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January 2005

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Kitchen, Ann M.; Gese, Erik M.; Karki, Seija M.; and Schauster, Edward R., "SPATIAL ECOLOGY OF SWIFT FOX SOCIAL GROUPS: FROM GROUP FORMATION TO MATE LOSS" (2005). *USDA National Wildlife Research Center - Staff Publications*. 28.

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## SPATIAL ECOLOGY OF SWIFT FOX SOCIAL GROUPS: FROM GROUP FORMATION TO MATE LOSS

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We examined social group formation, movements and denning relative to other group members, home-range use, and the response to social group disruption among 188 radiocollared swift foxes (*Vulpes velox*) in Colorado. We found that during the initial stages of pair formation mated foxes shared dens more frequently than during the remainder of their pair-bond. The average distance between mated pairs was influenced by season and time of day, with the greatest proximity in the breeding season ( $727.2 \text{ m} \pm 42.3 \text{ SE}$ ), and during diurnal hours ( $463.7 \pm 34.7 \text{ m}$ ). Female foxes spent more time in the core area of the group home range (60.71% of locations versus 54.66% for males) and males spent more time on the range boundary (19.34% of locations versus 15.61% for females). Home-range use was influenced by season, with females spending more time in the core area in the breeding and pup-rearing seasons than in the dispersal season. Males also spent the highest proportion of their time in the core area during the breeding season, but used the boundary area more frequently than the core area in the pup-rearing season. A sex difference also was found in the response of a swift fox to the death or disappearance of its mate. All females maintained their territory in the event of mate death or disappearance; however, 50% of males emigrated from their range when the female mate died or disappeared. These differences in space use between social group members provide important insights into the territorial behavior and mating system of the swift fox and indicate that the 2 sexes likely play different roles in care of young and home-range defense.

Key words: denning, dispersal, group formation, home-range use, spatial ecology, swift fox, *Vulpes velox*

Some carnivores have evolved to live in stable long-term groups and use space cooperatively (Gittleman 1989). The relative space use of social group members and their cohesiveness is influenced by how grouping affects the animals' abilities to forage, avoid predators, and care for young (Gittleman 1989). For example, numerous mammalian species benefit from living in groups and synchronizing space use through increased vigilance for predators (Bertram 1978). However, cohesiveness is often reduced by the need to effectively use resources such as small prey items (e.g., Packer and Ruttan 1988).

These 2 conflicting selective pressures (i.e., foraging efficiency and predator avoidance) may act on swift foxes to determine the level of cohesiveness of the group. Swift fox diets consist mainly of small rodents and insects (Kitchen et al.

1999; Lemons 2001), and thus their foraging efficiency would be increased by hunting alone rather than in a group (Packer and Ruttan 1988). Meia and Weber (1996) noted that red foxes (*Vulpes vulpes*) in the Swiss Jura Mountains use feeding patches serially to reduce competitive interactions between social group members. However, predation by coyotes (*Canis latrans*) is a significant cause of mortality for the swift fox (Kahn et al. 1997; Kitchen et al. 1999; Matlack et al. 2000; Sovada et al. 1998), and could be a strong selective influence for cohesiveness to increase vigilance for predators.

Season and time of day also can be influential in social group space-use patterns. Intra-social group dynamics vary temporally in many animals (e.g., Blundell et al. 2002; Kaunda 2000; Shimooka 2003). For example, the sleeping distance between members of wolf pairs decreased in the breeding season (Mech and Knick 1978). Examining seasonal changes in swift foxes' use of the home range and proximity to other social group members will help explain breeding, pup-rearing, and dispersal behaviors in this species.

Because of the need to act cooperatively, it is likely that the period of initial group formation plays an important role in the

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establishment of bonds between group members (Kleiman 1981), enabling them to efficiently coordinate their activities. This would necessitate increased proximity of the pair members during pair formation. White et al. (2000) noted that kit fox (*Vulpes macrotis*) pairs encountered each other more frequently during nocturnal hours during pair formation. However, how members of swift fox social groups behave relative to each other during this period has not been assessed.

In addition, evaluating the response of an individual to the death or disappearance of a group member is essential to discerning the respective roles of the individuals in the group. Moehlman (1989) noted that in families of medium to large canids (e.g., coyotes—Gese 1998), males often held territories, whereas in small canids (e.g., bat-eared foxes [*Otocyon megalotis*]), females maintained territories. However, the effect of body size on sex-biased dispersal versus territory maintenance may be an indirect one. For example, Greenwood (1980) argued that the direction of a sex-bias in dispersal is a consequence of the type of mating system exhibited by a species.

