



## Variation in mating system and group structure in two populations of swift foxes, *Vulpes velox*

JAN F. KAMLER\*, WARREN B. BALLARD\*, PATRICK R. LEMONS\* & KEVIN MOTE†

\*Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock

†Texas Parks and Wildlife Department, Pilot Point

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We studied 26 reproductive groups of swift foxes, *Vulpes velox*, from both high- and low-density areas during three field seasons in northwestern Texas, U.S.A., to examine whether differences in population density affect mating system and group structure. Although high- and low-density populations were only separated by 40 km and vegetation and diets were similar between sites, polygynous groups, communal denning and nonbreeding females occurred in the area of high density, whereas only monogamous pairs occurred in the area of low density. Annual survival of adult swift foxes was 66% in the area of high density, but 44% in the area of low density. Predation from coyotes, *Canis latrans*, was the only mortality factor that differed ( $P = 0.01$ ) between sites and contributed most to differences in survival. Although previous research indicated that variation in social systems among canids is related to bottom–up forces (i.e. food, habitat), the results of our study indicate that variation in social systems can also be related to top–down forces (i.e. predation, displacement by larger competitor).

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Polygamy is the predominant mating system of most mammals, occurring in more than 97% of species studied (Kleiman 1977). The major exception occurs within the family Canidae, in which most species tend to be monogamous (Kleiman 1977). Monogamy within Canidae probably evolved in relation to pair bonding and male care of the young (Kleiman & Eisenberg 1973). However, there is considerable interspecific variation in mating systems among canids, and both polygamy and monogamy have been documented (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).

Canids are also unique in that intraspecific variation in mating systems may be as great as interspecific variation, whereby both polygyny and monogamy occur 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*, varies considerably with food dispersion and abundance (Macdonald 1979a). Group sizes of grey wolves, *C. lupus*, and coyotes, *C. latrans*, often depend on prey size and availability (Bekoff & Wells 1980; Harrington et al. 1982; Messier & Barrette 1982). Both red foxes, *Vulpes vulpes*, and Arctic foxes, *Alopex lagopus*, show intraspecific variation in mating system and group structure as a result of differences in food and/or habitat resources (Macpherson 1969; Macdonald 1983; Hersteinsson 1984; Moehlman 1989). Mating systems have also been observed to change over time within the same population, shifting from polygyny to monogamy, when food resources decline (red foxes: von Shantz 1984; Zabel & Taggart 1989).

Among primate species, several factors have been suggested to affect social organization, including food distribution, risk of infanticide, conspecific competition, habitat dispersion, population density and predation risk (Wrangham 1980; van Schaik 1983, 1996; Dunbar 1988, 1996; Moore 1999). Similarly, among avian species, several factors are suggested to affect mating systems, including male age, nesting dispersion, breeding synchrony and breeding density (Birkhead & Møller 1992; Westneat & Sherman 1997). Under certain conditions, some of these factors might be more influential than others, but it is more likely that a combination of these

Correspondence and present address: W. B. Ballard, Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, TX 79409, U.S.A. (email: [warren.ballard@ttu.edu](mailto:warren.ballard@ttu.edu)). J. F. Kamler is now at the Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland.

factors influences the social organization and mating system of a given population. Thus, although differences in food abundance and habitat have been shown to affect intraspecific variation in reproductive strategies of canids, other factors such as mortality from predators might also affect reproductive strategies of canids, at least under certain conditions. In fact, some researchers have suggested that mortality from larger canids 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, separated by 40 km, in northwestern Texas, U.S.A., that differed in density by at least two-fold. Initial results suggested that density was related to differences in survival and mortality from coyotes, and not to differences in food or habitat resources. This provided a unique opportunity to determine whether the mating system and group structure of swift foxes differed with respect to predation pressure and density.

## METHODS

We studied 26 breeding groups of swift foxes (classified as warranted, but precluded as endangered from 1995 to 2001 under the Endangered Species Act; Clark 2001) at two sites in northwestern Texas between August 1998 and May 2001. Site 1 was situated on Rita Blanca National Grasslands (RBNB) and adjacent private lands in west-central Dallam County (36°31'N, 102°64'W). Site 2, approximately 40 km east of site 1, was situated on a private cattle ranch on the border of Dallam and Sherman counties (36°24'N, 102°19'W). Vegetation at both sites consisted of short-grass prairie, dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*), that was moderately to intensively grazed by cattle (*Bos taurus*). Although site 2 was more fragmented with agricultural lands, swift foxes used the short-grass prairie more than 97% of the time (Kamler 2002). Coyotes were the primary predator of swift foxes at both sites, but the density of coyotes at each site differed (Kamler et al. 2003a). At site 1, the RBNB is open year-round for hunting and trapping, but survivorship of coyotes was high (90%; Kamler et al. 2003a). At site 2, ranch owners encouraged hunting of coyotes to reduce livestock losses, and consequently, coyotes had low survival (54–56%; Kamler et al. 2003a).

