed. Our objective was to estimate swift fox litter size and annual survival rates of adult swift foxes found in an area of nontypical habitat (sagebrush steppe and shortgrass prairie transition) in southeastern Wyoming.

**STUDY AREA**

The study area (220 km²) was located in northwestern Albany County, Wyoming (42°N, 106°W), near the town of Medicine Bow. Area was mostly flat with numerous dry lake beds and several saline lakes, at an average elevation of 2,075 m. Mean maximum and minimum temperatures in July were 28 and 8°C; mean maximum and minimum temperatures in January were 0 and −12°C. Precipitation averaged 26 cm annually, including 98 cm of snow (Western Regional Climate Center, www.wrcc.dri.edu).

Plant communities consisted primarily of graminoids but were interspersed with patches of low-growing (<1 m) big sagebrush (Artemisia tridentata), greasewood (Sarcobatus vermiculatus), and saltbush (Atriplex gardneri). Primary grasses were buffalograss (Buchloe dactyloides), blue gramma (Bouteloua gracilis), needle-and-thread (Stipa comata), western wheatgrass (Agropyron smithii), and prairie junegrass (Koeleria macrantha). Shrub, shrub–grass and grass habitats were 29%, 29% and 26% of the study area, respectively (Olson 2000). Other predators present in the study area were badgers, coyotes, golden eagles (Aquila chrysaetos), and ferruginous hawks (Buteo regalis). No red foxes (Vulpes vulpes) were observed in the study area during this study. Land ownership of the area was primarily private, with some property belonging to state of Wyoming and Bureau of Land Management. Primary land use was cattle grazing. Human development was limited, consisting of fences, windmills, stock ponds, and secondary roads.

**MATERIALS AND METHODS**

**Capture.**—Swift foxes were captured between January and May from 1996 to 1999 using Tru-Catch live-traps (Manufacturing Systems Inc., Belle Fourche, South Dakota) baited with meat scraps and were immobilized with an intramuscular injection of Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa—Kreeger et al. 1990; Travaini and Delibes 1994) at an approximate dosage of 5 mg/kg body mass. Foxes were released at the site of capture after they had regained their balance and ability to run. Foxes were ear-tagged and fitted with 50-g radiocollars (Advanced Telemetry Systems Inc., Isanti, Minnesota) with a battery life of 12 months and an increased pulse rate to indicate death of foxes (8-h delay). We recorded body mass and sex and collected blood samples. Blood was tested at the Wyoming State Veterinary Laboratory for antibodies to disease agents (such as canine distemper and sylvatic plague). We considered all swift foxes to be adults in December in any year (Kitchen et al. 1999) because they are able to breed in their 1st year. We determined the age of foxes subjectively based upon tooth wear at the time of initial capture.

Foxes radiocollared in previous years were targeted for recapture to replace transmitters. After a fox was captured, we attempted to capture its mate by placing traps at the den of the collared fox. Traps were checked twice nightly (midnight and sunrise) and were closed when temperatures fell below −18°C. We trapped areas where we had observed unmarked foxes or signs of them, and those areas of suitable habitat...
not known to have foxes, after collared foxes and their mates were captured. We recorded observations of coyotes and their signs (tracks, scats) to document their distribution in the study area.

Number of young.—Foxes were considered a mated pair when a male and female were found using the same dens and home range. Number of young produced by swift foxes was estimated from observation of natal dens when young foxes began to emerge from dens (from mid-June through July). We observed dens from a distance using a spotting scope or binoculars in the evening and morning when swift fox young were most active, and counted number of young observed. Counts resulted in a minimum estimate of the number of young per fox pair. We frequently watched dens of fox pairs known to have young, to improve counts, but we gave emphasis to observation of dens of fox pairs for whom young had not been confirmed.

Survival.—We divided the year into 3 biological periods corresponding to reproductive biology of adult swift fox (Kitchen et al. 1999; Zoellick et al. 1989): pup-rearing (May–August), dispersal (September–November), and pair formation (December–March). Radiocollared swift foxes were relocated and their life status determined using truck-mounted and handheld telemetry equipment and permanent telemetry towers. Swift foxes were monitored weekly from March 1996–July 1997, every 1–3 weeks from August to December 1997, daily during the pup-rearing periods in 1998 and 1999, and twice weekly during dispersal and pair formation periods in 1998 and 1999. Cause of death was determined in the field from physical evidence, including condition of the carcass (trauma, consumed, intact, buried, puncture wounds) and presence of signs (tracks, scat, feathers) of other species. If cause of death could not be determined in the field, remains were examined for cause of death at the Wyoming State Veterinary Laboratory in Laramie. We estimated date of death as the midpoint between when a dead fox was last located alive and when its carcass was found, if the condition of carcass did not allow more precise timing.

