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DISPERSAL AND EXTRATERRITORIAL MOVEMENTS OF SWIFT FOXES (*VULPES VELOX*) IN NORTHWESTERN TEXAS

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ABSTRACT.—Dispersal plays an important role in the population dynamics of many carnivores, yet little information exists about the dispersal and movement patterns of swift foxes (*Vulpes velox*). We radio-collared and monitored 68 swift foxes for dispersal at 2 study sites in northwestern Texas from January 2002 to April 2004. Dispersal distance for juveniles (13.1 ± 0.3 km, *s*), adults (10 ± 4.7 km) and transients (25.4 ± 9.1 km) did not differ by age class ($F = 1.49$, df = 2, $P = 0.24$) or sex ($F = 0.23$, df = 1, $P = 0.63$) but differed by study site ($F = 4.72$, df = 1, $P = 0.04$). Mean dispersal distance from private ranches (PR) was greater than from National Grasslands (NG). Peak dispersal occurred during October–November (13 individuals) and January–February (7 individuals). Dispersal direction was influenced by land-use practices (i.e., toward rangelands and away from anthropogenic features). Direction of dispersal among foxes that occupied the NG was uniform ($n = 16$, $P = 0.08$), whereas foxes from PR dispersed in a northwesterly direction ($n = 18$, $P \leq 0.001$) away from a town and croplands. Three resident adult foxes made extraterritorial movements. Distances of these movements ranged from 0.2 km to 11.4 km. Distance of extraterritorial movements did not differ by sex ($F = 0.05$, $P = 0.83$), nor by duration of movement ($F = 1.11$, $P = 0.32$). Knowledge of movement distances and patterns is important for conservation and protection of swift foxes and their habitats.

Key words: swift fox, dispersal, extraterritorial movement.

Persistence of small isolated animal populations depends, in part, on their members' abilities to disperse (Brooker et al. 1999). Land-use practices that alter the landscape may interact or interfere with dispersal capabilities (Keitt et al. 1997). In fragmented landscapes, species that disperse over long distances will perceive a given habitat distribution as more connected than a species with short-range dispersal (Keitt et al. 1997). Landscape pattern can influence movement of species with varying degrees of magnitude. For example, those species that are more adaptable could potentially disperse greater distances and occupy more varied landscapes than those that are rigid in their requirements. Some have suggested that a mechanism must exist, either behavioral or evolutionary, that influences an animal to disperse among habitat patches in a disconnected landscape (Keitt et al. 1997).

Individual foxes sometimes make short-term excursions (hereafter called extraterritorial movements) outside of their established home ranges (Lidicker and Stenseth 1992). Many studies refer to this behavior as an extraterritorial movement. Extraterritorial movements have been documented for many species including wolverines (*Gulo gulo*), ferrets (*Mustela nigripes*), hyenas (*Crocuta crocuta*), meerkats (*Suricata suricatta;* Doolan and MacDonald 1996), dingoes (*Canis familiaris dingo;* Thomson et al. 1992), and wolves (*Canis lupus;* Van Ballenberghe 1983, Ballard et al. 1997). Extraterritorial movements are common among canid species, yet the nature and extent of these movements have been poorly documented (Van Ballenberghe 1983). In a study of wolves, Ballard et al. (1997) defined an extraterritorial movement as an individual temporarily leaving its territory for varying time periods and distances, and then returning to its original territory. These exploratory movements can be motivated by the need to search for a mate or to locate additional resources, better forage, or better living conditions. These excursions might also be a prelude to dispersal and occur commonly among younger age classes (usually juveniles).

