

Population ecology of swift foxes (*Vulpes velox*) in southeastern Colorado

Edward R. Schauster, Eric M. Gese, and Ann M. Kitchen

Abstract: Swift foxes (*Vulpes velox*) were once distributed across most of the shortgrass prairie of North America. The arrival of settlers and the concurrent loss of habitat, trapping, incidental poisoning, and shooting brought about a decline in its numbers until the swift fox remained only in the southern part of its historic range. A current understanding of swift fox population ecology is important to management and conservation efforts. We examined the population ecology of swift foxes on a native shortgrass prairie ecosystem in southeastern Colorado. From January 1997 to December 1998 we investigated home-range size and space use, spatial overlap, dispersal patterns, survival rates, and reproduction using a sample of 90 (42 males, 48 females) radio-collared foxes. Home ranges were largest ($9.4 \pm 4.9 \text{ km}^2$) and spatial overlap was greatest using nighttime locations when foxes were active, while daytime locations indicated that the use of dens was exclusive among social units, and space use ($2.8 \pm 2.2 \text{ km}^2$) was reduced during the day. Among resident foxes, survival rates were higher for adults than for juveniles. For dispersing foxes, adults that dispersed had higher survival rates than juvenile dispersers. Social units ranged in size from 2 to 4 foxes. About 58% of the social units produced pups; litter size averaged 2.4 pups at den emergence. Among the surviving pup cohort, some pups were philopatric, some dispersed long distances, while others dispersed to neighboring territories. Swift fox density was negatively associated with both coyote (*Canis latrans*) and lagomorph abundance but positively correlated with rodent abundance.

Résumé : L'aire de répartition du renard véloce (*Vulpes velox*) s'étendait jadis à toute la prairie à herbes courtes de l'Amérique du Nord. L'arrivée des colons et, en conséquence, la perte d'habitats, le trappage, les empoisonnements accidentels et la chasse, ont réduit les densités du renard au point où il ne survit plus que dans la partie sud de son aire traditionnelle. Pour des fins de gestion et de conservation, il importe de connaître l'écologie actuelle de l'espèce. Nous avons donc étudié l'écologie d'une population d'un écosystème naturel de prairie à herbes courtes du sud-est du Colorado. Un échantillon de 90 (42 mâles : 48 femelles) renards munis de colliers radio-émetteurs nous a permis, de janvier 1997 à décembre 1998, de déterminer la taille du domaine vital, l'utilisation de l'espace, les chevauchements spatiaux, les patterns de dispersion, les taux de survie et la reproduction. La taille des domaines ($9,4 \pm 4,9 \text{ km}^2$) et les recouvrements de domaines étaient axiaux lorsque calculés à partir des repérages de nuit au moment où les renards étaient actifs; les repérages de jour indiquaient que l'utilisation des terriers était réservée exclusivement à chacun des groupes sociaux et que l'utilisation de l'espace ($2,8 \pm 2,2 \text{ km}^2$) était réduite durant le jour. Chez les renards résidents, les taux de survie étaient plus élevés chez les adultes que chez les jeunes. Les adultes en phase de dispersion avaient une survie supérieure à celle des jeunes qui se dispersaient. La taille des groupes sociaux variait de 2 à 4 renards/groupe social. Environ 58 % des groupes sociaux ont produit des petits et la taille des portées était en moyenne de 2,4 renardeaux/portée. Parmi les survivants de la cohorte des renardeaux, quelques-uns étaient philopatriques, d'autres se sont dispersés sur de grandes distances et enfin d'autres ont gagné des territoires avoisinants. La densité des renards véloces était en corrélation négative avec l'abondance tant des coyotes (*Canis latrans*) que des lagomorphes, mais en corrélation positive avec celle des rongeurs.

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Introduction

Swift foxes (*Vulpes velox*) were once widely distributed across much of the short- and mixed-grass prairie of North America (Scott-Brown et al. 1987). Historically, swift foxes

ranged from the southern portions of the central Canadian provinces of Alberta and Saskatchewan south through the states of Montana, the Dakotas, eastern Wyoming, Nebraska, Colorado, and Kansas and the Oklahoma panhandle, eastern New Mexico, and northwestern Texas (Egoscue 1979; Scott-Brown et al. 1987; FaunaWest 1991). Swift foxes may have been found as far east as western Minnesota and Iowa (Swanson et al. 1945; Bowles 1975) in the United States and possibly western Manitoba in Canada, but this remains undocumented (Egoscue 1979; Carbyn 1998). During much of the 1800s swift foxes are believed to have been abundant, as evidenced by observations made by early naturalists and explorers (FaunaWest 1991). Johnson (1969) examined the returns of the American Fur Company and found that 10 614 swift fox pelts were traded at their posts covering western Montana and the Dakotas from 1835 to 1839 (Utley 1997).

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The records of the Hudson's Bay Company showed 117 025 pelts being purchased during 1835–1877 (Rand 1948).

The late 1800s and the advent of the 20th century heralded a dramatic change in abundance and distribution of swift foxes. The arrival of settlers and the subsequent conversion of prairie habitat to dry-land agriculture, initiation of rodent-control programs, intense trapping and poisoning campaigns (wolves, *Canis lupus*, and coyotes, *Canis latrans*, were the intended targets), indiscriminate shooting, and predation by domestic dogs (Bailey 1926; Hoffman et al. 1969; Scott-Brown et al. 1987) brought about a widespread decline in numbers of swift foxes until they remained only in small isolated populations scattered within the southern and western part of its historic range (Hillman and Sharps 1978; Kahn et al. 1997). Interspecific competition between the swift fox and other canids (coyotes and red fox, *Vulpes vulpes*) and a changing prey base may have maintained this restricted distribution until the mid-1900s (FaunaWest 1991). For the northern states of Montana, the Dakotas, Wyoming, and Nebraska there exist no reports of swift foxes being either taken by trappers or seen by observers for >50 years (Kilgore 1969; Chambers 1978; Hillman and Sharps 1978; Scott-Brown et al. 1987). The last record of a swift fox in Canada was made in 1928 and the species was formally declared extirpated in 1978. Nonetheless, swift fox populations in parts of the U.S.A. began to increase in the 1950s, possibly because of changing predator-control methods, the implementation of Executive Order 11643 banning the use of chemical toxicants on all federal lands in the U.S.A. after 1972 (Egoscue 1979), and changing socioeconomic factors resulting in declining numbers of ranches and farms across the Great Plains (Floyd and Stromberg 1981).

Today, swift foxes are considered to be relatively widespread; "the present known range is constricted and disjunct, with an identified population core present in the states of Wyoming, Colorado, and Kansas, an undetermined species distribution in the adjacent states of Nebraska, Oklahoma, Texas, and New Mexico, and a restricted species distribution in South Dakota and Montana" (Kahn et al. 1997). Recovery efforts in Canada began in 1973, with the first animals being reintroduced in 1978 (Scott-Brown and Reynolds 1984; Carbyn et al. 1993). There is still concern over the status and distribution of swift foxes throughout their present and historic range. Paramount in recovery efforts, management plans, and determination of the status of swift foxes on the Great Plains is an understanding of the population dynamics of this species. Many aspects of swift fox ecology and biology remain unknown (Scott-Brown et al. 1987). The objective of this study was to document the population demographics and ecology of swift foxes on a native shortgrass prairie ecosystem in southeastern Colorado. We examined home-range size, space use and social organization, den use, survival, reproduction, dispersal, and age structure of swift foxes on the U.S. Army's Pinon Canyon Maneuver Site (PCMS) in Colorado.