Number of swift fox deaths per fox month (fox month = number of foxes alive at beginning of month, all years combined) was compared among biological periods (test between 2 proportions) to test for differences in timing of fox deaths throughout the year.

We used the Kaplan–Meier product-limit estimator to estimate annual (April–March) and pup-rearing period survival rates (Pollock et al. 1989; Sovada et al. 1998), and the log-rank test (alpha = 0.05) to compare survival rates between years (Cox and Oakes 1984; Pollock et al. 1989). We used a time interval of 1 week for survival rate calculations.

RESULTS

Number of young.—Fifty-six swift foxes (29 males, 27 females) were captured and radiocollared between 1996 and 1999. Sixteen swift foxes were captured during March and April 1996 and 18 foxes between 9 March 1997 and 15 May 1997. Ten of the 18 foxes captured in 1997 had been captured and radiocollared in 1996. The 18 collared foxes captured in 1997 comprised 9 male–female pairs. During the winter and spring of 1998 we captured and collared 24 swift foxes, 7 of which had been collared in 1997. We had 7 fox pairs radiocollared during the summer of 1998. During the winter and spring of 1999 we captured 28 swift foxes, 13 of which had been collared in 1998. In spring of 1999 we had 9 pairs of foxes radiocollared. By the end of May 1999, however, 3 individuals from 3 of the pairs had died. We noted no evidence that capture, handling, and immobilization of foxes may have influenced our results. Only 1 fox died within 1 week of capture—this fox was killed by a coyote 7 days after capture—whereas all collared females observed with young had been immobilized.

Nineteen of 24 (79%) swift fox pairs brought young aboveground. Mean minimum number of young observed per litter for those 19 pairs plus 6 additional litters observed outside the study area (within 25 km) was 4.6 ± 0.4 SE (95% CI = 3.8–5.3, n = 25, range = 1–10). Minimum number of young per litter (1997, $\bar{X} = 5.3$, n = 8; 1998, $\bar{X} = 4.0$, n = 10; 1999, $\bar{X} = 4.6$, n = 7) did not differ (analysis of variance, $F = 1.07, d.f. = 2, 22, P = 0.36$) among years. We observed 2 instances of more than 1 adult female being present at a den.
Table 1.—Survival rates of adult swift foxes near Medicine Bow, Wyoming, 1996–1999, shown as annual rate and rate during pup-rearing period (May–August).

<table>
<thead>
<tr>
<th>Time period</th>
<th>No. of deaths</th>
<th>Survival rate</th>
<th>95% CI for survival rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April 1996–March 1997</td>
<td>5</td>
<td>0.69</td>
<td>0.47–0.92</td>
</tr>
<tr>
<td>April 1997–March 1998</td>
<td>12</td>
<td>0.40</td>
<td>0.25–0.55</td>
</tr>
<tr>
<td>April 1998–March 1999</td>
<td>8</td>
<td>0.66</td>
<td>0.50–0.82</td>
</tr>
<tr>
<td>Pup-rearing period</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>3</td>
<td>0.81</td>
<td>0.62–1.00</td>
</tr>
<tr>
<td>1997</td>
<td>6</td>
<td>0.68</td>
<td>0.47–0.90</td>
</tr>
<tr>
<td>1998</td>
<td>1</td>
<td>0.95</td>
<td>0.86–1.00</td>
</tr>
<tr>
<td>1999</td>
<td>6</td>
<td>0.74</td>
<td>0.55–0.92</td>
</tr>
</tbody>
</table>

with young. An uncollared adult fox that appeared to be a female was observed at the natal den of 1 fox pair in July 1997, where there was a minimum of 10 young. The 2 radiocollared adults at this den died in July 1997 and the 3rd adult was still observed with the young in August 1997. The young likely were from 2 separate litters because they appeared to be of 2 distinct sizes. Another fox had a litter in May 1999 and her mate was killed on 15 May 1999. In late May she moved her young to the natal den of an adjacent fox pair and spent the remainder of the pup-rearing period (June–August) in the den with this pair and the 2 combined litters (n = 6).