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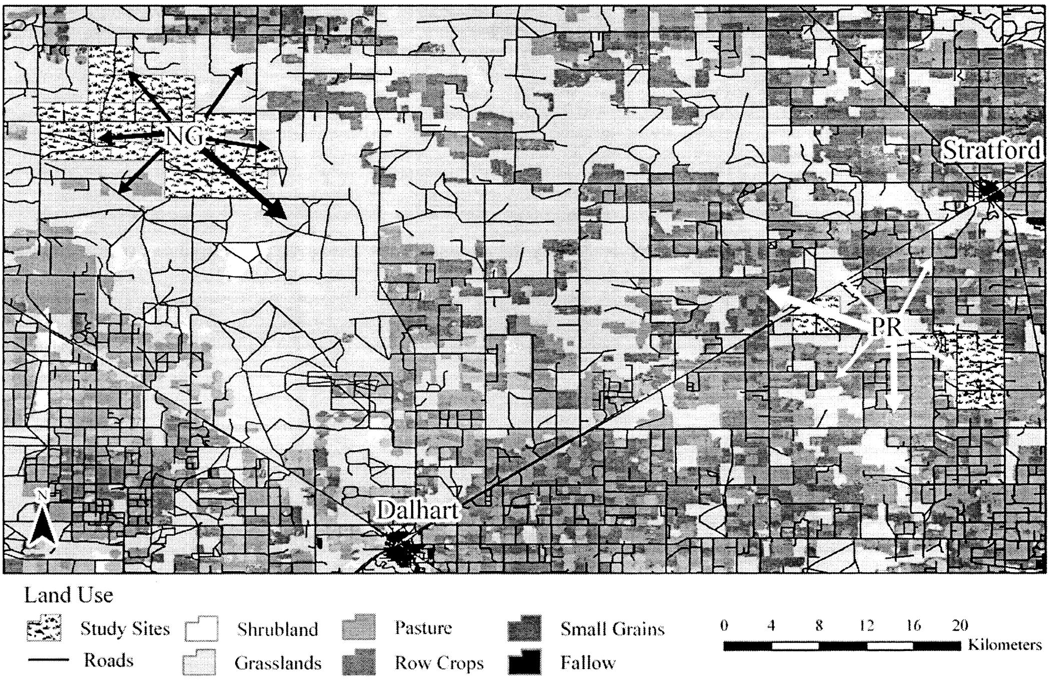

Fig. 1. Land-use map (1992) of Dallam County, Texas, including National Grasslands (NG) and Private Ranch (PR) study sites with swift fox dispersal directions from each study site, 2002–2004. The 2 largest arrows indicate our predicted directions of dispersal.

Few studies have focused primarily on dispersal and extraterritorial movements in swift foxes (Kamler et al. 2004a). Our objectives were to document and evaluate dispersal distances and directions of swift fox movements in fragmented and nonfragmented landscapes of northwestern Texas. We investigated dispersal distances of juvenile swift foxes and compared these distances to those traveled by resident and transient adult dispersers. We also determined survival rates of dispersing swift foxes. While monitoring swift foxes for dispersal we documented occasions of extraterritorial movements in adult swift foxes.

STUDY AREA

We conducted our research on two 100-km^2 study sites in northwestern Texas (Fig.1). Our Sherman County study area was on a private ranch (PR) located approximately 12 km south of Stratford, Texas (36°24′N, 102°19′W). The PR bordered Dallam County to the west and was surrounded by other ranches, Conservation Reserve Program (CRP) fields, and agricultural fields (Fig. 1). The PR consisted of rangelands, CRP lands, and cultivated fields; however, the PR was not a continuous tract of land. There was 3.5 km of land separating the 2 main sections of land. The 2nd study site was entirely native rangeland and included parts of the Rita Bianca National Grassland (NG) and private lands in Dallam County, Texas, approximately 55 km west of Stratford, Texas (36°3′N, 102°64′W). The National Grasslands were continuous tracts of land only divided by dirt roads (Fig. 1). Refer to Kamler et al. (2002) for a more detailed description of the study area.

METHODS

Capture and Handling

We captured and processed swift foxes from January 2002 to April 2004 with methods described by Kamler et al. (2002). Trapping occurred throughout both study sites and traps were placed opportunistically near active dens or where unmarked foxes were sighted. There were no mortalities associated with capture.

We did not trap between April and mid-June to avoid prolonged separation of mothers from their pups.

We recorded sex, age class, weight, and capture location for each fox. We also eartagged each swift fox with a unique identification number. We classified swift foxes as adults (>6 months old) or juveniles (young of the year). Age classes were based on morphological characteristics such as size, weight, and tooth wear at the time of capture. We placed radio-collars (40 g; Advanced Telemetry Systems, Inc., Isanti, MN) on swift foxes >6 months old. We monitored all animals until they recovered from sedation (Kamler et al. 2002).

