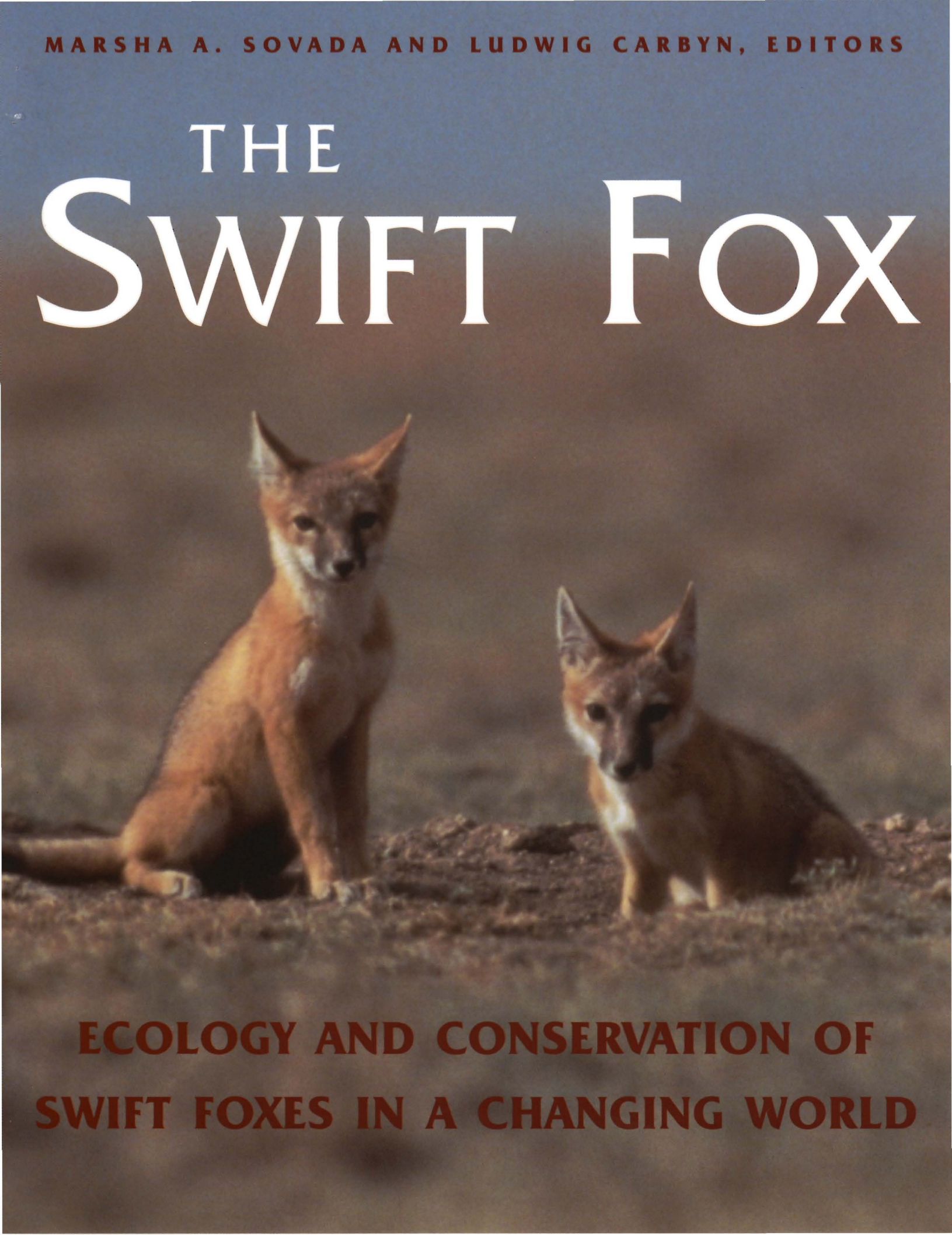
MARSHA A. SOVADA AND LUDWIG CARBYN, EDITORS

THE SWIFT FOX



ECOLOGY AND CONSERVATION OF SWIFT FOXES IN A CHANGING WORLD

Home Range, Habitat Use, Litter Size, and Pup Dispersal of Swift Foxes in Two Distinct Landscapes of Western Kansas

■ **Marsha A. Sovada, Christiane C. Slivinski, Robert O. Woodward and Michael L. Phillips**

Abstract: We radiocollared 41 adult swift foxes (Vulpes velox) *and 25 pups to investigate home range size during breeding/pup-rearing (March–August), use of habitats, and pup dispersal for populations in 2 distinctly different landscapes in western Kansas. One study area was dominated by dryland crops (76%; hereafter Cropland Area), the other was predominantly pasture (87%; hereafter Rangeland Area). We did not detect difference in home range size of individual foxes (P = 0.58) or families (P = 0.60) between the 2 landscapes. The 95% adaptive kernal estimates (ADK) of home range size (breeding/pup-rearing period) of adult foxes averaged 15.9 km² (n = 21, SE = 1.6) overall. Core areas of use, as defined by the 50% ADK estimates ($\bar{x}$ = 2.2 km², SE = 0.3), were also similar in size between the 2 landscapes (P = 0.74). Family home range size averaged 17.8 km² (n = 8, SE = 2.1). There was minimal overlap between home ranges of adjacent fox families (16%) and core areas were nearly exclusive. Swift foxes primarily used fallow/stubble and small grain fields in the Cropland Area and grasslands in the Rangeland Area. Mean litter size of pups observed at emergence from dens was 3.1 (n =11, SE = 0.4). Five of 10 monitored pups dispersed (i.e., did not return to family home range). Average dispersal distance was 14.7 km (SE = 4.8). The average date that pups first moved from their family home range was 26 October (range = 1 Oct–3 Dec). The average dispersal date was 5 November (range = 1 Oct–27 Dec).*

Knowledge of swift fox home range and habitat use is essential to understanding their population dynamics and habitat features necessary to sustain populations. Variation in home range size across a landscape might reflect the capacity of the habitat to support a population (Macdonald 1983). Optimal habitat for swift foxes is believed to be shortgrass and mixed-grass prairie in gently rolling to level landscapes (Cutter 1958, Kilgore 1969, Hillman and Sharps 1978, Hines 1980). However, populations of swift foxes are occasionally found in what is considered atypical landscapes for swift foxes, such as mixed agricultural areas (Kilgore 1969, Hines 1980), and sagebrush steppe and shortgrass prairie transition (Olson and Lindzey 2002). Favorable areas for swift foxes provide holes for shelter and protection (Scott-Brown et al. 1987) and have low potential for contact with humans and predators, such as coyotes (*Canis latrans*, Hillman and Sharps 1978).