The swift fox (*Vulpes velox*) is one of the smallest of the North American canids. The swift fox uses dens year-round (Floyd and Stromberg 1981; Kilgore 1969; Uresk and Sharps 1986), with the majority of diurnal hours spent in dens, often concurrently with a mate (Cutter 1958; Kitchen et al. 1999; Ralls and White 2003). Social groups generally consist of a mated pair, although groups of 3 adults also occur (Kilgore 1969). The members of social groups form long-term bonds, with groups holding shared home ranges year-round and most commonly remaining together until the death of 1 group member (Cypher 2003; Kilgore 1969). Many aspects of the behavioral ecology of the swift fox are relatively unknown, with only a few studies focusing on denning and helper behaviors (e.g., Covell 1992; Pruss 1994). By using data from a 4-year field study involving 188 radiocollared swift foxes, we present information on the behavior and relative roles of members of swift fox social groups in a spatial context from initial group formation to termination of the group bond.

Five predictions are tested in this study: foxes spend more time together during the period of pair formation as opposed to after formation because of the need to establish long-term pair-bonds; mated pairs are in closer proximity during the breeding and pup-rearing seasons than during the dispersal seasons because of the need to coordinate efforts of breeding and parental care; proximity of mates during nocturnal hours is influenced by the need to forage separately for small prey (decreasing proximity, that is, foraging farther apart), or the need for predator avoidance (increasing proximity); because of the strength of the pair-bond, mated pairs will synchronize behaviors and use the home range similarly; and response to death or disappearance of a pair mate may differ between sexes because of the likelihood of sex-biased dispersal patterns.

## MATERIALS AND METHODS

**Study site.**—The 1,040-km<sup>2</sup> study area, Pinon Canyon Maneuver Site, is located in Las Animas County, northeast of Trinidad, Colorado. The climate is semiarid with mean annual precipitation of

26–38 cm. Mean monthly temperatures range from  $-1^{\circ}\text{C}$  in January to  $23^{\circ}\text{C}$  in July. Elevations range from 1,310 to 1,740 m. The site consists of river canyons, limestone breaks, and open plains. The 2 main vegetation types are shortgrass prairie and pinyon pine (*Pinus edulis*)–juniper (*Juniperus monosperma*) communities (Shaw et al. 1989). The study area was primarily used for cattle ranching before 1982, at which time the United States Army acquired the Pinon Canyon Maneuver Site for military activities involving month-long, mechanized training sessions 3 or 4 times a year.

**Data collection.**—Foxes were captured by using double-door box traps (80 × 25 × 25 cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with chicken or mackerel parts (Covell 1992). Traps were deployed in the evening and checked the following morning. Trapping ceased during periods when nighttime temperatures dropped below  $-10^{\circ}\text{C}$ . A radiocollar (Advanced Telemetry Systems, Isanti, Minnesota) and ear tag (National Band and Tag Company, Newport, Kentucky) were attached to each fox and the weight, sex, and age of the animal were recorded. To recapture certain individuals to change their radiocollar, a trap-enclosure system as described by Covell (1992) was used. All foxes were released at the site of capture.

Radiocollared foxes were monitored to determine movement patterns, range space use, social groupings, and diurnal den use. Telemetry procedures followed recommendations by White and Garrott (1990). Locations were obtained by triangulating 2 or 3 bearings of the animal's position within 10 min. Triangulation angles were maintained between  $20^{\circ}$  and  $160^{\circ}$  (Gese et al. 1988). Aerial telemetry (Mech 1983) was used to locate missing animals. Relocation of each fox was attempted approximately every 1–3 days with locations obtained throughout the 24-h period to reduce bias in home-range estimates, space-use patterns, and movement analyses. When foxes were located in a den, the den location was recorded and marked. Telemetry error was determined by comparing telemetry locations with actual locations of stationary reference transmitters. Movement patterns and range space use were assessed by using Arcview 3.0 (Environmental Systems Research Institute, Inc., Redlands, California). Statistical analyses including analysis of variance and Wilcoxon tests were performed by using SAS (SAS Institute Inc. 2001). Animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) were followed and research protocols were approved by Institutional Animal Care and Use Committees at Utah State University and the National Wildlife Research Center.