We captured swift foxes using box traps (Kamler et al. 2002). We initially concentrated our trapping effort near the centre of both study sites, then expanded outward as capture of unmarked foxes decreased. Our research protocol (No. 00979BX) was approved by the Texas Tech University Institutional Animal Care and Use Committee. Swift foxes were ear-tagged, radiocollared, and aged by tooth wear, body size and reproductive condition (Rongstad et al. 1989). We classified foxes that were less than 10 months old as juveniles (i.e. from March to mid-January each year) and classified all other foxes as adults. We estimated the spring density of swift foxes by calculating the minimum number of adults that remained on each study site during May, which was the middle of the pup-rearing period. The area of

each study site was determined by the total area encompassed by all monitored foxes.

Foxes were considered to belong to the same family group if they used the same area and dens concurrently (Kitchen et al. 1999). Female foxes were considered to be breeders if they were pregnant when captured, or showed evidence of nursing during or after the pup-rearing period. We defined a breeding group as polygynous if two breeding females stayed in the same den (e.g. communal denning) with pups during the entire pup-rearing period. One adult male was always associated with a pair of breeding females, although the male sometimes stayed in a separate den nearby. We defined breeding groups consisting of one breeding female and one adult male as monogamous. We classified females as nonbreeders if they used the same territory as that of breeding adults during the pup-rearing period, but showed no evidence of current or former nursing. We compared mean group sizes between study sites using *t* tests (Zar 1996), and deemed results significant when  $P < 0.05$ .

We monitored den use, especially during the breeding (January–February) and pup-rearing (March–June) periods, by radiotracking swift foxes at night and by visiting their underground burrows during the day. Throughout the study, we also recorded independent telemetry locations (White & Garrott 1990) for study animals once or twice each week, separated by at least 12 h. We radiotracked from vehicles using null-peak systems, which consisted of dual, four-element Yagi antennas. For independent locations, we radiotracked 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). The mean error for reference collars (known locations) was 84 m (95% of errors were < 145 m).

We determined annual home range sizes for adult swift foxes using the minimum convex polygon method, as calculated by the Animal Movement program (Hooge & Eichenlaub 1997). We calculated home ranges for foxes using a minimum of 30 locations and 6 months of radiotracking data. Additionally, we pooled the locations for family members to calculate a total home range for each family group. Group home ranges were calculated only if more than one individual per group met the above criteria. For individual group members, we calculated home range overlap based on the percentage of home range area overlapping that of another family member. We compared mean home range sizes for individuals and family groups, and mean home range overlap, between sites using *t* tests (Zar 1996), and deemed results significant when  $P < 0.05$ .

We estimated annual survival and cause-specific mortality rates for adult swift foxes using the program Micromort (Heisey & Fuller 1985). Causes of mortality for swift foxes were determined by necropsy. We classified swift fox deaths as coyote predation if fox carcasses had haemorrhaging and puncture wounds consistent with that from coyote bite marks. We initially analysed the data by biological season to meet the assumption of constant survival (Heisey & Fuller 1985). Because preliminary

analyses indicated that survival did not differ between seasons or years, we grouped the data and compared survivorship between sites using *Z* tests (Heisey & Fuller 1985; Nelson & Mech 1986). Differences in survival and cause-specific mortality rates were deemed significant when  $P < 0.05$ .

## RESULTS

During the 3-year study, we radiocollared and monitored 31 adult swift foxes on site 1 and 21 adults on site 2. Of these, we determined annual home ranges for 23 adults on site 1 and 17 adults on site 2. Annual home range sizes ( $\bar{X} \pm \text{SE}$ ) for individuals were larger (Student's *t* test:  $t_{38} = 2.3$ ,  $N = 40$ ,  $P = 0.03$ ) on site 2 ( $10.7 \pm 0.9 \text{ km}^2$ ) than on site 1 ( $8.4 \pm 0.5 \text{ km}^2$ ). Group home range sizes also were larger ( $t_7 = -2.5$ ,  $N = 9$ ,  $P = 0.04$ ) on site 2 ( $16.6 \pm 2.4 \text{ km}^2$ ) than on site 1 ( $11.3 \pm 0.3 \text{ km}^2$ ). Home range overlap of family members did not differ ( $t_{36} = 0.7$ ,  $N = 38$ ,  $P = 0.46$ ) between site 2 ( $73.1 \pm 4.0\%$ ) and site 1 ( $78.8 \pm 6.5\%$ ).

