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David E. Andersen

Thomas R. Laurion

John R. Cary

Robert S. Sikes

Mary A. McLeod

See next page for additional authors

Authors
David E. Andersen, Thomas R. Laurion, John R. Cary, Robert S. Sikes, Mary A. McLeod, and Eric . M. Gese

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Aspects of Swift Fox Ecology in Southeastern Colorado

■ David E. Andersen, Thomas R. Laurion, John R. Cary, Robert S. Sikes, Mary A. McLeod and Eric M. Gese

Abstract: We studied the ecology of swift fox on the Piñon Canyon Maneuver Site (PCMS) in southeastern Colorado from March 1986 to September 1987. Forty-two foxes were captured 162 times; 23 were radiocollared. Mean minimum convex polygon home range size of 5 adult swift fox was 29.0 km² (range = 12.8 to 34.3 km²) and, although home ranges of adjacent social groups overlapped, core areas described by 50% harmonic means were almost entirely exclusive. Swift fox diet (as determined from scats) consisted primarily of small and medium-sized mammals (monthly mean % volume = 64%), arthropods ($\bar{x}$ = 19%), and small birds ($\bar{x}$ = 8%). Mean litter size (n = 5) was 3.4 (range = 2 to 5) and not all females produced litters. Kaplan-Meier estimates of annual survivorship were 0.45 for adults (n = 8) and 0.126 for juveniles (n = 14). Predation by coyotes was the primary cause (63%) of fox mortality. Fox carcasses collected off of the PCMS (where coyote hunting and trapping were permitted) indicated that juvenile mortality due to predation by coyotes was lower there than on the study site. We conclude that where coyotes are abundant, predation by coyotes is a significant source of mortality for swift fox and that den availability might be an important aspect of swift fox management.

Swift fox (*Vulpes velox*) formerly inhabited shortgrass and midgrass prairies of North America, from eastern New Mexico and northwestern Texas to southern Alberta and Saskatchewan, and from eastern Colorado, Wyoming, and Montana to western Iowa (Scott-Brown et al. 1987, Carbyn et al. 1994). By the mid-1950s, swift fox were uncommon in eastern and northern portions of their historic range, and rare or absent from other portions (Martin and Sternburg 1955, Glass 1956, Long 1965, Pfeifer and Hibbard 1970, Kerwin 1972, Hillman and Sharps 1978). Explanations for this range reduction include the loss of prairie habitat to agriculture (Chambers 1978, Russell and Scotter 1984) and both direct and indirect effects of poisoning campaigns directed primarily at the wolf (*Canis lupus*). Young (1944:336) noted that swift foxes often were the first to consume poisoned bait intended for wolves, and Carbyn (1986) suggested that exterminating the wolf in prairie habitats may have allowed coyote (*C. latrans*) densities to increase. As coyotes often prey upon swift and kit fox (*V. macrotis*) (Seton 1929:564, Kilgore 1969, Scott-Brown et al. 1986, O'Neal et al. 1987, Covell 1992, Cypher and Scrivner 1992, Disney and Spiegel 1992, Ralls and White 1995, Sovada et al. 1998), increases in coyote densities can in turn increase predation rates on swift and kit fox.

Swift fox are slowly becoming re-established in parts of their historical range, but populations are affected by a variety of human activities including hunting and trapping (Kilgore 1969, Linhardt and Robinson 1972, Loy 1981), indiscriminate shooting (Miller and McCoy 1965, Kilgore 1969, Hines 1980, Hines and Case 1991), poisoning programs for coyote control (Seton 1929, Bunker 1940, Hillman and Sharps 1978), and mortality caused by vehicles on roads (Cutter 1958, Hines 1980, Samuel and Nelson 1982, Scott-Brown et al. 1986, Hines and Case 1991). Additional sources of fox mortality include predation by golden eagles (*Aquila chrysaetos*) (Cameron 1984, Scott-Brown et al. 1986), American badgers (*Taxidea taxus*), red fox (*V. vulpes*), bobcats (*Lynx rufus*), domestic dogs (*C. familiaris*) (Scott-Brown et al. 1986, Disney and Spiegel 1992), and potentially great horned owls (*Bubo virginianus*) (Kilgore 1969).

Scott-Brown et al. (1987) reviewed available literature on swift fox and suggested the need for population studies and especially the need for information on rates and causes of mortality. These types of data, combined with information on general ecological patterns, are essential for species management. The current study was designed to provide information on swift fox ecology in southeastern Colorado pertinent to population management. We used radiocollared individuals to examine home range sizes and patterns of habitat use between neighboring individuals and also to assess mortality rates and causes of mortality. Additionally, regular observations of this population allowed us to gather data on reproduction and food habits.