Three of the 5 paired females not observed with young were 1 year old (2 in 1997, 1 in 1999), one was 2 years old (in 1999), and one was 3 years of age (in 1998). The 2-year-old female not observed with young lost a portion of her right rear leg in February 1999 (presumably in a leg-hold trap). Seven of 10 paired year-old females were observed with young between years. None of the original 1997 pairs (n = 10) were intact at the beginning of the 1998 pup-rearing period, but 3 of the 1998 pairs (n = 7) were intact at the beginning of the 1999 pup-rearing period and each produced young again in 1999.

Survival.—Annual survival rate of adult foxes did not differ between years (P > 0.10, Table 1). Mean annual survival rate for the 3 years was 0.58. Survival rates during pup-rearing periods (Table 1) differed only between 1997 and 1998 (P = 0.03). Only 1 collared fox died during the 1998 pup-rearing period.

Collared swift foxes died in all months except September; the maximum number of deaths occurred in July (6 deaths) and in October (6 deaths). The number of deaths per fox month did not differ among the biological periods (pup-rearing = 0.051, dispersal = 0.056, pair formation = 0.047; P > 0.7). Ten of the 14 foxes that died during the pup-rearing periods were killed by predators (coyotes, 5; raptor, 1; unknown predators, 4). Number of deaths was similar for the sexes (females, 19; males, 16). Predation by coyotes was the primary cause of swift fox deaths (8 males, 8 females), accounting for 46% of swift fox deaths and 73% of known-cause deaths. Coyotes or their signs were observed in all swift fox home ranges. Seven of the 14 resident swift foxes whose home range had been estimated (Olson 2000) and that were later killed by coyotes were killed outside their home range boundaries (95% isopleth using the fixed kernel method; Seaman et al. 1998). The single fox killed by a vehicle (3% of deaths), a yearling female captured on 31 January 1998, left the study area and was killed 67 km from its capture site in late March 1998. Other causes of deaths included predation by raptors (2 foxes, 6% of
deaths), by badgers (1 fox, 3%), and by unknown predators (7 foxes, 20%), as well as death from canine distemper (2 foxes, 6%) and from unknown causes (6 foxes, 17%).

Thirteen of 16 foxes (81%) whose blood was collected at capture had been exposed to canine distemper virus. Two foxes died of canine distemper—1 (female) was found at a den entrance and the other (male) in a den. Neither fox had been scavenged.

**DISCUSSION**

While mean number of young per litter (4.6) is only a minimum estimate, it was higher in this area of nontypical habitat on the margin of the species range than documented elsewhere in the species range. Average litter sizes estimated in Colorado are 2.9 (Covell 1992), 1.6 (Fitzgerald and Roell 1995), 3.4 (Kahn and Beck 1996), and 3.4 (O. J. Rongstad et al., in litt.). Hillman and Sharps (1978) document an average litter size of 4 in South Dakota, and Brechtel et al. (1993) an average of 3.9 in Canada. Three of the 5 paired females in our study area that were not observed with young were only 1 year old, suggesting 1-year-old females may be slightly less likely to produce young than older females, although 7 of 10 did produce young.

Production of young in swift fox is likely related to prey abundance, as has been demonstrated in the kit fox (Cypher et al. 2000; White and Ralls 1993; White et al. 1996). In work related to this study, we found a positive relationship between number of young observed and proportion of sage vegetation within the parent’s home range (Olson 2000). This relationship was likely driven by prey abundance. Sagebrush, greasewood, and sagebrush–grassland habitats had higher rankings of prey-relative abundance (based upon capture success of small mammals, counts of breeding birds, and pitfall trapping of insects) than grassland habitats (Olson 2000). Others have demonstrated that several types of prey frequently utilized by swift foxes are more abundant in shrub habitats than in pure grasslands. Higgins and Stapp (1997) found that 13-lined ground squirrels (*Spermophilus tridecemlineatus*) were more abundant in shrub-dominated sites than in grass-dominated sites. Stapp and Van Horne (1997) found that deer mice (*Peromyscus maniculatus*) preferred shrub microhabitats and Stapp (1997) found that beetles were trapped more often beneath shrubs. All of these species—13-lined ground squirrels, deer mice, and beetles—were important components of the swift fox diet in our study area (Olson 2000). More abundant prey in sage vegetation likely permitted foxes with a higher proportion of this habitat in their home ranges to raise larger litters. As suggested by Higgins and Stapp (1997), increased vertical cover provided by shrubs likely improved habitat quality for 13-lined ground squirrels by reducing predation risk, thus resulting in higher abundance. Increased vertical cover provided by sagebrush likely improves the habitat for small mammals in general as well as providing increased structure for nesting songbirds. These factors no doubt contributed to the higher overall prey abundance in habitats with some sagebrush component. Swift fox habitat quality on our study area was likely enhanced by the presence of low-growing sagebrush, as indicated by the high litter sizes observed.