Many factors likely were responsible for the decline in swift fox numbers, including inadvertent poisoning (aimed at gray wolves [*Canis lupus*]), intensive trapping, and increasing numbers of predators (Sovada et al. 1998). Modification of native grassland and the associated decline in prey species are also implicated in the decline of swift foxes (Egoscue 1979). European settlers converted large expanses of prairie to cropland; less conversion occurred in drier shortgrass prairie than tall or mixed-grass prairies (Samson and Knopf 1994, Samson et al. 1998). Replacement of native grazers such as American bison (*Bison bison*) and prairie dogs (*Cynomys* spp.) by domestic cattle, which have different grazing impacts on the prairies (Schwartz and Ellis 1981), might also have affected swift foxes and their prey. Habitat alteration likely caused increased risk of predation on swift foxes where escape habitat was destroyed and could have affected spacing patterns of swift foxes, thus influencing their encounters with predators such as coyotes. Furthermore, the number of coyotes (primary predator of swift foxes) has increased since presettlement which is directly related to human activity (Johnson and Sargeant 1977, Sovada et al. 1998).

In western Kansas swift foxes occupy areas with large expanses of gently rolling grasslands, as well as extensive areas of cultivated land. This successful occupation of a mostly cultivated landscape is unusual in the current distribution of swift foxes in North America (*see* Swift Fox Conservation Team 1997). Fox and Roy (1995) suggested that dryland winter wheat/fallow rotation sustains swift foxes in this intensively cropped region of Kansas. It is not clear why mixed agricultural areas in other parts of the swift fox distribution are not supporting populations of swift foxes.

We had an opportunity to study swift fox ecology in their traditional grassland landscape and adjacent areas of highly cultivated cropland. Our objectives were to estimate home range size and evaluate habitat use by swift foxes in these 2 strikingly different landscapes in western Kansas. We wanted to determine if foxes were behaving and living differently in the 2 landscapes. That is, do foxes in cropland compensate in some way for this apparent

stark environment in which they reside. Additionally, we report litter sizes, timing of dispersal, and dispersal distances for pups from both landscapes.

Study Areas

We studied populations of swift foxes on two 259-km^2 study areas in Sherman and Wallace counties of western Kansas during March 1996 through January 1997. The Cropland Area was relatively flat, approximately 76% cultivated fields (Fig. 1). Most fields were in a dryland winter wheat–fallow rotation; others were irrigated corn and sunflowers, milo, and sorghum. Ten percent of the land was enrolled in the U.S. Department of the Agriculture's Conservation Reserve Program (CRP) and seeded primarily to big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicium virgatum*). There were 125 km of roads and 20 occupied residences. The Rangeland Area was characterized by rolling hills, approximately 87% moderately to heavily grazed native pasture. Primary grasses included buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and hairy grama (*B. hirsuta*). A few cropland fields (wheat, sunflowers) were interspersed in the Rangeland Area. There were 66 km of roads and 10 occupied residences. Both study areas had few trees (<1% of landscape).

Annual precipitation was 50.5 cm (long-term average = 46.2 cm) and occurred primarily in spring and summer. Temperatures were characteristic of continental climate, with January the coldest month ($\bar{x}$ = -2.6°C, long-term average = -2.0°C) and July the warmest ($\bar{x}$ = 23.1°C; long-term average = 24.2°C; National Climate Data Center 1997).

Methods

We used 81-cm× 25-cm× 30-cm live traps to capture adult swift foxes beginning in March 1996. Traps were modified to a smaller mesh (2.5 × 2.5 cm) to reduce chance of injury to captured foxes. Traps first were placed within 3 randomly selected 10-km^2 blocks in each study area; blocks were separated from each other and study area boundaries by ≥1.6 km. Trapping effort expanded outward from the 10-km^2 blocks as capture of unmarked foxes within a block subsided. Our goal was to radiocollar 25 adult swift foxes in each study area. With the same traps, we began capturing juvenile foxes in August 1996 near dens of radiocollared adults. We attempted to capture as many pups as possible. Numbered eartags and a 39-g radiocollar detectable up to 3.2 km and containing a mortality sensor were attached to each captured swift fox. Gender, reproductive status (e.g., lactating), and general health were recorded for each fox. All foxes (adults and pups) alive in late January 1997 were recaptured and collars were removed. We noted any fur wear or abrasion caused by collars for all recaptured foxes.

We monitored radiocollared adult swift foxes from March 1996 through January 1997 from vehicles equipped with null-peak directional antennas. Foxes were systematically monitored for ≥4 nights every 2 weeks on each study area, and never on consecutive nights on the same area. We monitored foxes in two 6-hr nighttime periods, approximately 1900–0100 hr and 0100–0700 hr, with equal number of sampling periods in each 2-week period. Our goal was to locate each monitored fox 2 or 3 times in a 6-hr period, with locations for individual foxes ≥2 hours apart. We also attempted to obtain daytime (0700-1900 hr) locations of all adults approximately every 3 days, not coinciding with nighttime monitoring. When a den location was determined, we recorded the habitat the den was in. We attempted to locate each radiomarked pup 2 or 3 times per week.

Permanent tracking stations were established at every road/trail intersection, along roads at 0.4 km intervals, and at areas of higher elevation affording improved reception. Universal Transverse Mercator (UTM) coordinates were predetermined for each station with a Precision Lightweight Geographic Positioning System receiver (Rockwell International, Cedar Rapids, Iowa). Each fox location was estimated from bearings taken in rapid succession from 2–4 permanent tracking stations by one observer. To reduce error of the bearing angle, orientation of the tracking vehicle was determined at each station using a compass and the bearing was adjusted accordingly. Animal locations and 95% error ellipses were estimated using LOCATE II software (Nams 1990). Locations based on 2 bearings were estimated using a fixed standard deviation determined for each crew member based on field tests given early in the field season.

To reduce error in telemetry locations, we eliminated locations that were ≤3 km from a tracking station. We included locations 3 km from a tracking station only if the angle of intersection of bearings was >45° and <135°. The interval between first and last bearings for each triangulation was typically ≤3 minutes. Locations with areal error estimates >50 ha (LOCATE II) were eliminated from analysis during recording or processing of data.