Study Area

The 1040-km² Piñon Canyon Maneuver Site (PCMS) is located 52 km northeast of Trinidad in Las Animas County, Colorado (Fig. 1). The area was first settled in the late 1860s and has undergone 2 homesteading booms associated with cattle and sheep ranching. Cattle ranching has dominated in this area since the early 1950s (Friedman

1985). The PCMS was acquired by the U.S. Army in 1983 for use by mechanized infantry. All hunting, trapping, and predator control was prohibited on the area from 1983 until 1987. Beginning in January 1987 an experimental program of coyote population control to reduce coyote densities was initiated in the southwestern region of the PCMS, outside of the area of our intensive study site (Gese 1987). In areas surrounding the PCMS, coyotes have consistently been subjected to intense removal efforts by ranchers (Covell 1992). Because of the restrictions on many types of human use on the PCMS, this site provides an excellent opportunity to examine elements of swift fox ecology and population dynamics that are impacted by human activities elsewhere and to provide comparative data for managed populations.

Elevation on the PCMS ranged from 1,300 to 1,740 m and climate was semiarid with average annual precipitation ranging from 26 to 38 cm on different parts of the study site. Vegetation on the PCMS was composed of grasslands, shrublands, and woodlands (Shaw and Diersing 1990). Grasslands covered 55% of the total area (Firchow 1986) and were dominated by blue grama *(Bouteloua gracilis)*, western wheatgrass *(Agropyron smithii)*, and galleta *(Hilaria jamesii)*. Shrublands were composed of a grassland understory with an overstory of shrubs or succulents, including walking-stick cholla *(Opuntia imbricata)*, soapweed *(Yucca glauca)*, wolfberry *(Lycium pallidum)*, winterfat *(Ceratoides lanata)*, and bigelow sage *(Artemisia bigelovii)*. Woodlands were dominated by one-seed juniper *(Juniperus monosperma)* and piñón pine *(Pinus edulis)*, with a shrubby understory of wax current *(Ribes cereum)*, sumac *(Rhus trilobata)*, and true mountain mahogany *(Cercocarpus montanus)*.

A 75-km^2 intensive study area within the PCMS (Fig. 1) was selected in which we attempted to capture and radiocollar all swift fox. The intensive study area was outside of the area of coyote removal described above, and only the first removal effort (January 1987) occurred during the present study (Gese 1987). Habitat within the intensive study site was primarily short-grass prairie that graded into piñón/juniper shrub in association with limestone breaks or at the heads of canyons of tributaries to the Purgatoire River.

Methods

Trapping, Capture, and Radio Telemetry Monitoring

Swift foxes were captured using single- and double-door National live traps (61 x 24 x 24 cm and 81 x 24 x 24 cm, respectively) baited with chicken or pork. Traps were prebaited with a door wired open, and were set when the bait had been taken for 1–2 nights. Radiocollared foxes were recaptured by enclosing the entrance to their den with a small pen and an attached trap (Zoellick and Smith 1986). We usually recaptured radiocollared individuals in

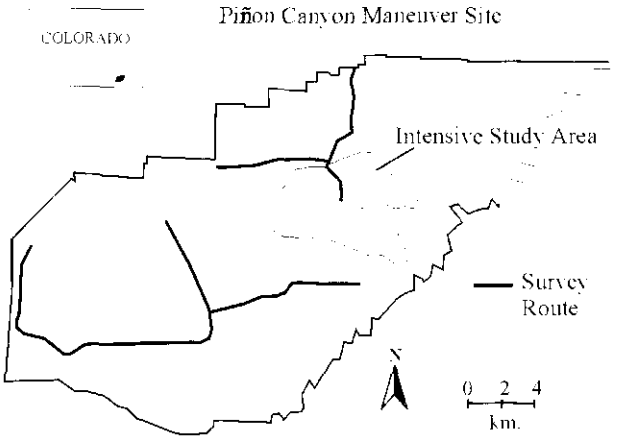

Figure 1. Map of the Piñon Canyon Maneuver Site located in southeastern Colorado. Boundaries of the intensive study area used to assess swift fox ecology and the 87-km truck survey route are indicated.

1–2 nights. Beginning May 1986, we attempted to capture and radiocollar pups as soon as possible after they appeared above ground and weighed >700 g. Pups were captured in traps set next to natal dens; no prebaiting was necessary. We manually restrained all individuals and recorded sex, weight, age class, and standard body measurements (total length, and length of tail, hindfoot, and ear). Individuals were classified as pup or adult based on their development at the time of first capture. We checked all females for evidence of lactation or for pregnancy by abdominal palpation.

