Den Site Activity Patterns of Adult Male and Female Swift Foxes, *Vulpes velox*, in Northwestern Texas

PATRICK R. LEMONS^{1,2}, WARREN B. BALLARD¹, ROBERT M. SULLIVAN³, and MARSHA A. SOVADA⁴

Lemons, Patrick R., Warren B. Ballard, Robert M. Sullivan, and Marsha A. Sovada. 2003. Den site activity patterns of adult male and female Swift Foxes, *Vulpes velox*, in northwestern Texas. Canadian Field-Naturalist 117(3): 424-429.

Activity of Swift Foxes (*Vulpes velox*) at den sites was studied in northwestern Texas during pup rearing seasons in 2000 and 2001 to determine role of males in parental care. Twenty-four percent of radio-collared females with a potential to breed successfully raised pups to eight weeks of age. We intensively monitored presence and absence of male and female Swift Foxes at two den sites each year. Females were present >2.6 times more at den sites than males during the pup rearing season. Female and male Swift Foxes largely stayed at dens during diurnal hours and were active away from dens during nocturnal and crepuscular hours. Females and males spent 12.4% and 3.0% more time at dens before pups emerged, than after pups emerged, respectively. Following depredation of one male parent, the female spent 29% less time at the den site. Decrease in time spent at the den by the female following loss of her mate suggested that loss of one parent might severely impact recruitment of Swift Foxes. Our observations indicated that intense Coyote (*Canis latrans*) depredation may severely impact pup-rearing success as well as the parental care within Swift Fox family groups.

Key Words: Swift fox, Vulpes velox, den sites, helping behavior, Texas.

Understanding the importance of parental behavior in rearing offspring is an important management consideration. Parental investment theory suggests that efforts parents dedicate to caring for young are at the expense of later reproduction (e.g., decreased fecundity in subsequent years or decreased survival) (Williams 1966; Trivers 1972). Increased parental investment can decrease survival of adults through increased susceptibility to depredation or decreased physiological fitness (Krebs and Davies 1998). This phenomenon has been documented in numerous species (Gustafsson and Sutherland 1988; Sterns 1992). For example, in Great Tits (Parus major), increased brood sizes increase susceptibility of parents to infection from malaria and haematozoans (Norris et al. 1994; Richner et al. 1995). Winter mortality in Kestrels (*Falco tinnunculus*) increased as parental effort in the previous summer increased (Daan et al. 1996). Knowing parental investment of species is important to understanding the impacts of changes in social structures on reproductive success.

Swift Fox reproductive behavior has not been thoroughly studied. Available literature suggests that Swift Foxes are primarily monogamous breeders, and both parents share in pup rearing (Kilgore 1969; Egoscue 1979; Scott-Brown et al. 1987; Samuel and Nelson 1992). However, roles of male and female Swift Foxes in parental care have not been identified. The role each parent has in pup rearing could be an important factor

in successful raising of pups as well as the impacts on future health of parents following pup rearing.

Additional females known as "helpers" have been documented at natal dens of Swift Foxes (Egoscue 1979; Scott-Brown et al. 1987; Covell 1992; Samuel and Nelson 1992; Kitchen et al. 1999). Red Foxes (Vulpes vulpes), Arctic Foxes (Alopex lagopus), and Kit Foxes (Vulpes macrotis) have also been documented with helpers at natal dens (Macdonald 1983; Macdonald and Moehlman 1983; Moehlman 1989; Spiegel and Tom 1996). Helpers have been documented to increase overall pup rearing success in family groups of Red Foxes, Arctic Foxes, and Blackbacked Jackals (Canis mesomelas) (Macdonald 1979, 1983; Moehlman 1979, 1989; Macdonald and Moehlman 1983). However, no information exists concerning the role helpers have in Swift Fox family groups and their impacts on pup rearing success.