Home Range Estimation

We estimated home range size and core area (defined below) with CALHOME software (Kie et al. 1996) based on nighttime location coordinates collected during the breeding/pup-rearing period (March–August). We considered only this period for home range estimation and analyses because sample sizes were insufficient for other periods. We calculated the adaptive kernel (ADK) estimates (Worton 1989, Gallerani Lawson and Rogers 1997) of home range. All analyses of home range were conducted with 95% ADK estimates. Core area was defined by the 50% ADK estimate. We also provide minimum convex polygon (MCP; Mohr 1947, White and Garrott 1990) estimates of home range to permit comparison with home

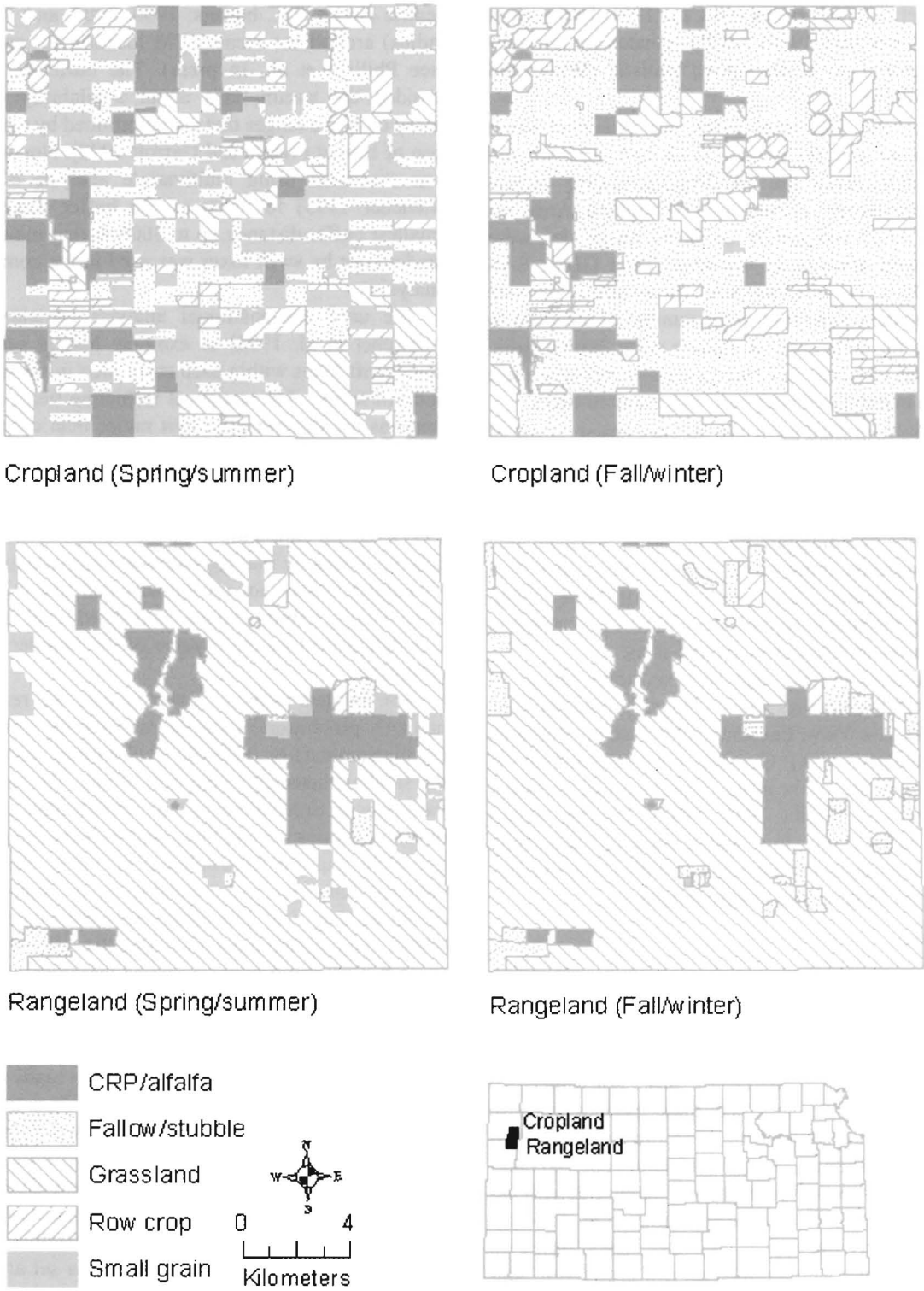


Figure 1. Cropland and Rangeland study areas (each 259 km²) in Sherman and Wallace counties of western Kansas with habitats delineated for 2 periods of the study, spring/summer (1 March–15 July) and fall/winter (16 July–31 January). UTM coordinates for the northwest corner of each study area are: Cropland—4355640 N, 273068 E; Rangeland—4336794 N, 269121 E.

range estimates among published studies of swift foxes (Andersen et al. 2002, Hines and Case 1991, Pechacek et al. 2000, Zimmerman 1998). MCP estimates are less suitable biologically as a descriptive statistic (White and Garrott 1990:148).

INDIVIDUALS: For individual foxes, we estimated home range and core area for animals with ≥60 locations and monitored throughout the breeding/pup-rearing period. Effect of landscape composition (Cropland Area vs. Rangeland Area) and gender on home range size were evaluated with analysis of variance (Proc GLM; SAS Institute 1988). For the analyses, we weighted the size estimates by the square root of the number of locations to compensate for differences in sample sizes. Within pairs, we examined variation in home-range size between male and female members of each pair with a paired t-test.

FAMILIES: We identified swift fox families based on use of shared dens and observations of radiomarked foxes. We estimated home range and core areas used by swift fox families that met the criteria of ≥60 locations collected throughout the breeding/pup-rearing period. We evaluated effect of landscape composition on home range size with analysis of variance (Proc GLM; SAS Institute 1988), weighted by the square root of the number of locations to compensate for differences in sample sizes.

We estimated overlap area between home ranges of adjacent swift fox families with a Geographic Information System (GIS; Arc/View, Environmental Systems Research Institute, Redlands, CA). Overlap was calculated as the mean of the product of the ratios of overlap size to overall home range size (Minta 1992, 1993). Overlap values potentially range from 0 to 1, with a value of 1 indicating adjacent home ranges of identical size with 100% overlap. We converted these values to percentages.