Radio-collars weighing between 35 and 50 g (<5% body weight, Eberhardt et al. 1982) and with a battery life of 150 to 200 days were affixed to all foxes captured in the intensive study site. Most radiocollars were equipped with mortality sensors. We used a portable receiver and hand-held 4-element Yagi antenna to locate animals during daylight hours ≥2 times/week. These daytime locations facilitated collection of scats and provided information on den use and date of death. Nighttime locations were obtained from simultaneous bearings recorded from 2 fixed-location receiving stations. Each station had a 13.7 m rotatable mast with paired 11-element Yagi antennas and a null-peak system (Mech 1983). Night tracking was conducted in 6-hour blocks, either 1800 to 2400 hours or 2400 to 0600 hours. Four to 12 locations were obtained on each animal during each 6-hour tracking period. The number of locations obtained for each animal depended upon weather conditions and the number of animals being tracked. Night tracking was conducted on 54 nights in 7 periods: from 15 July–7 August 1986; 23–30 September 1986; 23–30 October 1986; 3–7 January 1987; 17–22 January 1987; 11–21 February 1987; and 18–27 March 1987. Because night locations best represented home-range use during periods of fox activity, we performed all home range analyses using only nighttime locations.

Home Range Estimation and Core Areas of Activity

Prior to home range analyses, location data were screened for accuracy using a maximum error polygon size and rate of movement from a prior location. Error polygons are in part a function of azimuth precision, distance from the signal source to receiver, the number of simultaneous azimuths used to determine the location of the source of a signal, and the relation of azimuths to one another (White and Garrott 1990). Azimuth precision and the number of simultaneous azimuths used (2) were the same for all nighttime locations. However, because receiving stations were fixed, distance to individual animals and the relation of azimuths to one another varied among individuals, resulting in relatively large error polygons for some radiocollared foxes. Thus, we assessed location data for each fox separately. Error polygons for all but 2 foxes averaged <5 km^2, so for these individuals we excluded obvious outliers (<2% of locations) from further analyses. For the remaining 2 individuals we excluded all locations with error polygons >10 km^2. Five additional locations were removed from the overall data set based on calculated movement rates that seemed excessive (>0.20 m/sec compared to an average of 0.026 m/sec). In total, 46 locations were excluded from home range analyses based on excessive error polygons or consideration of rate of movement.

Home ranges were calculated from data that included at least 1 location from each nighttime tracking period. The number of tracking periods per fox ranged from 13 to 50. Home ranges were calculated using the minimum convex polygon method (100%; Mohr 1947, Southwood 1966) and we calculated 50% and 95% core activity areas using both harmonic mean (Dixon and Chapman 1980) and adaptive kernel (Worton 1989) estimators. To assess the extent to which home ranges might change over time, we calculated seasonal minimum convex polygon home ranges for the 3 adults (at time of capture) located most often across seasons (3 months comprised each season with spring beginning on 1 March).

Population Dynamics and Estimation of Survival Rates

To determine the relative abundance of swift fox on the PCMS, an 87-km survey route was driven in the morning after each new snowfall or after it ceased snowing in the winter of 1986–87. This route was driven 5 times from 2 December 1986 to 21 January 1987, but surveys were sometimes abbreviated if required by local weather conditions. The location of all swift fox tracks observed on the road were recorded. We compared sex and age composition of swift fox on the entire PCMS to foxes on the intensive study area by attempting to capture foxes in live traps placed near locations of tracks observed on the survey route.

We used cementum annuli of fox teeth (canines) to estimate the age structure of foxes trapped in areas adjacent to the PCMS where coyotes were not protected through hunting and trapping restrictions. Skulls of swift fox were obtained from trappers during the 1986–87 winter in Cheyenne Wells, Colorado, about 280 km northeast of the study site ($n = 43$), and Springfield, Colorado, about 160 km east of the study site ($n = 30$).

Deaths were recorded when indicated by the mortality sensor on radiocollars or when individuals remained motionless during nighttime tracking periods. Causes of death were determined from condition of carcasses and tracks and signs at the kill site. In a few cases, cause and date of death were recorded for untagged individuals that were found by investigators within the study area. Survival rates were calculated using Kaplan-Meier product limit estimators based on the staggered entry design described by Pollock et al. (1989). Annual (June 1986 through May 1987) survival rate was calculated for eight adults collared during this period. Survival rate of pups was calculated over an 11-month period (July 1986 through May 1987) and annual survival rate was estimated by extrapolation. Seasons for survival calculations were the same periods of time described for home range analyses.

Food Habits

We determined food habits from scats that were collected throughout the PCMS. Scats were collected most often during snow tracking, while obtaining day locations, or at den sites. Scats found around dens probably were pup scats; adults generally left the den site to defecate (determined from snow tracking). Scats were air dried and broken apart, and food remains were identified from reference materials collected locally. The percent volume of each item in individual scats was estimated visually (to the nearest 10%) and the mean of these estimates was calculated to give total percent volume for each month and season.

Results and Discussion

Radio Telemetry

Forty-two swift fox were captured 162 times on the PCMS. Twenty-three individuals (9 adults and 14 pups) captured within the 75-km^2 intensive study area were equipped with radiotransmitters (Table 1) and were located 995 times during the day and 1,539 times at night. Five pairs (or family groups when pups were present) were followed during 1986 and 1987.