A social group was defined as foxes that shared a range and concurrently shared dens (Kitchen et al. 1999). For the purposes of analyses, we defined seasons on the basis of energetic demands (due to climatic changes and prey abundance) and behavioral characteristics (including breeding, gestation, pup-rearing, and dispersal), which were applicable to swift foxes as follows: pup-rearing season (April 15–August 14), dispersal season (August 15–December 14), and breeding and gestation season (December 15–April 14). The diel period was divided into 4 time periods to assess differences in distances between mates and home-range use throughout the day. The crepuscular periods of “dawn” and “evening” spanned the 2 h before and after sunrise and sunset for the day of location, and “day” and “night” periods fell in between.

The behavior of social group members during pair formation was investigated by using pairs for which both members were being radiotracked during pair formation. We measured distance between the mates during nocturnal and crepuscular hours when locations on both animals were taken within 1 h, and frequency of shared diurnal denning, from date that the 1st den sharing event occurred and weekly thereafter (data for weeks 13 until the termination of the pair-bond were pooled). The distance between mates when locations of both

animals were taken within 1 h and the frequency of shared denning also were assessed seasonally for the entire duration of the pair-bond. The choice of a 1-h interval for use in the analysis was arbitrary; however, the average time between locations was <10 min. Proximity during the entire pair-bond was assessed by using a mixed-effects analysis of variance model of structure 3 (season)  $\times$  4 (time of day)  $\times$  (season  $\times$  time of day). Proximity during pair formation was assessed by using a repeated-measures analysis of variance model of structure 6 (week) with an unstructured covariance structure. The seasonal difference in den sharing was assessed by using a mixed-effects analysis of variance model of structure 3 (season). Tukey's adjusted post hoc *t*-tests were used for multiple comparisons.

The shared group home range for the entire pair-bond was described by using a fixed-kernel home-range estimator (Arcview 3.0). The core area was determined to be the area enclosed by the 50% isopleth, and the boundary area was defined as the area between the 75% and the 95% isopleths. The differential use of regions within the home range by season and diel period was investigated for each social group member by comparing the number of locations that fell in the core area versus those in the boundary area of the shared group home range. This was standardized by dividing number of locations for each area by the total number of locations obtained of each fox, and it was assessed by using a mixed-effects analysis of variance of structure 2 (area)  $\times$  2 (sex)  $\times$  3 (season)  $\times$  4 (time) with all interactions included. The size of the seasonal denning area of each member was assessed by using a minimum convex polygon. Only foxes with a known mate were used for these analyses. A Wilcoxon test was used to assess denning area because of departures from normality.

The response of swift foxes to disruption within the social group (i.e., death or desertion of a mate) was examined by assessing changes in mate association, home range, movements, and diurnal den use of the swift foxes after a disruption as compared to before the disruption. Only pairs for which the remaining fox was radiotracked for at least 6 months after the death or disappearance of the mate were included in analyses to fully examine the results of the disruption.

## RESULTS

We obtained 32,556 radiotelemetry, visual, and den locations of 188 swift foxes, with continuous data collection from January 1997 to December 2000. We had a total of 59 social units of which 55 (93%) were male–female pairs, and 4 (7%) were groups of 3 adults.

### Pair Formation

There were 9 mated pairs for which both members were radiotracked at the time of pair formation. We found that proximity of the foxes during the night and crepuscular hours was not influenced by the number of weeks (assessed for the first 6 weeks) since pair formation ( $F = 0.78$ , *d.f.* = 5, 28,  $P = 0.58$ ). However, diurnal denning behaviors of swift foxes were influenced by pair formation. Den sharing between a newly formed pair was highest during the beginning of the pairbond (<10 weeks), and then declined (Fig. 1). We were unable to test for an effect of season on proximity and denning during pair formation because of the small sample size. However, at least 1 pair formed during each season, and thus seasonal effects were unlikely to account for the differences seen between the beginning period of the pair-bond and the remainder of the bond.

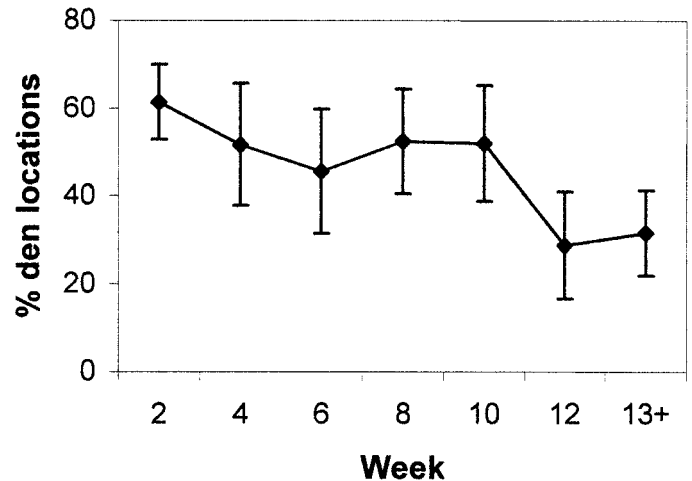


FIG. 1.—Percentage of den locations in which pairs of swift foxes were found together after initial pair formation ( $n = 9$ ), Pinon Canyon Maneuver Site, Colorado, 1997–2000.