Habitat Use

We delineated habitats of study areas (and surrounding areas when needed for analysis) from aerial photography (1:40,000) entered into GIS. We generated databases for habitat composition of each study area for each of 2 periods (spring/summer: 1 March–15 July; fall/winter: 16 July–31 January). We specified these periods because wheat harvest was completed about 15 July, which marked a significant and sudden change in the landscape and habitats available to foxes. Verification of habitat determinations was conducted by ground surveillance in mid-June and again in early September. Habitat classes, based on vegetation structure were defined as: row crop (corn, sunflowers, sorghum), small grain (wheat, milo), stubble/fallow, grassland (pasture), CRP/alfalfa, and other (e.g., farmyards). Swift foxes were never found in the few farmyards on the study areas, therefore we did not include this habitat class in the analyses. We did not include roads as a habitat class and the adjacent habitat on either side of roads was assigned to mid-road.

We defined available habitats based on a series of concentric circles (i.e., buffers: 1000, 2000, and 3000-meter radius) around the mean UTM location for each animal (see Phillips et al., In press). The buffering technique avoided the assumptions about availability of habitat based on home ranges that are determined by a prior selection of habitat (White and Garrott 1990). Nonrandom use was evaluated using multivariate analysis of variance (Rencher 1995) for each of the buffer distances. The smallest buffer distance up to 3000 m that indicated nonrandom use by swift foxes was used in the compositional analysis.

We used compositional analysis (Aitchison 1982, Aebischer et al. 1993) to examine habitat selection by adult swift foxes within each study area in spring/summer and fall/winter. The statistical technique treats individual foxes as the experimental unit rather than each location. Because sample sizes of locations were not the same for all animals, we weighted the differences in proportions by the square root of the number of locations (Aebischer et al. 1993). Given nonrandom habitat use, we then ranked habitat classes by making pairwise comparisons between all habitat classes for all animals and tested for differences among habitat classes. Threshold level of selection was determined by the inverse of the number of habitat categories.

For habitats with no detected use, we replaced the habitat's proportion of use (zero) with the value 0.0001 (spring/summer) or 0.000001 (fall/winter), depending on the smallest detected proportion of use. The replacement value was an order of magnitude smaller than the smallest observed proportion and thus, preserves the meaning of no use in the analysis (Aebischer et al. 1993). Similarly, for habitats that were not available to an individual fox (occurred only 8 of 210 times), we substituted the value 0.0001 (spring/summer) or 0.000001 (fall/winter). By using this substitution, we assumed that the individual fox responded to that habitat at random.

Use of Roads

We examined distance of locations to roads as a measure of the use of roads as travel lanes or foraging sites. The distance to a road was determined for every point from the nighttime telemetry locations within the buffer distance (3000 m, see Results) resulting from our analysis of habitat selection for individual foxes. We generated files with all possible coordinates (>10,000 points) within each fox's 3000 m buffer. The output cell size was set at 7 meters, which is the same cell size as the original habitat grid developed from the GIS. We then computed the mean distance from each generated point to the nearest road within the 3000 m buffer. Comparisons between the mean distance to roads for individual fox locations and the mean distance to roads for all possible generated points were made with a paired t-test.

Litter Size and Dispersal

Litter size was determined through observations at den sites at the time of emergence. Capture and radiomarking of pups was not attempted until pups were nearly full grown. We defined the onset of dispersal as when a pup left its family home range, without subsequent return movements. Pup locations were reviewed chronologically in relation to the family's 95% ADK home range. The date of dispersal was determined as the median of the date the pup was last known to be within the family home range and the date it was first known to be continually outside the family home range (Koopman et al. 2000). We measured dispersal distances from the point of capture to the furthest location.

Results

We radiocollared 41 adult foxes, 19 in the Cropland Area and 22 in Rangeland Area. Three of the 41 animals either died (1 killed by coyote) or their radios failed (evidenced by signal abnormality just prior to signal loss and observations of collared fox with no signal) within a week of capture. One male was captured in the Cropland Area, but was most frequently found in areas adjacent to that study area. Habitat composition where it resided was more similar to the Rangeland Area than the Cropland Area, therefore we assigned that fox to Rangeland Area for analyses (Fig. 2, see F8).

We radiocollared 25 pups (12 females, 13 males) from families with a radiomarked adult. One female pup captured on 31 October was not positively associated with a marked adult, but we assigned her to the family we assumed she belonged to. We gathered an average of 2.7 locations per week for each monitored pup. Of the 25 pups, 14 died, 1 radio failed, and 10 were tracked until the end of January when collars were removed (see Sovada et al. 1998 for mortality rates and causes). At recapture, all pups and adults were in good health and there was no evidence that collars caused adverse wear on the neck. Only slight hair matting was evident.

Home Range

INDIVIDUALS: Data from 11 (5 females, 6 males) adult foxes in the Cropland Area and 10 (4 females, 6 males) in the Rangeland Area met criteria for home range estimation. We observed that foxes could move >5 km in 1.5–2 hours, the interval between our locations, thus we assumed successive locations for individual foxes were independent (Swihart and Slade 1985). MCP results are given in Table 1.

The mean home range size (95% ADK) for adult foxes was 15.9 km^2 (SE = 1.6) and did not vary between the Cropland Area ($\bar{x}$ = 16.8 km^2, SE = 2.4) and the Rangeland Area ($\bar{x}$ = 15.0 km^2, SE = 2.1; $F_{1,19}$ = 0.32 P = 0.58; Table 1). We detected no effect of gender overall ($\bar{x}$ = 14.1, SE =2.2 [females], $\bar{x}$ = 17.2, SE =2.1 [males]; $F_{1,19}$ = 1.04, P = 0.32), and there was no interaction between area and gender ($F_{1,17}$ = 1.20, P = 0.29). MCP estimates of home range are given in Table 1.

The mean core area size (50% ADK) for adult foxes was 2.2 km^2 (SE = 0.3) and did not differ between the Cropland Area ($\bar{x}$ = 2.3 km^2, SE = 0.4) and the Rangeland Area ($\bar{x}$ = 2.1 km^2, SE = 0.3; $F_{1,19}$ = 0.11, P = 0.74; Table 1). Female core areas overall tended to be smaller ($\bar{x}$ = 1.6, SE = 0.3 [females], $\bar{x}$ = 2.7, SE = 0.4 [males]; $F_{1,19}$ = 4.20, P = 0.06). There was no interaction between area and gender ($F_{1,17}$ = 0.37, P = 0.55) on core area size.