Study area

The 1040-km² PCMS is located in Las Animas county, southeastern Colorado. The PCMS was acquired by the U.S.

Army in 1982 to facilitate brigade-size training of mechanized infantry units. Prior to its acquisition by the U.S. Army, the PCMS was a collection of cattle ranches where predator-control programs were managed by individual landowners. After 1983, grazing was not allowed on the site and during the period of our study the area was closed to recreational coyote hunting. Coyote removal continues on private lands adjacent to the PCMS. The climate is classified as midlatitude semiarid with mean monthly temperatures ranging from -1°C in January to 23°C in July (Andersen and Rosenlund 1991). The average annual precipitation of 32 cm fluctuates widely from year to year and among areas (U.S. Army²). Elevation varies from 1310 to 1740 m. Topography consists of broad, moderately sloping uplands, limestone hills, and sandstone canyons (U.S. Army²; Gese et al. 1988). The vegetation is dominated by shortgrass prairie and woodland communities consisting of pinyon pine (*Pinus edulis*) and one-seeded juniper (*Juniperus monosperma*) (Costello 1954; Kendeigh 1961). Grasslands constitute approximately 60% of the vegetative cover (Shaw et al. 1989), with blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), western wheatgrass (*Agropyron smithii*), galleta (*Hilaria jamesii*), and needle-and-thread (*Stipa comata*) predominating.

Methods

Capture and handling

Swift foxes were initially captured with double-door box traps (80 × 25 × 25 cm; Tomahawk Live Trap Company, Tomahawk, Wis.) baited with raw chicken (Covell 1992). Traps were deployed in the evening and checked the following morning. During periods when nighttime temperatures were below -9°C, traps were wired open to allow the fox to enter the trap but prevented the trap from closing. To recapture certain individuals for the purpose of changing their radio collar, we used a trap-enclosure system described by Covell (1992). Foxes were handled and restrained by personnel wearing thick leather gloves. Foxes were removed from the trap by placing a canvas bag over one end of the trap, opening the door, and allowing the fox to move into the bag. Once the fox was in the bag, the bag was collapsed around the animal, allowing the handler to secure its body and mouth. Once secured, the fox could then be safely removed from the bag. Each fox was weighed, sexed, aged by tooth wear and body size (Rongstad et al. 1989), ear-tagged, radio-collared, and released. Foxes were considered juvenile until the breeding season (15 December) following their birth, at which time they were considered adult. Foxes were radio-collared (Advanced Telemetry Systems, Isanti, Minn.) with a 30- to 50-g transmitter; the transmitter weighed <5% of body mass (Eberhardt et al. 1982). All radio collars included a mortality sensor that activated after 6 h without motion. No anesthesia was required during the handling of any fox.

Radiotelemetry and triangulation of locations

A portable receiver (Telonics Inc., Mesa, Ariz.) and a hand-held 4-element Yagi antenna was used to locate animals. Radiotelemetry techniques similar to those of White

²U.S. Army. 1980. Draft: Environmental impact statement for acquisition of training land in Huerfano, Las Animas and Pueblo Counties, Colorado. U.S. Army, Fort Carson, Colorado.

and Ralls (1993) and White et al. (1994) were used to determine home-range size, spatial organization, den use, dispersal, survival rate, and movement pattern. Telemetry procedures followed recommendations by White and Garrott (1990). Fox locations were triangulated using the LOCATE (Pacer, Truro, N.S.) software package with ≥ 2 bearings taken ≤ 10 min apart. Bearing angles were maintained between 20° and 160° (Gese et al. 1988) to minimize triangulation error. Telemetry error was determined with reference transmitters to be approximately $\pm 8^\circ$. We attempted to locate foxes at least once per day. Point locations were taken at ≥ 8 -h intervals and sequential locations were taken every 0.5 h. Attempts were made to point-sample all periods of the 24-h day equally. Aerial telemetry (Mech 1983) with fixed-wing aircraft and helicopters was used to locate missing animals. When foxes were located in a den, the den location and general description were recorded and the site was marked for future reference. Foxes sharing the same den concurrently were considered to belong to the same social unit.

Denning and foraging areas, spatial organization, and overlap

Daytime denning and nighttime foraging areas were determined using the CALHOME home-range analysis program (Kie et al. 1996). ArcView 3.0 (Environmental Systems Research Institute, Inc., Redlands, Calif.) was used to examine spatial organization and overlap of adjacent social units. Daytime (06:00–17:59) and nighttime (18:00–05:59) area use was estimated using the 95% adaptive kernel method (Worton 1989). Adequate location sample sizes were determined from area-observation curves (Odum and Kuenzler 1955), which showed that ≥ 15 locations within the daytime or nighttime period were required for estimating home ranges. Unless otherwise noted, animals that died or were determined to be missing were censored from the analysis for the season within which this event occurred. Three annual seasons were defined on the basis of changing energetic needs and behavioral characteristics: breeding/gestation (15 December – 14 April), pup rearing (15 April – 14 August), and dispersal (15 August – 14 December). A multiway analysis of variance (ANOVA) was used to examine individual estimates of denning- and foraging-area use and the influence of sex, age, season, year, and time; only main effects were examined. A one-way ANOVA followed by a Tukey's multiple-comparison test was used to identify differences within significant variables. The software program SYSTAT was used for statistical analysis (Wilkinson et al. 1992). Spatial organization and overlap were determined using the social group as the sampling unit; daytime and nighttime social group areas were determined by combining the locations of all individuals within the social group and using a 100% adaptive kernel estimator.

Dispersal

Dispersal has been defined as movement of an animal from one previously established home range to an area where another home range was subsequently established (Bowen 1982). We used this definition but considered only those individuals that moved > 2 km away from their previously established area of use to be "dispersers," in an effort to

eliminate those animals that were simply shifting their spatial use because of changing environmental conditions and not truly dispersing into new areas. Dispersal distances were calculated using the last known den in an individual's original home range and the first den site occupied once dispersal movement ceased, or the location of death. Seasonal rates at which resident foxes dispersed were extrapolated from daily rates using MICROMORT (Heisey and Fuller 1985), substituting the number of animals dispersing for the number of deaths (Fuller 1989). Only the number of days within the season that a fox spent as a resident were used in calculating the rate. Differences between seasonal rates of dispersal were examined with a z test (Heisey and Fuller 1985).

Reproduction

Reproductive output and social-group composition and structure were determined through observations conducted at the den site and telemetry records of foxes concurrently sharing dens. Litter size was determined visually at the time of den emergence (mid-May). We did not attempt to capture and radio-collar pups until late in the pup-rearing season (mid-August), when animals were almost full-grown and completely mobile. Thus, we were unable to assess natal mortality when pups were < 3 months old.