In Kit Foxes, helping behavior appears rare, which may be due to high mortality of individuals through intense Coyote depredation (Koopman et al. 2000; Kamler et al. 2003). In Swift Fox family groups in southeastern Colorado, 100% (n = 5) of helpers were found in Coyote reduction areas suggesting that increased Coyote depredation reduced occurrence of helpers (Covell 1992). It has been suggested that Swift Fox pup rearing success in family groups without helpers are more heavily impacted by intense Coyote depredation than in family groups with helpers (i.e., in

¹ Department of Range, Wildlife and Fisheries Management, Texas Tech University, Box 42125, Lubbock, Texas 79409 USA

² Current Address: Department of Natural Resource and Environmental Sciences, University of Nevada-Reno, 1000 Valley Road, Reno, Nevada 89512 USA

³ Texas Parks and Wildlife Department, P. O. Box 659, Canyon, Texas 79015 USA

⁴ U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street Southeast, Jamestown, North Dakota 58401 USA

social groups with helpers, if an adult dies helpers can take over) (Covell 1992). Understanding the roles of helpers in Swift Fox family groups and their impacts on pup rearing success is important to determining if Coyotes indirectly decrease Swift Fox recruitment.

We studied pup-rearing behavior of adult male and female Swift Foxes in northwestern Texas to determine their roles in parental care. Parental behavior was studied to determine if differences existed between two different landscapes, as pups aged, and with the depredation of a male in one family group. Frequency of helpers in Swift Fox family groups as well as proportion of known females breeding were also recorded to determine impacts of intense Coyote depredation within the populations studied.

Study Area

Research was conducted at two 93 km² study sites in northwestern Texas. The first study site was designated our continuous rangeland landscape and was located 55 km west of Stratford in Dallam County, Texas, predominantly within the Rita Blanca National Grasslands. The area was restored short-grass prairie habitat dominated by Blue Grama (*Bouteloua gracilis*) and Buffalograss (*Buchloe dactyioides*) and was moderately to heavily grazed by cattle.

The Rita Blanca National Grasslands study site averaged 1250 m in elevation. Average temperature was 12.6°C with an average maximum daily temperature of 21.5°C and an average minimum daily temperature of 3.6°C. Average precipitation was 0.40 m per year with 0.31 m of snow per year (National Oceanic and Atmospheric Administration 2000, 2001).

The second study site was designated our fragmented agriculture/rangeland landscape and was located on a private ranch in Sherman County, Texas approximately 12 km south of Stratford, Texas. This site was composed of a mixture of short-grass prairie rangeland (35%), cultivated fields (31%), and conservation reserve program (CRP) (35%). Crops included corn, winter wheat, and sorghum. CRP land had either been recently enrolled in the program and was planted to warm-season grasses including Sideoats Grama (*Bouteloua curtipendula*), Blue Grama, Sand Dropseed (*Sporobolus cryptandrus*), and Buffalograss, or had not been recently reenrolled in the program and was vegetated by Old World Bluestem (*Bothriochloa* spp.).

The Sherman County study site averaged 1125 m in elevation. Average temperature was 13.4°C (average maximum daily temperature was 21.8°C, average minimum daily temperature was 5.0°C). Average precipitation was 0.44 m per year with 0.41 m of snow per year (National Oceanic and Atmospheric Administration 2000, 2001).

Methods

We located radio-collared Swift Foxes approximately twice per week from January through June of 2000 and 2001. We identified potential breeding pairs

and pairs with helpers by monitoring foxes for shared den use. Radio-collars were equipped with mortality sensors allowing early detection of mortality and identification of causes of death. We identified dens used by radio-collared foxes and then monitored the dens where presence of pups was established.

Each year during the pup-rearing period (April through June), a den in each study site was monitored intensively with a den site activity station. Activity stations were placed 60 to 75 m from dens and consisted of a receiver, a Rustrak® recorder, and 12-volt battery placed in a weather-protected container, and a directional antenna placed on a mast 1.5 m above ground. Presence and absence of Swift Foxes at den sites were recorded once every 12 minutes on an 18.3 m tape advancing at 15.2 cm per hour. To calibrate the monitors, we placed a radio transmitter on a 0.2 m pole located 1 to 2 m behind the den. This transmitter was also recorded once every 12 minutes enabling our calibration of times on the tape to the actual time as marked on the tape with each daily visit.