Radiotelemetry

We radio-tracked collared foxes from January 2002 through July 2004. Throughout the study period, we obtained independent telemetry locations for each animal at least every other night during 1700–0700 hours when swift foxes are most active (Kilgore 1969). At least once per week foxes were tracked in the day to their dens. We considered locations independent if they were >3 hours apart. All radio-tracking was performed by a single observer with a vehicle-mounted, null-peak, 2,4-element Yagi antenna system. To prevent biased locations we began each radio-tracking session by finding a randomly chosen individual. Dispersing and lost foxes were relocated via aerial telemetry from a fixed-wing Cessna 173 (Cessna Aircraft Co., Wichita, KS). Radio-collars had an estimated 9-month lifespan; therefore, foxes that dispersed off the study site, or those that we were unable to recapture, were monitored from aircraft until May of the spring following capture.

We determined animal locations from azimuth angles of 40°–140°, made from readings (≤5 minutes between each location) from 3 or 4 telemetry locations (White and Garrott 1990). We calculated foxes' locations or point estimates using the maximum likelihood estimator in LOAS (location of a signal; Ecological Software Solutions, Sacramento, CA). Telemetry errors were based on readings of test collars placed in 30 different locations (White and Garrott 1990). Mean error was 47.4 m or 9° for known locations of reference collars. Locations of test collars were verified with a Garmin 72 geographic positioning system (GPS) unit (Garmin International, Inc., Olathe, KS). We tracked swift foxes to their diurnal resting sites (dens) using a handheld antenna 1–2 times per week. We recorded Universal Transverse Mercator (UTM) locations for each den with a GPS unit to assign grid coordinates (accuracy ≤5 m).

Dispersal

We used a Z test to compare dispersal rates between adults and juveniles. For dispersal analyses we defined residents as adults that (1) stayed in 1 area for about 1 year and (2) had a mate. Transients were adult foxes that were never observed with another fox and did not maintain a long-term continuous range. Transients were individuals who did not originate at our site, but rather moved through our study site, though they stayed long enough to be captured and relocated several times before moving off our study site. We classified juveniles as young of the year. Swift foxes tend to have circular home ranges (Kitchen et al. 1999, Kamler 2002), and Karki (2003) reported mean seasonal home ranges of <6 km^2 for adult foxes in Colorado. Koopman et al. (2000) defined dispersal for kit foxes (*Vulpes macrotis*) as movements >1.65 km from the natal range. Therefore, we classified fox movement ≥2 km from the center of home ranges as dispersal if individuals did not return or overlap their original home range (Kamler et al. 2004). We used the standard of Koopman et al. (2000) to calculate date of dispersal as the median of the date of the last location within the home range and the 1st location >2 km from the home range. Home ranges of juveniles, or natal range, encompassed all den locations of parents and, if parents were unknown, we used the initial capture locations as the center of the natal range (Koopman et al. 2000). For resident adult dispersing foxes, we calculated dispersal distance as the length between the center of the original home range and the farthest known location before contact was lost. For transients we used the initial capture locations and all relocations for each individual as the center of its range. In some instances there were <30 locations for a transient's known range on our study site. We suspect these individuals were attempting to find permanent residence and were unsuccessful within our study boundary. To avoid seasonal shifts confounding our results, we defined dispersing foxes such that the area they occupied before movement did not overlap with the area they occupied after movement. We used an analysis of variance (PROC GLM: dispersal distance = age * sex * location) and Tukey's post hoc analysis to assess the difference in dispersal distances of foxes.

We classified dispersal direction (direction of recovery from last known location) as northwest (210°–359°), northeast (0°–90°), southeast (91°–180°), or southwest (181°–209°). Angles of specified dispersal were chosen based on direction to the largest section of continuous rangeland from the center of each study site. We tested uniformity in dispersal direction using a Hodges-Ajne test for uniformity and a Batschelet test for uniformity versus a specified angle (Zar 1999). The PR had the largest rangeland available between 270° and 0°, so we used the northwesterly direction toward 315°; for NG we used the same criteria and chose the southeasterly direction toward 135°. We used SAS 8.02 (SAS Institute, Inc., Cary, NC) for all other statistical analyses and significance was determined at $\alpha = 0.05$.

Extraterritorial Movement

To determine if swift foxes showed signs of extraterritorial movement, we first used the Animal Movement Extension (Hooge et al. 1999) in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA) to calculate a 95% kernel home range for resident and juvenile swift foxes. Each fox had ≥35 locations and we only considered movements beyond the 95% kernel as possible extraterritorial movements. To be conservative in identifying movements for these analyses, we only used movements that were ≥2 km with a return. We used a 1-way ANOVA to compare distances (distance = sex) and duration (duration = sex) of movements between sexes. Sample sizes were too small to compare between study sites. Minimum straight-line distance was measured from the farthest movement location to the closest home range boundary defined by the 95% kernel estimate. The number of days was counted from the 1st movement location outside the home range to the next location within the home range.