Survival and causes of mortality

Possible causes of mortality were determined for radio-collared foxes, using the criteria of Disney and Spiegel (1992) and Ralls and White (1995). Physical evidence at the site of mortality, such as sign (tracks and (or) scat) of other species and condition, description, and location of the carcass were recorded. Carcasses were examined for diagnostic puncture wounds, hemorrhaging, and skeletal-muscular injuries to determine cause of death. In some cases, necropsies were performed by a veterinary pathologist (Wyoming State Diagnostic Laboratory, Laramie). During necropsy, canines and incisors were removed to determine the age at time of death using cementum annuli analysis (Linhart and Knowlton 1967) performed by a commercial laboratory (Matson's Laboratory, Milltown, Mont.). Annual and seasonal survival rates were extrapolated from daily rates using MICROMORT (Heisey and Fuller 1985). Following the recommendations of White and Garrott (1990), missing individuals were censored during the season in which contact was lost, unless otherwise specified. Differences between seasonal rates of survival were examined using a z test (Heisey and Fuller 1985).

Density

Density of swift foxes was determined at 5 sites in our study area. These estimates were then pooled and averaged to calculate an overall density of swift foxes on the PCMS within each season. At each site 100% adaptive kernel estimators were constructed for areas used by individual swift foxes, using the CALHOME home-range analysis program. All point locations for an individual fox were included within a season. These polygons were then loaded into ArcView 3.0 and overlaid on a 10 km long transect over which seasonal surveys had taken place. These transects were then buffered by the average radius of areas used by swift foxes at that site. The outermost boundary of either a swift fox's area of use or the transect buffer was employed to define the total

area of actual and potential use across a site. This was done to include some measure of space that was unoccupied but believed to be suitable for swift fox use. Across even the relatively small landscape of our 10 km long transect, swift foxes were distributed unevenly in a "patchy" manner. Density was then calculated as the total number of foxes at a site divided by the total area of actual and potential use.

Factors influencing swift fox density

To examine the relationships between swift fox density and abundance of coyotes, lagomorphs, and rodents, estimates of fox density were compared with the results of surveys conducted using 3 different methods along the same five 10 km long transects on which swift foxes were monitored (Schauster 2001): a spotlight survey (Ralls and Eberhardt 1997), an activity-index survey (Allen and Engeman 1995; Allen et al. 1996), and a scent-post survey (Linhart and Knowlton 1975). The numbers of lagomorphs (included were both desert cottontails, *Sylvilagus audubonii*, and black-tailed jackrabbits, *Lepus californicus*), rodents, and coyotes encountered during a survey were recorded and their abundance was examined for its influence on estimates of swift fox density. Detailed descriptions of each survey method can be found in Schauster (2001). The relative abundance of lagomorphs seen during the spotlight survey was standardized as the number of lagomorphs observed per kilometre, whereas the relative abundance of lagomorphs, rodents, and coyotes encountered during scent-post and activity-index surveys corresponded to the average daily rate of visitation recorded. Spotlight and scent-post surveys were conducted during all seasons except breeding/gestation in 1997. The activity index was added in 1998 and the analysis is for data collected during the 3 seasons in 1998. We used the software program SYSTAT to perform regression analyses between swift fox density and relative abundance of lagomorphs, rodents, and coyotes; a stepwise regression analysis was used to identify the best fitting model.

Results

Sex and age structure

From 8 January 1997 to 14 December 1998, 94 swift foxes were captured 227 times. Ninety animals were fitted with radio collars. Fifty-three percent of all captures were made during the breeding/gestation season and 13 and 33% during the pup-rearing and dispersal season, respectively. The sex ratio of radio-collared swift foxes was 42 males (M) to 48 females (F) and was not significantly different from parity ($\chi^2_{[1]} = 0.527$, $P = 0.47$). Of the 90 radio-collared swift foxes at the time of capture, 27.8% were juveniles ($n = 25$; 15M:10F) and 72.2% were adults ($n = 65$; 27M:38F). However, as previously mentioned, all individuals encountered during the breeding/gestation season were considered adult (i.e., juveniles were classified as adults after 9 months of age). Trapping was conducted early in the pup-rearing season, before pups began to wander widely from their natal dens, therefore none were encountered in this season. Consequently, juveniles were only captured during the dispersal season. During the dispersal season in 1997 and 1998, juveniles accounted for 93.3 and 64.7% of all captures, respectively. During our study, 14 foxes were followed for >20

Table 1. Multiway ANOVA showing the influence of sex, age, season, time, and year on estimated area used by 90 swift foxes (*Vulpes velox*) on the Pinon Canyon Maneuver Site (PCMS), Colorado, 1997–1998.

Source	df	F	P
Sex ^a	1	12.79	<0.0001
Age ^b	1	0.052	0.819
Season ^c	2	4.392	0.013
Time ^d	1	183.754	<0.0001
Year ^e	1	2.961	0.086
Error	312		

^aMale or female.

^bAdult or juvenile.

^cBreeding/gestation, pup rearing, or dispersal.

^dDay (06:00–17:59) or night (18:00–05:59).

^e1997 or 1998.

months and 13 remained alive at the end of the dispersal season in 1998. Twenty foxes were followed for 12–20 months, 28 foxes for 4–12 months, and an additional 28 foxes were followed for <4 months. Foxes were only captured in open shortgrass prairie habitat, though efforts were made to capture foxes in the woodland community (to test if foxes were absent from woodland habitat; lack of sign and sightings also indicated absence).

Denning and foraging areas, spatial organization, and overlap

During our study, 13 077 locations (845 in breeding/gestation 1997; 2064 in pup rearing 1997; 2776 in dispersal 1997; 2005 in breeding/gestation 1998; 2131 in pup rearing 1998; 3256 in dispersal 1998) were obtained for radio-collared swift foxes. For the 2 years combined, the daytime and nighttime seasonal numbers of locations for foxes that met the minimum requirement for estimating home ranges were 25.2 ± 7.3 and 21.7 ± 4.7 ($\bar{x} \pm \text{SE}$) for the breeding/gestation season, 33.9 ± 8.8 and 25.1 ± 6.2 for the pup-rearing season, and 38.8 ± 10.9 and 30.4 ± 7.8 for the dispersal season. The multiway ANOVA showed that 39% of the variation in size of area used was explained by the significant variables of sex, season, and time ($r = 0.627$). Seasonal daytime and nighttime area use averages were pooled across years, as the multiway ANOVA showed only a slight and insignificant yearly effect (Table 1). The estimated seasonal area used was 2.8 ± 3.0 km² during the day and 9.4 ± 4.9 km² during the night for the breeding season, 2.5 ± 1.8 and 6.6 ± 4.3 km² during the day and night, respectively, for the pup-rearing season, and 2.7 ± 2.2 and 7.6 ± 3.6 km² during the day and night, respectively, for the dispersal season. Area-use estimates varied across time, sex, season, and year (Table 2). Estimated areas of daytime and nighttime use were 2.7 ± 2.3 and 7.5 ± 4.2 km² for adult foxes and 3.0 ± 2.1 km² and 8.4 ± 3.9 km² for juveniles during the day and night, respectively.