To determine Swift Fox whelping dates, female foxes were systematically trapped until lactation was observed. Visual observations of dens were made at least twice per week to determine dates pups first emerged from dens, post emergent litter sizes, and number of pups successfully raised to eight weeks of age. We backdated four weeks from date pups were first observed to confirm whelping dates (Scott-Brown et al. 1987; Samuel and Nelson 1992). Observations were conducted with binoculars and spotting scopes from a distance of 75 to 100 m from the den between 3 hr before sunset to 30 minutes after sunset during the pup rearing period.

Presence and absence observations were combined across days and grouped by hour to determine activity of both male and female Swift Foxes. Differences in occurrence of male and female Swift Foxes at den sites were determined by comparing percentage of time spent at den sites. We also examined differences in time spent at den sites for pre- (first four weeks of monitoring) and post- (second four weeks of monitoring) emergent times as well as between landscapes. Sample variances (s²) for percentage of time spent at den sites were determined (Zar 1999).

Results

Twenty-five female Swift Foxes were monitored in 2000 (n = 12) and 2001 (n = 13). Of these, 17 females' fates were determined to pup rearing season. Five showed signs of whelping, of which four successfully raised pups to eight weeks of age. Of the 12 remaining possible breeding females, five did not breed as a result of mortalities within the breeding pair, and seven were non-breeding single females. Two possible were documented prior to whelping, and both did not successfully whelp due to Coyote depredation within the Swift Fox family group.

TABLE 1. Duration of den site monitoring and den attendance of Swift Foxes in northwestern Texas during pup rearing season,
2000 and 2001.

	Den site monitoring			Presence (%)	
Den site	Date started	Date ended	Number of days monitored	Male	Female
PR-2000	9 April 2000	6 June 2000	58	38.0	66.2
RB-2000	6 April 2000	1 June 2000	56	21.5	61.7
PR-2001	9 April 2001	4 June 2001	56	9.1	54.0
RB-2001	15 April 2001	19 May 2001	30	70.5	28.9

Den site activity was monitored for 3360 hours for both male and female Swift Foxes. Overall, female Swift Foxes spent more time $(63.1\%, s^2 = 0.5\%)$ at den sites than males $(24.3\%, s^2 = 1.5\%)$. Percentage of time spent at den sites was variable between sexes (Table 1). At each den, differences between amount of time females and males spent at dens were also variable (2000 Rita Blanca den: 40.3%; 2000 Sherman County den: 28.2%; 2001 Rita Blanca den: 47.9%; 2001 Sherman County den: 44.9%).

Female Swift Foxes were away from dens during nocturnal hours, and were likely to be present at dens during diurnal hours (Figure 1). Females left dens around dusk and returned around dawn (Figure 1). Male Swift Foxes showed this same activity pattern; however, the pattern was not as distinct as that of female Swift Foxes (Figure 2). We did not observe any seasonal shift in adult movement patterns as the pups aged during this study.

Percentage of time spent at den sites changed for both males and females as Swift Fox pups aged. Males spent 25.5% ($s^2 = 1.9\%$) of their time at dens prior to emergence and 22.4% ($s^2 = 0.6\%$) of their time at dens

following pup emergence. Females spent 68.0% (s² = 1.1%) of their time at den sites prior to emergence and 55.6% (s² = 3.7%) of their time at dens following pup emergence.

No difference in parental behavior was recorded for males or females when comparing the two landscapes. Males spent 24.0% ($s^2 = 0.006\%$) of their time at den sites on continuous rangeland and 26.3% ($s^2 = 4.2\%$) of their time at den sites on fragmented agriculture/rangeland. Females spent 66.8% ($s^2 = 14.9\%$) of their time at den sites on continuous rangeland and 61.3% ($s^2 = 0.7\%$) of their time at den sites on fragmented agriculture/rangeland.

