RELATIONSHIPS OF SWIFT FOXES AND COYOTES

IN NORTHWEST TEXAS

by

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ABSTRACT

Due to severe reductions in their distribution and numbers, the swift fox (*Vulpes velox*) was classified as warranted, but precluded as a threatened species by the U. S. Fish and Wildlife Service from 1995 to 2001. Several factors were likely responsible for the decline of the swift fox in the western Great Plains, including habitat loss and competition with coyotes (*Canis latrans*). From 1998 to 2001, we radio-collared and monitored 88 swift foxes and 29 coyotes at 2 study sites in northwestern Texas to investigate the ecology and relationships of both species. Initial results suggested that higher coyote numbers on site 1 resulted in lower survival, lower density, and lower recruitment of swift foxes compared to site 2. To test this hypothesis, we experimentally removed coyotes on site 1 during the final year of the study. Subsequently, swift foxes had increased survival, increased density, increased recruitment, and exhibited a source population due to lower predation by coyotes. We also found that high mortality from coyote predation affected the spatial distribution, mating system, and group structure of swift foxes. These results indicate that high coyote numbers can suppress swift fox populations due to heavy predation.

To determine if habitat loss also negatively affected swift foxes, we examined habitat selection of swift foxes at 2 spatial scales on site 2, which was comprised of shortgrass prairies grazed by cattle, non-native (CRP) grasslands that were ungrazed, dry-land agriculture, and irrigated agriculture. Habitat use was similar at both spatial scales, as swift foxes preferred shortgrass prairies, but used dry-land agriculture less than expected, and nearly completely avoided irrigated agriculture and CRP grasslands. These results indicate that swift foxes are habitat specialists, thus protection of shortgrass prairies might be necessary for their long-term existence.

We documented that the social organization of swift foxes was based entirely on female territories, as adult males emigrated after adult female deaths, but not vice versa. A female-based social organization, previously unknown among canids, likely evolved in swift foxes from the reduced importance of food provisioning by males.

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CHAPTER I

INTRODUCTION

The following chapters constitute partial fulfillment of the requirements for the degree of Doctor of Philosophy in Wildlife Science for the Graduate School at Texas Tech University. These chapters are the result of research conducted on swift foxes and coyotes on two study sites in northwestern Texas from 1998 to 2001. Chapters II through VII consist of six manuscripts that are intended for submission to peer-reviewed journals, whereas chapter VIII is a summary of all the chapters. Because chapters were written in formats for different journals, they might have different subheadings and reference styles. Chapter II focuses on the trapping methodology developed and used during the research. Chapters III and IV discuss the social organization, mating system, and group structure of swift foxes on both study sites. Chapter V documents the habitat use of swift foxes on the fragmented landscape of one study site. Chapter VI documents the spatial relationships of swift foxes and coyotes on one of the study sites. Chapter VII documents the effects of coyotes on density, survival, and recruitment of swift foxes on both study sites. All chapters represent my ideas, analyses, and writing ability. Each chapter has several co-authors who were determined using guidelines provided by Dickson and Conner (1978) and the CBE Style Manual Committee (1994). Authorships for chapters are as follows:

Chapter II. Jan F. Kamler, Warren B. Ballard, Rickey L. Gilliland, and Kevin Mote.

Chapter III. Jan F. Kamler, Warren B. Ballard, and Kevin Mote.

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Chapter V. Jan F. Kamler, Warren B. Ballard, Ernest B. Fish, Patrick R. Lemons, Kevin Mote, and Celine C. Perchellet.

Chapter VI. Jan F. Kamler, Warren B. Ballard, Rickey L. Gilliland, and Kevin Mote.

Chapter VII. Jan F. Kamler, Warren B. Ballard, Rickey L. Gilliland, Patrick R. Lemons, and Kevin Mote.

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CHAPTER II

IMPROVED TRAPPING METHODS FOR SWIFT FOXES AND SYMPATRIC COYOTES

Abstract

We compared capture rates of 2 types of trapping methods, single-set boxtraps and reverse double-set boxtraps, for capturing swift foxes (*Vulpes velox*) and other mesocarnivores. We also evaluated the use of pan-tension devices on No. 3 Soft Catch traps for capturing sympatric coyotes while excluding swift foxes. We captured 87 swift foxes 302 times in boxtraps in northwest Texas from August 1998 to January 2001. Capture rate for reverse double-set boxtraps was 48% higher (P=0.003) than single-set boxtraps, as reverse double-set boxtraps allowed easier access to bait and allowed for capture of 2 swift foxes. Capture rates between the 2 trap sets were not different (P=0.937) for striped skunks (*Mephitis mephitis*), suggesting that advantages of reversed double-set traps were unique to swift foxes. Use of pan-tension devices set at 2.15 kg on No. 3 Soft Catch traps allowed us to capture 32 sympatric coyotes (*Canis latrans*) while excluding swift foxes, which likely would have sustained serious injuries if captured. The capture rate of No. 3 Soft Catch traps for coyotes was 94%, whereas the exclusion rate for swift foxes was 100% despite 88 visits in 562 trapnights.

Introduction

From 1995 to 2001, the swift fox (*Vulpes velox*) was classified as warranted, but precluded as a threatened species by the United States Fish and Wildlife Service. Because of this classification, research on swift foxes recently increased throughout their range. During the 1990s, swift foxes were captured for research purposed in 7 states, and were re-introduced into Canada (Luce and Lindzey 1997, Schmitt 2000). In addition to these programs, swift foxes are often trapped along transects to determine presence/absence and monitor long-term population trends (Luce and Lindzey 1997, Schmitt 2000). Despite the wide use of boxtraps for capturing swift foxes, there is no published information concerning methodology or comparing capture rates of different types of trap sets. This information can be important to researchers and biologists, as the most efficient trap set may be preferred for capturing the nocturnal and secretive swift fox.

Coyotes (*Canis latrans*) are trapped for livestock depredation management, game management, and recreational purposes throughout the western United States (Cooke 1995, Gilliland 1995, Ballard et al. 2001), often in areas where they are sympatric with swift foxes or kit foxes (*Vulpes macrotis*). To reduce captures of nontarget species, including foxes, the United States Department of Agriculture's Wildlife Services has mandated since 1989 the use of pan tension devices in all of their operations (Phillips and Gruver 1996). Many researchers and recreational trappers also use pan tension devices to exclude nontarget species when capturing coyotes (Gruver et al. 1996, Kamler et al. 2000b). On No. 3 and larger leghold traps, pan tension devices are needed to exclude swift foxes because such a relatively large trap would likely cause serious damage to smaller animals (Kamler et al. 2000b). Although the effectiveness of pan tension devices for excluding nontarget species has been reported elsewhere (Phillips and Gruver 1996), the effectiveness for excluding large numbers of swift foxes has not been studied. This information would be valuable to government and recreational trappers, as swift foxes are fully protected in some western states, and have more restricted seasons than coyotes in other western states. Additionally, if swift or kit foxes cannot be effectively excluded from leghold traps set for coyotes, then the use of leghold traps could be severely restricted if swift or kit foxes are federally listed as a threatened or endangered species in the future.

The purpose of this paper was to compare capture rates of swift foxes using 2 different trap sets: single-set boxtraps, and reverse double-set boxtraps. Capture rates of striped skunks (*Mephitis mephitis*) was also compared to determine if effectiveness of different trap sets was similar between species. We also evaluated the use of Paws-I-Trip pan-tension devices on No. 3 Soft Catch traps for capturing sympatric coyotes while excluding swift foxes.

Study Area

We conducted research on 2 study sites in northwest Texas: a private cattle ranch on the border of Dallam and Sherman counties (36°24'N, 102°19'W), and the Rita Blanca National Grasslands in westcentral Dallam County (36°31'N, 102°64'W). Both study sites consisted of shortgrass prairies dominated by buffalograss (*Buchloe dactyoides*) and blue grama (*Bouteloua gracilis*), and were adjacent to agriculture and Conservation Reserve Program fields. Trapping occurred from August 1998 to January 2001 during all seasons except summer.

Methods

Swift foxes were captured using Havahart® cage traps (Woodstream Corp., Lititz, Pennsylvania, USA), referred to hereafter as boxtraps. Boxtraps (25.4 × 30.5 × 81.3 cm) were baited with prey species, including black-tailed prairie dogs (*Cynomys ludovicianus*), black-tailed jackrabbits (*Lepus californicus*), and desert cottontails (*Sylvilagus audubonii*), and checked once daily. Bait was obtained opportunistically from roadkill and collected after recreational hunters left prairie dog towns. Bait was frozen until time of use and carcasses were cut into smaller pieces. To prevent swift foxes from taking bait without springing traps, bait was tied securely to the bottom of the trap. Boxtraps were also staked to the ground to prevent swift foxes and other animals from moving the traps. Trapping effort was initially concentrated near the center of both study areas and expanded outward as capture of unmarked foxes decreased. Our trapping methods were approved by the Texas Tech University Animal Care and Use Committee.

During the study, two types of trap sets were used: Single-set boxtraps, and reverse double-set boxtraps. During preliminary trapping, we set a single boxtrap at each trap location (hereafter single-set boxtraps), as typically done in most studies. However, we noticed on several occasions that swift foxes would often dig at the rear of the boxtrap to get at the bait, apparently unaware that the bait could be obtained through the open door on the front of the boxtrap. Placing a second boxtrap facing the opposite direction adjacent to the first boxtrap (hereafter reverse double-set boxtraps) prevented this activity. Thus, swift foxes investigating bait at the back of 1 trap would clearly see the bait in the second trap through that open door. Also, since we observed swift foxes laying on the outside of boxtraps next to captured foxes (Kamler et al. 2000a), additional foxes potentially could be captured if an adjacent boxtrap was present. Throughout the study, both types of trap sets were used randomly along trap lines.

We recorded the following data each day boxtraps were checked: species captured, and type of trap set. Capture rate was defined as the number of animals captured, divided by the number of trapnights. Capture rate was calculated from individual traps in each set type, thus 1 double-set = 2 trapnights. Preliminary analyses indicated that capture rates for each set type were similar among years and between study sites, and therefore data were pooled across years and study sites. Capture rates were compared between the 2 set types using Yates-corrected chi-square tests. High numbers (*n*=258) of a nontarget species, striped skunks, also were captured in boxtraps during the study. Therefore, we compared capture rates for striped skunks to determine if effectiveness of different trap sets was unique to swift foxes, or was similar to another mesocarnivore species.

Coyotes were captured with Victor Soft Catch® No. 3 traps (Woodstream Corp., Lititz, Pennsylvania, USA). All traps were equipped with the Paws-I-Trip™ pan tension system (M-Y Enterprises, Homer City, Pennsylvania, USA) to reduce capture of smaller nontarget animals (Phillips and Gruver 1996). The Taos Lightening Spring™ (J.C.

Conner Trapping Supply, Newcomerstown, Ohio, USA), a double torsion spring, was also added to traps to increase capture rates (Gruver et al. 1996). Traps were also equipped with a metal baseplate (3/16" thick) with center D-ring for chain attachment, and a 38-cm chain equipped with an in-line T-bar shock spring and 2 stop-shock springs. Soft Catch traps were set according to Woodstream Corporation's recommended procedures described by Linhart and Dasch (1992). Before each trap was set, a device that measured pan tension was used to set tension on traps at 2.15 kg. The tension of 2.15 kg was used because that was within the weight range of swift foxes captured during the study. Trap sets were baited with a variety of baits, urines, and lures and checked once daily. Trapping effort was concentrated in areas where swift foxes were captured to increase the likelihood that study animals shared the same area for purposes of another study. Leghold traps were placed along animal trails and near coyote sign to increase capture success. All trapping of coyotes was conducted by R. L. Gilliland, a Wildlife Services employee with > 25 years of trapping experience.

We recorded the following data each day leghold traps were checked: Animals captured, animals that sprung traps, and animal tracks on pan. A visit was defined as an incident when an animal stepped on or within the margin of the pan and was either captured or excluded. An exclusion was defined as when an animal stepped on the pan but did not spring the trap. Capture rate for coyotes was defined as the number of coyotes captured divided by the number that stepped on pans (Phillips and Gruver 1996). Exclusion rate for swift foxes was calculated by dividing the number of swift foxes that were excluded by the number that stepped on the pan (Phillips and Gruver 1996).

Results

Eighty-seven swift foxes were captured 302 times in 2,498 trapnights from August 1998 to January 2001. The capture rate of swift foxes in reverse double-set boxtraps, 14.1 % (198 captures/1,406 trapnights), was greater (Yates chi-square = 9.10, *P*=0.003) than in single-set boxtraps, 9.5 % (104 captures/1,092 trapnights). In contrast, the capture rate of striped skunks in reverse double-set boxtraps, 10.2 % (144 captures/1,406 trapnights), did not differ (Yates chi-square = 0.01, *P*=0.937) from single-set boxtraps, 10.4 % (114 captures/1,092 trapnights).

Two swift foxes were captured in adjacent traps 28 times, comprising 28% of the total captures in reverse double-set boxtraps. Swift foxes captured in adjacent traps consisted of juvenile litter mates (*n*=13), a juvenile and adult (*n*=13), and an adult mated pair (*n*=2). In contrast, 2 striped skunks were captured in adjacent traps just 7 times, comprising only 10% of the total captures in reverse double-set boxtraps.

The capture rate of coyotes was 94% (32 captured/34 stepped on pan) using No. 3 Soft Catch traps with a pan tension set at 2.15 kg. The exclusion rate of the No. 3 Soft Catch traps for swift foxes was 100% (88 foxes excluded/88 stepped on pan) in 562 trapnights.

Discussion

Capture rates of swift foxes can be increased nearly 50% using reverse double-set boxtraps as compared to the traditional single-set boxtraps. We believe that reverse double-set boxtraps increased capture rates for 2 reasons: 1) They allowed swift foxes easier access to bait, and 2) they allowed for capture of 2 swift foxes. As stated previously, by placing 2 adjacent traps facing opposite directions, swift foxes could clearly see bait through the open door of one trap if they investigated the back of the other trap. Additionally, because swift foxes are attracted to other foxes captured in boxtraps (Kamler et al. 2000a), swift foxes could be captured in adjacent traps as they investigated other captured foxes.