FAMILIES: We identified 10 families in the Cropland Area and 11 families in the Rangeland Area (Fig. 2). Of the 21 families, 7 lost a pair member early in the study; 3 of the 7 surviving pair members associated with a new mate. When the new pair bonds were identified, location data for these foxes were assigned to the new family and home range estimations were calculated accordingly. Radiocollars failed on females of 2 families (F4 and F8, Fig. 2), but pups were present and both females were observed

Table 1. Average 95% and 50% adaptive kernal (ADK) estimates and 100% minimum convex polygon (MCP) estimates of home range size (km^2) during the breeding/pup-rearing period (March–August), and standard errors for female and male swift foxes, all foxes combined, and swift fox families residing in Cropland and Rangeland study areas and overall in western Kansas.

	n	$\bar{x}$ no. locations	95% ADK		50% ADK		100% MCP	
			$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Cropland								
Female	5	176	13.1	2.2	1.6	0.4	16.5	4.3
Male	6	176	19.7	3.7	2.9	0.6	23.6	3.7
All foxes	11	176	16.8	2.4	2.4	0.4	20.4	2.9
Families	5	279	18.7	3.1	2.5	0.3	25.3	4.1
Rangeland								
Female	4	193	15.2	4.6	1.7	0.4	19.1	6.9
Male	6	206	14.9	2.1	2.4	0.4	24.2	1.2
All foxes	10	201	15.0	2.1	2.1	0.3	22.3	2.7
Families	3	270	16.3	2.6	2.9	0.6	23.2	1.4
Overall								
Female	9	184	14.1	2.3	1.6	0.3	17.6	3.6
Male	12	191	17.2	2.1	2.7	0.4	23.9	1.9
All foxes	21	188	15.9	1.6	2.2	0.3	21.3	1.9
Families	8	276	17.8	2.1	2.7	0.3	24.5	2.5

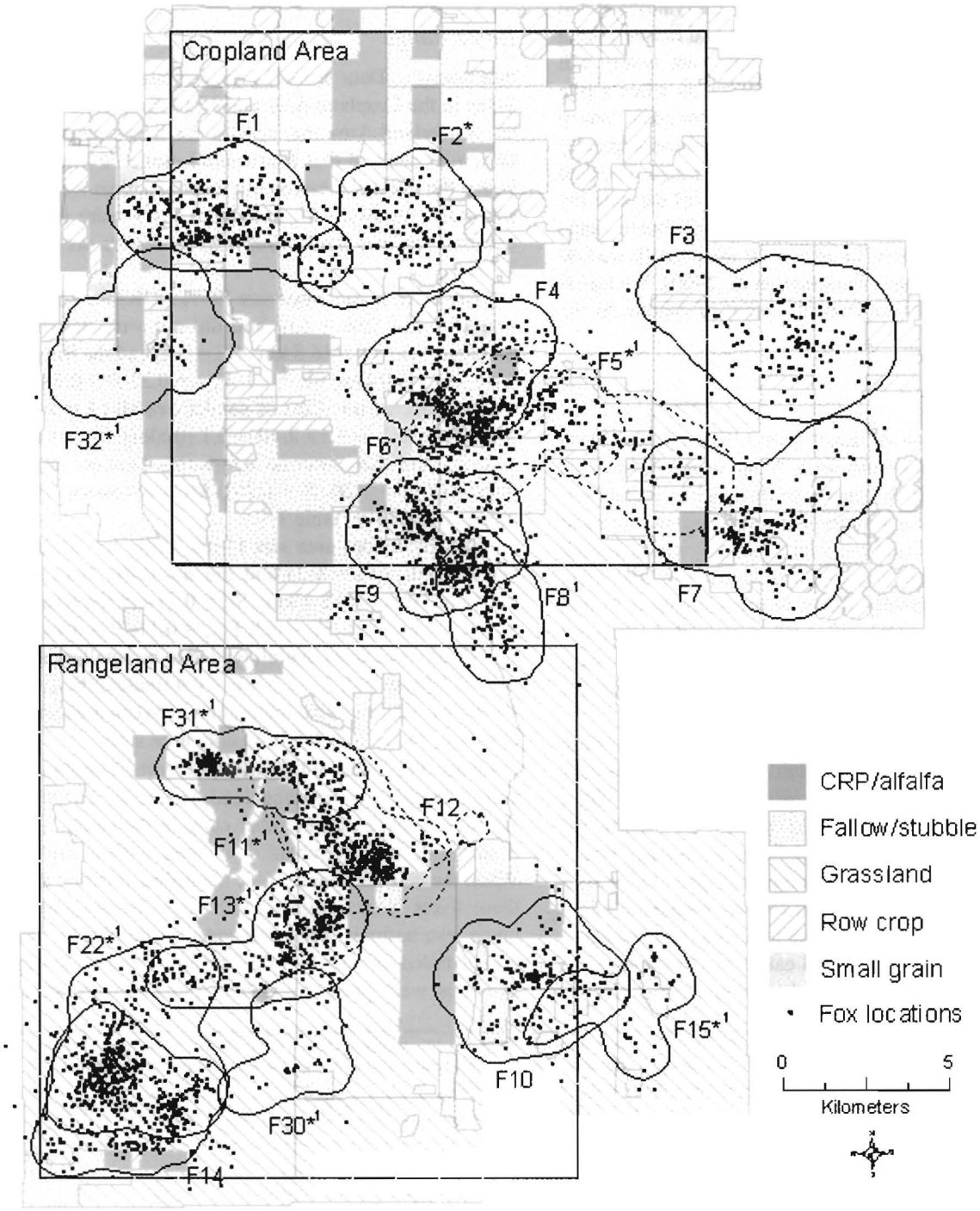


*Figure 2. Home ranges, estimated with the 95% adaptive kernal method, of swift fox families in the Cropland and Rangeland study areas of western Kansas, March 1996 through January 1997. Superscript 1 indicates only 1 member of the pair was monitored and * indicates data for the family did not meet the criteria (60 locations and monitored throughout the breeding/pup- rearing period) for analyses. Families 5 and 6 in Cropland and 11 and 12 in Rangeland (dashed home ranges) each had a shared pair member, i.e., a mate died in 1 family and the remaining pair member associated with a new fox forming a new family unit. Habitats in study areas and outside the study area were identified for the fall/winter (July–31 January) period of the study. Note: T22, this female's mate died in April and she did not attach to a new male and did not appear to be a helper to Family 14.*

throughout the study. We considered these to be stable functioning family units containing a pair and pups. We used telemetry locations from the males to estimate area used, however these estimates are not included in analyses of home range size. We did not know the status of one pair member of 3 families. One family included a second female (yearling) that seemed to be a "helper" female, because she remained in the family home range and occasionally shared a den with the adults (Kilgore 1969, Covell 1992).