Swift Fox pups were born 6 April – 14 April. Den site activity stations were started immediately following determination of presence of pups (Sherman County dens: 9 April 2000, 9 April 2001; Rita Blanca dens: 6 April 2000, 14 April 2001) and run until early June (Table 1). Visual observations confirmed estimated whelping dates through documentation of emergence of pups in early May (Rita Blanca dens: 7 May 2000, 9 May 2001; Sherman County dens: 5 May 2000, 6 May 2001).

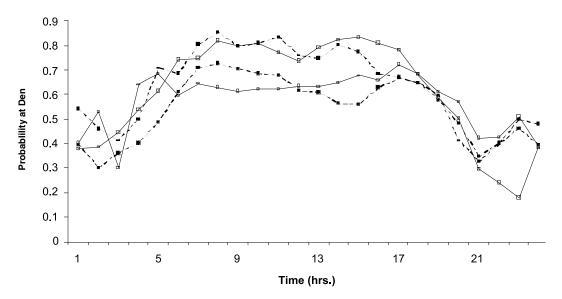


FIGURE 1. Probability of finding individual radio-collared female Swift Foxes at dens on an hourly basis based on individual dens in northwest Texas during pup rearing season (April – June), 2000 and 2001.

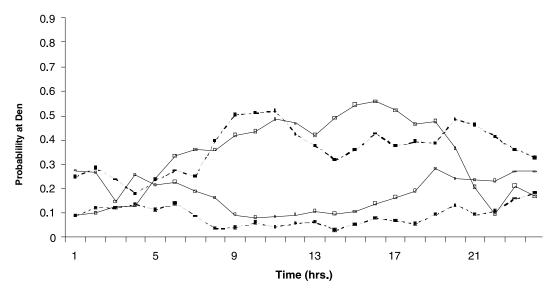


FIGURE 2. Probability of finding individual radio-collared male Swift Foxes at dens on an hourly basis based on individual dens in northwest — Texas during pup rearing season (April – June), 2000 and 2001.

Swift Fox litter sizes averaged 3.5 pups (range 2–5, n = 4). In 2000, both monitored fox pairs successfully raised all pups from 4 to 8 weeks of age (2000 Rita Blanca den: 5 pups; 2000 Sherman County den: 2 pups). In 2001, the Sherman County den raised 3 pups from 4 to 8 weeks of age. In 2001 4 pups emerged from the Rita Blanca den in 2001. However, the male was killed (11 May 2001) by Coyotes and the female died (19 May 2001) from a vehicle collision. On 23 May 2001, one pup was observed running within 150 m of the den, but no other observations of pups were made and we assumed the remaining pups died.

Following depredation of the male, the female spent 29.2% less time at the den when comparing the final 8 days (47.7%) to the first 4 weeks (76.9%) of occupation.

Discussion

During the pup-rearing season, male and female Swift Foxes were active away from dens primarily during crepuscular and nocturnal hours. However, this pattern of behavior was more distinct for females than males. Differences were documented between amount of time male (24.3%) and female (63.1%) Swift Foxes spent at den sites. Overall, females spent 2.6 times more time at dens than males during the pup-rearing season. Impacts of unequal parental care in Swift Foxes are unknown. Since males and females contribute to pup rearing, losses of either parent could have consequences for pup survival.

However, despite unequal parental care, males likely make important contributions to successful pup rearing. In Colorado, loss of a male parent resulted in a decrease in the number of pups that survived to emergence from a Swift Fox den (Covell 1992). This same phenomenon has been documented in several bird species when removal of males during nesting season resulted in decreased reproductive success (Krebs and Davies 1993). Furthermore, the importance of males to reproductive success likely increased when food resources were scarce (Krebs and Davies 1993). Although our sample size was small, our data suggested a similar pattern. Following the loss of the male parent at the Rita Blanca den during 2001, the amount of time spent at the den by the remaining female declined by 29.2%. This was probably the result of decreased food availability to pups following loss of the male, causing the female to spend more time away from the den searching for food.