Daytime and nighttime seasonal use areas overlapped between adjacent swift fox social groups (Figs. 1 and 2). Spatial overlap was most pronounced at night, suggesting that nighttime foraging areas were commonly used by members of different social groups. Overlap of daytime denning areas appeared to be less conspicuous and restricted, suggesting

Table 2. Estimated area use by 90 swift foxes on the PCMS, 1997–1998, showing the influence of sex, time, and season.

Year and season	Males			Females		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Estimated daytime home range						
1997						
Breeding/gestation	3.30	3.41	9	2.82	1.82	7
Pup rearing	3.88	1.91	14	2.63	1.46	15
Dispersal	3.12	2.33	16	2.96	1.81	18
1998						
Breeding/gestation	3.19	4.38	10	2.15	1.74	11
Pup rearing	2.28	1.49	15	1.53	1.70	18
Dispersal	2.50	1.86	13	2.43	2.53	20
Estimated nighttime home range						
1997						
Breeding/gestation	4.87	—	1	4.96	—	1
Pup rearing	8.17	4.14	14	6.41	4.86	15
Dispersal	8.81	2.36	15	7.71	3.21	16
1998						
Breeding/gestation	11.54	5.30	12	8.12	3.89	12
Pup rearing	7.78	4.63	13	4.71	3.17	18
Dispersal	8.07	3.62	14	6.41	3.87	22

that these areas were not commonly shared and may be to some degree exclusive, which is indicative of territoriality. We found a significant difference in the amount of spatial overlap between adjacent pairs for daytime and nighttime use areas ($t = 9.105$, $P < 0.001$). Overlap between pairs of adjacent social groups was 0.08 ± 0.12 (range 0–0.53) during the day and 0.22 ± 0.24 (range 0–0.90) during the night for the breeding season ($t = 5.572$, $P < 0.001$), 0.08 ± 0.16 (range 0–0.67) during the day and 0.20 ± 0.19 (range 0–0.90) during the night for the pup-rearing season ($t = 7.303$, $P < 0.001$), and 0.120 ± 0.24 (range 0–1.0) for the day and 0.20 ± 0.19 (range 0–0.82) for the night during the dispersal season ($t = 3.837$, $P < 0.001$). A multiway ANOVA showed no significant effect due to season or year on the amount of overlap between adjacent social units during either daytime or nighttime.

Den use

The number of dens used did not appear to vary with season or sex. Foxes used the lowest number of dens during the breeding/gestation season and the highest number during the pup-rearing season. Over both years, the number of dens used was 4.97 ± 2.55 ($n = 30$) for the breeding/gestation season, 7.26 ± 2.75 ($n = 66$) for the pup-rearing season, and 5.84 ± 2.22 ($n = 62$) for the dispersal season. Adult females used 6.15 ± 2.53 ($n = 89$) dens per season, while males used 6.42 ± 2.81 ($n = 69$). However, when the numbers of dens used are compared across sex and season, males seemed to use a larger number of dens only in the pup-rearing season. Adult females used 5.06 ± 2.57 ($n = 16$) dens during the breeding/gestation season, 6.78 ± 2.61 ($n = 36$) during the pup-rearing season, and 6.00 ± 2.32 ($n = 37$) during the dispersal season, whereas adult males used 4.86 ± 2.63 ($n = 14$), 7.83 ± 2.84 ($n = 30$), and 5.60 ± 2.08 ($n = 25$) dens, respectively, during the same seasons.