Some researchers use boxtraps with doors that open on both ends to capture swift foxes (Scott-Brown et al. 1987). We believe that these boxtraps would be more efficient at capturing swift foxes than single-door boxtraps, as 2-door boxtraps would alleviate the problem concerning access to bait by swift foxes. However, even for 2-door boxtraps, placing 2 traps together would still likely increase capture rates as opposed to single set traps, because multiple swift foxes could be captured together in adjacent traps.

Because capture rates were similar between trap sets for striped skunks, the greater efficiency of reverse double-set boxtraps may be unique to swift foxes. Striped skunks appeared to be more persistent at obtaining bait from traps than swift foxes. For example, we observed that if striped skunks dug at the rear of boxtraps to obtain bait, they eventually would go around to the open door and enter from the front. In contrast, swift foxes would dig at the rear of the boxtraps then apparently would leave after not obtaining the bait. Also, swift foxes are more social than striped skunks (Rosatte 1987, Scott-Brown et al. 1987); and therefore, striped skunks are less likely to investigate other striped skunks captured in traps. The lower occurrence of double captures for striped skunks compared to swift foxes support this conclusion.

The 94% capture rate of coyotes in our study was similar to other studies that used Paws-I-Trip pan tension devices on leghold traps (Phillips and Gruver 1996). This capture rate was also similar to other studies that used No. 3 Soft Catch traps to capture coyotes (Phillips et al. 1992, Phillips and Mullis 1996). Swift foxes visited these trap sets on a regular basis most likely because of the lures and urines that were used to attract coyotes. On several occasions, swift foxes would dig up leghold traps without springing them. We would move trap sets after these instances to avoid future risk of traps springing due to increased pressure applied by foxes digging.

Our results indicate that in areas where coyotes and swift foxes are sympatric, coyotes can be effectively captured and swift foxes can be effectively excluded from No. 3 Soft Catch traps equipped with pan tension devices set at 2.15 kg. This information may be valuable to researchers and trappers because swift foxes, and closely related kit foxes, are sympatric with coyotes over most of the western United States. Since swift foxes have closed or restricted trapping seasons in all the states where they occur, coyote trapping can occur in those states with little fear of capturing swift foxes if pan tension devices are set at the appropriate weight. In a study that covered several western states, Phillips and Gruver (1996) used leghold traps with pan tension devices set at 1.4-1.8 kg that excluded 15 swift and kit foxes. However, whether that lower weight could exclude higher numbers of swift or kit foxes was not known. Regardless, our study indicates that pan tension devices can be set as high as 2.15 kg on No. 3 leghold traps without reducing the capture rate of coyotes, while excluding high numbers of swift foxes.

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CHAPTER III

A FEMALE-BASED SOCIAL ORGANIZATION AMONG CANIDS

Introduction

Members of the family Canidae are distinguished from other carnivore families by exhibiting monogamy and male care of the young (Moehlman 1989, Geffen et al. 1996). Although canids exhibit a high degree of flexibility in their social organization within and among species (Moehlman 1989, Geffen et al. 1996), a social organization based on female territories, which is more typical of other carnivore families, was unknown among the 36 species within Canidae. Here we describe the social organization of a small canid, the swift fox (*Vulpes velox*), where adult females maintained territories and family structure, and adult males emigrated.

The swift fox is a small canid (2-3 kg) that occurs in the western grasslands of the United States and Canada. Their diet varies seasonally, with a predominance (> 80%) of insects during summer, but switching primarily to small rodents during winter (Kitchen et al. 1999, Lemons 2001). Swift foxes are secretive, as they are primarily nocturnal and are the most den-dependent canid species in North America (Egoscue 1979). Adult social groups reportedly consisted of a monogamous pair, with an occasional trio of two females and one male (Egoscue 1979).

Methods

Our field work occurred from May 1998 to January 2001 on two 100-km^2 study sites consisting of shortgrass prairie in northwestern Texas, U.S.A. Swift foxes were captured in boxtraps, equipped with radiocollars, and then monitored on a weekly basis. During the 2.5 year study, 88 swift foxes were captured and monitored, and these comprised 8-10 separate family groups per year.

Results

All juveniles ($n = 53$) were independent of the mother (i.e., no longer denned together) by 6 months of age, and most dispersed from their natal territory during their first winter. However, four juvenile females did not disperse, and subsequently stayed with their respective family units for an additional year before dispersing. Nonbreeding females within family groups are common among canid species (Moehlman 1989). We also recorded two cases of communal denning, where two adult females had litters and shared a common den with one adult male. Although communal denning has not previously been reported for swift foxes, it has been reported for other fox species (Frame and Frame 1976, Moehlman 1989).

The above information indicates that swift foxes have a female-biased social group, similar to that reported for other fox species. However, we also documented the following unusual features that indicated their social organization was based entirely on female territories. (1) Three cases in which a reproductive adult female died, and subsequently the associated adult male emigrated from the territory. After the female deaths, all three males began making extra-territorial movements within 1-2 weeks, and finally emigrated from the area within 5-7 weeks. If two females denned communally and only one died, the male did not emigrate. (2) Early dispersal occurred for three of five juveniles after the death of their mothers. The three juveniles dispersed within 3-5 weeks of their mothers' death, even though it was 1-4 months before the typical dispersal period. (3) Two cases in which the adult male died, but both adult females and five associated juveniles never exhibited unusual movements. A transient male eventually replaced the dead male in each case. (4) One case in which an adult female maintained her territory alone for 13 months, even through a reproductive season during which she did not breed.

Discussion

We conclude from the above information that the social organization of swift foxes is based entirely on female territories, in addition to the occurrence of non-breeding females and occasional polygyny. If neither adult died, mated pairs tended to stay together, suggesting that monogamy is also exhibited among swift foxes. Compared to previous studies, deaths of adults (n = 11) in our study were high, due primarily to coyote (*Canis latrans*) predation (7 of 11), which allowed us on several occasions to monitor the movements of others after the death of an individual. Previous studies tended to focus on home range size and overlap, and did not discuss movements of family members after an adult's death. However, there were two confirmed cases of adult male emigration after adult female deaths during a recent study in New Mexico (unpublished data, R. L. Harrison, Univ. New Mexico).

Variation in social organization among canid species has been related to body size, where small species exhibit female-biased sex ratios with occasional polygyny, and large species exhibit male-biased sex ratios with occasional polyandry (Moehlman 1989, Geffen et al. 1996). Among large canids, an extreme form of a male-biased social organization was reported among African hunting dogs (*Lycaon pictus*), where groups of males maintained territories and family units, and females emigrated (Zabel and Taggart 1989). Under that social system, although females produced and nursed pups, groups of males were the limiting factor, as they were necessary to provision food in the form of medium and large-sized ungulates (Zabel and Taggart 1989). Among medium-sized canids, such as coyotes, blackbacked jackals (*C. mesomelas*), and even red foxes (*Vulpes vulpes*), adult males maintain territories and provide food to young in the form of medium and small-sized prey (Moehlman 1989). Among these species, after the death of an adult male, litters often fail (Zabel and Taggart 1989) and adult females disperse (Hamlin 1997, Gese 1998), suggesting that food provisioning by males is necessary for survival of young, and males themselves are important to the social structure of the family group. In contrast, among the small, insectivorous bat-eared foxes (*Otocyon megalotis*), adult females exhibited communal denning and were known to maintain territories and successfully raise litters in the absence of males (Moehlman 1989), suggesting that food provisioning by males was not necessary. Similarly, among the small, insectivorous Blanford's foxes (*V. cana*), although males often accompanied young, they did not provide food, as pups were entirely dependent on their mother's milk until they began to forage for themselves (Geffen and Macdonald 1992). The major food resource of small, insectivorous foxes are readily available to young (i.e., insects), and insects are not large enough to merit transmission back to the den by adults (Geffen and Macdonald 1992). Additionally, because most fox species do not regurgitate (Geffen and Macdonald 1992), males of insectivorous species likely provide little food to young. A similar pattern occurred among swift foxes. During our study, at least one female successfully raised pups without a male. Additionally, although male swift foxes often accompany young (Pruss 1994, Lemons 2001) and sometimes bring food back to the den (Pruss), their diet is primarily insectivorous during summer when young were weaned (Kitchen et al. 1999, Lemons 2001), suggesting that food provisioning by males may not be necessary. We hypothesize that the minimal role of males in raising young allowed for the evolution a female-based social organization in swift foxes. Under this social system, reproducing females are the limiting factor, whereas adult males are easily replaced as their food provisioning is not necessary. Whether a female-based social organization occurs among other small, insectivorous fox species is unknown, but deserves further investigation.

Our results indicate that variation in social systems among canid species are related to diet and importance of food provisioning by males, and not necessarily body size, although these factors might be related (i.e., insectivorous fox species tend to be small). Thus, among most canid species, males provide food for young and consequently share or even dominate the structure of the family group. However, if food provisioning by males is not required due to a highly insectivorous diet, as is the case with swift foxes, then males have a minimal role in the family structure and social organization.

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CHAPTER IV

VARIATION IN MATING SYSTEM AND GROUP STRUCTURE OF SWIFT FOXES RELATED TO MORTALITY AND DENSITY

Abstract

We examined 26 reproductive groups of swift foxes, *Vulpes velox*, from both a high and low density during 3 field seasons in northwestern Texas. Although populations were only separated by 40 km, swift foxes exhibited polygyny, communal denning, and nonbreeding females in the area of high density, whereas only monogamy with no additional females occurred in the area of low density. Density did not appear to be related to habitat or food resources, as vegetation and diets were similar between sites. Furthermore, home ranges were larger on the area of high density, suggesting that foxes were not food stressed in the area of low density. Spring density of swift foxes was related to differences in predation from coyotes, *Canis latrans*, as coyotes were the major cause of fox mortality in the area of low density, but not in the area of high density. Our data indicate that differences in density from high mortality can affect the mating system and group structure of swift foxes, even over short distances. Although previous research indicated that variation in social systems among canids was related to bottom-up forces (i.e., food, habitat), our study indicates that variation in social systems also can be related to top-down forces (i.e., predation, displacement by larger competitor).

Introduction

Polygamy is the predominate mating system of most mammals, occurring in >97% of species studied (Kleiman 1977). The major exception occurs within the family Canidae, as most canid species tend to exhibit monogamy (Kleiman 1977). Monogamy within Canidae likely evolved in relation to pair bonding and male care of the young (Kleiman & Eisenberg 1973). There is considerable interspecific variation in mating systems among canids, however, and both polygamy and monogamy have been exhibited (Bekoff et al. 1981; Moehlman 1989; Geffen et al. 1996). Several factors are suggested to contribute to the variation of mating systems among canid species, including body size (Moehlman 1989) and resource availability (Geffen et al. 1996).

Also unique to canids, intraspecific variation in mating systems may be as great as interspecific variation, as both polygyny and monogamy have been exhibited within the same species (Moehlman 1989). Food availability, habitat availability, and resource dispersion have been suggested as major factors contributing to intraspecific variation in reproductive strategy and group structure in canids (Macdonald 1983, Geffen et al. 1996). For example, the social system of golden jackals, *Canis aureus*, varied considerably with food dispersion and abundance (Macdonald 1979). Group sizes of gray wolves, *C. lupus*, and coyotes, *C. latrans*, often depend on prey size and availability (Bekoff & Wells 1980; Harrington et al. 1982; Messier & Barrette 1982). Populations of arctic foxes, *Alopex lagopus*, differed in mating system and group structure as a result of differences in food resources (Macpherson 1969; Hersteinsson 1984; Moehlman 1989). Populations of red foxes, *Vulpes vulpes*, differed in mating system and group structure, apparently as a result of differences in food resources, mortality, and climate (Voigt & Macdonald 1984). Mating systems can also change over time within the same population, as decreases in food resources resulted in a shift from polygyny to monogamy in populations of red foxes (von Shantz 1984; Zabel & Taggart 1989).

Among avian species, which also are predominately monogamous, breeding density was related to the use of alternative reproductive strategies within the same species (Westneat & Sherman 1997; Richardson & Burke 2001). Consequently, higher breeding densities in monogamous bird species increased the occurrence of polygamy, as more birds were available to mate (Westneat & Sherman 1997; Richardson & Burke 2001). Whether variation in density alone affects reproductive strategies in canids is not known. Although differences in food abundance and habitat affected intraspecific variation in reproductive strategies of canids, these factors often affect density (Clark 1972; Ballard & Van Ballenberghe 1997; Strand et al. 2000), thereby compounding their effects. Additionally, high mortality from larger predators can affect density of smaller canids (Johnson & Sargeant 1977; Peterson 1995; Cavallini 1996; Crabtree & Sheldon 1999). Consequently, high mortality also might contribute to variations in social systems of small canids (Voigt & Macdonald 1984; Cavallini 1996), although this hypothesis has not been tested.

We studied two populations of swift foxes in northwestern Texas that differed at least 2-fold in density, apparently as a result of differences in predation from coyotes. These populations were only separated by 40 km, and vegetation was similar between areas. Additionally, diets of swift foxes did not differ between sites during our study

(Lemons 2001), suggesting that food resources were similar between sites. This provided a unique opportunity to determine if mating system and group structure of swift foxes differed with respect to predation pressure and density.

Study Area

We conducted research between August 1998 and May 2001 on two 100-km^2 study sites in northwestern Texas. Site 1 was located on Rita Blanca National Grasslands (RBNG) and adjacent private lands in west-central Dallam County (36°31'N, 102°64'W). Vegetation consisted of shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyoides*) that was moderately to intensively grazed by cattle (*Bos taurus*). Although RBNG was open year around for hunting and trapping, during our study swift foxes were not exploited by humans, whereas coyotes were lightly exploited by hunters.

Site 2, approximately 40 km east of site 1, was located on a private cattle ranch located on the border of Dallam and Sherman counties (36°24'N, 102°19'W). Vegetation on this site also consisted shortgrass prairie dominated by blue grama and buffalograss that was moderately to intensively grazed by cattle. This site was surrounded by a more fragmented landscape, although swift foxes used shortgrass prairie >97% of the time (Kamler 2002). To reduce livestock losses, coyote hunting was permitted and encouraged by ranch owners on this site, and consequently coyotes were heavily exploited. However, swift foxes were not exploited by humans.

Methods

We captured, radio-collared, and monitored 49 swift foxes on site 1, and 39 swift foxes on site 2. Swift foxes were captured using box traps (Kamler 2002), and trapping effort initially was concentrated near the center of both study sites and expanded outward as capture of unmarked foxes decreased. Swift foxes were ear-tagged, radio-collared, and aged by tooth wear, body size, and reproductive condition (Rongstad et al. 1989). Foxes were classified as juveniles until the breeding season following their birth, whereas all other foxes were considered adults.