For estimation of family home range size (95% ADK), criteria were met by 5 families in the Cropland Area ($\bar{x}$ = 18.7 km^2, SE = 3.1) and 3 in the Rangeland Area ($\bar{x}$ = 16.3 km^2, SE = 2.6; Table 1). Home range size of families was similar between the Cropland and Rangeland areas ($F_{1,6}$ = 0.30, P = 0.60). The mean home range size for all families was 17.8 km^2 (n = 8, SE = 2.1). The size of core area (50% ADK) used by families was also similar between the Cropland Area ($\bar{x}$ = 2.5 km^2, SE = 0.3) and the Rangeland Area ($\bar{x}$ = 2.9 km^2, SE = 0.6, $F_{1,6}$ = 0.26, P = 0.63). For 8 families with sufficient data, we detected no difference in home range size between females ($\bar{x}$ = 15.0 km^2, SE = 2.4) and males ($\bar{x}$ = 17.0 km^2, SE = 1.9) within families (t_7 = 0.67, P = 0.52). The females tended to have smaller core areas ($\bar{x}$ = 1.6, SE = 0.3) than males ($\bar{x}$ = 2.5 km^2, SE = 0.3; t_7 = -2.13, P = 0.07).

OVERLAP OF FAMILY HOME RANGES: Our data included 5 pairs of families with adjacent home ranges appropriate (fit criteria for home range estimation) for evaluating home-range overlap. The mean overlap of home ranges was 16% (range 0–32%, SE = 6) and 2 of the 5 families had core areas that overlapped (3% and 18%).

Habitat Selection

We observed consistent nonrandom habitat use by swift foxes in both landscapes in both time periods only within the 3000-m buffered area (P <0.10; Table 2). This

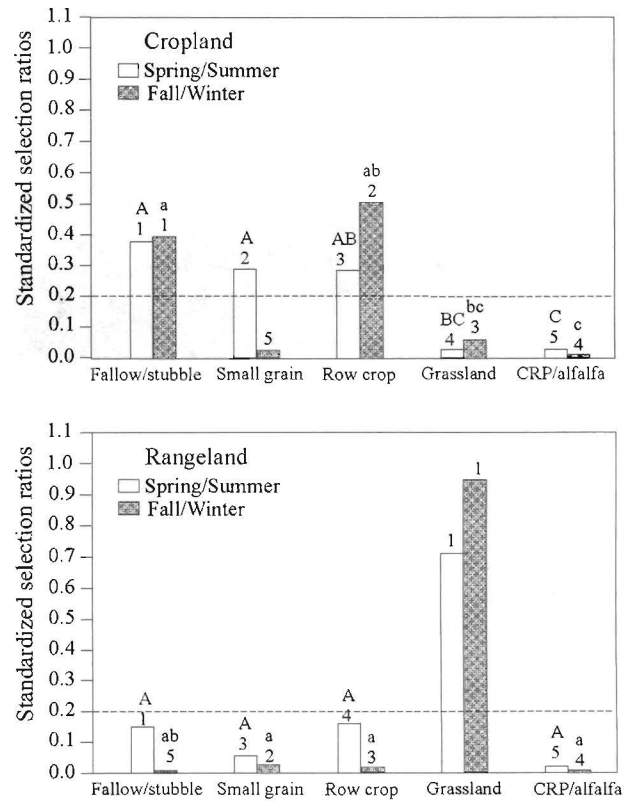


Figure 3. Standardized selection ratios for swift foxes on Cropland and Rangeland study areas in western Kansas in 2 periods (spring/summer: 1 March–15 July; fall/winter: 16 July–31 January) in 1996–1997. Numbers above the histogram bars are the rank of each habitat within the period. Habitats with the same letter above the bar are not significantly different from each other (P >0.05) within each period. The dashed line represents a threshold level of selection determined by the inverse of the number of habitat categories (i.e., 1/5 = 0.2).

Table 2. Results of MANOVA tests evaluating habitat selection by swift foxes at each buffer distance.

	Buffer Distance (m)		
	1000	2000	3000
Spring/Summer			
Cropland			
Fox (n=13)			
Wilks' Λ	0.545	0.634	0.289
P	0.199	0.340	0.016
Rangeland			
Fox (n=11)			
Wilks' Λ	0.646	0.329	0.239
P	0.484	0.068	0.025
Fall/Winter			
Cropland			
Fox (n=10)			
Wilks' Λ	0.695	0.404	0.280
P	0.643	0.184	0.069
Rangeland			
Fox (n=8)			
Wilks' Λ	0.550	0.214	0.104
P	0.355	0.118	0.030

MIKE BLAIR, KANSAS DEPT. OF WILDLIFE AND PARKS

Swift fox den in the Cropland Study Area.

MIKE BLAIR, KANSAS DEPT. OF WILDLIFE AND PARKS

Swift fox den in the Rangeland Study Area.

area included 88% of locations in spring/summer and 95% of locations in fall/winter. During spring/summer in the Cropland Area, fallow/stubble, small grain, and row crop where the highest ranked habitats in their use by foxes, but these habitats did not differ from each other (Fig. 3, P >0.10). Grassland and CRP/alfalfa were the lowest ranked habitats used by foxes and fell below the selection threshold. They were selected less than fallow/stubble, small grain, and row crop. In the Rangeland Area in spring/summer, grassland had the highest ranked selection factor and was selected more often than all other habitats (Fig. 3, P <0.01). Fallow/stubble, small grain, row crop, and CRP/alfalfa were not different from each other (P >0.33–0.88).

During fall/winter in the Cropland Area, fallow/stubble ranked first in selection by foxes among habitats (Fig. 3), followed by row crop, grassland, CRP/alfalfa, and small grain. No difference was detected in relative use of fallow/stubble and row crop (P = 0.76) or row crop and grassland (P = 0.08), but there was a difference between fallow/stubble and grassland (P = 0.05). Foxes in the Rangeland Area in fall/winter selected habitats similarly to that of spring/summer; grassland had the highest rank and was different from all other habitat categories (P <0.02).