Annual survival rates of swift foxes on our study area (0.69, 0.40, 0.66) were generally higher than those documented in other areas of the species’ range. Although annual survival rates we observed varied, survival functions between years did not differ, suggesting annual survival functions for swift foxes on our study area were from the same underlying survival curve (Pollock et al. 1989). Estimated annual survival rates for foxes on the Pinyon Canyon Maneuver Site in Colorado were 0.52 (O. J. Rongstad et al., in litt.), 0.53 (Covell 1992), and 0.64 (Kitchen et al. 1999). Sovada et al. (1998) reported an annual survival rate of 0.43 in western Kansas and Zimmerman (1998) a rate of 0.46 in Montana. In our study, swift
foxes were susceptible to death and predation year-round, and the likelihood of dying did not appear to be greater during any particular biological period. Despite the relatively low annual survival rates, most fox pairs (79%) produced young, and foxes formed new pairs rapidly following the death of a mate. All indications suggest that production of young was sufficient to replace those foxes that died.

Others have also reported coyote predation to be the primary cause of swift fox mortality, accounting for up to 80% of known-cause deaths (Brechtel et al. 1993; Carbyn et al. 1994; Covell 1992; Kitchen et al. 1999; O. J. Rongstad et al. 1989, in litt.; Sovada et al. 1998). Coyote predation was also identified as the primary cause of death of kit foxes in California (Cypher et al. 2000; Disney and Spiegel 1992; Ralls and White 1995). Sovada et al. (1998) reported that 8 of 9 swift fox deaths caused by coyotes were located near the boundary of the fox’s home range as estimated by the minimum convex polygon method. Kitchen et al. (1999) stated that 11 of 11 swift fox deaths caused by coyotes occurred outside the fox’s home range as estimated by the adaptive kernel method (85% isopleth). Our results further corroborate these findings. Swift foxes appear more vulnerable to coyotes in areas they are not familiar with, possibly because they do not know the location of dens that could provide refuge. Swift foxes have been known to carry antibodies for canine distemper virus (Miller et al. 2000); however, the 2 deaths caused by canine distemper virus were the first documented for swift foxes from this pathogen. Since these 2 deaths were observed, canine distemper virus was determined to be the cause of death in a swift fox from Colorado (E. Williams, in litt.). Canine distemper is endemic, common in the Intermountain West, and has been previously diagnosed in Albany county, Wyoming (Thorne et al. 1982). The virus is spread through direct contact and all canids are susceptible. Animals in poor physical condition are more susceptible to the disease, and its impacts upon small carnivore populations can be significant (Monson and Stone 1976). Persistence of our study population, large litter sizes, and high antibody prevalence rate in foxes tested suggested, however, that canine distemper did not have a major impact on this swift fox population during our study.

Although our study population was located in habitat not typically associated with swift foxes (sagebrush steppe and shortgrass prairie transition) on the periphery of the species’ geographical range, mean litter size was higher and survival rates similar to or higher than those observed elsewhere in the range. Extensive areas of sagebrush interspersed with short bunchgrasses exist throughout Wyoming (Risser et al. 1981). Much of this type of habitat in Wyoming has not been impacted by large-scale habitat modifications such as dry land farming, and vegetation remains largely unchanged from its condition in the 1800s (Knight 1994). It is not surprising that swift foxes can use habitat with a significant shrub component considering that the very similar kit fox extensively uses shrub-dominated plant communities throughout the southwestern United States (Zoellick et al. 1989). Areas of transition between sagebrush steppe and shortgrass prairie should be considered an important component of the swift fox distribution because of their potential to provide quality swift fox habitat.

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LITERATURE CITED


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