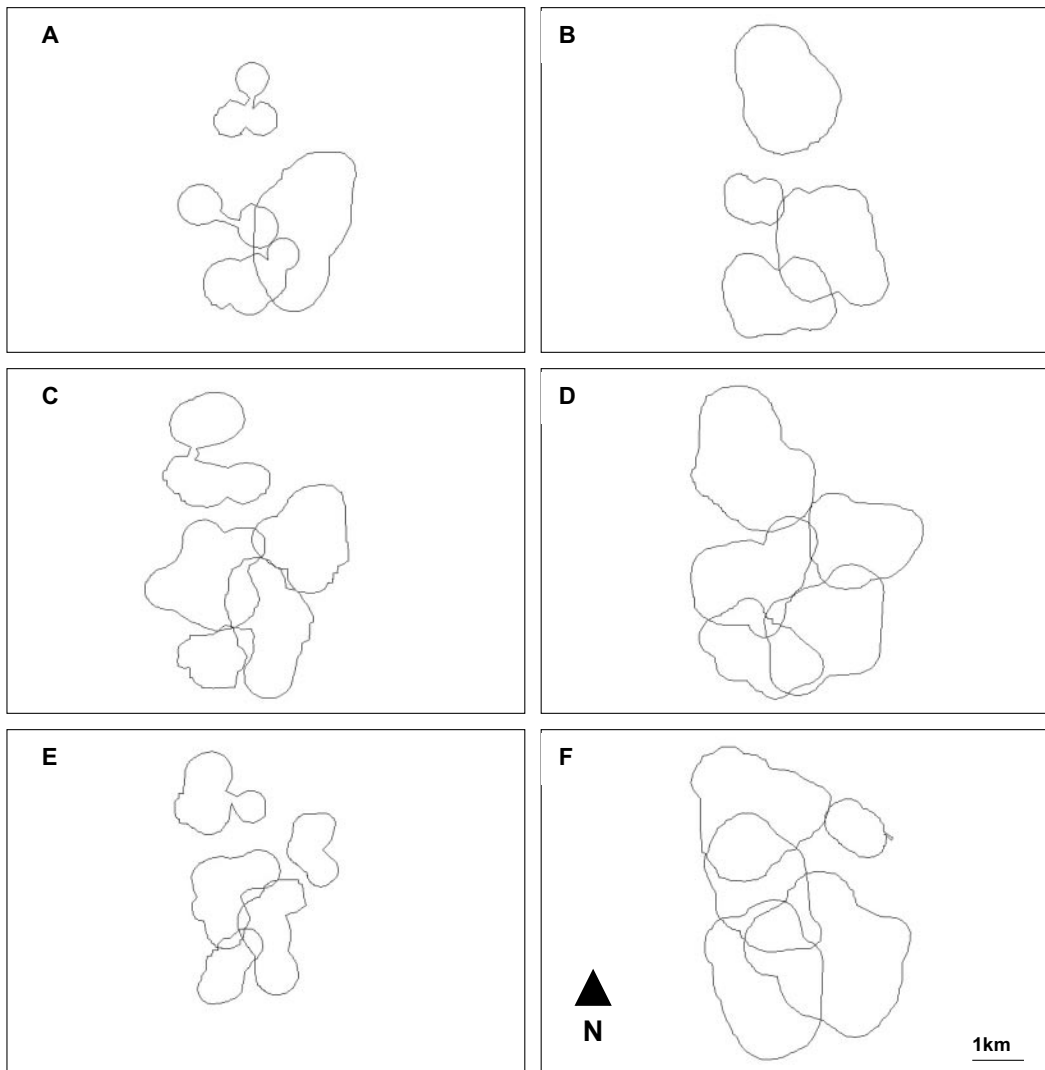
Dispersal

During our study we followed the movements of 13 animals as they dispersed. In some cases, dispersal started in one season and continued into the next. Of 6 adults (2M:4F), 5 began dispersal movements during the breeding/gestation season (3 in 1997 and 2 in 1998), whereas only 1 adult female dispersed in the 1998 dispersal season. In 1 case during the breeding/gestation season of 1997, movement of an adult female seemed to commence shortly (about 14 days) after the death of her mate. One adult in the breeding/gestation season of 1998 actually started dispersing as a juvenile in the previous dispersal season and continued moving in the breeding/gestation season after she was considered an adult. Total distance moved during dispersal was 11.9 ± 8.79 km (range 4.99–29.0 km) and the total number of days spent dispersing before a new area of use was established was 28.3 ± 20.8 (range 6–67 days). All adults that dispersed remained alive and established new denning and foraging areas. In contrast, only 3 (37.5%) of 8 juveniles (6M:2F) remained alive and established new denning and foraging areas. For juvenile dispersers, the total distance moved was 12.6 ± 3.17 km (range 8.4–15.9 km), while the total number of days spent dispersing was 32.1 ± 13.7 (range 15–50 days). In general, dispersal rates for adults peaked during the breeding/gestation season, decreasing considerably, although not significantly, during the pup-rearing and dispersal seasons (Table 3). A significant year effect on dispersal rates of juveniles during the dispersal season was found ($z = 1.87$, $P < 0.05$).

Reproduction

Of 15 radio-collared females that survived through the breeding/gestation season of 1997, 93.3% were believed to be paired and breeding females. These females composed 13 of 18 suspected parental social units, 16 of which were suspected to comprise or confirmed as comprising 1 adult

Fig. 1. Home-range overlap and spatial organization of 4–5 swift fox (*Vulpes velox*) social units during daytime in the breeding/gestation season (A), nighttime in the breeding/gestation season (B), daytime in the pup-rearing season (C), nighttime in the pup-rearing season (D), daytime in the dispersal season (E), and nighttime in the dispersal season (F) in 1997 on the Pinon Canyon Maneuver Site (PCMS) in Colorado.



male and 1 adult female. In the other 2 cases, the trios were made up of 2 females with 1 male or 2 males with 1 female. Through visual observation at suspected natal den sites we documented that 13 of these 18 (72%) parental social units sired litters. The observed litter size for 1997 was 2.1 ± 0.8 pups (range 1–3 pups). Of this cohort, we later trapped 12 individuals and found the sex ratio to be 6M:6F. In 1998, of 25 radio-collared females surviving through the breeding/gestation season, 84% were believed to be paired and breeding females. These females composed 23 of 25 suspected social units. In 1998 we had at least 5 social units that were trios, 3 of which were made up of 2 females and 1 male. In addition, we suspected that 1 social unit was a quartet consisting of 2 females and 2 males. In this case it appeared that 2 juveniles had remained in their natal territory and were contributing to the following year's reproductive effort by helping to raise the current litter. Through visual observation we were able to document 12 of 25 (48%) parental social units siring litters. The observed litter size for 1998 was 2.4 ± 1.2 pups (range 1–5 pups). Of this 1998 cohort, we were

later able to trap and radio-collar 11 individuals, and found the sex ratio of juveniles to be 9M:2F ($\chi^2_{[1]} = 0.035$, $P = 0.82$). Owing to the presence of radio-collared female pups from 1997, we were also able to document swift foxes breeding during their first breeding/gestation season. Twelve of 13 (92%) female pups from the 1997 cohort were believed to be paired, and in 6 cases (46%) we documented that breeding had occurred. The litter size for females breeding in their first year (1998) was 2.0 ± 1.2 pups (range 1–4 pups).

Survival rates

Overall survival rates during our study varied between seasons and years (Table 4). Annual survival rates for all radio-collared foxes of known fate were 0.75 ($n = 53$) and 0.55 ($n = 80$) for 1997 and 1998, respectively ($z = 1.85$, $P < 0.05$). Annual survival rates for residents were 0.88 ($n = 53$) and 0.57 ($n = 80$) for 1997 and 1998, respectively ($z = 8.54$, $P < 0.001$). Seasonal rates of survival for resident males and females varied between adults and juveniles (Table 5). Sur-

Fig. 2. Home-range overlap and spatial organization of 6 swift fox social units during daytime in the breeding/gestation season (A), nighttime in the breeding/gestation season (B), daytime in the pup-rearing season (C), nighttime in the pup-rearing season (D), daytime in the dispersal season (E), and nighttime in the dispersal season (F) in 1998 on the PCMS.