Spring densities of adult swift foxes were more than twice as high on site 2 as on site 1 during all 3 years of the study (Table 1). 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 1). On site 2, three of 10 adult groups consisted of two adult females that denned communally throughout the pup-rearing period, along with an associated adult male that usually denned less than 30 m away. There were also four nonbreeding females (three yearlings and one 2-year-old) present among the 10 groups. Overall mean group size was larger ( $t_{24} = 3.4$ ,  $N = 26$ ,  $P < 0.01$ ) on site 2 than on site 1 (Table 1).

Of the three pairs of adult females that denned communally, we recaptured both females of one pair in early March when both were presumably in late pregnancy (based on unusually enlarged abdomens). Both of these females were more than 2 years old and were similar in age based on tooth wear. When captured prior to March, both had elongated and darkened nipples, suggesting that they had nursed the previous year (Mech et al. 1993). An

alternative explanation is that one of these females was pseudopregnant and did not actually give birth, as pseudopregnant canids also may have enlarged abdomens and can sometimes nurse (Asa & Valdespino 1998). However, pseudopregnant females in family groups are typically yearlings that are reproductively suppressed by aggression from dominant females (Asa 1997). Because dominant female foxes are highly aggressive towards subordinates during breeding and birthing periods, breeders do not allow subordinate females in the natal den during the first month after birth (Macdonald 1979b; von Shantz 1984). Thus, we classified this group as polygynous because both females showed evidence of pregnancy in early March and evidence of nursing the previous year, and both females were several years old and similar in age, had denned communally with pups throughout the entire birthing and pup-rearing period (March–May), and had been associated with a single adult male. Females in the second pair were also more than 2 years old and similar in age based on tooth wear, and both females showed signs of nursing when they were captured the previous year. Both females also denned communally with pups throughout the entire birthing pup-rearing period and were associated with an adult male. Because circumstances were similar to the first case, we assumed that both females of this pair also gave birth and were a polygynous group. Females in the third pair were yearlings based on tooth wear and body size, and neither showed signs of nursing the previous year when initially captured. Although neither female was recaptured during the pregnancy period, and thus, pregnancy could not be confirmed, both denned communally with pups during the entire pup-rearing period and were associated with an adult male. Both of these females showed signs of previous nursing when captured the following autumn based on elongated nipples (nipples were not elongated in yearlings that did not nurse). Although one or both of these yearlings could have been pseudopregnant and nursed another's pups without giving birth, we also assumed that both had given birth and were a polygynous group. Overall, the females within each polygynous group appeared to be of the same age, indicating that they may have been sisters.

**Table 1.** Adult spring density and group structure of swift foxes monitored at two study sites in northwestern Texas from 1999 to 2001

	Spring density (no. adult foxes/km <sup>2</sup> )	Monogamous matings (N)	Polygynous matings (N)	Nonbreeding females* (N)	Mean group size
<b>Site 1</b>					
1999	0.09	5	0	0	2.0
2000	0.09	5	0	0	2.0
2001	0.11	6	0	0	2.0
Summary	0.10	16	0	0	2.0
<b>Site 2</b>					
1999	0.31	1	2	3	3.7
2000	0.19	3	0	1	2.3
2001	0.25	3	1	0	2.3
Summary	0.25	7	3	4	2.7

\*Nonbreeding females associated with reproductive groups.

During the study there were 16 confirmed adult mortalities on site 1, and six on site 2. Overall, swift fox deaths were caused by coyote predation ( $N = 14$ ), vehicles ( $N = 4$ ) and other unknown causes ( $N = 4$ ). Annual survival was 66% on site 2, and 44% on site 1, although this difference was not statistically significant ( $Z$  test:  $Z = 1.53$ ,  $P = 0.08$ ). Cause-specific mortality rates differed statistically between sites for coyote predation ( $Z = 2.55$ ,  $P = 0.01$ ), but not for vehicles ( $Z = 1.47$ ,  $P = 0.10$ ) or other unknown causes ( $Z = 0.51$ ,  $P = 0.53$ ).

## DISCUSSION

Spring density of swift foxes was more than twice as high on site 2 as on site 1 during all 3 years of the study. Survival was also 50% higher on site 2 than site 1, and thus, differences in density were probably related to differences in adult survival. Predation from coyotes was the largest cause of mortality overall, and the only mortality factor that differed between sites, suggesting that coyote predation strongly influenced differences in swift fox survival and density between sites. There were fewer deaths from coyote predation at site 2 probably because the density of coyotes was lower as a result of increased rates of hunting and trapping of coyotes at this site (Kamler 2002). In addition to predation, coyotes spatially displaced swift foxes from their home ranges (Kamler et al. 2003b). Predation and spatial displacement are common among canid species, and can result in population suppression of smaller canids by larger canids (Johnson & Sargeant 1977; Peterson 1995; Crabtree & Sheldon 1999). 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 for food or territories.