Numerous studies have documented the direct impacts of Coyote depredation on Swift Fox populations (Hines 1980; Covell 1992; Carbyn et al. 1994; Sovada et al. 1998; Kitchen et al. 1999. The increased Coyote densities following removal of large predators (i.e., wolves) throughout the range of the Swift Fox may have impacted Swift Fox populations indirectly. Covell (1992) suggested that Coyote reduction increased the proportion of helpers (i.e., non-breeding adult females assisting in rearing of young) found in Swift Fox family groups. We documented two trios prior to whelping, and neither successfully whelped due to Coyote depredation within the trio. Several studies have suggested that presence of helpers in family groups increased pup survivorship (Macdonald 1979, 1983). Our results show, however that depredation by Coyotes in Swift Fox family groups may indirectly result in a decrease in success of whelping or decreased pup survival and therefore, recruitment.

Our study suggested that Coyotes have indirect effects on success of reproduction in Swift Fox populations. Our study documented 23.5% (4 of 17) of potentially breeding females successfully raised pups to eight weeks of age. Of the remaining potentially breeding females, 70.6% (n = 12) did not whelp pups due to high mortality rates documented in this study, and 5.9% (n = 1) lost the entire litter due to depredation of the male parent and the following mortality of the female parent during pup rearing. Importance of understanding direct and indirect effects of Coyotes on Swift Fox populations may aid in determining causes of depressed Swift Fox populations.

Management Implications

High mortality rates directly, as well as indirectly, affect Swift Fox populations. High mortality of Swift Foxes in this study resulted in indirect losses of Swift Foxes through decreased breeding and pup rearing success. Control of Coyotes particularly during times preceding and during the breeding season may help improve Swift Fox reproductive success. Control may directly enhance populations of Swift Fox through decreased Coyote depredation (Kamler et al. 2003), but also may increase breeding pairs, breeding success, and pup rearing success, therefore increasing recruitment of Swift Foxes.

Acknowledgments

This project was funded by Texas Tech University, Texas Parks and Wildlife Department, United States Forest Service, Northern Prairie Wildlife Research Center, the United States Department of Agriculture's Wildlife Services program, National Fish and Wildlife Foundation, the Zoological Society of Houstson, and a Section 6 Grant E-1-12 from the U. S. Fish and Wildlife Service Endangered Species Program. Kansas Department of Wildlife and Parks and BWXT Pantex loaned us equipment. We thank the many landowners in Sherman and Dallam counties that allowed us to conduct research on their land. A special thanks goes to F. Pronger, who contacted us about Swift Foxes, then allowed us to use his ranch as a second study site. Our research protocol, number 00979BX, was approved by the Texas Tech University Animal Care and Use Committee. This is Texas Tech University, College of Agricultural Sciences and Natural Resources technical publication T-9-932.

Literature Cited

Carbyn, L. N., H. J. Armbruster, and C. Mamo. 1994.
The Swift Fox reintroduction program in Canada from 1983 to 1992. Pages 247-271 in Restoration of endangered species: conceptual issues, planning and implementation.
Edited by M. L. Bowles and C. J. Whelan. Cambridge University Press, Cambridge, United Kingdom.