We recorded independent telemetry locations (White & Garrott 1990) for study animals 1-2 times per week and > 12 hours apart. We radio-tracked from vehicles using null-peak systems which consisted of dual, 4-element Yagi antennas. We conducted radio-tracking primarily during 1800-0900 hours, when swift foxes were likely to be most active (Kitchen et al. 1999). We calculated location estimates using the maximum likelihood estimation option in the program Locate II (Pacer, Inc., Truro, Nova Scotia, Canada). Mean error for reference collars (known locations) was 84 m (95% of errors were < 145 m).

Foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999). We determined annual home range sizes for adult swift foxes using the minimum convex polygon (MCP) method (Mohr 1947), as calculated by Animal Movement program (Hooge & Eichenlaub 1997). We calculated home ranges for foxes with >30 locations and >6 months of radio-tracking.

Mean home ranges sizes were compared between sites using *t*-tests (Zar 1996), and deemed significant when $P < 0.05$.

Spring density of swift foxes was estimated by minimum number of adults that remained on each study site during the birthing period (April-May). Area of study sites were determined by the total area encompassed by all monitored foxes. Spring densities (foxes/km^2) were compared between study sites using the Wilcoxon rank sum test (Zar 1996). Causes of mortality for swift foxes were determined by necropsy. We classified swift fox deaths as coyote predation if fox carcasses had hemorrhaging and puncture wounds consistent with that from coyote bite marks.

Results

During the 3-year study, we radio-collared 26 adult swift foxes on site 1, and 21 adults on site 2. Of these, annual home ranges were determined for 23 adults on site 1, and 17 adults on site 2. Annual home range sizes (mean ± SE) were larger ($P = 0.02$) on site 2 (10.7 ± 0.9 km^2) than site 1 (8.4 ± 0.5 km^2).

Spring density of adult swift foxes was greater ($P = 0.05$) on site 2 than site 1 (Table 4.1). There were 16 confirmed adult mortalities during the study, with 10 on site 1, and 6 on site 2. Coyote predation was responsible for all 10 adult deaths (100%) on site 1, but only 2 adult deaths (33%) on site 2. Most adult deaths (60%) on site 2 were due to vehicle collisions.

During the study, we monitored 16 adult groups on site 1, and 10 adult groups on site 2. On site 1, all 16 adult groups were monogamous pairs and no nonbreeding females were present (Table 4.1). On site 2, 3 of 10 adult groups consisted on 2 adult females and 1 adult male that communally denned and raised pups. There were also 4 nonbreeding females present among the 10 groups. Overall mean group size was larger ($P = 0.03$) on site 2 than site 1 (Table 4.1).

Discussion

Spring density of swift foxes was more than twice as high on site 2 than site 1 during all 3 years of the study. This difference in density was likely related to the greater occurrence of coyote predation on site 1, as 5 X more adult swift foxes died from coyote predation on site 1 than site 2. The largest cause of mortality in most swift fox populations was predation by coyotes (Sovada et al. 1998; Kitchen et al. 1999; Olsen & Lindzey 2002), suggesting that coyotes are major predators of swift foxes throughout their range. Of all swift foxes killed by coyotes during this study, none were consumed, similar to that reported by previous studies (Sovada et al. 1998; Kitchen et al. 1999). This suggests that coyotes killed swift foxes for reasons other than food, such as competition or territorial reasons. In addition to predation, coyotes spatially displaced swift foxes from their home ranges (Kamler 2002). Predation and spatial displacement is common among canid species, and can result in population suppression of smaller canids. For example, wolves, *Canis lupus*, spatially displace and kill coyotes (Fuller & Keith 1981; Carbyn 1982; Crabtree & Sheldon 1999), resulting in the suppression of coyote numbers where they are sympatric (Carbyn 1982; Peterson 1995; Crabtree & Sheldon 1999). Similarly, coyotes spatially displace and kill red foxes (Voigt & Earle 1983;

Sargeant & Allen 1989; Harrison et al. 1989), resulting in suppression of red fox populations (Johnson & Sargeant 1977; Peterson 1995). A similar relationship occurred between coyotes and swift foxes (Kamler 2002). Fewer deaths from coyote predations on site 2 were the result of lower coyote numbers due to the heavy exploitation of coyotes by humans on that site (Kamler 2002).

The difference in swift fox densities between sites resulted in differences in their mating system and group structure. In the area of low density, all adult groups consisted of monogamous pairs with no nonbreeding females. In contrast, in the area of high density, 30% of all adult groups consisted of polygynous groups (2 females, 1 male). Additionally, nonbreeding females were present in 40% of the adult groups. Intraspecific variation in mating system and group structure has been reported in other canid species, however, never in adjacent populations studied simultaneously. Several reasons might explain why the lower density of swift foxes, due to heavy predation by coyotes, decreased the occurrence of polygyny and group formation. First, high mortality created vacant territories for both adult females and juveniles to establish their own territories. Secondly, high mortality reduced the number of available females for both communal denning and nonbreeding status. Voigt and Macdonald (1984) suggested that these same factors might have contributed to differences in mating system and group formation of red foxes in Ontario and England, as red foxes in Ontario experienced high mortality and spatial displacement from coyotes, but those in England did not.

Cavallini (1996) suggested that the plasticity in social systems of small canids might have evolved as an adaptation to predation and displacement by larger canids. A more plastic social system would be necessary for small canids due to the unpredictability in spatial constraints imposed by larger canids (Cavallini 1996). Thus, small canids should be opportunistic in their mating systems and group structures, as territories of larger canids wax, wane, and shift. Cavallini (1996) suggested that a comparision of fox populations under different predation pressures would help test his hypothesis. The results of our study support his hypothesis, as swift foxes had different mating systems and group structures under different predation pressures. This suggests that social systems of swift foxes, and possibly other small canids, are opportunistic, as they take advantage of areas with fewer predators by increasing their breeding opportunities via polygyny and communal denning.

The resource dispersion hypothesis (RDH) suggested that group formation of canids was dependent on heterogeneity of food and habitat distribution (Macdonald 1983). This hypothesis has been supported by studies on several canid species, including golden jackals (Macdonald 1979) and red foxes (Macdonald 1983; Poule et al. 1994). Similarly, differences in food type and abundance affected group size in coyotes (Bekoff & Wells 1980; Messier & Barrette 1982), and both group size and mating system in arctic foxes (Macpherson 1969; Hersteinsson 1984) and red foxes (von Shantz 1984; Zabel & Taggart 1989). However, it is unlikely that habitat or food resources resulted in different mating systems and group structures between our study sites. Vegetation was similar between study sites, as swift foxes occupied short-grass prairie habitat on both sites. Lemons (2001) showed that swift fox diets were similar between sites during our study, suggesting that food resources were similar. Additionally, home range sizes were smaller on the area of low density, suggesting that foxes were not food stressed on that site. Thus, although previous studies showed that "bottom-up" factors, such as food and habitat, affected mating systems and group structures in canids, our study suggests that "top-down" factors, such as predation and spatial displacement, also can affect these parameters.

Because density among canids is also related to food abundance (Clark 1972; Ballard & Van Ballenberghe 1997; Strand et al. 2000), density alone might have a strong influence on mating system and group structure of canids. However, changes in food resources alone affected variation in the mating system and group structure of red foxes, as density remained similar even after food resources decreased (von Shantz 1984; Zabel & Taggart 1989). Our results, along with others, suggest that both density and food resources can each act independently to influence mating system and group structure among canids. For example, at a given density, decreases in food resources might cause individuals to become more aggressive, thereby excluding additional group members, and reproduction itself might be reduced due to abortion or resorption of fetuses (von Shantz 1984; Zabel & Taggart 1989). However, at a given level of food abundance, decreases in density due to high mortality might influence young females to breed in a vacant territory rather than forego reproduction (decreasing nonbreeding females), and adult females might choose to establish their own natal den rather than den communally (decreasing polygyny). Thus, throughout the range of medium and small-sized canids, bottom-up and top-down forces might act separately or in combination to affect variations in mating systems and group structures. However, due to the widespread suppression of smaller canids by larger canids (Johnson & Sargeant 1977; Peterson 1995; Cavallini 1996), influences of high mortality and spatial displacement on social systems of small canids might be greater than previously believed.

Our results indicate there can be considerable plasticity in the mating systems and group structure within a canid species, even between adjacent populations. Similar plasticity has been shown in other canid species, such as gray wolves (Harrington et al. 1982), red foxes (Voigt & Macdonald 1984; von Shantz 1984; Zabel & Taggart 1989; Cavallini 1996) and arctic foxes (Macpherson 1969; Hersteinsson 1984), that have been studied extensively. Furthermore, these variations can result from several forces acting independently or in combination, including differences in density, food resources, habitat, and mortality. There has been considerable discussion in the literature concerning reasons for the variation in social systems among canid species (Bekoff et al. 1981; Moehlman 1989; Geffen & Macdonald 1992; Geffen et al. 1996), and generalizations about particular species are often concluded from just one or a few studies. Our data, along with others, indicate that generalizations about mating systems and group structures of any canid species should be done with caution. Only after studies have been conducted under a variety of conditions, including areas with different food resources, habitat, and mortality patterns, should generalizations be made about a species.

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Table 4.1-Adult spring density and group structure of swift foxes monitored at 2 study sites in northwestern Texas, 1999 to 2001.

	Spring Density (no. adults/area)	no. monog. matings[a]	no. polyg. matings[b]	no. nonbreed.[c]	mean group size
SITE 1					
1999	0.09 fox/km^2	5	0	0	2.0
2000	0.09 fox/km^2	5	0	0	2.0
2001	0.11 fox/km^2	6	0	0	2.0
Summary	0.10 fox/km^2	16	0	0	2.0
SITE 2					
1999	0.31 fox/km^2	1	2	3	3.7
2000	0.19 fox/km^2	3	0	1	2.3
2001	0.25 fox/km^2	3	1	0	2.3
Summary	0.25 fox/km^2	7	3	4	2.7

[a] Number of monogamous mated pairs.
[b] Number of polygynous groups (2 breeding females, 1 adult male).
[c] Number of nonbreeding yearling females associated with the reproductive groups.

CHAPTER V

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

Abstract

Distribution and numbers of swift foxes (*Vulpes velox*) in the western Great Plains have declined since historical times. Human-induced changes to the environment, especially conversion of native prairie to agriculture, have been hypothesized as the primary reason for the decline of the swift fox. No studies have occurred in fragmented landscapes to assess the effects of human impacts. From 1998 to 2001, we monitored movements of 42 swift foxes in a landscape interspersed with four habitat types: native shortgrass prairies that were grazed by cattle, nonnative (CRP) grasslands that were ungrazed, irrigated agriculture, and dry-land agriculture. Annual adult survival ranged from 0.52 to 0.55, whereas 6-month survival of juveniles (5 to 11 months of age) ranged from 0.55 to 0.66. Overall, the primary causes of mortality were from vehicle collisions (42% of deaths) and coyote (*Canis latrans*) predation (33%). Annual home range size (mean ± SE) of adult males (10.8 ± 1.6 km^2) was similar ($P = 0.90$) to adult females (10.5 ± 1.1 km^2). We determined habitat use at 2 spatial scales: within study area, and within home ranges. Habitat use was similar at both spatial scales, as swift foxes selected shortgrass prairies, but had lower than expected use of dry-land agriculture, complete avoidance for irrigated agriculture, and nearly complete avoidance of CRP grasslands.

Our results indicate that swift foxes are more specialized in their habitat selection than other North American canids, thus protection of native shortgrass prairies might be necessary for their long-term existence.

Introduction

The distribution of swift foxes (*Vulpes velox*) in the western Great Plains has been severely reduced since historical times (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 have hypothesized that habitat loss, as a result of conversion of prairies to agricultural fields, was one 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 occurred in areas interspersed with both native prairies 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 cineroargenteus*) (Bekoff 1982; Fritzell 1987; Samuel and Nelson 1982; Voigt 1987). Consequently, these species have benefited from fragmentation and other human-induced changes to the environment, and have increased their distributions since the 1800s (Bekoff 1982; Fritzell 1987; Samuel and Nelson 1982; Voigt 1987). In contrast, the distribution of swift foxes became severely reduced in concert with human reductions of mixed-grass and shortgrass prairies (Egoscue 1979; Scott-Brown et al. 1987), suggesting that swift foxes might be habitat specialists. However, factors other than habitat loss also might contribute to the range reduction of swift foxes, such as competition with coyotes (Scott-Brown et al. 1987; Sovada et al. 1998).

All but one previous study of swift foxes occurred 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). However, the selection of agricultural fields compared to other habitats has not been studied. Clearly, more research is needed on the ecology of swift foxes in fragmented landscapes, as this information could help elucidate the importance of different habitat types needed to maintain swift fox populations. Because the effects of human-altered habitats on swift foxes have not been previously studied, this information would also have important implications for conservation efforts on swift foxes.

Our objectives were to determine the habitat use, home ranges, and survival of swift foxes in a fragmented landscape in northwestern Texas. Our study area consisted of shortgrass prairies that were grazed by cattle, nonnative (CRP) grasslands that were ungrazed, irrigated agriculture, and dry-land agriculture. We focused on habitat use at two different scales: within study area, and within home ranges. Specifically, we tested the null hypotheses that (1) there were no differences in habitat use compared to availability within the study area, (2) there were no differences in habitat use compared to availability within individual home ranges, and (3) there were no differences in home range size between sexes.

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 enrolled in the Conservation Reserve Program (hereafter CRP grasslands). Vegetation on ranches consisted of shortgrass-prairie species that were dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyoides*) and were moderately to intensively grazed by cattle (*Bos taurus*). The Conservation Reserve Program, created with the passage of the 1985 Farm Bill, retired highly erodible land from agricultural production and converted 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 were planted to warm-season grasses, dominated by old world bluestem (*Andropogon* spp.) and sideoats grama (*Bouteloua curtipendula*). We considered CRP in our study area to be nonnative grasslands, as these areas were dominated by old world bluestem and had vegetation that was taller and thicker than the shortgrass 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 corn-winter wheat plantings 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 wheat-grain sorghum plantings followed by a fallow year. 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. Additional meso-carnivores that occurred on the study site included striped skunks (*Mephitis mephitis*), badgers (*Taxidea taxus*), and raccoons (*Procyon lotor*).

