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HABITAT USE, HOME RANGES, AND SURVIVAL OF SWIFT FOXES IN A FRAGMENTED LANDSCAPE: CONSERVATION IMPLICATIONS

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Habitat loss might be one of the primary reasons for the decline of the swift fox (*Vulpes velox*) in the western Great Plains of North America. From 1998 to 2001, we monitored 42 swift foxes in a landscape interspersed with native short-grass prairies, nonnative grasslands enrolled in the Conservation Reserve Program, irrigated agricultural fields, and dryland agricultural fields. Survival estimates ranged from 0.52 to 0.66 for both adults and juveniles, and the primary causes of death were vehicle collisions (42% deaths) and coyote (*Canis latrans*) predation (33%). Annual home-range size was similar for males and females (10.8 and 10.5 km^2, respectively). Within the study area, swift foxes selected only short-grass prairies and had lower-than-expected use or complete avoidance of all other habitat types. Our results indicate swift foxes are more specialized in habitat selection than other North American canids; thus, protection of native short-grass prairies might be necessary for their long-term existence.

Key words: habitat use, home range, survival, swift fox, Texas, *Vulpes velox*

The distribution of swift foxes (*Vulpes velox*) in the western Great Plains of North America has been severely reduced since the mid-1800s (Egoscue 1979; Scott-Brown et al. 1987). Consequently, the swift fox was classified as ''warranted, but precluded'' as a threatened species by the United States Fish and Wildlife Service from 1995 to 2001. In Canada, swift foxes were extirpated by the 1930s but were recently reintroduced after being classified as an endangered species (Carbyn et al. 1994). Previous researchers hypothesized that habitat loss, as a result of conversion of prairies to agricultural fields, was one of the primary factors that led to the decline of the swift fox (Egoscue 1979; Scott-Brown et al. 1987). Although research on swift foxes increased during the 1990s, no studies were carried out in areas interspersed with both native and human-altered habitats.

Most canid species in temperate North America are habitat generalists, including coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*—Bekoff 1982; Fritzell 1987; Kamler and Ballard 2002; Samuel and Nelson 1982). Consequently, these species have benefited from fragmentation and other human-induced changes to the environment and have increased their range since the 1800s (Bekoff 1982; Fritzell 1987; Kamler and Ballard 2002; Samuel and Nelson 1982). In contrast, the distribution of swift foxes became severely reduced in

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concert with conversion of mid- and short-grass prairies to agriculture (Egoscue 1979; Scott-Brown et al. 1987), suggesting swift foxes may be habitat specialists. Factors other than habitat loss, however, also might contribute to the range reduction of swift foxes, such as competition with coyotes (Scott-Brown et al. 1987; Sovada et al. 1998).

Although swift and kit foxes (*Vulpes macrotis*) were considered conspecifics based on initial genetic analysis (Dragoo et al. 1990), a more recent study using larger sample sizes and more advanced genetic analyses concluded they were separate species (Mercure et al. 1993). Mitochondrial deoxyribonucleic acid differentiation between these 2 species was similar to that between these taxa and the arctic fox (*Alopex lagopus*), a species commonly placed in a different genus (Mercure et al. 1993). The latter study supported previous studies that supported separate species status based on morphological data (Rohwer and Kilgore 1973; Stromberg and Boyce 1986; Thornton and Creel 1975). Consequently, although previous research indicated that kit foxes were not negatively affected by human-altered habitats (Cypher and Frost 1999; Zoellick et al. 2002), swift foxes have a different evolutionary history and occupy a different biome; thus, they might be affected differently by human-altered habitats.

All but one previous study of swift foxes took place in continuous native habitat. Thus, there is a lack of knowledge concerning their habitat selection, especially in agricultural and other human-altered environments that now occupy most of the Great Plains. In the only exception, swift foxes were found to occupy continuous, dry-land agriculture in western Kansas (Matlack et al. 2000; Sovada et al. 1998). The selection of agricultural fields compared with other habitats, however, has not been studied. Clearly, more research is needed on the ecology of swift foxes in fragmented landscapes because this information could help elucidate the importance of different habitat types needed to maintain swift fox populations. This information also would have important implications for conservation efforts on swift foxes because the effects of human-altered habitats on swift foxes are unknown.

We determined habitat use, home ranges, and survival of swift foxes in a fragmented landscape in northwestern Texas. Our study area consisted of short-grass prairies that were grazed by cattle and nonnative grasslands that were ungrazed, which were enrolled in the United States Department of Agriculture's Conservation Reserve Program (CRP). It also included irrigated agricultural fields and dry-land agricultural fields. Our primary goals were to compare habitat use and availability within the study area and to determine major sources of mortality.