Home Range Estimates

We had sufficient data to estimate home range size for five adult swift foxes (2 females and 3 males). Minimum convex polygon home ranges averaged 29.0 km^2 (range 12.8 to 34.3 km^2, Table 2) and are similar to previous reports for swift fox (Hines and Case 1991), but somewhat larger than those reported for kit foxes (Spiegel and Bradbury 1992, Zoellick et al. 1992). Minimum convex

Table 1. Summary data for swift foxes captured and equipped with radio transmitters on a 75 -km^2 intensive study area of the Piñon Canyon Maneuver Site in Colorado, March 1986–November 1987. Table includes mortality data for 4 additional animals that were n ot radio-collared.

Animal No.	Sex	Date of Capture dd/mm/yy	No. Times Captured	No. Dens	Radio-days	Daytime Locations	Nighttime Locations	Cause of Death	Date of Death or Last Day Monitored dd/mm/yy
Adults									
1	M	30/03/86	6	4	89	17	0	coyote	27/06/86
2	F	25/0586	13	20	493	156	285		30/09/87
3	M	15/0586	17	23	503	151	312		30/09/87
4	F	04/06/86	2	5	56	18	18	coyote	30/07/86
5	M	28/05/86	5	15	282	104	217	coyote	06/03/87
18	M	21/12/86	5	8	210	74	94	eagle	19/07/87
23	F	09/02/87	6	7	233	67	34		30/09/87
36	M	12/05/87	3	11	141	40	0		30/09/87
37	F	03/06/87	4	5	119	27	0		30/09/87
Pups									
6	F	07/06/86	5	—	56	0	24	coyote	02/08/86
7	M	07/06/86	7	—	55	0	7	coyote	01/08/86
8	F	07/06/86	16	17	480	145	195		30/09/87
11	M	07/06/86	8	—	113	0	38	coyote	28/09/86
13	M	20/06/86	7	12	194	72	104	coyote	31/12/86
14	M	28/05/86	4	-	29	0	3	eagle	26/06/86
15	F	27/11/86	1	—	15	2	0	coyote	12/12/86
16	M	27/11/86	3	—	39	9	13	coyote	05/01/87
17	F	20/12/86	2	12	265	90	195	coyote	11/09/87
38	M	04/06/87	5	4	98	3	0	badger	10/09/87
39	F	04/06/87	5	2	118	2	0		30/09/87
40	F	06/06/87	6	4	97	8	0	coyote	11/09/87
41	F	01/07/87	1	4	71	4	0	coyote	10/09/87
42	M	04/07/87	1	4	88	6	0		30/09/87
Unmarked									
—	F (adult)							vehicle	21/04/86
—	M (pup)							suspected coyote	07/06/86
—	M (pup)							suspected coyote	07/06/86
—	M (pup)							unknown	01/07/86

Table 2. Minimum convex polygon (100% MCP) home range size estimates (km ^{2}) and harmonic mean and adaptive kernel estimates of core activity areas (km^2) from night locations for adult swift foxes radio -tracked on the Piñon Canyon Manuever Site, Colorado, 19 86–1987.

Fox number	Number of locations	Tracking nights	Months monitored	MCP	Core activity areas: Harmonic mean 50%	Harmonic mean 95%	Adaptive kernal 50%	Adaptive kernal 95%
Male								
3	312	50	16	34.3	3.6	18.5	3.5	16.4
5	217	43	10	32.3	4.8	23.8	5.5	23.4
18	94	21	7	33.5	4.9	23.3	6.3	30.1
Female								
2	285	48	16	31.4	1.9	24.9	1.9	23.9
23	34	13	7	12.8	1.7	14.0	3.5	20.1

polygon estimates of home ranges of adjacent individuals or family pairs overlapped appreciably (Fig. 2). Sizes of 50% core activity areas of individuals or families were similar regardless of whether the harmonic means or adaptive kernel estimates were used and ranged from 1.3 to 6.3 km^2 depending on the estimator (Table 2). The core activity areas of adjacent, same-sex adults were almost entirely exclusive of one another (Fig. 2), suggesting some degree of territoriality. These data are important because swift foxes previously were not believed to be territorial (Hines 1980, Samuel and Nelson 1982, Cameron 1984, Scott-Brown et al. 1987). Similarly, earlier studies of kit fox indicated no tendency toward territoriality (Morrel 1972, McGrew 1979) whereas recent studies using telemetry have demonstrated territoriality for kit fox (White et al. 1994).