Methods

From August 1998 to January 2001, we captured, radio-collared, and monitored 42 swift foxes (21 adult, 21 juvenile). Swift foxes were captured using box traps (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. Swift foxes were ear-tagged, radio-collared, and aged by tooth wear, body size, and reproductive condition (Rongstad et al. 1989). Foxes were classified as juveniles until the breeding season following their birth, whereas all other foxes were considered adults.

We recorded independent telemetry locations (White and Garrott 1990) for study animals 1-2 times per week and > 12 hours apart. We radio-tracked from vehicles using null-peak systems which consisted of dual, 4-element Yagi antennas. We conducted radio-tracking primarily during 1800-0900 hours, 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, Nova Scotia, Canada). Mean error for reference collars (known locations) was 84 m (95% of errors were < 145 m).

Foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999). We determined annual home range sizes for swift foxes using the minimum convex polygon (MCP) method (Mohr 1947), as calculated by Animal Movement program (Hooge and Eichenlaub 1997). We calculated home range sizes for foxes with >30 locations and >6 months of radio-tracking. Due to emigrations and early deaths, annual home range sizes were calculated for only 17 adult swift foxes (6 male, 11 female). Mean home ranges sizes were compared between sexes using *t*-tests (Zar 1996), and deemed significant when $P < 0.05$.

Habitat types were delineated using geographic information system (GIS) data that were ground-truthed. Habitat selection was determined at 2 spatial scales: within study area, and within home ranges. At the study-area scale, we determined habitat selection (use versus available) for both adults and juveniles. For each age class, an availability polygon (Miller et al. 1999) was calculated using locations from all radio-collared individuals within that age class. 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 (version 3.2, Environmental Systems Research Institute, Inc., Redlands, CA). Expected number of locations for each habitat type was calculated by multiplying total locations by percentage of available habitat types. We then compared total locations within habitat types to expected using chi-square goodness-of-fit tests (Neu et al. 1974; White and Garrott 1990).

At the home-range scale, we determined habitat composition by overlaying individual home range polygons onto the GIS map of habitat types. Percentage of different habitat types within home-range polygons was considered available. We determined habitat use by plotting all locations for each fox onto the GIS map of habitat types. Expected number of locations for each habitat were calculated by multiplying total locations by percentage of habitat types within the home-range polygon. We then compared actual habitat use to expected with chi-square goodness-of-fit tests. Selection indices (observed/expected) were also calculated for illustrative purposes.

Survival rates were determined for swift foxes using MICROMORT (Heisey and Fuller 1985). Annual survival of adults were 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 (Aug.-Jan.) were calculated for juveniles during each of the 3 years of the study. These survival rates corresponded to 5 to 11 months-of-age, after which time most juveniles dispersed. Causes of mortality were determined by necropsy. We classified swift fox deaths as coyote predation if fox carcasses had hemorrhaging and puncture wounds consistent with that from coyote bite marks. 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 for 6-month survival of juveniles (Heisey and Fuller 1985, Zar 1996).

Results

We obtained 958 locations on 21 adults, and 246 locations on 25 juveniles during the study. Annual home range size (mean ± SE) of adult males (10.8 ± 1.6 km^2, n=6) was similar (P = 0.90) to adult females (10.5 ± 1.1 km^2, n=11). Three juveniles remained on the study site and became adults during their second year.

At the study-area scale, the availability polygon for adults (9,659 ha) included 47% shortgrass prairie, 25% dry-land agriculture, 15% irrigated agriculture, and 13% CRP grasslands. The availability polygon for juveniles (10,185 ha) included 46% shortgrass prairie, 25% dry-land agriculture, 15% irrigated agriculture, and 15% CRP grasslands. For both adults and juveniles, there was a strong selection for shortgrass prairie, whereas there was lower than expected use of dry-land agriculture, complete avoidance for irrigated agriculture, and nearly complete avoidance of CRP grasslands (Table 5.1).

At the home range level, 13 adult swift foxes had home ranges that encompassed several different habitat types, whereas 4 foxes had home ranges that encompassed only shortgrass prairie (Table 5.2). All swift foxes used shortgrass prairie more than expected, although two foxes did not show statistical significance ($P < 0.10$, Table 5.2). Swift foxes exhibited a lower than expected use of dry-land agriculture, and complete avoidance of both irrigated agriculture and CRP grasslands (Table 5.2).

Annual survival of adults did not differ between years (*Z* = 0.13, *P* = 0.87, Table 5.3). Similarly, 6-month survival of juveniles did not differ among years (*G* = 0.21, d.f. = 2, *P* = 0.90, Table 5.3). There were 12 confirmed deaths of swift foxes during the study. Five (42%) were from vehicle collisions, 4 (33%) were from coyote predation, and 3 (25%) were from unknown causes.

Discussion

Our results indicate that swift foxes selected for shortgrass prairie habitats, rarely used dry-land agriculture, completely avoided irrigated agriculture, and nearly completely avoided CRP grasslands. Although swift foxes occupied continuous dry-land cropfields in western Kansas (Matlack et al. 2000; Sovada et al. 1998), differences in body condition and mortality suggested that 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, as all swift foxes used dry-land agriculture considerably less than expected. The highest percentage of dry-land agriculture in any home range was only 21%, whereas most home ranges contained much less, and four contained none, suggesting that this habitat was not as productive or useful for swift foxes as shortgrass prairie.

In our study, irrigated agriculture was completed avoided by all swift foxes even though it comprised 15% of the study area. There were considerable differences between irrigated and dry-land agriculture 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 intermittently watered by a center-pivot irrigation system, which continuously rotated when used, and chemicals were applied through the water-irrigation system. Thus, the higher disturbance likely made foxes avoid these areas, and insecticide applications likely reduced food resources, as insects were a major part of their diet on our study area (Lemons 2001). Our results support the hypothesis that conversion of prairies to agriculture contributed to the decline of the swift fox, as both types of agriculture 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 comprised 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 visibility. We did not determine prey abundances in the different habitat types of our study area. However, any differences in prey abundances were not likely so great as to cause the nearly total avoidance of this habitat. We believe that avoidance of CRP grasslands was probably due to the tall and dense vegetation of this habitat type. Historically, the distribution of swift foxes was limited in the eastern Great Plains by relatively tall vegetation, as they did not occupy tall-grass prairie regions (Egoscue 1979; Scott-Brown et al. 1987). Swift foxes are the smallest canid species in North America (Egoscue 1979; Scott-Brown et al. 1987), and tall vegetation probably limits their visibility and movements. On our study site, the ungrazed vegetation of CRP grasslands was considerably taller than swift foxes, whose mean shoulder height ranged from 29-30 cm (Kamler 2002). Thus, swift foxes would have severely reduced visibility when moving through this vegetation. Swift foxes were vulnerable to coyote predation, as 44% of known deaths were from coyotes. Thus, taller vegetation might also increase their vulnerability to predation, as swift foxes would less likely see coyotes approaching. Additionally, larger predators such as coyotes are faster and more mobile in taller vegetation than swift foxes, making escapes less likely if larger predators were encountered. 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 were not beneficial to swift foxes, and, in fact, may have further restricted their available habitat.

Home ranges of swift foxes in our study were larger (10-11 km^2 versus 7-8 km^2) than those reported from Colorado (Kitchen et al. 1999) and Wyoming (Olsen and Lindzey 2002). Home ranges in our study site might have been larger because they contained habitats, such as agriculture, that essentially were not used by swift foxes, thereby requiring larger areas to meet their annual needs. 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 any previous study. Previous studies reported 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). On our study site, coyotes were heavily exploited by both local landowners and recreational hunters, which likely decreased the impacts of coyotes compared to 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, as they sometimes hunted in road ditches within 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 adult swift foxes 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, as they depended primarily on shortgrass prairie, and nearly completely avoided all other types of habitats. Thus, protection of native prairies might be necessary for the long-term conservation of swift foxes. Swift foxes were negatively affected by major roads, and their distribution on our study site was restricted by all human-altered habitats, including agriculture and CRP grasslands. 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; Samuel and Nelson 1982; Voigt 1987). 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. Thus, protection of any native habitats for swift foxes also must account for the possible negative effects of other canids, especially coyotes, in order to ensure long-term viability of swift fox populations.

Because much of the Great Plains consists of agricultural and CRP fields, we recommend several management practices to help conserve vulnerable populations of swift foxes. We suggest that CRP fields should be planted with local, native species of grasses, because tall, nonnative grasslands were completely avoided by swift foxes. Additional management practices on CRP fields could also benefit swift foxes. For example, some type of disturbance, such as limited grazing or fire, would reduce vegetation height on CRP fields, allowing them to be more useful to swift foxes. Although swift foxes sometimes used dry-land agriculture, irrigated agriculture was completed avoided. Thus, conversion of irrigated agriculture to dry-land agriculture could also benefit swift foxes. Finally, due to habitat loss, swift foxes are now absent from large areas of their former range. Thus, habitat restoration, including conversion of agricultural fields back to native rangelands, may be necessary to re-establish swift foxes in parts of their former range.

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and Use Committee. This is a Texas Tech University, College of Agricultural Sciences and Natural Resources technical publication.

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Table 5.1-Habitat use observed (obs), compared to expected (exp), at the study site level for adult and juvenile swift foxes monitored from 1998 to 2001 in northwestern Texas.

		Prairie[a]	D-Agr.[b]	I-Agr.[c]	CRP[d]		
	no. loc.	(obs/exp)	(obs/exp)	(obs/exp)	(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] Shortgrass prairie

[b] Dry-land agriculture

[c] Irrigated agriculture

[d] CRP grasslands (nonnative and ungrazed)

Table 5.2-Habitat selection indices (observed/expected) within home ranges of swift foxes monitored from 1998 to 2001 in northwestern Texas. Selection indices > 1 indicate preference, whereas indices < 1 indicate avoidance.

ID	no. loc.	Prairie[a] (obs/exp)	Dry-Agr.[b] (obs/exp)	χ^2	*P*-value
109F[c]	33	1.38	0.56	10.14	0.006
83F	40	1.11	0.00	3.40	0.065
86M	47	1.08	0.00	2.78	0.095
70F	50[e]	----	----	----	----
47F	42	1.15	0.45	2.76	0.097
52F	43[e]	----	----	----	----
71M	30[e]	----	----	----	----
2F[d]	61	1.22	0.09	12.56	0.002
6M	63	1.17	0.25	7.31	0.007
12F	53	1.22	0.31	7.27	0.007
53M	60[e]	----	----	----	----
49M	48	1.04	0.63	0.39	0.387
49M	49	1.22	0.10	8.50	0.004
54F	45	1.06	0.28	1.34	0.247
54F	45	1.20	0.12	6.83	0.009
9F	84	1.12	0.10	8.45	0.004
9F	62	1.16	0.11	7.83	0.005

[a] Shortgrass prairie

[b] Dry-land agriculture

[c] Also had 18% irrigated agriculture within home range, but no locations.

[d] Also had 1% CRP grasslands within home range, but no locations.

[e] Only shortgrass prairie occurred within the home range.

Table 5.3-Survival estimates for swift foxes monitored in northwestern Texas from 1998 to 2001. Included are annual estimates for adults and 6-month estimates for juveniles, along with 95% confidence intervals (CI).

	n[a]	deaths	Survival	95% CI
Adults				
Jan. 1999-Dec. 1999	10	4	0.55	0.31-0.99
Jan. 2000-Dec. 2000	13	2	0.52	0.21-1.00
Juveniles				
Aug. 1998-Jan. 1999	8	2	0.66	0.38-1.00
Aug. 1999-Jan. 2000	9	2	0.60	0.30-1.00
Aug. 2000-Jan. 2001	8	2	0.55	0.23-1.00

[a] Number of foxes monitored during that period.

CHAPTER VI

SPATIAL RELATIONSHIPS BETWEEN SWIFT FOXES AND COYOTES IN NORTHWESTERN TEXAS

Abstract

Interspecific competition among canids can result in mortalities and spatial displacement of smaller canids by larger canids. To investigate mortalities and spatial relationships of swift foxes (*Vulpes velox*) and coyotes (*Canis latrans*), we captured and radio-tracked both species at Rita Blanca National Grasslands in northwestern Texas. At least 89% of swift fox mortalities were caused by coyotes, resulting in a relatively low annual survival of 0.47 for foxes. Annual home ranges of swift foxes occurred near the periphery and outside coyote home ranges, and did not overlap, or only slightly overlapped, coyote core areas. Swift foxes that shifted home ranges and established dens within a coyote's core area were killed by coyotes shortly thereafter. Our data indicated that spatial displacement of swift foxes was not due to behavioral avoidance of coyotes, but rather increased predation of swift foxes within coyote core areas. Most mortalities caused by coyotes occurred in the immediate vicinity of swift fox dens, suggesting that coyotes made an active effort to kill swift foxes.

Introduction

Interspecific competition among canids often results in spatial displacement of smaller species by larger species. For example, coyote (*Canis latrans*) home ranges tend to occur near the periphery or outside wolf (*C. lupus*) home ranges (Fuller and Keith 1981), indicating that wolves spatially displace coyotes. Similarly, red fox (*Vulpes vulpes*) home ranges occur near the periphery or outside of coyote home ranges (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). Spatial displacement among canids might result from behavioral avoidance of larger species by smaller species (Voigt and Earle 1983, Sargeant et al. 1987, Harrison et al. 1989), although the mechanisms of spatial displacement are poorly understood.

In addition to spatial displacement, interspecific killing of smaller canids by larger canids has been well documented. For example, wolves kill coyotes (Carbyn 1982, Paquet 1992, Thurber et al. 1992), whereas coyotes kill red foxes (Sargeant and Allen 1989). Other fox species, including gray foxes (*Urocyon cinereoargenteus*), kit foxes (*V. macrotis*), and swift foxes (*V. velox*), also have been killed by coyotes (Ralls and White 1995, Cypher and Spencer 1998, Sovada et al. 1998, Fedriani et al. 2000). However, no spatial avoidance was found between coyotes and either gray foxes (Neale and Sacks 2001), kit foxes (White et al. 1994), or swift foxes (Kitchen et al. 1999). However, interspecific competition and spatial relationships among canids can vary among regions. For example, coyotes and wolves overlapped completely in space use in Manitoba (Paquet 1992) and Alaska (Thurber et al. 1992). Paquet (1992) and Thurber et al. (1992) suggested that competition was reduced in those regions due to abundant food resources for wolves, which allowed for effective resource partitioning between species. Thus, competition and spatial relationships between coyotes and smaller canid species may also differ among regions depending on food resources.