### Pair Dynamics

*Proximity of male and female mates.*—A significant difference was found in the proximity of paired males and females depending on season ( $F = 4.28$ , *d.f.* = 2, 47,  $P = 0.02$ ) and time of day ( $F = 99.58$ , *d.f.* = 3, 47,  $P < 0.0001$ ). Post hoc *t*-tests adjusted for multiple comparisons (Tukey's adjustment) showed that a significantly smaller distance occurred between male and female mates during the breeding season as compared to the pup-rearing season (Tukey's adjusted  $P = 0.04$ ; Fig. 2a). No significant difference was found in proximity during the dispersal season compared to the pup-rearing season (Tukey's adjusted  $P = 0.86$ ) or compared to the breeding season (Tukey's adjusted  $P = 0.31$ ). A significant difference was found in proximity of male and female mates between all time periods of the day (Tukey's adjusted  $P < 0.0001$ ), except between dawn and evening periods (Tukey's adjusted  $P = 0.06$ ). The distance between mates was greatest during the night, and least during the day (Fig. 2b).

We observed 4 stable trios in the swift fox population, and measured proximity during nocturnal and crepuscular hours. Among these trios, females and males (hereafter referred to as female–male dyads;  $936.7 \text{ m} \pm 99.7 \text{ SE}$ ,  $n = 8$ ) were in general closer together than male–male dyads ( $1,080.5 \pm 242.0 \text{ m}$ ,  $n = 3$ ) or the female–female dyad ( $1,070.8 \text{ m}$ ). On average, the 2 females in a trio were closest during the pup-rearing season ( $963.2 \text{ m}$ ) as compared to the breeding ( $1,326.9 \text{ m}$ ) or dispersal ( $922.4 \text{ m}$ ) seasons. Females were closest to males in the breeding season ( $820.1 \pm 143.7 \text{ m}$ ) as compared to the dispersal ( $1,055.5 \pm 160.2 \text{ m}$ ) or pup-rearing ( $1,115.7 \pm 179.2 \text{ m}$ ) seasons. Males were also closer to males in the breeding season ( $972.9 \pm 285.1 \text{ m}$ ) than in the pup-rearing season ( $1,402.9 \pm 293.8 \text{ m}$ ). No male–male dyads were collared and tracked through the dispersal season.

*Concurrent diurnal den use by mates.*—A seasonal difference was found in den sharing between mated pairs ( $F = 10.54$ , *d.f.* = 2, 47,  $P < 0.001$ ; Fig. 3a), with pairs spending significantly more time together in dens during breeding season