MATERIALS AND METHODS

Study area.—Research was conducted on a 110-km^2 area on the border of Dallam and Sherman counties in northwestern Texas (36°24′N, 102°19′W). The center of the study site was located on a private ranch surrounded by other ranches, agricultural fields, and nonnative grasslands. Vegetation on ranches consisted of short-grass–prairie grass species and was dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) and was moderately to intensively grazed by cattle (*Bos taurus*). With the passage of the 1985 Farm Bill, CRP was created with the goal of retiring highly erodible land from agricultural production and converting it to permanent cover. Across the United States, CRP fields were planted with a variety of grass species. In our study area, most CRP fields were enrolled in 1985 and planted to warm-season grasses, dominated by old world bluestem species (*Andropogon*) and sideoats grama (*Bouteloua curtipendula*). These areas had vegetation that was taller and thicker than the short-grass prairie that historically dominated this region (Barbour and Billings 1988). As required by federal law, CRP fields were not grazed. Irrigated agricultural fields consisted of consecutive crops of corn (approximately April to September) and winter wheat (September to

June) followed by a fallow 10-month period. Crops were watered by center-pivot irrigation. Chemical applications, including fertilizers, herbicides, and pesticides, were applied through the irrigation system. Dry-land agricultural fields were not irrigated and consisted of consecutive crops of grain sorghum (June to September) and wheat (September to June) followed by a fallow 12-month period. Chemicals were not applied to dry-land agriculture. To reduce livestock losses, coyote hunting was permitted by the owner of the private ranch, and consequently, coyotes were heavily exploited (Kamler 2002). However, swift foxes were not exploited by humans.

Capture and radiotelemetry.—From August 1998 to January 2001, we radiocollared and monitored 42 swift foxes (21 adults, 21 juveniles). Swift foxes were captured in Havahart® cage traps (Woodstream Corp., Lititz, Pennsylvania) during all months of the year except April to July (Kamler 2002). Trapping effort for swift foxes was initially concentrated near the center of the study site and expanded outward as capture of unmarked foxes decreased. Most traps (>95%) were set along fences that separated fields. All fence lines within the study area were trapped, and all habitat types were represented when trapping. Captured foxes were ear-tagged and fitted with radiocollars (Advanced Telemetry Systems, Inc., Isanti, Minnesota), and their age was determined by tooth wear, body size, and reproductive condition (Rongstad et al., in litt.). Foxes were classified as juveniles until approximately 11 months of age (the following March), whereas all other foxes were considered adults. Swift foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999).

We recorded independent telemetry locations (White and Garrott 1990) for study animals 1–2 times per week and >12 h apart. We radiotracked foxes from vehicles using null-peak systems, which consisted of dual, 4-element yagi antennas (Advanced Telemetry Systems, Inc., Isanti, Minnesota). Most radiotracking (>90%) occurred during 1800–0900 h, when swift foxes were likely to be most active (Kitchen et al. 1999). We calculated location estimates using the maximum likelihood estimation option in program Locate II (Pacer, Inc., Truro, Canada). Mean error for reference collars (determined for known locations) was 84 m (95% of errors were <145 m).

Home range analysis.—We determined annual home-range sizes for swift foxes using the minimum convex polygon method (Mohr 1947), as calculated by animal movement software (Hooge and Eichenlaub 1997). Because the 95% adaptive kernel method (Worton 1989) was used in previous studies to determine home ranges of swift foxes (Kitchen et al. 1999; Pechacek et al. 2000), we also calculated home ranges using this method for comparison purposes. We calculated home-range sizes for foxes with >30 locations and >6 months of radiotracking. As a result of emigrations and early deaths, annual home-range sizes were calculated for only 17 adult swift foxes (6 males and 11 females). Mean home-range sizes were compared between sexes using *t*-tests (Zar 1996) and were deemed significantly different when $P < 0.05$.

Habitat-use analysis.—Habitat types were delineated using geographic information system (GIS) data obtained from quadrangle maps and were ground-truthed by visual inspection. Habitat selection (used as compared with available) was determined at the study-area scale for both adults and juveniles. Using locations from all radiocollared individuals within each age class, an availability polygon (Miller et al. 1999) for each age class was determined using the minimum convex polygon method. Percentage of different habitat types within polygons was considered available. To determine use, we plotted all locations on a GIS map of habitat types using ArcView software (version 3.2, Environmental Systems Research Institute, Inc., Redlands, California). Expected number of locations for each habitat type was calculated by multiplying total number of locations by percentage of available habitat types. We then compared total number of locations within habitat types with those expected using chi-square goodness-of-fit tests (Neu et al. 1974; White and Garrott 1990).