Daytime telemetry revealed an average of 6.1 dens/family in the Cropland Area and 5.6 dens/family in the Rangeland Area during the spring/summer however, we mightn't have located all dens based on our sampling schedule. In the Cropland Area, dens were predominately located in fallow/stubble habitat (31 of 43 dens) and in the Rangeland dens were largely in grassland (28 of 34 dens). Additional information regarding dens on the study site can be found in Jackson and Choate (2000).

Use of Roads

The distances of fox locations from roads were not different from random locations (P >0.17), although there was variability among foxes and no clear pattern was evident. Male foxes in the Rangeland Area tended to be located closer to roads than expected (t_7 = 2.08, P = 0.08).

Litter Size and Dispersal

Ten families raised ≥1 pup (post-emergence average litter size = 3.1, SE = 0.4) with an average of 3.1 pups (n = 7, SE = 0.5) in the Cropland Area and 3.0 pups (n = 3, SE = 0.7) in the Rangeland Area. Three females died prior to whelping, revealing 7, 4, and 3 embryos upon necropsy and one female that died post-partum showed 3 recent placental scars. Information on pups was unknown for 2 families, and 2 others probably did not have pups.

Average dispersal distance was 14.7 km (SE = 4.8) for 10 pups (4 Rangeland Area, 6 Cropland Area). Of these, a female and 2 males dispersed ≥20 km (20, 22, 32 km respectively) from their family home ranges. Two female pups dispersed, but stayed near (5 and 6 km) the edge of their family home range. Two male pups moved from the family home range (3 and 5 km), but continued occasional use of the periphery of the family home range. One female pup remained in the family home range, and 2 other females appeared to remain in the area used by their parents, but we had insufficient data to adequately estimate their family home range.

The average date pups first left the family home range was 26 October (n = 10, range = 1 Oct–3 Dec). The average date pups dispersed from their family home range was 5 November (n = 5, range = 1 Oct–27 Dec).

Discussion

The average home range size of 15.9 km^2 that we observed for swift foxes was midrange compared to other studies. However, other estimates are quite variable and difficult to compare because of differences in estimation techniques, criteria used, and periods of evaluation (Gallerani Lawson and Rodgers 1997). Using the same 95% ADK method as we used, Kitchen et al. (1999) reported an average home range size of 7.6 km^2 for swift foxes (>30 animals and >60 locations per breeding, rearing, and dispersal seasons) on the Piñon Canyon Maneuver Site in

southeastern Colorado during 1997–98. Pechacek et al. (2000) estimated home range sizes of 11.7 km^2 (95% ADK) and 7.7 km^2 (100% MCP) for 10 swift foxes in southeastern Wyoming. Hines and Case (1991) reported an average MCP home range size of 32.3 km^2 (range 7.7–79.3 km^2) for 7 swift foxes in Nebraska, which is larger than our MCP home range estimate ($\bar{x}$ = 21.3 km^2). However, >50% of their study animals were followed ≤5 nights and only in winter or very early spring. Andersen et al. (2002) reported a similar average MCP home range size (29.0 km^2, range 12.8–34.3 km^2) on the Piñon Canyon Maneuver Site (1986–87), reporting on 5 swift foxes with 34 locations ($\bar{x}$ = 188 locations) over a minimum period of 7 months. Zimmerman et al. (2002) estimated an average MCP home range size of 10.4 km^2 (range 7.3 to 16.9 km^2) for 5 swift foxes in Montana.

Swift foxes use a broad array of plant and animal foods (Hines and Case 1991, Kitchen et al. 1999, Sovada et al. 2001), and there is no evidence that food is a limiting factor. Initially, we had expected home range size would be larger in the Cropland Area than the Rangeland Area based on different types and distribution of food resources. Spiegel (1996) suggested that spacing patterns for kit foxes (*Vulpes macrotis*) are influenced by differences in fox density, and type and abundance of prey. However, Sovada et al. (2001) reported no fundamental differences in foods used by foxes between cropland areas and rangeland areas. Although there are no data on abundance of prey, we can assume similar (or more than adequate) abundance of prey based on similar diet and similar home ranges. Therefore, there must be some other factors influencing spacing patterns. However, without long-term studies, it is difficult to assess the impact of abundance of prey on fox densities.

Similar to Spiegel (1996), Sargeant (1972) indicated that territory size for red foxes (*Vulpes vulpes*) is a reflection of population density and he further proposed that red foxes have innate minimum and maximum spatial requirement. Studies of red fox spatial patterns confirm this suggestion (Sargeant et al. 1975, Trewhella et al. 1988) and our findings suggest the same might be true for swift foxes. Because food resources are not limiting, except perhaps under extreme environmental conditions, swift fox spacing patterns might be more related to fox density on our study areas. Other accounts in the literature suggest fox densities might be influenced by factors such as disease (Lindström 1991), human inflicted mortality (Sargeant 1982), and interspecific competition (Voigt and Earle 1983, Sargeant et al. 1987, Harrison et al. 1989). The swift fox populations in this study suffered relatively high mortality due to predation by coyotes (Sovada et al. 1998), and thus may be at a lower density than the landscape can actually support. Further research is necessary to determine mechanisms regulating densities.

Earlier studies suggested that swift foxes are not territorial (Cameron 1984, Hines 1980); however more recent data, including ours, provide evidence to the contrary. Andersen et al. (2002) reported nearly total exclusion of an individual swift fox's core area (50% MCP estimates) from other same-sex individuals. Pechacek et al. (2000) found that the area used by mated pairs had minimal overlap with areas used by adjacent pairs (95% ADK).

Although considered a hallmark species of mixed-grass and shortgrass prairie, swift foxes have adapted to a variety of habitats (e.g., Kilgore 1969, Olson and Lindzey 2002). Results of this study suggest that swift foxes were well adapted to use fallow, stubble, and small grain fields in landscapes dominated by dryland cropping practices (winter wheat–fallow rotation) and minimal grassland habitat. In the cropland landscape, fallow/stubble fields likely provide excellent habitat for foraging and denning and we expected and recorded significant use of this habitat. We had expected foxes to use grasslands more than they did the cropland landscape despite the limited availability of this habitat. The grassland, not surprisingly, was the selected habitat in areas where rangeland dominated the landscape.