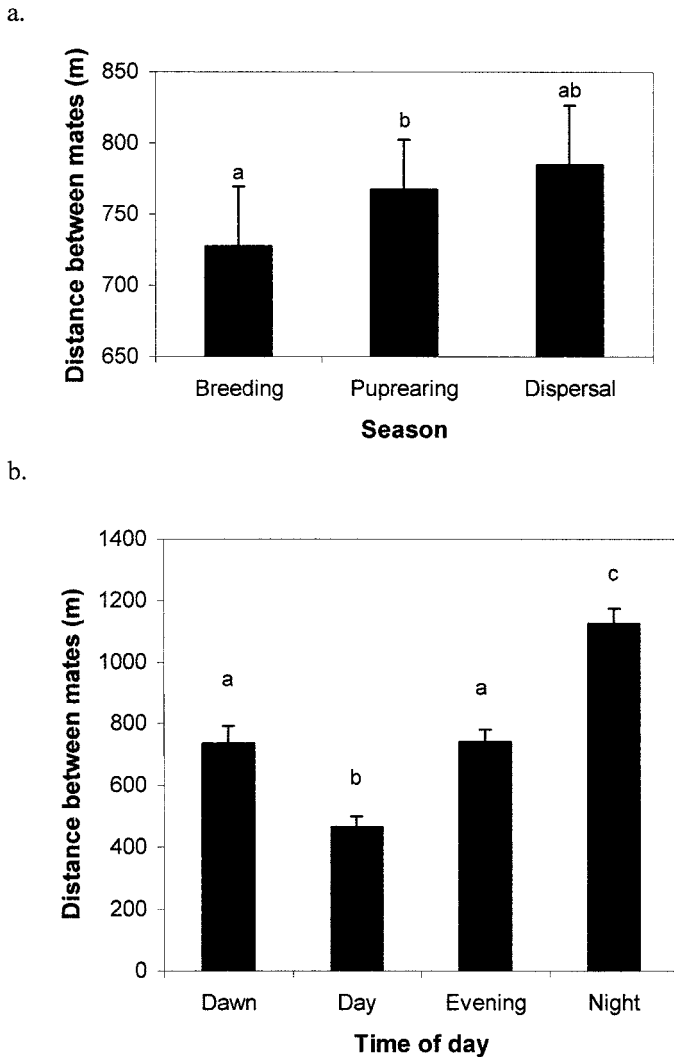


FIG. 2.—Proximity of swift fox mates by a) season and b) time of day ( $n = 48$ ), Pinon Canyon Maneuver Site, Colorado, 1997–2000. Different letters denote classes significantly different from each other.

than in the pup-rearing season (Tukey's adjusted  $P = 0.001$ ). No significant difference was found between the time spent together in the dispersal season as compared to the breeding (Tukey's adjusted  $P = 0.16$ ) or pup-rearing (Tukey's adjusted  $P = 0.23$ ) seasons.

Overall, males and females of trios shared dens more frequently ( $53.8\% \pm 9.6$  SE) than did female–female (37%) or male–male ( $45.0\% \pm 5.0$ ) dyads. Trios of swift foxes showed a similar seasonal difference to that of mated pairs, with higher rates of den sharing in the breeding season as compared to the pup-rearing season and the dispersal season (Fig. 3b). However, the 1 female–female combination that was tracked during the pup-rearing season showed a higher rate of den sharing in the pup-rearing season (52% of denning locations were shared), than in other seasons (39% in the breeding season and 20% in the dispersal season).

**Home-range use.**—Overall, females spent more time ( $60.7\% \pm 1.2\%$  of locations) in the core area of the shared home range than did males ( $54.7\% \pm 1.2\%$ ;  $F = 25.92$ ,

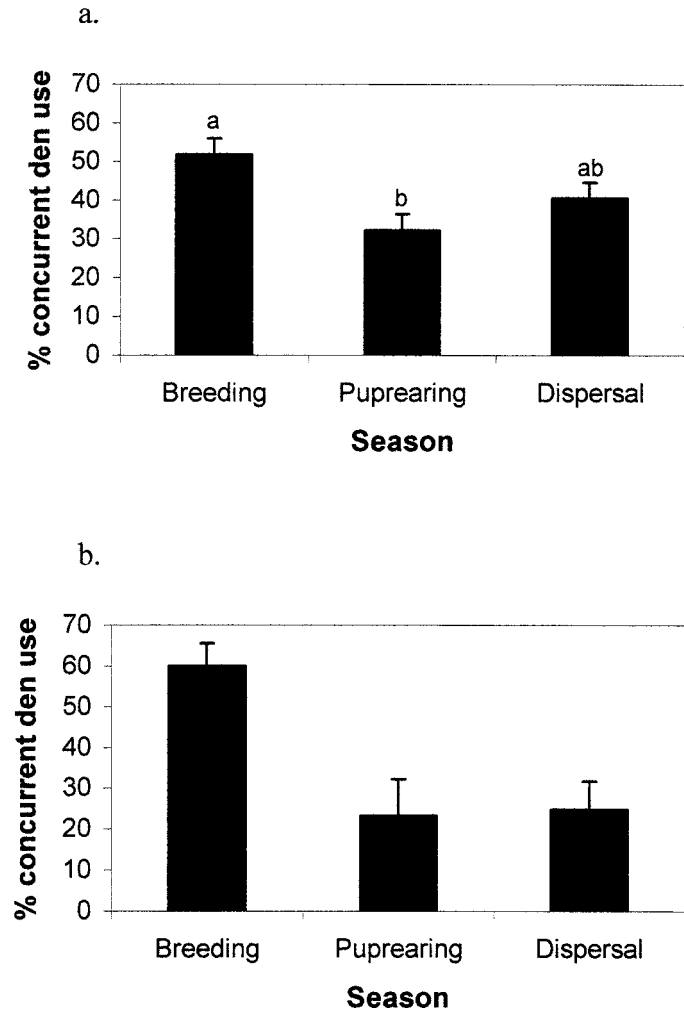


FIG. 3.—Concurrent den use in a) pairs ( $n = 48$ ) and b) trios ( $n = 4$ ) of swift foxes, Pinon Canyon Maneuver Site, Colorado, 1997–2000. Different letters denote classes significantly different from each other.