Survival analysis.—Survival rates were determined for swift foxes using MICROMORT software (Heisey and Fuller 1985). Annual survival of adults was calculated only for 1999 and 2000 because adults were not monitored for a full 12 months during other years of the study. Six-month survival rates (August–January) were calculated for juveniles during each of the 3 years of the study. These survival rates were mainly for foxes 5–11 months of age, after which time most juveniles dispersed. Causes of mortality were determined by necropsy. We classified

TABLE 1.—Habitat use observed (Obs) compared with expected (Exp) for adult and juvenile swift foxes (*Vulpes velox*) monitored from 1998 to 2001 in northwestern Texas.

	Number of locations	Short-grass prairie[a] Obs (Exp)	Dry-land agriculture Obs (Exp)	Irrigated agriculture Obs (Exp)	CRP grassland[b] Obs (Exp)	χ^2	*P* value
Adults (*n* = 21)	958	932 (446)	26 (242)	0 (142)	0 (127)	991.38	<0.0001
Juveniles (*n* = 21)	246	234 (112)	11 (60)	0 (36)	1 (38)	244.94	<0.0001

[a] Grazed by cattle.
[b] Conservation Reserve Program (CRP) grassland was nonnative vegetation and ungrazed.

swift fox deaths as coyote predation if fox carcasses had hemorrhaging and puncture wounds consistent with that from coyote bites. For adults, data were initially analyzed by biological season to meet the assumption of constant survival (Heisey and Fuller 1985). Because preliminary analyses indicated that survival did not differ among seasons, data were grouped and compared between years for adults using *z*-tests (Heisey and Fuller 1985; Nelson and Mech 1986). Likelihood ratio tests (*G* statistic) were used to make multiple comparisons across years and for 6-month survival of juveniles (Heisey and Fuller 1985; Zar 1996).

RESULTS

We obtained 958 locations for 21 adults and 246 locations for 25 juveniles during the study. Annual home-range size (minimum convex polygon) of adult males (10.8 km^2 ± 1.6 *SE*, *n* = 6) was similar (*P* = 0.90) to that of adult females (10.5 ± 1.1 km^2, *n* = 11). Overall home-range size for foxes using the 95% adaptive kernel method was 11.7 ± 1.0 km^2, *n* = 17. Three juveniles remained on the study site and became adults during their 2nd year.

At the study-area scale, the availability polygon for adults (9,659 ha) included 47% short-grass prairie, 25% dry-land agricultural fields, 15% irrigated agricultural fields, and 13% CRP grasslands. The availability polygon for juveniles (10,185 ha) included 46% short-grass prairie, 25% dry-land agricultural fields, 15% irrigated agricultural fields, and 15% CRP grasslands. For both adults and juveniles, there was a strong selection for short-grass prairie, whereas there was lower-than-expected use of dry-land agricultural fields, complete avoidance of irrigated agricultural fields, and nearly complete avoidance of CRP grasslands (Table 1). Use of dry-land agricultural fields occurred during both planted and fallow periods.

Annual survival of adults did not differ between years (*z* = 0.13, *P* = 0.87; Table 2). Similarly, 6-month survival of juveniles did not differ among years (*G* = 0.21, *d.f.* = 2, *P* = 0.90; Table 2). There were 12 confirmed deaths (7 adults, 5 juveniles) of swift foxes during the study, 5 (42%) from

TABLE 2.—Survival estimates for swift foxes (*Vulpes velox*) monitored in northwestern Texas from 1998 to 2001. Included are annual estimates for adults, 6-month estimates for juveniles, and 95% *CI*.

	n[a]	Deaths	Survival	95% *CI*
Adults				
January 1998–December 1999	10	4	0.55	0.31–0.99
January 1999–December 2000	13	2	0.52	0.21–1.00
Juveniles				
August 1998–January 1999	8	2	0.66	0.38–1.00
August 1999–January 2000	9	2	0.60	0.30–1.00
August 2000–January 2001	8	2	0.55	0.23–1.00

[a] Number of foxes monitored.

vehicle collisions, 4 (33%) from coyote predation, and 3 (25%) from unknown causes.

Discussion

Our results indicate that swift foxes selected for short-grass–prairie habitats, rarely used dry-land agricultural fields, completely avoided irrigated agricultural fields, and nearly completely avoided CRP grasslands. Preliminary analysis of habitat use within individual home ranges of swift foxes also showed similar results (Kamler 2002). Although swift foxes occupied continuous dry-land agricultural fields in western Kansas (Matlack et al. 2000; Sovada et al. 1998), differences in body condition and mortality suggested that these foxes were less fit than those in adjacent areas of continuous native prairies (Matlack et al. 2000). This suggests that dry-land agricultural fields are marginal for swift foxes and might provide only sink habitats (Pulliam 1988). Our results support this conclusion because both adult and juvenile swift foxes used dry-land agricultural fields considerably less than expected, suggesting that this habitat was not as productive or useful for swift foxes as short-grass prairie.