RESULTS

From January 2002 to April 2004, we radiocollared 68 swift foxes (43 adults, 25 juveniles) for dispersal and monitored these foxes through the dispersal period. Eighteen of 25 juveniles dispersed and survived until the end of May; 4 died before dispersal characteristics could be determined; and we eventually lost radio contact with 3 foxes. Adults were either transients or were residents that stayed on the study site, though they still moved without return (Table 1). Juveniles had higher dispersal rates (86%) than adults (8%; $Z = 4.39$, $P \leq 0.001$).

Dispersal distances did not differ by age class ($F = 1.49$, df = 2, $P = 0.24$) or sex ($F = 0.23$, df = 1, $P = 0.63$). However, dispersal distances differed by study site ($F = 4.72$, df = 1, $P = 0.04$). Swift foxes on the PR dispersed greater distances than those on the NG (Table 2). Peak dispersal occurred during October–

TABLE 1. Average dispersal distances of juvenile, transient, and adult swift foxes in northwestern Texas, 2002–2004.

Status	n	Dispersal distance (km) $\bar{x} \pm s$	Range
Juvenile	18	19.5 ± 18.7	2.5–63.5
Transient	10	29.4 ± 24.2	2.1–61.0
Resident	5	34.0 ± 26.5	7.7–67.7

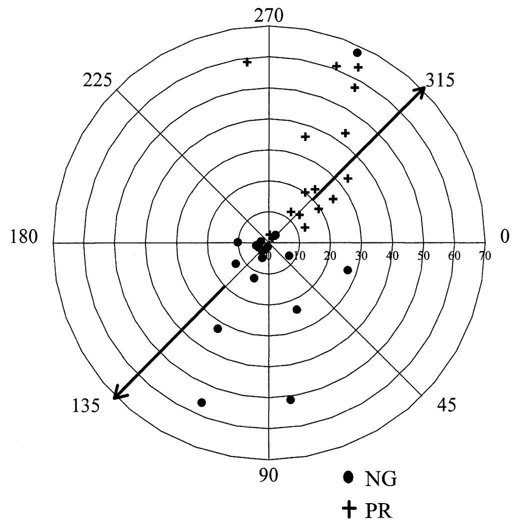

Fig. 2. Direction and distance of swift fox dispersal on the National Grasslands (NG) and Private Ranch (PR) study sites, 2002–2004. Arrows indicate the predicted directions tested.

TABLE 2. Average dispersal distances of juvenile, transient, and resident adult swift foxes on National Grasslands (NG) and on private ranches (PR) in northwestern Texas, 2002–2004.

			Dispersal distance (km)	
Location	Status	n	$\bar{x} \pm s$	Range
NG	Juvenile	7	9.3 ± 8.7	2.5–27.1
	Transient	6	25.4 ± 22.2	3.3–54.4
	Resident	3	43.8 ± 31.8	7.7–67.8
TOTAL		16	21.8 ± 22.5	2.5–67.8
PR	Juvenile	11	25.9 ± 20.8	2.6–63.5
	Transient	4	35.5 ± 29.1	2.2–61.0
	Resident	2	19.3 ± 8.3	13.5–25.6
TOTAL		17	27.4 ± 21.4	2.2–63.5

TABLE 3. Summary of swift fox extraterritorial movements in northwestern Texas, 2002–2004. NG = National Grasslands, PR = private ranches, F = female, M = male.

Foxes	Movements	Total duration (days)	Movements >2 km	Duration >2 km (days)	Greatest distance (km)
NGF 254	1	1	0	0	0.20
NGF 266	4	8	2	2	3.41
NGF 277	1	19	1	6	8.94
NGM 078	4	22	1	2	3.98
NGM 090	5	23	0	0	0.39
NGM 249	5	23	2	10	9.20
NGM 270	19	44	18	41	4.20
NGM 271	2	12	2	12	5.00
NGM 276	12	104	3	33	11.39
PRF 040	12	28	1	3	7.22
PRF 095	7	28	1	1	8.73
PRM 099	12	41	4	28	11.43
PRM 224	1	1	0	0	1.71

November (n = 13 foxes), with a 2nd dispersal pulse in January–February (n = 7 foxes).