Distribution and abundance of swift foxes has been considerably reduced compared to historical times (Egoscue 1979, Scott-Brown et al. 1987). Consequently, from 1995-2001 swift foxes were classified as warranted, but precluded as a threatened species by the United States Fish and Wildlife Service. Although human impacts in the Great Plains were primarily responsible for the reduction of swift foxes during the early 1900s (Egoscue 1979), competition from coyotes might be suppressing and reducing current swift fox populations (Scott-Brown et al. 1987). Thus, information concerning relationships between coyotes and swift foxes is needed to further enhance conservation efforts for swift foxes. To determine spatial relationships of swift foxes and coyotes in northwestern Texas, we captured and radio-tracked both species on Rita Blanca National Grasslands from August 1998 to January 2000. We plotted annual home ranges of swift foxes against those of coyotes. We also determined survival rates and causes of mortality for radio-collared swift foxes.

Study Area

The study was conducted on 100 km^2 area of rangeland located on Rita Blanca National Grasslands (RBNG) and adjacent private lands (36°31'N, 102°64'W) in Dallam County, Texas. Rangeland vegetation consisted of shortgrass prairies dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyoides*) that was moderately to intensively grazed by cattle (*Bos taurus*). Although trapping and hunting was permitted on RBNG, during our study no trappers used this area and coyotes were only lightly exploited by hunters.

Methods

From August 1998 to January 2000, we captured, radio-collared, and released 18 swift foxes and 12 coyotes. Swift foxes were captured using box traps, whereas coyotes were captured using padded leg-hold traps (Kamler et al. in review). Trapping effort for swift foxes was initially concentrated near the center of the study area and expanded outward as capture of unmarked foxes decreased. Trapping effort for coyotes was concentrated in areas where swift foxes were captured to increase the likelihood that study animals shared the same area. All study animals were ear-tagged, radio-collared, and aged by tooth wear, body size, and reproductive condition (Gier 1968, Rongstad et al. 1989). Foxes were classified as juveniles until the breeding season following their birth. All other foxes were considered adults. All coyotes were classified as adults because all were aged > 1 year.

We recorded independent telemetry locations (White and Garrott 1990) for study animals 1-2 times per week and > 12 hours apart. We radio-tracked from vehicles using null-peak systems which consisted of dual, 4-element Yagi antennas. We conducted radio-tracking primarily during 1800-0900 hours, when swift foxes and coyotes were likely to be most active (Andelt 1985, Kitchen et al. 1999). We calculated location estimates using the maximum likelihood estimation option in the program Locate II (Pacer, Inc., Truro, Nova Scotia, Canada). Mean error for reference collars (known locations) was 84 m (95% of errors were < 145 m).

Foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999). Coyotes have been classified in their social organization as residents and transients. Resident groups, which consist of breeders (mated pair) and often pack associates (yearling offspring that have not dispersed), are territorial and have non-overlapping home ranges with adjacent resident groups (Andelt 1985, Gese et al. 1988, Kamler and Gipson 2000). Transients are solitary coyotes that have relatively large, poorly defined home ranges that overlap those of other coyotes (Andelt 1985, Gese et al. 1988, Kamler and Gipson 2000). Therefore, we classified coyotes in our study as resident or transient based on the above criteria.

We determined annual home range sizes for swift foxes and coyotes using the 95% minimum convex polygon (MCP) method (Mohr 1947), as calculated by Animal Movement program (Hooge and Eichenlaub 1997). We also calculated 65% MCP home ranges for coyotes to determine core areas (Shivik et al. 1996). We calculated home ranges for study animals with >40 locations and >9 months of radio-tracking. Because 1 resident coyote was killed before 40 locations were obtained, we estimated a minimum home range and core area with 23 locations, although this was not included in statistical analyses. We did not calculate home ranges for transient coyotes because they were radio-tracked intermittingly throughout the year and had < 30 total locations.

Annual survival rates were determined for swift foxes using MICROMORT (Heisey and Fuller 1985). Causes of mortality for swift foxes were determined by necropsy. We classified deaths as coyote predation if fox carcasses had hemorrhaging and puncture wounds consistent with that from coyote bite marks.

Results

We captured and monitored 12 adult swift foxes (5 male, 7 female), 6 juvenile swift foxes (4 male, 2 female), and 12 adult coyotes (6 male, 6 female) from August 1998 to January 2000. Mean (±SE) annual home ranges for 8 adult swift foxes was 7.6 ± 0.9 km^2 (Fig. 6.1). Home ranges were not determined for other adults due to emigration or early deaths. Of 12 coyotes captured, 10 were residents and 2 were transients. Mean annual home ranges for 7 resident coyotes was 12.5 ± 1.1 km^2 (Fig. 6.1). Due to early deaths, home ranges were not calculated for 3 resident coyotes. However, based on 23 locations, an estimated home range was determined for 1 of these coyotes for illustrative purposes (Fig. 6.1). Additionally, core areas (65% MCP) for resident coyotes are shown in Fig. 6.1.

Annual survival rate (mean ± SD) for swift foxes was 0.47 ± 0.01. Of 9 confirmed swift fox deaths, 8 (89%) were confirmed or suspected as being caused by coyotes, and the remaining death was unknown. Thus, coyotes were responsible for 100% of known causes of death. Of the 9 fox deaths, 5 (56%) were within 20 m of the den entrances of the swift foxes. Three swift foxes were killed shortly after (4-9 weeks) shifting their home ranges and establishing dens within coyote core areas (Fig. 6.1).

Discussion

Home ranges of swift foxes occurred near the periphery and outside of coyote home ranges. Additionally, home ranges of swift foxes did not overlap, or only overlapped slightly, the core areas of coyote home ranges. Although the mechanisms for spatial displacement are poorly understood, previous researchers have suggested that behavioral avoidance was the mechanism for spatial displacement among sympatric canids (Voigt and Earle 1983, Sargeant et al. 1987, Harrison et al. 1989). However, our data suggested that intensive coyote predation within core areas was most likely responsible for the observed spatial pattern. For example, all swift foxes (n = 3), including a pregnant female, were killed shortly after shifting their home ranges and establishing dens within coyote core areas. This indicated that swift foxes did not behaviorally avoid coyote core areas, but rather swift foxes that established dens in coyote core areas were killed shortly thereafter. Carbyn (1982) found a similar relationship between wolves and coyotes in Manitoba. In that study, coyotes did not avoid wolves, but wolves consistently killed coyotes in core areas, resulting in higher coyote survival near the periphery of wolf-pack territories (Carbyn 1982).

Interestingly, most coyote predation occurred in the immediate vicinity of swift fox dens, suggesting that coyotes ambushed swift foxes as they attempted to leave their dens. Additionally, during a night of spotlight surveys, we observed a coyote sitting near a complex of swift fox dens, with its ears and eyes focused on den entrances. Thus, our data and observations suggested that coyotes actively made an effort to kill swift foxes, at least within core areas of coyote home ranges. We found no clear indication that coyotes fed on any of the swift foxes they killed, suggesting that swift foxes were killed for reasons other than food, such as competition or territorial reasons.

In addition to excluding swift foxes from coyote core areas, coyotes were responsible for at least 89% of all swift fox deaths, resulting in a relatively low annual survival of 0.47. Our results differed from the only previous study that investigated swift fox-coyote spatial relationships (Kitchen et al. 1999). Kitchen et al. (1999) reported that home ranges and core areas of swift foxes and coyotes in Colorado overlapped completely. Additionally, coyotes were responsible for only 48% of all swift fox deaths, resulting in a higher survival of 0.64. Kitchen et al. (1999) also found that of the coyote-caused swift fox mortalities, all occurred outside or near the periphery of swift fox home ranges (i.e., none were near fox dens). Their results suggested that coyotes had less impact on swift fox populations than in our study.

Reasons for different swift fox-coyote spatial patterns between regions may be related to greater occurrences of coyote predation on swift foxes in our study, especially within coyote core areas. However, reasons for greater occurrences of coyote predation in our study were not clear. Palomares and Caro (1999) found that interspecific predation among carnivores was common, although killings increased when prey became less available. Other studies also found that interspecific competition and predation increased as carnivores became more food stressed. For example, Koehler and Hornocker (1991) found that cougar (*Puma concolor*) predation on bobcats (*Lynx rufus*) and coyotes increased as food resources became scarce. Ballard (1982) found that the number of kills contested by wolves and brown bears (*Ursus arctos*) was higher in areas of low prey density. Interspecific predation among carnivores, including lynx (*Lynx canadensis*) predation on red foxes, increased as snowshoe hare (*Lepus americanus*) populations decreased (O'Donoghue et al. 1995, Stephenson et al. 1991). Interspecific competition between coyotes and gray foxes, including predation on gray foxes, differed considerably between two regions in California (Neale and Sacks 2001, Fedriani et al. 2000), apparently due to differences in food abundances (Neale and Sacks 2001). In Nevada, increased predation on kit foxes by coyotes was probably related to a cyclic decline in black-tailed jackrabbit (*Lepus californicus*) population (O'Neal et al. 1987). Thus, although coyotes kill swift foxes throughout their range, these studies suggest that coyote predation might be greater in areas where coyotes are more food stressed due to lower prey availability.

In our study, smaller spatial requirements of swift foxes allowed them to persist near the periphery and outside of adjacent coyote home ranges, and prevented their complete displacement. However, resident coyotes limited the available habitat and carrying capacity for swift foxes. Conservation efforts for swift foxes should consider these results, especially in areas where swift foxes appear to be declining. Thus, not only should conservation efforts focus on available habitat and carrying capacity for swift foxes, but interspecific competition with coyotes must also be considered. Effects of coyotes on swift foxes vary spatially and possibly temporally throughout their range, and may depend on coyote densities, human exploitation of coyotes, and food resources of coyotes.

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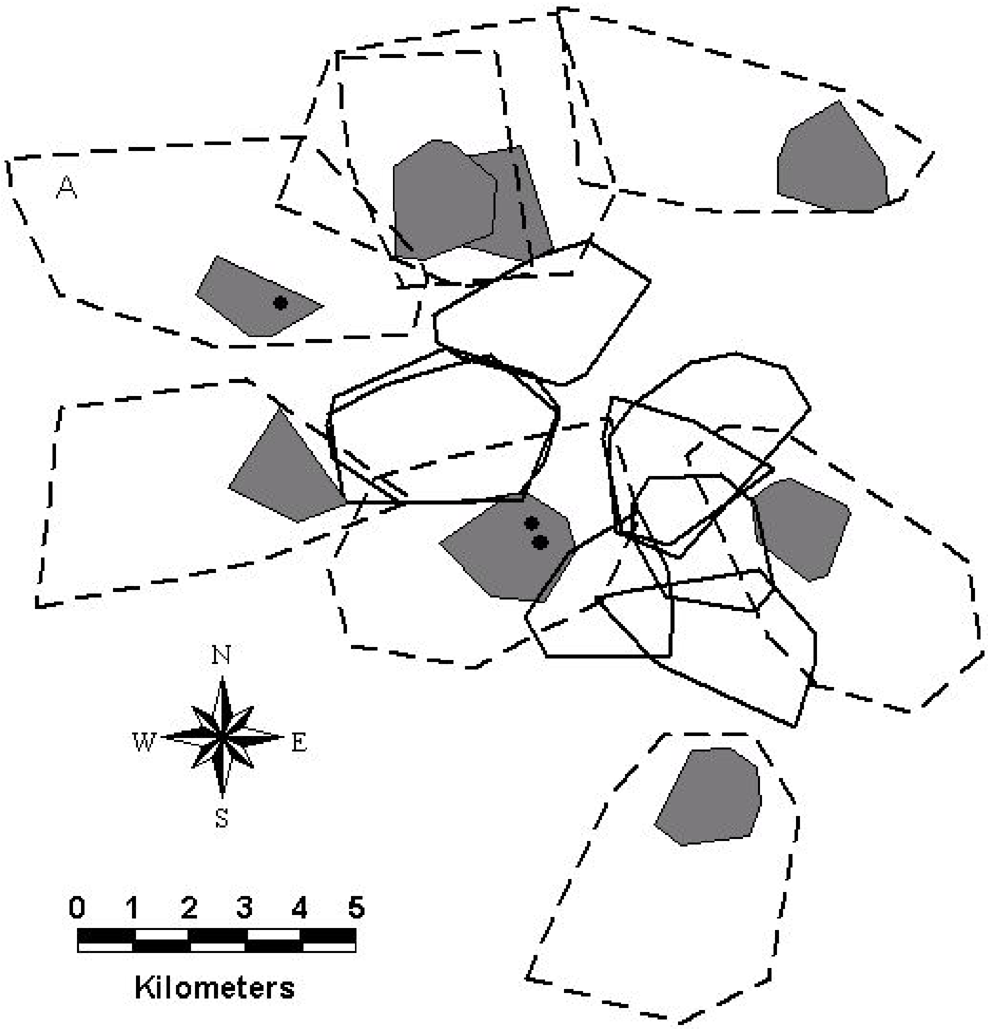

Fig. 6.1-Annual home ranges of swift foxes (solid polygons; n = 8) and resident coyotes (dashed polygons; n = 8) monitored on Rita Blanca National Grasslands, Texas, during 1998 and 1999. Solid gray polygons represent core areas of coyotes. "A" represents estimated core area and home range for a coyote based on 23 locations. Dots represent dens inhabited by three swift foxes shortly before they were killed by coyotes.