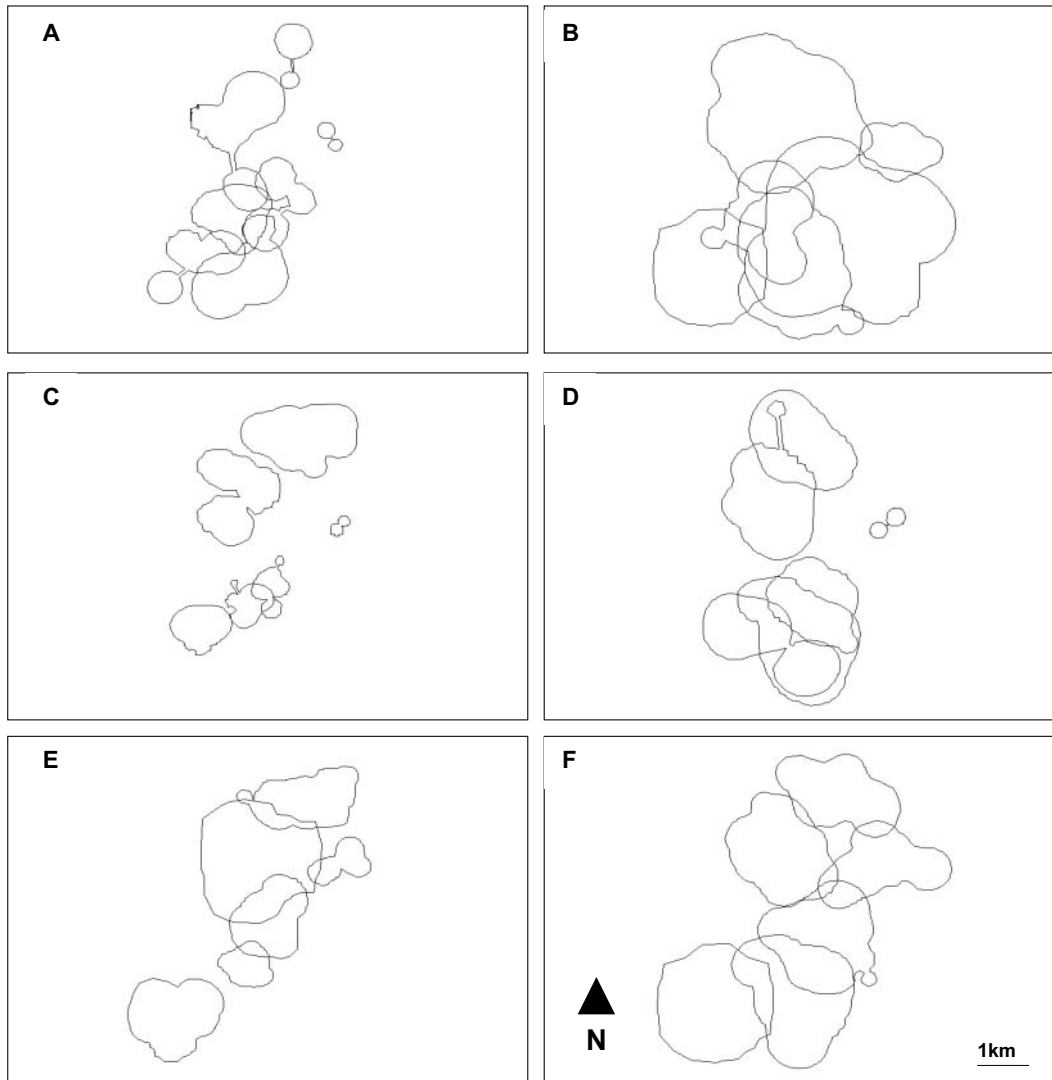


Table 3. Dispersal rates of swift foxes of known fate on the PCMS, 1997–1998.

Year and season	Adults			Juveniles		
	Rate	Variance	<i>n</i> ^a	Rate	Variance	<i>n</i> ^a
1997						
Breeding/gestation	0.12	0.00398	3			
Pup rearing	0.03	0.00106	1			
Dispersal	0	—	0	0.31	0.0223	3
1998						
Breeding/gestation	0.07	0.00168	3			
Pup rearing	0.03	0.00055	1			
Dispersal	0.03	0.00061	1	0.74	0.0304	4

^aNumber of foxes dispersing during that interval.

vival rates for adult males varied significantly between the pup-rearing season in 1997 and all seasons within 1998 and between the dispersal season in 1997 and all seasons within 1998 (all $z > 1.88$, all $P < 0.05$). Survival rates for adult females differed between the following seasons: breeding/gestation 1997 and dispersal 1997, breeding/gestation 1997 and breeding/

gestation 1998, pup-rearing 1997 and breeding/gestation 1998, breeding/gestation 1998 and pup-rearing 1998, and breeding/gestation 1998 and dispersal 1998 (all $z > 1.78$, all $P < 0.05$). For adults, sex influenced survival rates during the following seasons: dispersal 1997, pup-rearing 1998, and dispersal 1998 (all $z > 1.74$, all $P < 0.05$). Age class was a

Table 4. Survival rates for swift foxes of known fate on the PCMS, 1997–1998.

Year and season	Rate	Variance	95% confidence interval	
			Lower	Upper
1997				
Breeding/gestation	0.92	0.00277	0.82	1.0
Pup rearing	0.97	0.00104	0.91	1.0
Dispersal	0.90	0.00205	0.82	1.0
1998				
Breeding/gestation	0.80	0.00363	0.69	0.92
Pup rearing	0.87	0.00256	0.77	0.97
Dispersal	0.83	0.00292	0.73	0.96

significant factor for females during both dispersal seasons (both $z > 1.90$, both $P < 0.05$); however, this result should be weighed against the small sample of radio-collared juvenile females. Overall survival rates for dispersing foxes (Table 6) were considerably lower than those for resident foxes. Among dispersers, adults fared better than juveniles during dispersal, but the difference was significant only during the 1998 dispersal season ($z = 1.66$, $P < 0.05$); however, this result could be due to the small sample of dispersing foxes.

In 30 cases, age at time of death was determined by cementum annuli analysis (Fig. 3). In 13 cases (43.3%), foxes died when <3 years old (range 0–3 years old). In addition, 8 foxes (26.6%) were found to have survived for >5 years (range 5–7 years old). Only 7 foxes (23.3%) were found to have died between 3 and 5 years of age.

Causes of mortality

We documented 35 swift fox mortalities during the study. In 22 of the 35 (62.8%) cases, predation was determined to be the cause of death, in 10 cases (28.6%) the cause could not be determined and was classified as unknown, in 2 cases (5.7%) capture-related injuries and (or) stress could not be ruled out, and 1 swift fox (2.8%) was found drowned in a cattle-watering tank (the sides were too high for escape). Coyotes were considered the probable predator in 18 (81.8%) of the predation mortalities. In 2 additional cases (9%) it could not be determined whether mortality was caused by coyotes or bobcats (*Felis rufus*). In 2 other cases (9%) avian predation was determined to be the most likely cause of death.

Density

Fox density varied seasonally from $0.179 \pm 0.095/\text{km}^2$ during the 1997 pup-rearing season to $0.301 \pm 0.180/\text{km}^2$ during the 1998 dispersal season (Table 7). Overall, seasonal densities increased between 1997 and 1998. This may have been due to our improved understanding of where foxes were as the study progressed and not to an actual increase in density. It was difficult to assess whether vacant, but suitable, areas were unoccupied during the first seasons of our study and swift foxes dispersed into these areas during the pup-rearing and dispersal seasons of 1997, or animals were

there from the beginning and were simply missed during our earlier trapping efforts. However, these areas were routinely traveled during our normal research activities and swift foxes and (or) active denning sites were not casually seen at first. Only later, during the pup-rearing and dispersal seasons of 1997, did we begin to record observations of uncollared animals in these areas and these animals were subsequently radio-collared during our next trapping effort.

Factors influencing swift fox density

Swift fox density was negatively correlated with the relative abundance of lagomorphs encountered during spotlight ($r = -0.59$, $P = 0.002$) and scent-post surveys ($r = -0.47$, $P = 0.017$). In contrast, swift fox density was positively correlated with rodent abundance from activity-index surveys (Fig. 4; $r = 0.481$, $P = 0.069$). As in the spotlight and scent-post surveys, the relative abundance of lagomorphs and coyotes determined from activity-index surveys was negatively correlated with swift fox density (Fig. 4). Stepwise regression analysis of the activity-index data (i.e., relative abundance of coyotes, lagomorphs, and rodents) versus swift fox density identified the best fitting model as that which included the lagomorph and coyote abundance indices only ($r = 0.76$, $P = 0.006$). The model showed that swift fox density = $0.493 - 0.009(\text{coyote abundance}) - 0.004(\text{lagomorph abundance})$.

Discussion

Our finding of parity in the sex ratio of radio-collared foxes is consistent with earlier work on the PCMS (Rongstad et al. 1989; Covell 1992) and other studies carried out in northern Colorado (Fitzgerald et al.³; Cameron 1984) and Kansas (Zumbaugh 1984; Jackson and Choate 2000). However, Rongstad et al. (1989) and Covell (1992) both reported a higher number of juveniles captured during their studies: 18 of 42 (43%) and 59 of 109 (54%), respectively. In addition, Fitzgerald et al.³ found that juveniles composed 45% of all captures on the Pawnee National Grassland in northern Colorado. These findings, however, are likely an artifact due to capture goals, strategies, and (or) seasons.