The areas delineated by daytime locations (essentially den locations) and the 50% core activity areas were similar, indicating that swift fox spent most of their time in the vicinity of a den even during the active nocturnal period. That various areas within an individual's home range were used with different intensities is further demonstrated by the fact that 95% activity areas were 5–13 times larger than 50% activity areas (Table 2). The size of an individual's home range can vary among different areas and also temporally (Gittleman and Harvey 1982). In the present study, home ranges varied seasonally and were smallest during the summer for both sexes (Fig. 3). The summer range of female number 2 was especially restricted (Fig. 3A), as she was rearing a litter during this time. Winter ranges of all animals were by far the largest and included virtually the entire area of the overall minimum convex polygon calculated for each individual (Fig. 3).

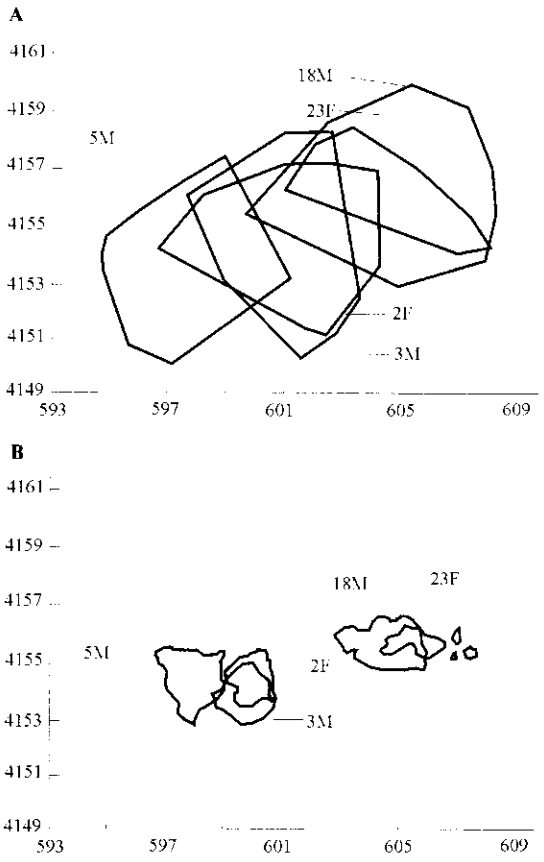

*Figure 2. Home ranges of adult swift foxes (*n = 5*) in the intensive study area of the Piñon Canyon Maneuver Site, Colorado, 1986–1987. A) Range boundaries calculated using the 100% minimum convex polygon method. B) Core activity areas using 50% harmonic mean estimators. Labels associated with each range boundary indicate the individual foxes' identification number and sex.*

Not surprisingly, mated pairs and family group members had home ranges that were similar. Pup movements initially were restricted to only a small portion of their parents' home range, but by September they appeared to be using most of their family group's range. Dispersal in this species has been reported as early as August (Kilgore 1969), but we observed no dispersal of pups until November and December.

Movement Data

Swift fox are assumed to be primarily monogamous, but some polygamy has been reported in both this species (Kilgore 1969) and in kit foxes (Egoscue 1962, 1975). If one mate dies, the surviving adult may move to another adult's home range, or stay and accept an ingressing mate. As a consequence, most movements outside of family group ranges probably are by the young of the year when they disperse or are forced out of their natal home range. We observed only 4 instances of ingress and egress; 3 of these involved pups and 1 involved an adult. Two juvenile females moved into the area and replaced mates lost to