CHAPTER VII

EFFECTS OF COYOTES ON SWIFT FOXES IN NORTHWESTERN TEXAS

Abstract

The distribution of swift foxes (*Vulpes velox*) in the western Great Plains has been dramatically reduced since historical times. Because coyotes (*Canis latrans*) have been identified as the largest cause of mortality in swift fox populations, we studied the effects of coyotes on swift foxes in northwestern Texas. We radio-collared and monitored 88 swift foxes and 29 coyotes at 2 study sites from 1998 to 2000. On site 1, coyotes had relatively high abundance (41 ± 6.8 scats/transect) and survival (0.90), whereas swift foxes had low survival (0.47), low density (0.24-0.31 foxes/km^2), low recruitment (0.25 young/adult). Consequently, swift foxes had a sink population due to heavy predation from coyotes. On site 2, coyotes had low abundance (19 ± 4.9 scats/transect) and survival (0.54), whereas swift foxes had high survival (0.69), high density (0.68-0.77 foxes/km^2), high recruitment (1.3 young/adult). Consequently, swift foxes had a source population due to low predation by coyotes. These initial results suggested that lower coyote numbers were beneficial to swift foxes. To test this hypothesis, we experimentally removed 227 coyotes on site 1 during the final year of the study. Subsequently, coyotes had decreased abundance (18 ± 4.5 scats/transect), whereas swift foxes had increased survival (0.63), increased density (0.68 foxes/km^2), increased recruitment (1.2 young/adult), and had a source population due to lower predation by coyotes. All parameters remained consistent on site 2. Our results indicate that high coyote numbers can suppress swift fox populations due to heavy predation. Our findings also indicate that reductions in coyote numbers can change a sink population of swift foxes into a source population, and thus has important implications for conservation efforts of swift foxes.

Introduction

The distribution of swift foxes (*Vulpes velox*) in the western Great Plains has been severely reduced since historical times. 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. Initially, this species was decimated by several human-induced factors, including inadvertent poisoning, trapping pressure, rodent control programs, and habitat loss (Egoscue 1979, Scott-Brown et al. 1987). However, Scott-Brown et al. (1987) speculated that current populations might be suppressed due to competition with coyotes (*Canis latrans*). Coyotes negatively affected other fox species (Voigt and Earle 1983, O'Neal et al. 1987, Sargeant et al. 1987, Cypher and Spencer 1998), including red foxes (*V. vulpes*) and kit foxes (*V. macrotis*), thus may negatively affect swift foxes as well.

Recent research indicated the largest cause of mortality among swift foxes was predation from coyotes (Sovada et al. 1998, Kitchen et al. 1999, Olsen and Lindzey 2002), suggesting that coyotes might be suppressing swift fox populations. However, previous studies were only descriptive in nature, as no studies manipulated coyote numbers to determine the effects on swift foxes. This information could have important implications for conservation efforts of swift foxes. For example, coyotes might affect overall survival, density, and recruitment of swift foxes, thus limiting their recovery, or even decreasing their populations in some areas.

To investigate relationships between swift foxes and coyotes in northwestern Texas, we captured and radio-collared both species at 2 study sites from 1998 to 2001. The objectives of our study were to determine home ranges, survival, and densities of both species. We also determined recruitment rates for swift foxes. Initial data indicated that higher coyote numbers on site 1 resulted in lower swift fox survival, lower density, and lower recruitment compared to site 2. Therefore, we experimentally removed coyotes from site 1 during the final year of the study to determine if population parameters of swift foxes increased.

Study Area

Research was conducted on 2, 100-km^2 study sites in northwestern Texas. Site 1 was located on Rita Blanca National Grasslands (RBNG) and adjacent private lands in west-central Dallam County (36°31'N, 102°64'W). Vegetation consisted of shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyoides*) that was moderately to intensively grazed by cattle (*Bos taurus*). Although RBNG was open year around for hunting and trapping, during our study swift foxes were not exploited by humans, whereas coyotes were lightly exploited by hunters.

Site 2, approximately 40 km east of site 1, was located on a private ranch surrounded by other ranches, agricultural fields, and Conservation Reserve Program (CRP) fields on the border of Dallam and Sherman counties (36°24'N, 102°19'W). Vegetation on ranches consisted shortgrass prairie dominated by blue grama and buffalograss that was moderately to intensively grazed by cattle. Agricultural fields consisted primarily of winter wheat and corn irrigated by center pivot, and grain sorghum that was not irrigated. CRP, created with the passage of the 1985 Farm Bill, retired highly erodible land from agricultural production and converted it to permanent cover. CRP fields in our study area were enrolled in 1985 and were planted to warm-season grasses, dominated by old world bluestem (*Andropogon* spp.) and sideoats grama (*Bouteloua curtipendula*). To reduce livestock losses, coyote hunting was permitted and encouraged by ranch owners on this study site, and consequently coyotes were heavily exploited. However, swift foxes were not exploited by humans.

Additional carnivores that occurred on both study sites included striped skunks (*Mephitis mephitis*), badgers (*Taxidea taxus*), and raccoons (*Procyon lotor*). Additional ungulates included pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Other mammals on the study sites included porcupines (*Erithizon dorsatum*), black-tailed jackrabbits (*Lepus californicus*), desert cottontails (*Sylvilagus audobonii*), black-tailed prairie dogs (*Cynomys ludovicianus*), Ord's kangaroo rats (*Dipodomys ordii*), ground squirrels (*Spermophilus* spp.), gophers (*Geomys* and *Cratogeomys* spp.), eastern moles (*Scalopus aquaticus*), shrews (*Notiosorex* and *Cryptotis* spp.), prairie voles (*Microtus ochrogaster*), hispid cotton rats (*Sigmodon hispidus*), northern grasshopper mice (*Onychomys leucogaster*), woodrats (*Neotoma* spp.), pocket mice (*Chaetodipus* and *Perognathus* spp.), harvest mice (*Reithrodontomys* spp.), and *Peromyscus* spp. (Lemons 2001). Predatory avian species that were summer residents included great-horned owls (*Bubo virginianus*), barn owls (*Tyto alba*), burrowing owls (*Athene cunicularia*), turkey vultures (*Cathartes aura*), Swainson's hawk (*Buteo swainsoni*), northern harriers (*Circus cyaneus*), ferruginous hawks (*Buteo regalis*), American kestrels (*Falco sparverius*), and prairie falcons (*Falco mexicanus*). Migratory winter species included merlins (*Falco columbarius*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), and rough-legged hawks (*Buteo lagopus*).

Methods

From August 1998 to January 2001, we captured, radio-collared, and monitored 49 swift foxes and 12 coyotes on site 1, and 39 swift foxes and 17 coyotes on site 2. Swift foxes were captured using box traps, whereas coyotes were captured using padded leg-hold traps (Kamler et al. in review). Trapping effort for swift foxes was initially concentrated near the center of both study sites and expanded outward as capture of unmarked foxes decreased. Trapping effort for coyotes was concentrated in areas where swift foxes were captured to increase the likelihood that study animals shared the same area. All study animals were ear-tagged, radio-collared, and aged by tooth wear, body size, and reproductive condition (Gier 1968, Rongstad et al. 1989). Foxes were classified as juveniles until the breeding season following their birth. All other foxes were considered adults. All coyotes were classified as adults because all were aged > 1year.

We recorded independent telemetry locations (White and Garrott 1990) for study animals 1-2 times per week and > 12 hours apart. We radio-tracked from vehicles using null-peak systems which consisted of dual, 4-element Yagi antennas. We conducted radio-tracking primarily during 1800-0900 hours, when swift foxes and coyotes were likely to be most active (Andelt 1985, Kitchen et al. 1999). We calculated location estimates using the maximum likelihood estimation option in the program Locate II (Pacer, Inc., Truro, Nova Scotia, Canada). Mean error for reference collars (known locations) was 84 m (95% of errors were < 145 m).

Foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999). Coyotes have been classified in their social organization as residents and transients. Resident coyotes tend to live in family groups with relatively small home ranges that overlap little with other resident groups (Andelt 1985, Gese et al. 1988, Kamler and Gipson 2000). Transients are solitary coyotes that have relatively large, poorly defined home ranges that overlap those of other coyotes (Andelt 1985, Gese et al. 1988, Kamler and Gipson 2000). Therefore, we classified coyotes in our study as resident or transient based on the above criteria.

We determined annual home range sizes for swift foxes and coyotes using the 95% minimum convex polygon (MCP) method (Mohr 1947), as calculated by Animal Movement program (Hooge and Eichenlaub 1997). We calculated home ranges for foxes with >40 locations and >9 months of radio-tracking. Due to emigrations and early deaths, annual home ranges were calculated only for 14 swift foxes (7 male, 7 female) on the treatment site, and 13 (4 male, 9 female) on the comparison site. Home ranges were not calculated for transient coyotes because they were monitored intermittingly throughout the year and had < 30 total locations. Home range sizes for coyotes were compared only in 1999, as coyote removal efforts eliminated all radio-collared coyotes from 1 study site in 2000. On each site, preliminary analysis indicated home range sizes of swift foxes and coyotes did not differ between sexes, thus sexes were pooled and compared between sites and years. Differences between mean home range sizes were calculated using t-tests (Zar 1996), and deemed significant when $P < 0.05$.

Annual survival rates were determined for swift foxes and coyotes using MICROMORT (Heisey and Fuller 1985). Causes of mortality were determined by necropsy. We classified swift fox deaths as coyote predation if fox carcasses had hemorrhaging and puncture wounds consistent with that from coyote bite marks. Because a major highway occurred in the middle of only 1 study site, we censored foxes that died from vehicle collisions. For each study site, data were initially analyzed in intervals of biological seasons to meet the assumption of constant survival (Heisey and Fuller 1985). Because preliminary analyses showed that survival did not differ among seasons, data were grouped and compared between sites and years using *Z*-tests (Heisey and Fuller 1985, Nelson and Mech 1986). Differences in survival and cause-specific mortality rates were deemed significant when $P < 0.05$.

Relative coyote abundance was estimated during 1999 and 2000 by scat deposition rates determined from seasonally walking 3 transects (2 km each) per study site and enumerating the number of scats deposited (Clark 1972, Cavallini 1994). For each study site, seasonal collections on each transect were combined for annual numbers that were compared between sites and years using *t*-tests. Too few fox scats were collected on transects to estimate their abundance. Therefore, fall fox density on each site was estimated by the minimum number of individuals captured per trapping area in 1998, 1999, and 2000. Trapping area was determined using the 100% minimum convex polygon method for all trapping locations. To verify that number of individuals captured was not related to trapping pressure, we also calculated catch-per-unit-effort (no. captured/100 trapnights) as index to relative abundance. Fall densities and relative abundances were compared between sites and years using Yate's corrected chi-square tests (Zar 1996). Recruitment rates for swift foxes was determined by the minimum number of juveniles per reproducing adult that survived until dispersal or 1 year of age. Recruitment rates were compared between sites and years using Fisher's exact tests.

Coyote removal, conducted by personnel from the United States Department of Agriculture's Wildlife Services program, was initiated on site 1 in January 2000. Coyotes were removed by aerial gunning 3 consecutive days every 3 months for a year. Coyotes were also removed from a buffer zone approximately 2 km around site 1 to decrease coyote immigration into the area.

Results

Differences Between Sites (1998-1999)

Annual survival of coyotes was greater ($Z = 2.04$, $P = 0.03$) on site 1 compared to site 2 (Table 7.1). On site 1, the only known coyote death was due to human hunting. On site 2, all 5 coyote deaths were from human hunting. Relative coyote abundance (mean ± SE) was greater ($P = 0.05$) on site 1 (41.0 ± 6.8 scats/transect) than site 2 (19.0 ± 4.9 scats/transect). Annual home range size (mean ± SE) of coyotes was greater ($P = 0.02$) on site 1 (12.5 ± 0.4 km^2, n = 7) compared to site 2 (8.9 ± 1.2 km^2, n = 7).

Annual survival of swift foxes was not statistically different ($Z = 1.24$, $P = 0.15$) between sites, although it was less on site 1 than site 2 (Table 7.1). On site 1, at least 89% (8/9) of fox deaths were due to coyote predation. On site 2, only 27% (2/7) of fox deaths were due to coyote predation.

Fall density of swift foxes was lower on site 1 than site 2 in both 1998 (Yate's $O^2 = 4.01$, $P = 0.04$) and 1999 (Yate's $O^2 = 3.65$, $P = 0.05$, Table 7.2). Relative abundance of swift foxes was not significantly different between sites in 1998 (Yate's $O^2 = 0.73$, $P = 0.39$) and 1999 (Yate's $O^2 = 1.64$, $P = 0.20$), although it was higher on site 2 in both years (Table 7.2). Recruitment rates were lower on site 1 than site 2 in both 1998 ($P = 0.04$) and 1999 ($P = 0.04$, Table 7.2). Annual home range sizes (mean ± SE) of swift foxes were not statistically different ($P = 0.11$) between site 1 (7.6 ± 0.9 km^2, n = 8) and site 2 (10.2 ± 1.1 km^2, n = 9).

Differences Within Sites After Coyote Removal (2000)

During 2000, 227 coyotes were removed from site 1. The number removed each 3-day period was 97, 54, 13, and 63. On site 1, relative coyote abundance (18.0 ± 4.5 scats/transect) decreased ($P = 0.02$) compared to the previous year. On site 2 (comparison site), relative coyote abundance (26.0 ± 12.5 scats/transect) was similar ($P = 0.32$) to the previous year. Annual survival of coyotes on site 2 during 2000 remained similar ($Z = 0.07$, $P = 0.93$) to the previous year (Table 7.1).

On site 1, annual survival of swift foxes was not statistically different ($Z = 0.90$, $P = 0.28$) between years, although it increased in 2000 (Table 7.1). Deaths from coyote predation (n = 3) decreased compared to the previous year. Fall density of swift foxes increased from that found in both 1998 (Yate's $\chi^2 = 4.23$, $P = 0.04$) and 1999 (Yate's $\chi^2 = 5.03$, $P = 0.02$, Table 7.2). Relative fox abundance increased from that found in both 1998 (Yate's $\chi^2 = 5.97$, $P = 0.01$) and 1999 (Yate's $\chi^2 = 5.00$, $P = 0.02$, Table 7.2). The recruitment rate of swift foxes also increased from that found in both 1998 ($P = 0.03$) and 1999 ($P = 0.03$, Table 7.2). Annual home range size of swift foxes (8.9 ± 1.0 km^2, n = 6) was similar ($P = 0.40$) to the previous year.

On site 2 (comparison site), annual survival of swift foxes remained similar ($Z = 0.13$, $P = 0.87$) between 2000 and the previous year (Table 7.1), and only 1 death occurred from coyote predation. Fall density remained similar between 2000 and both 1998 (Yate's $\chi^2 = 0.03$, $P = 0.87$) and 1999 (Yate's $\chi^2 = 0.01$, $P = 0.99$, Table 7.2). Relative fox abundance remained similar between 2000 and both 1998 (Yate's $\chi^2 = 0.01$, $P = 0.91$) and 1999 (Yate's $\chi^2 = 0.50$, $P = 0.48$, Table 7.2). The recruitment rate remained similar to both 1998 (*P* = 0.51) and 1999 (*P* = 0.51, Table 7.2). Annual home range size (9.5 ± 1.6 km^2, n = 4) also remained similar (*P* = 0.72) to the previous year.