Several studies have reported estimates of areas used by swift and San Joaquin kit foxes (*Vulpes macrotis*), principally in the form of home-range sizes (Morrell 1972; Hines 1980; Fitzgerald et al.³; Sharps and Whitcher 1984; Hines and Case 1991). Overall, home-range sizes reported for swift foxes are highly variable, ranging from 1.6 to 3.2 km² (Sharps and Whitcher 1984) during the spring in South Dakota to 17.3 km² for adult males in Nebraska (Hines 1980). As recently as Kahn et al. (1997), swift fox research has been conducted under the assumption that “there is no evidence from studies in the literature that swift fox exhibit signs of territoriality.” Most authors, however, have summed all locations across the 24-h period in their estimates of home-range size. Thus, any exclusive spatial-area use that may have a temporal aspect (i.e., daytime locations that may delineate core denning areas) may be confounded by larger foraging areas that are shared among adjacent social units. Rongstad et al. (1989) first noted that core activity areas (using either

³J.P. Fitzgerald, R.R. Loy, and M. Cameron. 1983. Status of swift fox on the Pawnee National Grassland, Colorado. Unpublished report, University of Northern Colorado, Greeley.

Table 5. Survival rates for resident swift foxes of known fate on the PCMS, 1997–1998.

Year and season	Adults			Juveniles		
	Rate	Variance	<i>n</i> ^a	Rate	Variance	<i>n</i> ^a
Resident males						
1997						
Breeding/gestation	0.84	0.0103	16			
Pup rearing	1.0	—	16			
Dispersal	1.0	—	15	1.0	—	7
1998						
Breeding/gestation	0.85	0.00639	27			
Pup rearing	0.77	0.00834	22			
Dispersal	0.77	0.00988	19	0.44	0.0652	8
Resident females						
1997						
Breeding/gestation	1.0	—	18			
Pup rearing	0.94	0.00348	18			
Dispersal	0.83	0.00772	18	1.0	—	7
1998						
Breeding/gestation	0.75	0.00768	31			
Pup rearing	0.96	0.00178	26			
Dispersal	0.96	0.00159	28	0.13	0.0720	3

^aNumber of radio-collared foxes monitored during that season.

Table 6. Survival rates for adult and juvenile dispersing swift foxes of known fate on the PCMS, 1997–1998.

Year and season	Rate	Variance	95% confidence interval		<i>n</i> ^a
			Lower	Upper	
Dispersing adults					
1997					
Breeding/gestation	1.00	—	—	—	3
Pup rearing	1.00	—	—	—	1
Dispersal					
1998					
Breeding/gestation	0.03	0.01270	0.00	1.00	3
Pup rearing	1.00	—	—	—	1
Dispersal	1.00	—	—	—	1
Dispersing juveniles					
1997					
Breeding/gestation					
Pup rearing					
Dispersal	0.00	0.00016	0.00	1.00	3
1998					
Breeding/gestation					
Pup rearing					
Dispersal	0.39	0.13500	0.06	1.00	4

^aNumber of foxes dispersing during that season.

daytime locations or a 50% kernel estimator) were almost exclusive of one another, suggesting some degree of territoriality. White and Ralls (1993) and White et al. (1994) demonstrated that San Joaquin kit foxes are territorial, when previously they were assumed to be nonterritorial (Morrel 1972; McGrew 1977). Our results concur with the finding of territoriality of den areas by Rongstad et al. (1989).

Mean litter size, based on counts of pups at the time of emergence, was slightly lower than previously reported for

swift foxes in the PCMS; Rongstad et al. (1989) and Covell (1992) reported a litter size of 3.4 and 3.8 pups, respectively. In northern Colorado, Fitzgerald et al.³ reported a mean litter size of 3.6 pups. In contrast to Zumbaugh (1984), who reported that only 10% of juveniles breed in their first year, we found a much higher proportion (>90%) to have bred, and documented that at least 50% of these yearlings raised litters. If this indicates that swift foxes share the canid ability to rebound quickly from low numbers through increased

Fig. 3. Age structure of swift fox mortalities determined from cementum annuli, PCMS, 1997–1998.

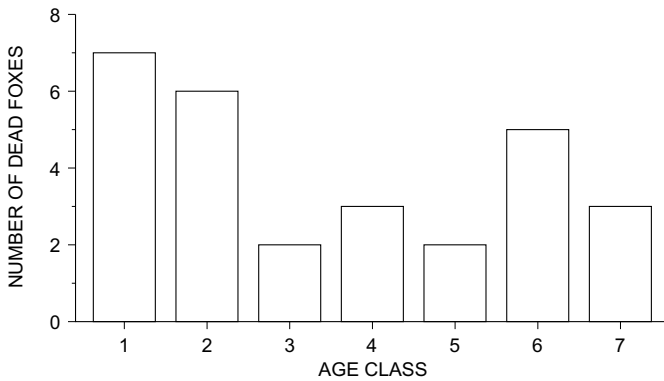


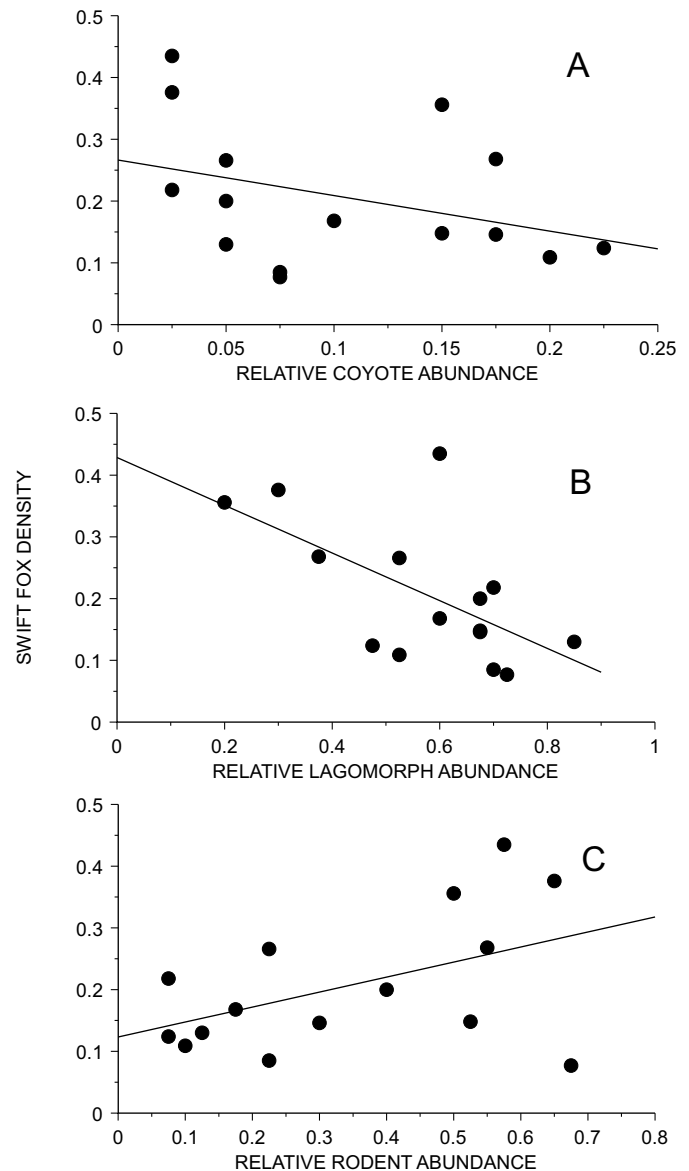
Table 7. Density estimates for swift foxes on the PCMS, 1997–1998.