- Covell, D. F. 1992. Ecology of the Swift Fox (Vulpes velox) in southeastern Colorado. Thesis. University of Wisconsin, Madison, Wisconsin, USA.
- Daan, S., C. Deerenberg, and C. Dijkstra. 1996. Increased daily work precipitates natural death in the kestrel. Journal of Animal Ecology 65: 539-544.
- Egoscue, H. J. 1979. *Vulpes velox*. Mammalian Species 122: 1-5.
- Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335: 813-815.
- Hines, T. D. 1980. An ecological study of *Vulpes velox* in Nebraska. Thesis, University of Nebraska, Lincoln, Nebraska, USA.
- Kamler, J. F, W. B. Ballard, R. L. Gilliland, P. R. Lemons II, and K. Mote. 2003. Impacts of coyotes on swift foxes in northwestern Texas. Journal of Wildlife Management 67: 317-323.
- Kilgore, D. L. 1969. An ecological study of the Swift Fox (*Vulpes velox*) in the Oklahoma Panhandle. American Midland Naturalist 81: 512-533.
- Kitchen, A. M., E. M. Gese, and E. R. Schauster. 1999. Resource partitioning between Coyotes and Swift Foxes: space, time, and diet. Canadian Journal of Zoology 77: 1645-1656.
- Koopman, M. E., B. L. Cypher, and J. H. Scrivner. 2000. Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). Journal of Mammalogy 81: 213-222.
- Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioural ecology. Third edition. Blackwell Science, Oxford, United Kingdom.
- **Krebs, J. R.,** and **N. B. Davies.** 1998. Behavioural ecology: an evolutionary approach. Fourth Edition. Blackwell Science, Oxford, United Kingdom.
- **Macdonald, D. W.** 1979. 'Helpers' in fox society. Nature 282: 69-71.
- **Macdonald, D. W.** 1983. The ecology of carnivore social behaviour. Nature 301: 379-384.
- Macdonald, D. W., and P. D. Moehlman. 1983. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 *in* Perspectives in ethology. *Edited by* P. Bateson and P. Klopfer. Plenum Press, New York, USA.
- Moehlman, P. D. 1979. Jackal helpers and pup survival. Nature 277: 382-383.
- Moehlman, P. D. 1989. Intraspecific variation in canid social systems. Pages 143-163 *in* Carnivore behavior, ecology, and evolution. *Edited by* J. L. Gittleman. Volume 1. Cornell University Press, Ithaca, New York, USA.
- National Oceanic and Atmospheric Administration. 2000. Annual climatological summary. National Climatic Data Center, Asherville, North Carolina, USA.
- National Oceanic and Atmospheric Administration. 2001. Annual climatological summary. National Climatic Data Center, Asherville, North Carolina, USA.
- Norris, K., M. Anwar, and A. F. Read. 1994. Reproductive effort influences the prevalence of haematozoan parasites in great tits. Journal of Animal Ecology 63: 601-610.
- Richner, H., P. Christie, and A. Oppliger. 1995. Paternal investment affects prevalence of malaria. Proceedings of the National Academy of Sciences of the USA 92: 1192-1194.
- Samuel, D. E., and B. B. Nelson. 1992. Foxes (*Vulpes vulpes* and allies). Pages 485-490 *in* Wild mammals of North America. *Edited by* J. A. Chapman and G. A. Feldhamer. Johns Hopkins University Press. Baltimore, Maryland, USA.

- Scott-Brown, J. M., S. Herrero, and J. Reynolds. 1987. Swift Fox. Pages 432-441 in Wild furbearer management and conservation in North America. Edited by M. Nowak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.
- Sovada, M. A., C. C. Roy, J. B. Bright, and J. R. Gillis. 1998. Causes and rates of mortality of Swift Foxes in western Kansas. Journal of Wildlife Management 62: 1300-1306.
- Spiegel, L. K., and J. Tom. 1996. Reproduction of San Joaquin kit fox in undeveloped and oil-developed habitats of Kern County, California. Pages 53-69 in Studies of the San Joaquin kit fox in undeveloped and oil-developed areas. Edited by L. K. Spiegel. California Energy Commission, Sacramento, California, USA.
- Sterns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in Sexual selection and the descent of man 1871-1971. Edited by B. Campbell. Aldine, Chicago, Illinois. USA.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100: 687-690.
- Zar, J. H. 1999. Biostatistical Analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Received 23 January 2002 Accepted 2 January 2004