We determined the dispersal direction of 35 foxes (16 from NG, 18 from PR). Direction was not uniform for all foxes ($C_{0.05\ (2),\ 34} = 8$, $P = 0.03$), so we tested a specified direction of dispersal based on fragmented or continuous landscapes (NG 135°, PR 315°; Fig. 2) for each study site. Dispersal directions for foxes from NG were not directional ($C_{0.05\ (2),\ 16} = 4$, $P = 0.08$), whereas foxes from PR moved directionally toward 315° ($C_{0.05\ (2),\ 18} = 1$, $P \leq 0.001$). Dispersal directions for all foxes were northeast (10% NG, 7% PR), southeast (28% NG, 7% PR), southwest (7% NG, 3% PR) and northwest (7% NG, 31% PR). Swift foxes dispersed towards rangelands at greater frequencies than towards other land types (Fig. 1).

We monitored 13 resident adults, only 3 of which had movements <2 km outside a 95% confidence interval (Table 3). Movement distances ranged from 0.2 km to 11.4 km. Average movement distance did not differ between sexes ($F = 0.05$, $P = 0.83$), nor by duration of movement ($F = 1.11$, $P = 0.32$).

DISCUSSION

Knowledge of dispersal is important to the management of many species. The average juvenile dispersal distances that we report were similar to those reported in other studies of swift foxes ($\bar{x}$ = 14.7 km in Kansas, Sovada et al. 2003; $\bar{x}$ = 12.6 km in Colorado, Schauster 2001; $\bar{x}$ = 12.1 km in Canada, Moehrenschlager 2000). Sovada et al. (2003) reported 3 juvenile foxes dispersing ≥20 km with 32 km being the greatest distance. We documented 9 foxes that dispersed ≥20 km. Four were juveniles with the greatest dispersal distance being

63 km; and 5 were adults with the greatest dispersal distance being 67 km (Table 2). Unlike Kamler et al. (2004), we did not have juvenile females that were philopatric to the natal home range. However, 6 juveniles (2 females, 4 males) stayed ≤5 km from their natal home range. No juveniles were found denning with the parents. Juvenile males tended to use the periphery of their natal home ranges. Timing of dispersal by juveniles was similar to that of Sovada et al. (2003) in Kansas, where peak dispersal occurred in October–November; however, dispersal timing in our study had a 2nd peak in January–February. Kilgore (1969) in Oklahoma and Covell (1992) in Colorado reported dispersal occurring earlier during August–September and September–October.

Transient foxes may be dispersing foxes that were displaying extraterritorial movements, because they moved into our study area and then out of our study area before settling down. Ultimately, we do not know whether these foxes moved onto our study site and then moved large distances off the study site.

The predominant direction of dispersal by swift foxes from PR was northwesterly. This direction was likely influenced by the presence of the town of Stratford located to the northeast and the predominance of cropland to the southeast and southwest (Fig. 1). We believe that the direction of dispersal in this study can be explained by swift fox avoidance of crop lands and areas with tall-structured vegetation such as Conservation Reserve Program (CRP) lands (Kamler 2002, Nicholson 2004). Nicholson et al. (2006) reported that swift foxes use short-structured vegetation more than would be expected.

Determining a justifiable distance for classifying specific movements as extraterritorial can be difficult. Foxes that moved <2 km could have found the resources they were looking for without the need to move any farther. However, those movements could also be extreme outliers from the determined 95% kernel home range. Average movement distance for all foxes was 6.3 km, with 2 foxes exploring distances ≥11 km with return. We had evidence of mate swapping following bouts of extraterritorial movements by resident adults. Kitchen (2004) described extra-pair copulation, breeding trios, and mate switching in Colorado. Our findings were similar in that the new mates taken by adult foxes were younger, and mate swapping occurred with neighboring foxes with prior short-term exploratory movements.

The dispersal distances we report suggest that swift fox subpopulations have a reasonable chance for interchange and may be better connected than previously thought. The dispersal pattern we observed suggests that swift foxes were capable of moving long distances using suitable grassland habitat to facilitate that movement. Dispersal, no matter what the distance, helps maintain genetic diversity within a population.

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