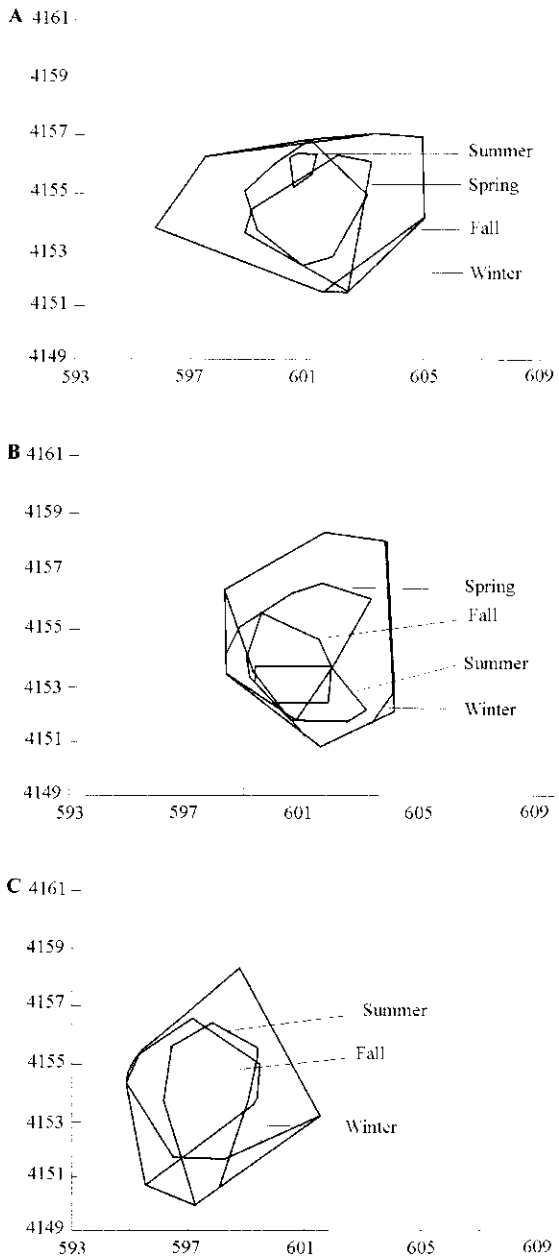

Figure 3. Seasonal[a] home ranges calculated by the 100% minimum convex polygon method for 3 adult swift fox in the intensive study area of the Piñon Canyon Maneuver Site, Colorado, 1986–1987. A) Female number 2; B) Male number 3; C) Male number 5. Outermost boundaries indicate the overall minimum convex polygon ranges for each individual.
[a] - Seasonal periods, Spring = March-May, Summer = June–August, Fall = September–November, and Winter = December–February.

predation, and a single juvenile male presumably became the mate of a female that was occupying a territory with a male litter mate. One adult male moved outside of his previously known home range and into an adjacent territory when both his mate and the mate of the female in the adjoining territory were killed.

Population Dynamics and Mortality

Nineteen swift fox mortalities were recorded (Table 1): 12 fox (63%) were killed by coyotes, 2 were suspected of being killed by coyotes, 2 were killed by eagles, 1 was most likely killed by a badger (judging from tracks, fresh excavations, and fox remains at the den site), 1 was hit by a vehicle, and 1 pup died of unknown causes in a den. Pups suffered the highest mortality. Forty-two percent of the individuals that were classified as adults at initial capture survived at least 10 additional months (n = 9, SE = 0.21 months), whereas >50% of radiomarked pups were killed within 100 days of capture (Table 1). Estimated annual survival rate was 0.45 for adults, and the 11-month survival rate was 0.15 (a rate of 0.126 on an annual basis) for pups. Survivorship curves for both adults and juveniles beginning in June 1987 were similar to curves from 1986 (Fig. 4).

The high level of predation by coyotes that we documented is consistent with subsequent findings for swift fox in this same area in 1989–1991, when coyotes accounted for 85% of fox mortality (Covell 1992). In the closely related kit fox, Disney and Spiegel (1992) reported that coyotes and domestic dogs accounted for about 75% of all fox mortality on their developed study site. White et al. (1995) documented considerable overlap in habitat and food use by coyotes and kit foxes, and reported that 65% of all verified kit fox mortalities in their study were attributable to coyotes. Given the level of predation of coyotes on these arid-land foxes and the resource competition between coyotes and foxes (White et al. 1994), the potential exists for coyotes to suppress fox populations where densities of the former are high, especially in times of low prey availability.

In the present study, only 3 of 14 radiocollared pups were alive at the end of the study period. Eleven of 14 pup mortalities (including data for 3 pups that were not radiocollared) were caused or suspected of being caused by coyotes (Table 1). Death of the uncollared pups was inferred from the fact that they were not captured after their presumed father was killed by coyotes. Further, 7 of the 10 pups killed by coyotes in the study area were removed from the population before October; only 3 were killed in December and January. These data indicate that predation by coyotes was occurring well before hunting or trapping normally would have occurred had these activities been allowed on the study site.

In contrast to the low pup survival on the PCMS, 55 of 73 swift fox carcasses (75%) obtained from nearby areas outside the PCMS in southeastern Colorado after the 1986–87 winter were juveniles (Table 3). The preponderance of juveniles in this sample suggests much lower levels of predation by coyotes on juvenile foxes outside as compared to inside the PCMS, even if juvenile swift fox are substantially more vulnerable to harvest. As the density of the unexploited population of coyotes likely was