We expected the low selection of CRP/alfalfa. Several fox family home ranges bordered or included CRP fields, but we seldom located foxes using the CRP field (see Fig. 2). CRP lands in western Kansas were originally seeded to tall grass species that are not native to the area, primarily big blue stem, Indian grass, and switch grass. Swift foxes prefer open plains habitat that allows relatively good visibility to detect potential predators (Kilgore 1969, Hines 1980), thus CRP likely provided little security for the foxes. For conservation of the species in Kansas and similar areas, we recommend CRP lands be planted to native shortgrass and mixed-grass species rather than the currently applied tall grass species. If the landowners are given incentives under the CRP provisions, landowners might be more likely to plant native shortgrass and mixed-grass species that benefit swift foxes and other native wildlife species.

Although we do not have sufficient data to closely examine use of row crops during various stages of growth, we believe that foxes avoided these fields when their visibility was obstructed by the vegetation. Foxes were located in row crop habitat mostly (80% of row crop locations) when the crops were very short (prior to July) or after harvest (after September).

We did not observe frequent use of roads by foxes. However, other studies have indicated that swift fox movements and den locations are associated with roads (Hines and Case 1991, Pruss 1999). Road associations were a major source of vehicle-related mortality for juvenile foxes in the Cropland Area where there was more vehicle traffic (Sovada et al. 1998). Adult foxes seemed to be more cautious of roads.

We found that litter sizes ($\bar{x}$ = 3.1) were medial in rela-

tion to published average swift fox litter sizes of 2.3–5.7 (Kilgore 1969, Hillman and Sharps 1978, Covell 1992, Carbyn et al. 1994, Anderson et al. 2002, Olson and Lindzey 2002). Similar to our study, sample sizes were small in most published accounts. Regardless, our data suggest litter size was similar between landscapes.

Average dispersal distances that we found were similar to other studies ($\bar{x}$ = 12.6, Schauster 2001; $\bar{x}$ = 12.1, Moehrenschlager 2000). Timing of the onset of pup dispersal that we observed was later than reports from southern portions of the swift fox range. Kilgore (1969) reported dispersal in August/September in Oklahoma and Covell (1992) reported dispersal in September/October in southern Colorado. These differences might be related to earlier whelping in more southerly populations (Asa and Valdespino 2002). Schauster (2001) found the juvenile females dispersed later than males, often delaying dispersal until next breeding/gestation period, when they were considered adults. In our study, 6 of 7 pups that remained close to or within their family home range were females. We were unable to determine if they might have delayed dispersal until late winter/early spring or until after their first breeding/gestation.

Swift fox populations in Kansas have experienced major changes since presettlement. Despite trapping efforts, poisoning campaigns, and significant habitat modification, this small prairie fox has survived and adapted to a new and vastly different landscape within its historic range. However, the future of swift fox populations in Kansas remains uncertain despite the present, relatively healthy, populations. Agricultural cropping practices are changing toward more irrigation rather than dryland farming. Larger monotypic crop fields are becoming more common, replacing the smaller fields in dryland fallow–winter wheat rotations. Such changes likely will not benefit the swift fox that presently is able to use fallow fields for foraging and denning. However, there are suitable habitats within the region that currently are not occupied by the species (Sovada and Scheick 1999). Factors limiting or delaying expansion of swift foxes into these unoccupied portions of their historic range in Kansas continue to be unknown. Given the high mortality rates and unremarkable reproductive rates for the swift fox in Kansas, their ability to expand current distribution in the state can only be a slow unsure process, if not impossible without help from wildlife managers. We recommend continued long-term research and monitoring of swift fox populations to gain insight into population dynamics, dispersal abilities, and other aspects of ecology in landscapes with diverse habitat composition and changing agricultural practices. Ultimately, knowledge gained will be useful to guide management decisions to ensure a thriving population of swift foxes in Kansas.

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In 1998, biologists and endangered species experts from fifteen states, three provinces, and seven countries met at an International Symposium on Swift Foxes, held in Saskatoon, Saskatchewan, to exchange information and identify the "state-of-the-science" of swift fox ecology and status in North America. Papers presented at the symposium, together with others written afterwards, are brought together in this peer-reviewed volume, which is divided into five major sections. Papers in Part I (Setting the Stage) consider swift fox conservation issues in general. Part II (Distribution and Population Shifts) explores what is known about the current distribution of the species on the North American continent. Part III (Censusing and Techniques) is devoted to evaluations of scent stations for surveying fox presence and abundance, along with a review on mitigating capture-related injuries. The papers in Part IV (Population Ecology) attempt to better understand the dynamics of changes in distribution and abundance of swift foxes on the continent, particularly as related to loss of suitable habitats, ecosystem modification brought on by human activities, and climate change. Part V discusses the current knowledge of swift fox taxonomy, physiology, and disease-related issues. Broad-ranging and comprehensive, *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World* will provide invaluable information for scientists, resource managers, and students.

Part I – Setting the Stage

- A Review of the Ecology, Distribution, and Status of Swift Foxes in the United States
- The Socio-Economic Context for Swift Fox Conservation in the Prairies of North America
- A Design for Species Restoration—Development and Implementation of a Conservation Assessment and Conservation Strategy for Swift Fox in the United States
- Canada's Experimental Reintroduction of Swift Foxes into an Altered Ecosystem

Part II – Distribution and Population Shifts

- The Historic and Recent Status of the Swift Fox in Montana
- The Status and Ecology of Swift Foxes in North-central Montana
- Swift Fox Detection Methods and Distribution in the Oklahoma Panhandle
- Current Swift Fox Distribution and Habitat Selection Within Areas of Historical Occurrence in New Mexico
- A Literature Review of Swift Fox Habitat and Den-Site Selection

Part III – Censusing and Techniques

- Swift Fox Detection Probability Using Tracking Plate Transects in Southeast Wyoming
- Scent-Station Survey Techniques for Swift and Kit Foxes
- Reducing Capture-Related Injuries and Radio-Collaring Effects on Swift Foxes

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- A Review of Small Canid Reproduction
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- Home Range, Habitat Use, Litter Size, and Pup Dispersal of Swift Foxes in Two Distinct Landscapes of Western Kansas
- Using Tooth Sectioning to Age Swift Fox
- Den Ecology of Swift, Kit and Arctic Foxes: A Review
- Coyote and Kit Fox Diets in Prairie Dog Towns and Adjacent Grasslands in Mexico
- Assessing Restoration of Swift Fox in the Northern Great Plains
- Captive Breeding of the Swift Fox at the Cochrane Ecological Institute, Alberta

Part V – Taxonomy/Physiology/Disease

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