Differences in mating system and group structure of swift foxes also occurred between study sites. In the area of low density (site 1), all adult groups consisted of monogamous pairs with no nonbreeding females. In contrast, in the area of high density (site 2), 30% of all adult groups consisted of polygynous groups (two females and one male), and nonbreeding females were present in 40% of groups. Because mortality still occurred on site 2, mating systems and group structures there were not homogenous among family groups. Our results are similar to those of Covell (1992), who found that polygynous mating groups among swift foxes in Colorado occurred only when coyote numbers were artificially reduced. During our study, coyote numbers were reduced on site 1 during 2000 (Kamler et al. 2003a); however, this reduction occurred too late (January) to affect the breeding density of adult foxes for that year. Among canids, communal denning of two breeding females was also reported for the closely related kit foxes, *Vulpes macrotis* (Egoscue 1962), and red foxes (Macdonald 1979b; Zabel & Taggart 1989), as well as bat-eared foxes, *Otocyon megalotis* (Nel et al. 1984), coyotes (Camenzind 1978) and grey wolves (Mech 1970).

Several reasons might explain why the lower density of swift foxes, due to predation by coyotes, decreased group

size and the occurrence of polygyny. First, high mortality created vacant territories for both adult females and juveniles to establish their own territories. Second, high mortality reduced the number of available females for both communal denning and nonbreeding status. Voigt & Macdonald (1984) indicated that these same factors might have contributed to differences in mating system and group formation between two populations of red foxes.

The resource dispersion hypothesis predicts that group formation of canids is dependent on heterogeneity of food and habitat distribution (Macdonald 1983). Similarly, differences in food resources are also thought to affect mating systems within canid species (Camenzind 1978; Hersteinsson 1984; Zabel & Taggart 1989). However, differences in food resources are unlikely to account for the differences in mating systems and group structures on our study sites. Food items consumed by swift foxes on both study sites included 53–68% insects, 38–49% small rodents, 14–15% large rodents, 4–11% lagomorphs and 7–15% birds (Lemons 2001). Because swift foxes are omnivorous and opportunistic feeders (Scott-Brown et al. 1987; Sovada et al. 2001), their diets probably reflect the general abundance of available food items (Sovada et al. 2001). These relatively small differences in diet indicate that food resources were relatively similar between sites. Thus, it is unlikely that differences in food resources contributed to the two-fold difference in density between sites or major differences in mating system or group structure.

Differences in habitat resources are also unlikely to account for the differences in mating system and group structure between sites. Although we did not measure habitat quality, short-grass prairie habitat, which historically occurred in this region (Barbour & Billings 1988), dominated both study sites and was used by swift foxes more than 97% of the time on both sites (Kamler 2002). Although more agricultural land occurred on site 2, home ranges of swift foxes were noncontinuous on both sites due to habitat availability and spatial displacement by coyotes (Kamler 2002; Kamler et al. 2003b), indicating that foxes had limited access to available resources on both sites. Additionally, den sites of swift foxes have been found in a variety of natural and human-altered habitats (Cutter 1958; Kilgore 1969), suggesting that den sites were not a limiting factor on either site. However, limiting factors related to resource dispersion could have occurred at a finer scale than that investigated during this study. Regardless, we believe that differences in mating system and group structure of swift foxes in our study were related to the two-fold difference in density, which was affected most by differences in survival and coyote predation. Thus, our study strongly suggests that 'top-down' factors, such as predation and spatial displacement, also can influence mating system and group structure of small canids. 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.

The plastic social system of swift foxes might be an adaptation to the evolutionary constraints imposed on their spacing patterns and densities by larger canids

(Cavallini 1996). Thus, in areas with fewer coyotes, swift foxes may benefit by increasing mating opportunities via polygyny, and by increasing group size to include non-breeding females, which might help to increase pup survival (Moehlman 1979). However, because density of swift foxes was affected by mortality from coyotes, density alone might have affected the mating system and group structure of swift foxes at each site. For example, among avian species that are predominantly socially monogamous, breeding density is related to the use of alternative reproductive strategies within the same species (Westneat & Sherman 1997; Richardson & Burke 2001). Consequently, higher breeding densities in socially monogamous bird species increase the occurrence of polygamy, as the number of available mates increases (Westneat & Sherman 1997; Richardson & Burke 2001). Similarly, population density alone strongly influences social systems of primates (Moore 1999). However, other population parameters related to density, such as socioeconomic behaviours, also influence mating systems both in birds (Westneat & Sherman 1997) and in primates (Moore 1999). Thus, differences in the mating systems of swift foxes and other canids probably result from a complex mix of interacting factors, both intrinsic and extrinsic, which express themselves according to each set of unique circumstances at a given time. The importance of various factors in the evolution of mating systems might be impossible to determine, especially due to lack of knowledge about the specific circumstances under which various social traits evolved.

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