$d.f. = 1, 176$ ,  $P < 0.001$ ). The seasonal variation in relative use of core and boundary of the range also differed by sex ( $F = 3.45$ ,  $d.f. = 2, 240$ ,  $P = 0.03$ ). Females used the core area the most during the breeding and pup-rearing seasons as opposed to the dispersal season. Males also used the core area the most during the breeding season, but used the boundary the most in the pup-rearing season (Fig. 4a). The time of day also influenced area use ( $F = 328.54$ ,  $d.f. = 3, 516$ ,  $P < 0.001$ ), with boundary use highest during nocturnal periods and core-area use highest in diurnal periods for both sexes (Fig. 4b). No difference was found between sexes in relative area use by time of day ( $F = 0.98$ ,  $d.f. = 3, 516$ ,  $P = 0.40$ ).

In addition to home-range use being influenced by sex and seasonal changes, we found that sizes of the diurnal denning areas of foxes varied between sexes for the pup-rearing and breeding seasons. The prediction that females held smaller denning areas than males for these seasons was supported (breeding: females,  $0.8 \text{ km}^2 \pm 0.1$  SE; males,  $1.0 \pm 0.1 \text{ km}^2$ ;  $U = 2,031.0$ ,  $P = 0.041$ ; pup-rearing: females,  $0.9 \pm 0.1 \text{ km}^2$ , males,  $1.0 \pm 0.1 \text{ km}^2$ ;  $U = 2,245.0$ ,  $P = 0.012$ ). No significant