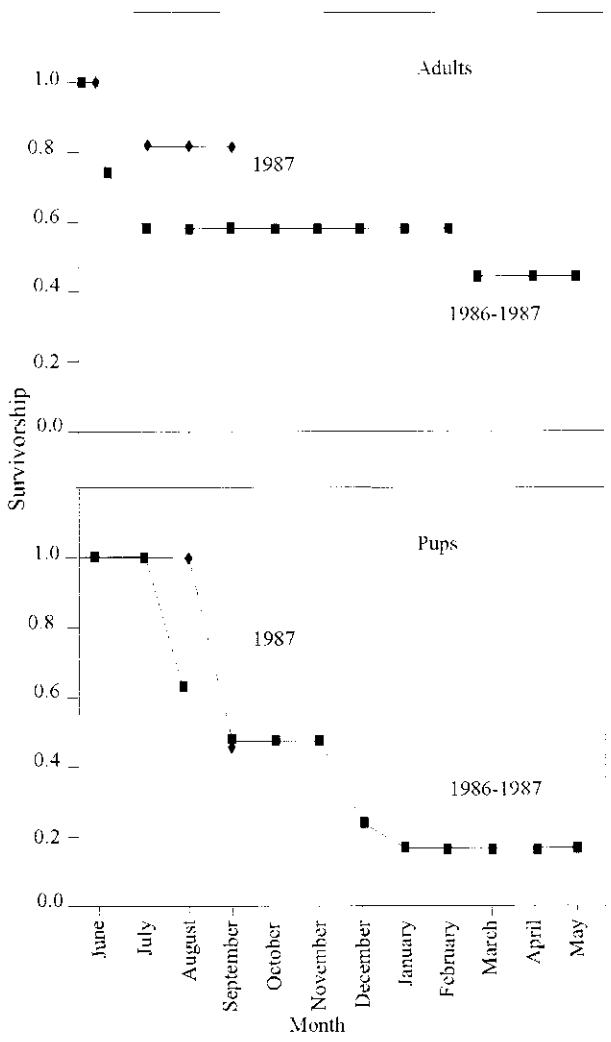

*Figure 4. Staggered-entry Kaplan-Meier survival rate estimates for adult (*n = *8) and juvenile (*n = *14) swift foxes on the intensive study area of the Piñon Canyon Maneuver Site in southeastern Colorado, 1986–1987.*

higher on the PCMS than off the site, these circumstantial data underscore the negative correlation between coyote density and swift fox survivorship, especially for juvenile foxes.

Litter size, estimated from litters that emerged at dens (n = 4 in 1986 and 1987) and from the number of fetuses in a female that was killed by a vehicle (1986), averaged 3.4 (range = 2–5). This estimate is conservative as mortalities may have occurred prior to the time that young emerged. Although mean litter sizes as large as 5 and 5.7 have been reported (Kilgore 1969), most populations average somewhat smaller litters (3.8—Covell 1992, 3.4—Hillman and Sharps 1978), and Scott-Brown et al. (1987) reported an average litter size of only 2.4 young in 37 litters at a captive breeding facility in Alberta. Based on

Table 3. Age of swift foxes harvested during the 1986 –87 trapping season in southeastern Colorado, based on *cementum annuli* from canine teeth of skulls collected from trappers.

Location	Age (Years)				
	Pups	Yearling	2	3	4
Cheyenne Wells County	21	4	3	0	2
Springfield County	34	5	2	1	1
Total	55	9	5	1	3
	(75%)	(12%)	(7%)	(1%)	(4%)

Table 4. Percent volume of food items found in swift fox scats (n = 582) by month 1986 -1987 at the Piñon Canyon Maneuver Site, Colorado.

	Winter			Spring			Summer			Fall		Winter
	Jan	Feb	March	Apr	May	June	July	August	Sept	Oct	Nov	Dec
Food Item	(25)	(34)	(22)	(30)	(26)	(88)	(164)	(67)	(38)	(31)	(33)	(24)
Cricetidae	42.3	0	0	35.5	9.4	0	3.2	6.1	0	2.2	11.8	17.3
Geomyidae [a]	4.1	36.7	24.3	22.5	11.3	20.3	19.2	22.3	3.0	7.6	17.1	10.1
Heteromyidae [b]	5.2	23.8	63.1	12.0	12.9	0	6.2	0	10.2	50.7	17.2	0
Sciuridae	0	0	0	0	1.3	3.3	6.3	0	0	0	0	0
Leporidae	2.4	10.5	0	0	0	1.3	10.5	7.6	4.1	2.1	9.2	12.4
Unidentified	9.7	7.6	7.1	0	6.1	22.2	2.6	2.2	15.3	31.2	24.0	39.7
Total Mammals	63.7	78.6	94.5	70.0	41.0	47.1	48.0	38.2	32.6	93.8	79.3	79.5
Birds	5.9	1.8	4.1	1.0	33.7	26.3	11.6	3.0	6.3	0	1.7	1.0
Arthropods	25.6	13.2	0.7	6.3	9.5	16.8	34.3	50.3	49.2	2.5	12.0	5.0
Vegetation	0	0.7	0	1.0	0	1.2	0.5	0	0	0	0	0.4
Soil	4.8	5.7	0.7	21.7	15.8	5.4	4.6	7.1	5.7	3.8	7.0	14.1
Reptiles	0	0	0	0	0	3.2	1.0	1.4	6.2	0	0	0

[a] Yellow-face pocket gopher *(Pappogeomys castanops)* .
[b] Silky pocket mouse *(Perognathus flavus)* and Ord's kangaroo rat *(Dipodomys ordii)*.

timing of emergence above ground (pups on our study area were born in early to late May), and assuming a gestation period of 51 days (Scott-Brown et al. 1987), breeding probably occurred between 1 and 15 March.