Year and season	No. of foxes/km ²	
	Mean	SE
1997		
Breeding/gestation	0.193	0.058
Pup rearing	0.179	0.095
Dispersal	0.193	0.081
1998		
Breeding/gestation	0.242	0.121
Pup rearing	0.201	0.085
Dispersal	0.301	0.180

breeding among yearlings (e.g., coyotes, Gier 1968; Knowlton et al. 1999), especially when environmental conditions are favorable, it may bode well for the recovery and successful management of this species. Worthy of mention with respect to reproductive effort and den abandonment is the observation that adult males routinely abandoned the natal den earlier than their female mates. The pup-rearing season was the only season in which males used more dens than females, perhaps because of the conflict between the needs of a lactating mother with dependent pups and the space limitations of an underground den. The female usually abandoned the natal den within a couple weeks of the adult male and was then routinely located with him in a separate den from the pups. In the short time between den emergence and pup independence, den abandonment (with no pup abandonment) was more likely, owing to limited space and resultant overcrowding from growing pups. The assumption that den abandonment is related to rising levels of ectoparasite infestation (Kilgore 1969) is as yet unconfirmed.

There is no shortage of research showing that predation, mainly from coyotes, is one of the major sources of mortality within swift fox populations (Rongstad et al. 1989; Covell 1992; Carbyn et al. 1993; Fitzgerald et al.⁴; Sovada et al. 1998; Kitchen et al. 1999); our results provide further corroboration. However, the annual survival rates in our study appear to be some of the highest reported in the literature

Fig. 4. Relationships between swift fox density and relative abundance of coyotes (A), lagomorphs (B), and rodents (C) on the PCMS.



(Rongstad et al. 1989; Covell 1992; Sovada et al. 1998). Perhaps improved environmental conditions on the PCMS have elevated fox survival rates since the earlier swift fox research was conducted. Kitchen et al. (2000) found significantly smaller coyote home ranges and higher lagomorph counts during fieldwork in the 1990s than were found during work conducted on the same site in the 1980s, indicating a higher prey base and coyote density. Changes in canid survival rates and density in relation to increasing prey biomass have been reported (Keith 1983; Fuller 1989; Knowlton et al. 1999).

Although much has been written about dispersal in the canid family (Bekoff 1977; Gese and Mech 1991; Waser

⁴J. Fitzgerald, B. Roell, L. Dent, M. Schafer, L. Irby, J. Eussen, and D. Finley. 1996. Population dynamics of the swift fox (*Vulpes velox*) in northern Colorado. Unpublished report, University of Northern Colorado, Greeley.

1996), definitive conclusions about the physiological and behavioral mechanisms that cause dispersal have remained elusive. One problem is that dispersal is a relatively infrequent event whose timing can be sudden and unpredictable. In the case of swift foxes, little has been reported in the literature other than distances moved, how long movement took, and when it commenced (Fitzgerald et al.³; Sharps and Whitcher 1984; Carbyn and Killaby 1989; Rongstad et al. 1989; Covell 1992). Unfortunately, we can do little better. A few observations are worth noting, however. First, 2 of our adult dispersers in 1997 were seen to disperse during the breeding/gestation season in response to loss or lack of a mate; this was similarly observed on the PCMS by Rongstad et al. (1989). Second, juvenile males generally dispersed earlier in the dispersal season than females. Juvenile females typically dispersed later in the dispersal season or during the first breeding/gestation season when they were considered adults. Harris and White (1992) and Harris and Trehwella (1988) suggested that dispersal of juvenile male red fox cubs may be related to affiliative and (or) agonistic interactions within the social group and to the cubs' social development, while juvenile females' dispersal may have different causes and occur at a later point in their development. Covell (1992) noted a higher reproductive output in breeding pairs with helpers. Von Schantz (1984) noted that the presence of additional females in red fox social groups was a response to a resource surplus and high territory quality rather than a result of intergroup social relationships. Perhaps the breeding pair adopts a "wait-and-see" attitude toward juvenile females (and possible following-year helpers) until the scarcity of resources that accompanies winter conditions during the breeding season is realized.

In northern Colorado, swift fox densities have been found to be 0.2–0.4/km² in poor habitats and 0.7–1.1/km² where better conditions exist (Fitzgerald et al.³). On the PCMS, Rongstad et al. (1989) documented densities of 0.07 foxes/km² during 1986–1987, and found that the swift fox population was declining as a result of high coyote predation rates and low recruitment. After a period of coyote removal on the southwestern third of the site from 1987 to 1988 (Gese and Rongstad 1989), Covell (1992) found that densities had increased to 0.15 foxes/km² (1989–1991), with apparent population stability. Even though our density estimates were the highest reported for the PCMS, our survey data indicated that the abundance of lagomorphs and coyotes was negatively correlated with swift fox density. High coyote density may contribute to increased swift fox mortality, and thus affect overall population stability. However, several studies on kit foxes (Egoscue 1975; O'Neal et al. 1987; Zoellick et al. 1987) have shown that lagomorph abundance has a positive influence on fox densities. However, on the PCMS, black-tailed jackrabbits were associated with shrub–grassland areas with dense areas of bigelow sage (*Artemisia bigelovii*), sand sagebrush (*A. filifolia*), winterfat (*Ceratoides lanata*), fourwing saltbush (*Atriplex canescens*), and black greasewood (*Sarcobatus vermiculatus*). Dense shrub communities are generally marginal habitat for swift foxes. In addition, Kitchen et al. (1999) found the percent volume of lagomorphs (both jackrabbits and cottontails) in coyote scats to be an important food item throughout the year, whereas swift foxes ate relatively few jackrabbits and relied on cottontails as an im-

portant food resource only at specific times during the year. Earlier research carried out on the PCMS by Gese et al. (1988) also showed that coyotes preferentially used these shrub–grassland habitats. On the PCMS, lagomorph abundance (i.e., jackrabbit numbers) may reflect not only less suitable habitat for swift foxes but also areas of increased coyote presence and activity.

Recently, the population dynamics of San Joaquin kit foxes have been shown to be strongly influenced by precipitation and its subsequent effect on food supply (White and Garrott 1999; Dennis and Otten 2000). Data from a local National Oceanic and Atmospheric Administration Automated Weather Observing Site showed that although the work of Rongstad et al. (1989) was conducted during a 2-year period of above-average rainfall, it followed a period of less than normal precipitation. Perhaps a declining food base also contributed to the low densities observed by Rongstad et al. (1989). For 5 years preceding our study, average precipitation on the PCMS was 37.0 cm (i.e., 5 cm above average), and thus our results may reflect a period of increasing food supply and improving conditions. Rainfall on the shortgrass prairies of southeastern Colorado and its influence on swift fox population dynamics have not been investigated. It does seem plausible that the unpredictability of storms on the shortgrass prairie and their typically localized nature could have a strong influence on the population dynamics of swift foxes on relatively small spatial scales.

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