Discussion

Our study indicated that coyotes can suppress swift fox populations through heavy predation. Of 14 swift foxes killed by coyotes during the study on both sites, none were consumed, suggesting that coyotes killed swift foxes for reasons other than food. Swift foxes were likely killed by coyotes due to interspecific competition, as this phenomenon has occurred between coyotes and other fox species. For example, previous research indicated that coyotes suppressed populations of red foxes (*Vulpes vulpes*) by interspecific competition (Voigt and Earle 1983, Sargeant et al. 1987). Additionally, coyotes killed relatively high numbers of gray foxes (*Urocyon cineroargenteus*) and kit foxes (*V. macrotis*) due to interspecific competition (O'Neal et al. 1987, Fedriani et al. 2000). In general, interspecific killing among carnivores is common in nature (Palomares and Caro 1999). In addition to foxes, populations of other small carnivores have been negatively related to coyotes (Robinson 1961, Litvaitis and Harrison 1989, Rogers and Caro 1998, Crooks and Soule 1999, Henke and Bryant 1999), including bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), badgers (*Taxidea taxus*), and striped skunks (*Mephitis mephitis*), suggesting that coyotes are capable of suppressing several species of small carnivores.

Prior to coyote removal, our results indicated that human reductions in coyote numbers were beneficial to swift foxes. In fact, human reductions in coyote numbers may have overcome the negative effects of habitat fragmentation. Initially, we believed that populations of swift foxes should have been more productive on site 1 compared to site 2, as site 1 contained unbroken expanses of native vegetation that was less impacted by humans. However, coyotes numbers were relatively high on site 1 as they were lightly exploited by humans. Consequently, due to heavy predation by coyotes, swift foxes exhibited a sink population due to low survival, low density, and low recruitment. In contrast, site 2 occurred on a private ranch surrounded by a fragmented landscape consisting of highways, human dwellings, other ranches, agricultural fields, and CRP fields. However, coyote numbers were relatively low on this site as coyotes were heavily exploited by both the local landowners and hunters. Consequently, due to low predation by coyotes, swift foxes exhibited a source population due to high survival, high density, and high recruitment during all 3 years of the study. Habitat fragmentation and other human-induced changes to the landscape have contributed to the decline of swift foxes in the western Great Plains (Egoscue 1979, Scott-Brown et al. 1987). However, our results indicate that reductions in coyote numbers by humans can compensate for the negative effects of habitat fragmentation, at least in local areas.

The coyote removal program we conducted on site 1 was successful in decreasing the local coyote population by approximately 56%. Consequently, within 1 year the swift fox population changed from a sink to a source, as survival, density, and recruitment increased. Coyote reduction programs have previously been used for a wide variety of purposes, including livestock operations and game management. For example, most coyote reduction programs are conducted to decrease livestock losses (Andelt 1987, Knowlton et al. 1999), primarily calves, sheep, and goats. Coyote reduction is generally effective in localized areas for this purpose (Knowlton et al. 1999), although it is controversial (Andelt 1987). Coyote reduction programs also have been used to increase numbers of game species, including deer (*Odocoileus* spp.) and pronghorn (*Antilocapra americana*), although these programs were not always successful (Connolly 1978, Smith et al. 1986, Ballard et al. 2001). Ballard et al. (2001) reviewed 40 previous studies and concluded that predator reductions enhanced only those deer populations that were well below their carrying capacity. Our results indicate that coyote reduction programs can be successful for increasing numbers of swift foxes. However, our results might not be applicable to all swift fox populations. Previous research in other areas showed the negative effects of coyotes on swift foxes were not as great as in our study (Kitchen et al. 1999, Olsen and Lindzey 2002), suggesting that coyote reductions might not be as beneficial in those areas. Thus, similar to that found for deer management, coyote reductions might enhance only those swift fox populations that are well below their carrying capacity, such as that found on site 1 during our study.

Prior to coyote removal on the national grasslands (site 1), swift foxes exhibited a sink population as a result of low recruitment and low survival. Our annual survival estimate for swift foxes at that site, 0.47, was similar to that reported in most previous studies. For example, annual survival of swift foxes was 0.52-0.53 in Colorado (Rongstad et al. 1989, Covell 1992), 0.46 in Montana (Zimmerman 1998), 0.45 in Kansas (Sovada et al. 1998), and 0.40 during 1 of 3 years in Wyoming (Olsen and Lindzey 2002). A source population, positive recruitment, and annual survival > 0.60 occurred only after we removed coyotes on the national grasslands, and during all 3 years on site 2 where coyotes were already reduced by humans. Annual survival > 0.60 was reported only by Kitchen et al. (1999) in Colorado, and Olsen and Lindzey (2002) in Wyoming (2 of 3 years). Unfortunately, no previous studies determined recruitment rates for swift foxes. Thus, whether other populations of swift foxes were sink or source was not known. Our results suggest that recruitment rates for swift foxes should be determined in future studies, as other swift fox populations with relatively low survival also might exhibit sink populations.

The severe negative effects that coyotes have on swift foxes might be the result of previous wolf (*Canis lupus*) extirpations, and the effect this had on canid hierarchy. Wolves are known to suppress coyote populations, but not fox populations, as canid competition is most intense in more similarly-sized species (Peterson 1995). For example, predation and displacement of coyotes by wolves has been reported in Canada, Alaska, Yellowstone National Park (YNP), and Minnesota (Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982, Peterson 1995, Crabtree and Sheldon 1999). Similar to coyote predation on swift foxes, wolves killed but did not consume coyotes (Carbyn 1982, Peterson 1995), suggesting that wolves killed coyotes for reasons other than food. After wolves were introduced into YNP in the mid-1990s, wolf killings of coyotes resulted in a 50% sustained reduction in the coyote density (Crabtree and Sheldon 1999). This information suggests that prior to European colonization, wolves suppressed coyote densities at approximately 50% of their carrying capacity in central North America. The historic suppression of coyotes by wolves allowed for relatively abundant red fox populations in the northern Great Plains (Johnson and Sargeant 1977, Peterson 1995). Similarly, in the western Great Plains, the historic occurrence of wolves apparently allowed swift fox populations to thrive, as wolves suppressed coyotes populations but not the smaller swift foxes (Johnson and Sargeant 1977, Sovada et al. 1998).

Management Implications

Coyotes can suppress swift fox populations by heavy predation, apparently due to competition or territorial behavior, as swift fox carcasses were not consumed. Consequently, human reductions in coyote numbers were beneficial to swift foxes. In human-altered areas, constant reductions in coyote numbers by hunters and local landowners resulted in a source population of swift foxes, even though natural habitat was restricted and fragmented. Thus, even fragmented and relatively small areas of natural habitat can support viable populations of swift foxes, if coyotes numbers are constantly reduced. Although habitat loss and fragmentation has severely restricted the distribution of swift foxes in the western Great Plains (Egoscue 1979), protecting remaining natural and contiguous habitats may not be adequate to maintain viable swift fox populations in the long term. In unbroken expanses of natural habitat on Rita Blanca National Grasslands, swift foxes exhibited a sink population due to high numbers of coyotes. Under these circumstances, coyote hunting should not be restricted, and, in fact, may need to be encouraged by wildlife managers. The coyote reduction program we conducted on the national grasslands was successful in changing a sink population of swift foxes into a source. Thus, if natural or protected areas are little hunted by humans, then local coyote reduction programs should be conducted if conservation of swift foxes is a desired management objective. However, before conducting a coyote reduction program, wildlife managers need to determine if swift foxes are below their carrying capacity, as coyote reductions may not be beneficial otherwise.

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Table 7.1-Annual survival estimates and 95% confidence intervals (CI) for swift foxes and coyotes monitored at 2 study sites in northwestern Texas, 1999 and 2000.

	Site 1			Site 2		
	n[a]	Survival	(95% CI)	n	Survival	(95% CI)
Swift foxes						
1999	23	0.47	(0.28-0.77)	22	0.69	(0.47-0.99)
2000[b]	30	0.63	(0.42-0.94)	20	0.66	(0.36-1.00)
Coyotes						
1999	12	0.90	(0.74-1.00)	12	0.54	(0.32-0.93)
2000[b]	--	-----	-------------	10	0.56	(0.29-1.00)

[a] Number of animals used in analysis for that year.

[b] Coyotes were removed from site 1 during 2000.

Table 7.2-Estimates of fall density, relative abundance, and recruitment for swift foxes monitored at 2 study sites in northwestern Texas, 1998 to 2000.

	Fall Density (no. captured/area)	Relative Abundance (no. trapped/100 trapnights)	Recruitment (no. young/adult)
Site 1			
1998	0.31 fox/km^2	9.7 fox/100 trapnight	0.25 young/adult
1999	0.24 fox/km^2	9.8 fox/100 trapnight	0.25 young/adult
2000[b]	0.68 fox/km^2	16.4 fox/100 trapnight	1.20 young/adult
Site 2			
1998	0.77 fox/km^2	12.1 fox/100 trapnight	1.30 young/adult
1999	0.68 fox/km^2	13.8 fox/100 trapnight	1.30 young/adult
2000[b]	0.73 fox/km^2	11.5 fox/100 trapnight	1.00 young/adult

[b] Coyotes were removed from site 1 during 2000.

CHAPTER VIII

SUMMARY

Although research on swift foxes (*Vulpes velox*) has recently increased, none has documented trapping methods or compared various types of trap sets. We compared capture rates of 2 types of trapping methods, single-set boxtraps and reverse double-set boxtraps, for capturing swift foxes and other mesocarnivores. We also evaluated the use of pan-tension devices on No. 3 Soft Catch traps for capturing sympatric coyotes (*Canis latrans*) while excluding swift foxes. We captured 87 swift foxes 302 times in boxtraps in northwest Texas from August 1998 to January 2001. Capture rate for reverse double-set boxtraps was 48% higher (*P*=0.003) than single-set boxtraps, as reverse double-set boxtraps allowed easier access to bait and allowed for capture of 2 swift foxes. Capture rates between the 2 trap sets were not different (*P*=0.937) for striped skunks (*Mephitis mephitis*), suggesting that advantages of reversed double-set traps were unique to swift foxes. Use of pan-tension devices set at 2.15 kg on No. 3 Soft Catch traps allowed us to capture 32 sympatric coyotes while excluding swift foxes. Due to their small size, swift foxes could have sustained serious injuries if captured. The capture rate of No. 3 Soft Catch traps for coyotes was 94%, whereas the exclusion rate for swift foxes was 100% despite 88 visits in 562 trapnights.

Members of the family Canidae are distinguished from other carnivore families by exhibiting monogamy and male care of the young. Although canids exhibit a high degree of flexibility in their social organization within and among species, a social organization based on female territories, which is more typical of other carnivore families, was unknown among the 36 species within Canidae. Our research on swift foxes was the first to document a social organization of canids based entirely on female territories. We found that adult females maintained territories and family structure, and adult males emigrated. We based our conclusion on the following movement patterns: (1) when adult females died, adult males always emigrated from their territories, (2) when adult females died, most juveniles emigrated from their territories, (3) when adult males died, adult females and juveniles never exhibited unusual movements, and (4) one female maintained a territory for 13 months without a male. This social organization probably evolved as a result of their insectivorous diet during summer, which reduces the importance of male care of the young.

Little is known concerning swift fox mating system and adult group structure, especially in areas with different densities. We examined 26 reproductive groups of swift foxes from both a high and low density during 3 field seasons in northwestern Texas. Although populations were only separated by 40 km, swift foxes exhibited polygyny, communal denning, and nonbreeding females in the area of high density, whereas only monogamy with no additional females occurred in the area of low density. Density did not appear to be related to habitat or food resources, as vegetation and diets were similar between sites. Furthermore, home ranges were larger on the area of high density, suggesting that foxes were not food stressed in the area of low density. Spring density of swift foxes was related to differences in predation from coyotes as coyotes were the major cause of fox mortality in the area of low density, but not in the area of high density.

Our data indicate that differences in density from high mortality can affect the mating system and group structure of swift foxes, even between short distances. Although previous research indicated that social systems among canids was related to bottom-up forces (i.e., food, habitat), our study indicates that social systems also can be related to top-down forces (i.e., predation, displacement by a larger competitor).

Distribution and numbers of swift foxes in the western Great Plains have been dramatically reduced since historical times. Human-induced changes to the environment, especially conversion of native prairie to agriculture, have been hypothesized as the primary reason for the decline of the swift fox. Despite a recent increase in research, there have been no studies in fragmented landscapes to assess the effects of human impacts on swift foxes. From 1998 to 2001, we monitored movements of 42 swift foxes in a landscape interspersed with 4 habitat types: native shortgrass prairies that were grazed by cattle, nonnative (CRP) grasslands that were ungrazed, irrigated agriculture, and dry-land agriculture. Annual adult survival ranged from 0.52 to 0.55, whereas 6-month survival of juveniles (5 to 11 months of age) ranged from 0.55 to 0.66. Overall, the primary causes of mortality were from vehicle collisions (42% of deaths) and coyote predation (33%). Annual home range size (mean ± SE) of adult males (10.8 ± 1.6 km^2) was similar ($P = 0.90$) to adult females (10.5 ± 1.1 km^2). We determined habitat use at 2 spatial scales: within study area, and within home ranges. Habitat use was similar at both spatial scales, as swift foxes exhibited a strong preference for shortgrass prairies. Swift foxes had lower than expected use of dry-land agriculture, complete avoidance for irrigated agriculture, and nearly complete avoidance of CRP grasslands. Our results indicate that swift foxes are more specialized in their habitat selection than other North American canids, thus protection of native shortgrass prairies might be necessary for their long-term existence.

Interspecific competition among canids can result in mortalities and spatial displacement of smaller canids by larger canids. To investigate mortalities and spatial relationships of swift foxes and coyotes, we captured and radio-tracked both species at Rita Blanca National Grasslands in northwestern Texas. At least 89% of swift fox mortalities were caused by coyotes, resulting in a relatively low annual survival of 0.47 for foxes. Annual home ranges of swift foxes occurred near the periphery and outside coyote home ranges, and did not overlap, or only slightly overlapped, coyote core areas. Swift foxes that shifted home ranges and established dens within a coyote's core area were killed by coyotes shortly thereafter. Our data indicated that spatial displacement of swift foxes was not due to behavioral avoidance of coyotes, but rather increased predation of swift foxes within coyote core areas. Most mortalities caused by coyotes occurred in the immediate vicinity of swift fox dens, suggesting that coyotes made an active effort to kill swift foxes.