Although our sample sizes were small, pregnancy rates of swift fox on the PCMS were low. Whereas all 3 females captured on the area in 1986 were pregnant, only 2 of 5 females in 1987 produced young. No young were found for female number 23 (see Table 1 for animal identification numbers), a successful breeder in 1986, and females numbers 8 and 17 failed to rear young in 1987. Although these latter females were only 1-year old, both females and males are capable of breeding during their first year (Scott-Brown et al. 1986). Furthermore, female number 17 was lactating when captured on 26 June 1987, but it is unclear when her pups were lost. Female number 8 did not have a mate during 1987 when breeding normally would have occurred.

Food Habits

We examined 582 scats to identify prey items. Food items varied considerably among months, years, and family groups, but generally were comparable to previous food habits studies for both swift foxes (Cutter 1958, Zumbaugh et al. 1985, Uresk and Sharps 1986, Hines and Case 1991, also see Egoscue 1979) and kit foxes (White et al. 1996, and sources therein). Overall, mammals were the most frequent food item in scats (Table 4), making up >50% by volume of scats for 7 months. Both black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) occur on the site, and, although we found only cottontail remains at den sites and made no attempt to identify lagomorph hairs to species in scats, swift foxes will prey on both genera of lagomorphs opportunistically (Cutter 1958). Insects were the second most frequent prey and accounted for up to 50% by volume of scats during August and September. However, the importance of insect prey probably is exaggerated in scat analysis because of the large proportion of indigestible chitin in arthropods (Scott-Brown et al. 1987). Like most previous studies, our results show that swift foxes will take birds opportunistically. Zumbaugh et al. (1985) reported that avian prey were present in almost 20% of stomachs they examined from foxes collected from trappers and fur dealers in Kansas, and Cutter (1958) found birds in 10% of scats examined from northern Texas. However, unlike the population of swift fox studied by Uresk and Sharps (1986) in South Dakota, where avian prey was an important food item throughout the year, swift fox on our study site preyed heavily on ground-nesting birds only during May and June, when avian material comprised 33% of scats. Soil appeared consistently in scats but was most common in April, May, and December, which may be a result of individuals ingesting soil while cleaning out or enlarging dens in anticipation of a litter. We observed this digging in 1987 at dens frequented by females, and noted that even unmated females sometimes dug additional entrances and enlarged dens.

In interpreting our data on food habits, one should bear in mind that volumetric analysis of scats can bias results

and overestimate the importance of species with indigestible body parts such as hair, feathers, and exoskeletons, and underestimate highly digestible forms like soft-bodied invertebrates. Given that we, like previous studies based at least partially on analysis of stomach contents for this species (e.g., Cutter 1958, Kilgore 1969, Zumbaugh et al. 1985), found vertebrates to be the major prey items, we feel that our results are probably a conservative estimate of the importance of vertebrate prey because mammals and birds have a greater percentage of body mass that is easily digestible compared to arthropods, and foxes can selectively avoid indigestible components owing to the prey's larger size.

Den Activity

Swift fox on the PCMS spent most of the daylight hours in or very near a den but typically used multiple dens. Two individual foxes used >20 different dens each. Members of a pair often were found in the same den (45% of 214 locations for 4 females where both members of a pair were radiocollared) and they were more likely to be in the same den in the winter than in late summer. Male number 3 was in the den with his mate (number 2) all 12 times that she was located in January 1987. In contrast, 3 females were located in dens 22 times, but only twice with mates. Given that predation seems to be the cause of most mortality of swift fox on the PCMS, it may be that the more dens available throughout a pair's area of activity, the higher is the survival rate of that pair and their offspring (Waser 1980). Access to a den may be important in evading predation and swift fox spend most of their time in the vicinity of a den. Recent work by Wires (1995) suggests that visibility from the den location to allow foxes to detect approaching predators was a key feature in den use by kit foxes in California (see also Cypher and Spencer 1998), and this may also be important for swift fox.

Management Considerations

Although drastic range reductions have resulted in concern about the status of swift fox throughout much of their historic range, relatively little is known about their population dynamics. Our results show that coyote predation was a significant source of mortality in both adults and juveniles in a swift fox population in southeastern Colorado during a period when the coyote population on the study area was not being exploited through hunting or trapping (Gese et al. 1989). Samples of swift fox trapped in adjacent areas where coyote harvest was not restricted had higher proportions of juveniles than suggested by survival rates we found on the PCMS. Low adult and juvenile survival rates might necessitate immigration from surrounding areas to maintain the swift fox population on the PCMS. High coyote densities and predation rates might play a major role in limiting density and growth rates of swift fox populations. Availability and distribution of suitable dens and den sites may influence predation pressure, and may be important considerations in swift fox conservation.

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