In our study, irrigated agricultural fields were completely avoided by all swift foxes, even though it comprised 15% of the total area. There were considerable differences between irrigated and dry-land agricultural fields in our study site that might have resulted in differential use by swift foxes. Dry-land fields were never artificially watered, and no chemicals were applied. In contrast, irrigated fields were watered by a center-pivot irrigation system that continuously rotated during crop growth (except during wheat growth in late fall–winter), and chemicals were applied through the irrigation system. Foxes may have avoided these areas due to the higher disturbance and chemical applications, which reduce the availability of insects for food. Insects were a major part of the diet of swift foxes in our study area (Lemons 2001). Our results support the hypothesis that conversion of prairies to agricultural fields contributed to the decline of the swift fox because both types of agricultural fields limited the distribution of swift foxes in our study site.

Only 1 of 1,204 swift fox locations was in CRP grasslands, even though this habitat represented 13% and 15% of the study area for adults and juveniles, respectively. Several factors might have contributed to the nearly complete avoidance of CRP grasslands, such as prey abundance, restricted mobility, and reduced vision. We did not determine prey abundances in the different habitat types of our study area. Any differences in prey abundances were likely not so great, however, as to cause the nearly total avoidance of this habitat. We believe that avoidance of CRP grasslands was probably a response to the tall and dense vegetation of this habitat type. Historically, swift foxes did not occupy tallgrass prairie regions in central North America (Egoscue 1979; Scott-Brown et al. 1987), indicating their distribution was limited by tall vegetation. Swift foxes are one of the smallest canid species in North America (Egoscue 1979; Scott-Brown et al. 1987), and tall vegetation probably limits their vision and movements. In our study site, the ungrazed vegetation of CRP grasslands was considerably taller than swift foxes, whose mean shoulder height ranged from 29 to 30 cm (Kamler 2002). Thus, swift foxes would have severely reduced vision when moving through this vegetation. Swift foxes were vulnerable to coyotes, as at least 33% of deaths were caused by coyote predation. Taller vegetation might increase their vulnerability to predation because swift foxes would be less likely to see coyotes approaching, whereas coyotes would move more efficiently than swift foxes in dense vegetation. The nearly complete avoidance of tall vegetation by swift foxes in our study area, even by less-experienced juveniles, suggested that swift foxes may be obligate users (Morrison et al. 1998) of relatively short vegetation. Although CRP took large amounts of agricultural lands out of production in the Great Plains, our results indicated that replanting nonnative grasses and prohibiting grazing on these areas may have, in fact, further restricted available habitat for swift foxes.

The home-range size of swift foxes in our study (11.7 km^2) was identical to that reported from Wyoming (11.7 km^2—Pechacek et al. 2000) and larger than that reported from Colorado (7.6 km^2—Kitchen et al. 1999). Survival of swift foxes in our study was similar to that reported elsewhere, where survival ranged from 0.40 to 0.69 (Kitchen et al. 1999; Olsen and Lindzey 2002; Sovada et al. 1998). However, the primary cause of death in our study, vehicle collisions, was greater than in previous studies. Previous researchers indicated that predation from coyotes was the primary cause of death (Carbyn et al. 1994; Kitchen et al. 1999; Olsen and Lindzey 2002; Sovada et al. 1998). In our study site, coyotes were heavily exploited by both local landowners and recreational hunters, which likely decreased the impacts of coyotes compared with other studies (Kamler 2002). All roadkill deaths of swift foxes occurred on a 2-lane highway within our study area. Swift foxes appeared naive to the threat of vehicles because they sometimes hunted in road ditches within a few meters of passing vehicles. Most roadkill deaths (3 of 5) were adults, suggesting that swift foxes never learned to avoid vehicles. When we censored from analysis the foxes that died from vehicle collisions, annual survival of adults increased to 72% and 66%, respectively, for the 2 years of the study. This indicates that survival would increase in areas with fewer roads. Thus, protection of relatively isolated areas with few roads would benefit swift foxes.

Our results indicated that swift foxes are habitat specialists because they depended nearly exclusively on short-grass prairie. Swift foxes avoided all human-altered habitats, including agricultural fields and CRP grasslands, which restricted their distribution on the study site. Thus, protection of native prairies might be necessary for the long-term conservation of swift foxes. In contrast, generalist species such as coyotes, red foxes, and gray foxes have thrived in human-altered habitats and have expanded their distributions since the 1800s (Bekoff 1982; Fritzell 1987; Kamler and Ballard 2002; Samuel and Nelson 1982). Unfortunately, swift foxes also are negatively affected by other canids, primarily coyotes and possibly red foxes (Sovada et al. 1998), thereby compounding the negative effects of human-altered habitats. Protection of native habitats for swift foxes also should account for the possible negative effects of other canids, especially coyotes, to ensure long-term viability of swift fox populations.

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