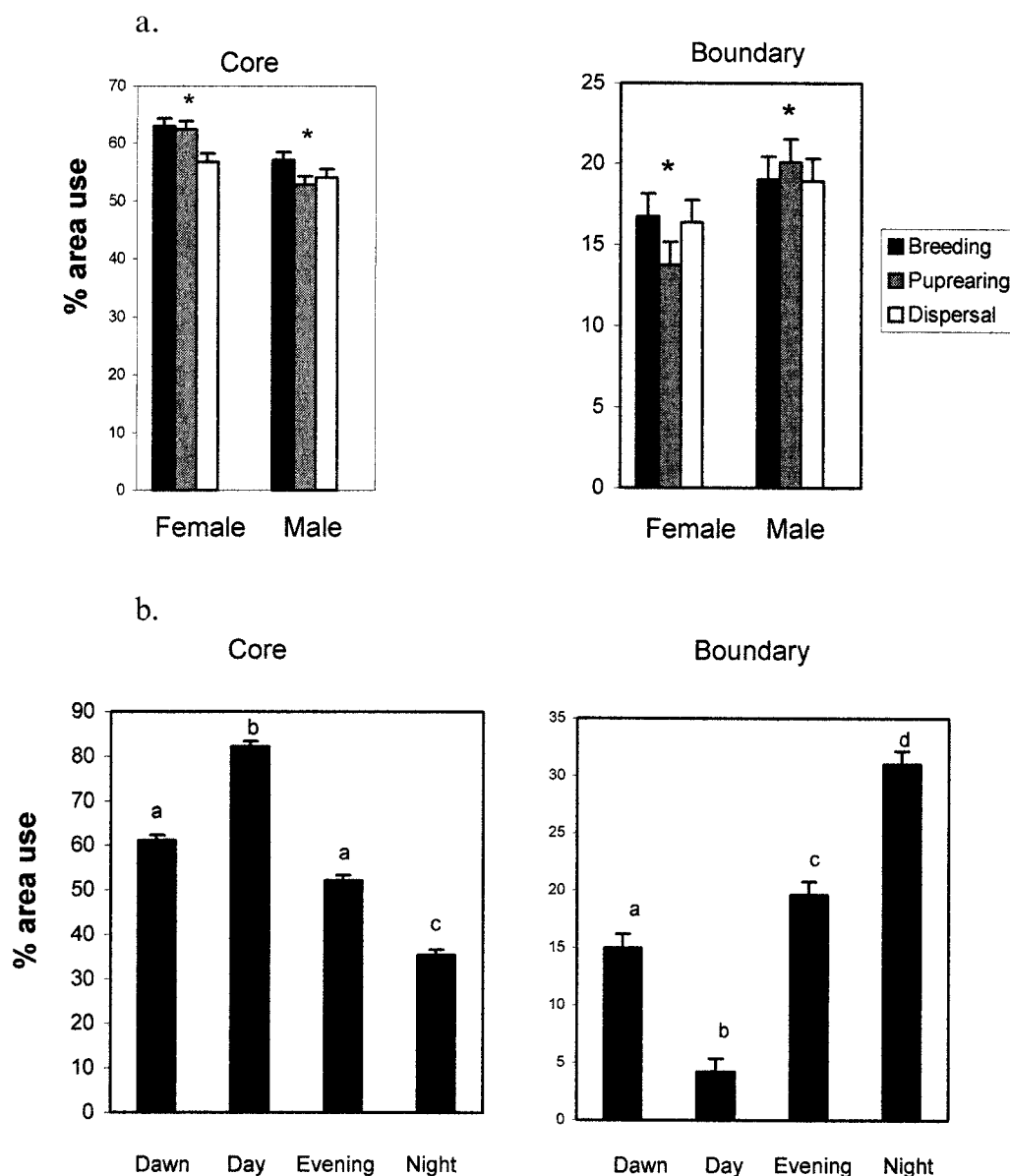


FIG. 4.—Relative use of core and boundary areas of swift foxes by a) sex and season and b) time of day ( $n = 90$ ), Pinon Canyon Maneuver Site, Colorado, 1997–2000. Different letters denote classes significantly different from each other. Group differences denoted by asterisks.

difference was found in the size of denning areas between males and females in the dispersal season (females,  $0.8 \pm 0.1$  km<sup>2</sup>; males,  $0.7 \pm 0.1$  km<sup>2</sup>;  $U = 3,880.0$ ,  $P = 0.21$ ).

#### Response to Loss of Mate

Over the study period, we were able to track the response of mates for at least 6 months for 28 foxes that died or disappeared. In 10 cases, the female died or disappeared before the male. Five (50%) of these males left their home range, whereas the other 5 remained. Of the 5 that left, the time before they left ranged between 1 week and 3 months. Four of them moved to a neighboring range, and at least 3 of these settled with another mate. The 5th male moved approximately 8 km, and settled with another mate. In addition, of the 5 males that stayed in their original range, 3 likely did so because there apparently was an unpaired female in the area at the time of the

death or disappearance of their mate. These males initiated a pair-bond with the new females within 2 months.

Eighteen females lost their mate to death or disappearance during the study. In contrast to the behavior of the males, all females remained and held their territories. At least 5 females had paired with new mates within a month, and a further 4 had already paired with new mates when the new mate was radiocollared during the months after the original mate's death.

In the 4 trios studied, the individual that died or disappeared from the group 1st was 1 of the same-sex members of the group. In all cases, the remaining male and female continued a stable pair-bond until the death of 1 of the 2 foxes.

#### DISCUSSION

The synchrony of pair activities in socially monogamous animals depends largely on the strength of the pair-bond and

the need to coordinate activities such as feeding, breeding, or territory defense (Kleiman 1981). Many factors may influence the space-use patterns of swift foxes relative to other group members. Factors promoting proximity include predator avoidance (Bertram 1978), parental care (Kleiman 1981), and the possible need for mate guarding (Kranz 1991), whereas factors promoting separation include the need to forage for small prey (White et al. 2000).

Swift foxes showed seasonal variation in their relative movements, with foxes geographically closer during the breeding season than during the pup-rearing season or dispersal season. This may occur due to mate guarding of females. Seasonal mate guarding during the breeding period is common in canids and many other animals including jackals (*Canis mesomelas* and *C. adustus*—Loveridge and Macdonald 2001), porcupines (*Erethizon dorsatum*—Sweitzer 2003), and many bird species (e.g., Blomqvist et al. 2002; Davis 2002). Mate guarding is especially common in species in which females are often fertilized by extrapair males (e.g., Komdeur 2001), and extrapair paternity has been documented in island foxes (Roemer et al. 2001) and swift foxes (Kitchen 2004).