Finally, we studied the effects of coyotes on swift foxes in northwestern Texas, because coyotes had been identified as the largest cause of mortality in most swift fox populations. We radio-collared and monitored 88 swift foxes and 29 coyotes at 2 study sites from 1998 to 2000. On site 1, coyotes had relatively high abundance (41 ± 6.8 scats/transect) and survival (0.90), whereas swift foxes had low survival (0.47), low density (0.24-0.31 foxes/km^2), low recruitment (0.25 young/adult), and exhibited a sink population due to heavy predation from coyotes. On site 2, coyotes had low abundance (19 ± 4.9 scats/transect) and survival (0.54), whereas swift foxes had high survival (0.69), high density (0.68-0.77 foxes/km^2), high recruitment (1.3 young/adult), and exhibited a source population due to low predation by coyotes. These initial results suggested that lower coyote numbers were beneficial to swift foxes. To test this hypothesis, we experimentally removed 227 coyotes on site 1 during the final year of the study. Subsequently, coyotes had decreased abundance (18 ± 4.5 scats/transect), whereas swift foxes had increased survival (0.63), increased density (0.68 foxes/km^2), increased recruitment (1.2 young/adult), and exhibited a source population due to lower predation by coyotes. All parameters remained consistent on site 2. Our results indicate that high coyote numbers can suppress swift fox populations due to heavy predation. Our findings indicate that reductions in coyote numbers can change a sink population of swift foxes into a source population, and thus has important implications for conservation efforts of swift foxes.

APPENDIX A

SUMMARY OF SWIFT FOXES AND COYOTES CAPTURED FROM 1998 TO 2001 IN NORTHWESTERN TEXAS

Table A.1-Summary of swift foxes and coyotes captured from August 1998 to March 2001 on a private ranch in Sherman (SH) and Dallam (DM) counties, Texas.

ID	collar no.	Sex	Age	Site	Period Monitored	Fate
Swift foxes						
1	151.892	M	A	SH	08/19/98-09/10/98	dead-unknown
2	151.673	F	J	SH	08/20/98-09/11/98	
2[a]	151.284	F	Y	SH	08/30/99-09/20/99	dispersed
3	151.182	F	J	SH	08/21/98-01/30/99	dispersed
4	151.792	F	J	SH	08/22/98-09/11/98	dead-unknown
5	151.271	M	J	SH	09/04/98-01/10/99	dispersed
6	151.382	M	A	SH	09/04/98-01/24/00	dispersed
7	not collared	M	J	SH	09/06/98	
8	151.662	F	J	SH	09/06/98-10/17/98	killed-coyote
9	151.613	F	J	SH	09/08/98	
9[a]	150.893	F	Y	SH	01/09/00	
9[a]	151.891	F	A	SH	11/05/00-03/15/01	killed-coyote
12	151.053	F	A	SH	10/03/98-10/10/99	killed-coyote
26	151.013	F	J	SH	11/22/98-01/22/99	dispersed
30	151.552	F	J	SH	12/14/98-01/22/99	dispersed
47	150.753	F	J	DM	02/28/99	
47[a]	150.923	F	Y	DM	09/30/99-10/11/99	dispersed
48	150.084	F	J	DM	03/01/99-03/30/99	dispersed
49	150.045	M	A	DM	03/01/99	
49[a]	150.943	M	A	DM	09/29/99	
49[a]	150.934	M	A	DM	08/25/00-08/26/00	dispersed
50	150.312	F	A	DM	03/02/99-03/25/99	killed-vehicle
52	150.103	F	A	DM	03/04/99	
52[a]	151.152	F	A	DM	10/01/99-10/15/99	killed-vehicle
53	150.163	M	A	DM	03/04/99	
53[a]	150.873	M	A	DM	11/27/99-02/19/00	dispersed
54	150.123	F	A	DM	03/05/99	
54[a]	150.984	F	A	DM	10/01/99-08/09/00	killed-vehicle
65	150.533	M	J	DM	10/01/99-12/27/99	dispersed
66	151.116	F	J	SH	10/03/99-01/13/00	dispersed
67	151.252	F	J	SH	10/05/99-10/29/99	dispersed
68	150.805	F	J	DM	10/05/99-01/31/00	dispersed
69	150.853	F	J	DM	10/05/99-10/12/99	killed-vehicle
70	150.703	F	A	DM	10/07/99-06/15/00	unknown
71	151.054	M	A	DM	10/21/99-02/20/00	dispersed
72	150.764	F	J	DM	10/23/99-02/20/00	dispersed
80	150.613	M	J	DM	08/24/00-12/24/00	dispersed

Table A.1 (cont.)

ID	collar no.	Sex	Age	Site	Period Monitored	Fate
Swift foxes						
81	150.914	F	J	DM	08/25/00-10/14/00	killed-vehicle
83	150.974	F	A	DM	08/26/00-05/08/01	alive
84	150.994	F	J	DM	08/26/00-09/04/00	dispersed
85	150.674	F	J	DM	08/26/00-10/03/00	killed-coyote
86	150.953	M	A	DM	08/27/00-05/08/01	alive
87	150.815	F	J	DM	08/29/00-10/24/00	dead-unknown
109	151.662	M	A	DM	11/01/00-05/08/01	alive
110	150.634	M	J	DM	11/03/00-01/19/01	dispersed
113	150.754	F	J	DM	12/16/00-05/08/01	alive
114	150.729	F	J	DM	12/16/00-05/08/01	alive
115	150.714	M	A	DM	12/17/00-05/08/01	alive
117	150.327	M	A	SH	01/05/01-05/09/01	alive
120	150.784	F	Y	SH	03/23/01-05/08/01	alive
Coyotes						
27	150.564	F	Y	SH	12/06/98-06/05/00	unkown
28	150.383	M	Y	SH	12/09/98-02/13/99	dispersed-killed
29	150.593	M	Y	SH	12/10/98-12/29/99	dispersed-killed
31	150.553	F	Y	SH	12/15/98-10/26/99	killed-hunters
32	150.583	M	A	SH	12/21/98-10/24/99	unkown
51	150.644	M	Y	SH	03/04/99-11/20/99	killed-hunters
55	150.623	M	Y	SH	03/07/99-05/09/01	alive
56	150.515	F	A	SH	03/08/99-06/05/00	killed-vehicle
57	150.423	F	Y	SH	03/09/99-04/01/99	unknown
58	150.663	F	Y	SH	03/29/99-04/09/01	unkown
59	150.261	M	A	SH	03/31/99-05/08/01	alive
60	150.362	M	Y	SH	04/01/99-01/09/00	killed-hunters
78	150.483	F	Y	SH	03/20/00-01/06/01	unkown
79	150.522	F	Y	SH	04/06/00-01/06/01	unkown
82	150.823	M	A	SH	08/26/00-09/20/00	killed-hunters
88	150.442	M	A	DM	09/06/00-11/02/00	killed-hunters
89	not collared	M	J	SH	09/07/00	
90	150.503	M	A	SH	09/09/00-04/08/01	dispersed

[a] re-captured and fitted with new radio-collar.

Table A.2. Summary of swift foxes and coyotes captured from August 1998 to March 2001 on Rita Blanca National Grasslands in Dallam County, Texas.

ID	collar no.	Sex	Age	Period Monitored	Fate
Swift foxes					
10	150.728	M	A	09/12/98	
10[a]	151.313	M	A	09/04/99	
10[a]	151.173	M	A	11/01/99	
10[a]	151.593	M	A	09/15/00-10/17/00	killed-coyote
11	151.934	F	J	09/15/98	
11[a]	151.036	F	Y	11/01/99	
11[a]	151.952	F	A	11/15/00-03/22/01	unkown
13	151.783	F	J	10/12/98-11/29/98	killed-coyote
14	151.412	M	J	10/12/98-12/10/98	killed-coyote
15	150.833	F	J	10/17/98-02/05/00	unknown
16	151.433	F	J	10/18/98-01/20/00	unknown
17	151.994	M	J	10/18/98-03/20/99	dead-unkown
18	151.703	M	A	10/19/98-12/01/98	killed-coyote
19	150.813	M	J	10/19/98-03/29/99	killed-coyote
20	150.711	F	A	10/19/98-11/20/98	killed-coyote
21	151.954	F	A	10/20/98-03/13/98	killed-coyote
22	151.514	M	A	10/20/98-03/30/99	disperse
23	150.796	M	A	10/22/98-01/21/00	unknown
24	151.266	M	J	10/24/98-10/27/98	killed-coyote
25	151.725	F	A	10/26/98-08/31/99	unknown
45	150.147	F	A	02/20/99-08/09/99	killed-coyote
46	150.024	M	A	02/22/99-04/02/00	killed-coyote
61	151.774	F	J	04/01/99-04/08/99	dispersed
62	151.735	M	A	09/04/99	
62[a]	151.314	M	A	04/08/00	
62[a]	151.412	M	A	11/17/00-01/05/01	unknown
63	151.234	M	A	09/06/99	
63[a]	151.425	M	A	09/20/00-05/08/01	alive
64	151.134	F	J	09/07/99-03/01/00	dispersed
73	151.015	M	A	11/05/99-12/19/99	dispersed
74	151.095	F	J	11/12/99-02/13/00	dispersed
75	151.193	F	A	12/20/99	
75[a]	151.702	F	A	10/12/00-05/06/01	killed-coyote
76	150.635	F	J	01/08/00-01/22/00	killed-vehicle
77	150.575	F	J	01/13/00-07/13/00	killed-coyote
91	151.904	M	J	09/13/00-09/20/00	dispersed
92	151.937	F	J	09/14/00-09/27/00	killed-coyote

Table A.2 (cont.)

ID	collar no.	Sex	Age	Period Monitored	Fate
Swift foxes					
93	151.784	F	A	09/14/00-04/01/01	killed-coyote
94	151.376	M	J	09/15/00-02/20/01	dispersed
95	151.604	M	J	09/15/00-01/25/01	killed-trapper
96	151.464	F	J	09/15/00-05/08/01	alive
97	151.645	M	J	09/16/00-02/25/01	dispersed
98	151.584	M	J	09/16/00-09/28/00	dispersed
99	151.973	F	J	09/16/00-09/24/00	dispersed
100	151.354	F	J	09/21/00-05/08/01	alive
101	151.473	F	J	09/26/00-12/24/00	dispersed
102	151.514	M	A	09/27/00-05/08/01	alive
103	151.393	M	J	09/27/00-11/10/00	killed-coyote
104	151.624	F	A	09/27/00-05/08/01	alive
105	151.634	F	J	09/27/00-01/25/01	killed-trapper
106	151.614	M	J	09/27/00-10/04/00	dispersed
107	151.553	F	A	09/28/00-05/08/01	alive
108	151.252	F	J	10/01/00-12/13/00	dispersed
111	151.733	M	A	11/14/00-03/15/01	killed-coyote
112	151.264	M	A	11/30/00-05/08/01	alive
116	151.993	M	J	01/04/01-01/05/01	dispersed
118	not collared	M	J	03/01/01	
119	151.054	M	A	03/04/01-05/08/01	alive
Coyotes					
33	150.544	F	Y	01/08/99-01/02/00	killed-hunters
34	150.504	F	Y	01/10/99-04/18/99	killed off site-hunters
35	150.654	M	Y	01/10/99-01/05/00	killed-control program
36	150.684	M	A	01/14/99-01/07/00	killed-control program
37	150.284	F	Y	01/16/99-04/18/99	killed off site-hunters
38	150.883	M	Y	01/18/99-01/04/00	disperse
39	150.772	F	A	01/22/99-01/07/00	disperse-killed
40	150.462	M	A	01/24/99-09/16/99	unknown
41	150.904	M	Y	01/25/99-01/07/00	killed-control program
42	150.324	M	A	02/17/99-01/06/00	killed-control program
43	150.604	F	Y	02/17/99-01/07/00	killed-control program
44	150.344	F	A	02/20/99-01/06/00	killed-control program

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[a] re-captured and fitted with new radio-collar.

APPENDIX B

BODY MEASUREMENTS OF SWIFT FOXES AND COYOTES CAPTURED FROM 1998 TO 200 IN NORTHWESTERN TEXAS

Table B.1-Mean standard measurements (± SD) of adult swift foxes and coyotes captured from August 1998 to January 2001 in Sherman and Dallam counties, Texas.

Species (*n*)	Body mass (kg)	Body length (cm)	Shoulder height (cm)	Hindfoot length (cm)	Tail length (cm)	Ear length (cm)
PRIVATE RANCH						
Swift foxes						
male (7)	2.6 (±0.2)	51.1 (±2.3)	29.9 (±0.8)	12.0 (±0.4)	29.0 (±0.9)	6.4 (±0.1)
female (8)	2.5 (±0.2)	49.0 (±1.5)	29.3 (±0.8)	11.5 (±0.2)	27.9 (±0.9)	6.2 (±0.3)
Coyotes						
male (10)	12.2 (±0.7)	87.4 (±2.4)	52.4 (±1.3)	18.2 (±0.8)	32.9 (±2.1)	10.7 (±0.6)
female (6)	11.8 (±1.1)	85.1 (±2.8)	50.8 (±2.3)	17.4 (±0.8)	31.7 (±1.1)	10.5 (±0.3)
NATIONAL GRASSLANDS						
Swift foxes						
male (10)	2.6 (±0.2)	50.4 (±1.6)	30.2 (±0.9)	12.0 (±0.4)	29.7 (±1.4)	6.4 (±0.3)
female (9)	2.2 (±0.1)	48.2 (±1.1)	28.8 (±0.7)	11.3 (±0.3)	27.7 (±1.8)	6.1 (±0.2)
Coyotes						
male (6)	13.8 (±1.3)	86.8 (±3.3)	52.2 (±1.3)	18.3 (±0.3)	32.4 (±1.2)	11.0 (±0.2)
female (6)	11.7 (±1.4)	85.2 (±1.8)	50.7 (±2.0)	17.9 (±0.7)	33.2 (±2.4)	10.5 (±0.3)