Reduced proximity of the paired foxes during the pup-rearing season suggests that the sexes may play different roles in parental care. Shared parental care is common in canids (Kleiman 1981); however, we found that mated pairs were on average further apart in the pup-rearing season than in the breeding season and shared dens less in the pup-rearing season than in any other season. In addition, the males spent less time in the core area of the home range during the pup-rearing season as compared to the breeding season or dispersal season, whereas the female spent more time in the core area. Thus, although swift fox males have been documented to participate directly in parental care (Pruss 1994), males may not have an equal role in guarding and care of the young at the den. Instead, they appear to spend more time in territory maintenance. A greater investment in territorial behaviors by males also has been documented in other monogamous species (e.g., Rathbun 1979; Smythe 1978).

In addition to seasonal differences in relative space use and movements between the sexes, we found variation through the diel period, with swift foxes exhibiting a lower level of proximity during nocturnal hours than during diurnal hours. This may indicate that pairs are foraging separately as a mechanism to increase foraging efficiency of the small prey that they eat, instead of foraging together for predator vigilance. This is supported by observations of the closely related kit fox hunting alone (O'Farrell 1984; White et al. 2000). The Ethiopian wolf (*Canis simensis*) also preys primarily on small prey, mainly rodents, and is generally a solitary hunter (Sillero-Zubiri 1994).

Behavior of swift foxes toward each other differed during pair formation from that exhibited during the remainder of the relationship. Foxes spent more time denning communally during the initial weeks of their pair-bond than in the remainder of the bond. These results imply that swift foxes engage in behaviors that facilitate the development of the cooperation that is necessary for long-term group cohesiveness.

The spatial response of swift foxes to the loss of a mate differed between the sexes, indicating that the ecological costs and benefits of range retention differ between males and females. This study shows that the female will retain her home range after the loss of her mate, whereas 50% of males emigrated after losing their mates. Kamler (2002) also documented 5 instances of mate loss; in 3 cases a male emigrated from the range after the death of his mate, and in 2 cases females retained their range after mate loss. Philopatry to natal ranges by females has been documented in the bat-eared fox, and appears to be more common among smaller canids (Moehlman 1989). In many larger canid species, female emigration is more common, for example, in African hunting dogs (*Lycaon pictus*—Frame and Frame 1976) and coyotes (Gese 1998).

The sex that is likely to leave a territory after mate loss in any species (i.e., adult dispersal) may be correlated with the sex that most commonly exhibits natal dispersal. Indeed, a slight bias toward male natal dispersal occurs in the swift fox (Karki 2003), and this trend also is seen in red foxes (von Schantz 1981) and arctic foxes (*Alopex lagopus*—Kullberg and Angerbjörn 1992). Numerous hypotheses have been proposed to explain differences between sexes in dispersal patterns in canids, including body size (Moehlman 1989), resource availability (Smale et al. 1997), sex ratio (Sanders and Gaines 1991), and parental behavior (Wolff 1993). Many authors have argued that inbreeding avoidance is the ultimate cause of sex-biased dispersal (Dobson et al. 1997; Packer and Pusey 1993; Wolff et al. 1988).

In summary, we present new information on space-use patterns from the formation to the termination of swift fox social groups. We found that foxes spend more time denning together during pair formation, and that proximity varied seasonally and throughout the diel period. Home-range space-use patterns varied between the sexes, as did the response to mate loss. This information provides important insights into the territorial behavior and mating system of the swift fox.

## ACKNOWLEDGMENTS

Funding and logistical support were provided by the Welder Wildlife Foundation, Sinton, Texas; the United States Army, Directorate of Environmental Compliance and Management, Fort Carson, Colorado, through the United States Fish and Wildlife Service, Colorado Fish and Wildlife Assistance Office, Golden, Colorado; and the Utah Cooperative Fish and Wildlife Research Unit at Utah State University. Additional support was provided by the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center, Logan Field Station at Utah State University. We thank T. Warren, G. Belew, R. Bunn, and B. Rosenlund for support and project coordination. We thank M. Klavetter, E. Bergman, K. Bly, J. Bolis, C. Bromley, R. Cavallaro, L. Gorman, S. Hahn, C. Hamblin, K. Hansen, R. Hare, E. Joyce, S. Kiffe, J. King, S. Langeland, S. Lupis, S. McLellan, J. Milner, M. Pangraze, L. Schafer, L. Schleub, L. Schutte, J. Stamp, H. Tall, J. Weber, W. Weber, M. Wedermyer, B. Wirschansky, and T. Young for assistance in the field and P. Terletzky for geographical help. K. Mock, D. Ramsey, J. Bissonette, K. Sullivan, and T. Edwards provided helpful comments on the manuscript.

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*Submitted 27 February 2004. Accepted 26 October 2004.*

*Associate Editor was Nancy G. Solomon.*