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Adult male emigration and a female-based social organization in swift foxes, *Vulpes velox*

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Members of the family Canidae are distinguished from other carnivore families by pair bonding and male care of the young. Because of the importance of food provisioning and territorial defence by males, social structure among canids is shared or even dominated by males. However, small, insectivorous species of canids show little male parental care, although whether social structure differs from other canids is unknown. We combined data from three independent research projects on a small canid, the swift fox, to help elucidate the social organization of this species. Based on data on movements of 35 adult mated pairs and the fate of litters, we found that adult females maintained territories and family structure, whereas adult males tended to emigrate. This is the first evidence of a female-based social organization among any canid species. This type of social organization probably resulted from the decreased importance of territorial defence and food provisioning by males, as their diet is primarily insectivorous during summer when young are weaned. Our results, along with others, indicate that variations in social structure among canid species are strongly influenced by the importance of food provisioning and territorial defence by males.

Most species within the Carnivora are solitary. Under this social system, only adult females maintain a family structure with young, whereas males are solitary and do not show male parental care. The major exceptions are within the family Canidae, as all these species show pair bonding and paternal care (Kleiman & Eisenberg 1973). Owing to the importance of food provisioning and territorial defence by males, social organization and group structure of most canid species appear to be shared by both sexes. For example, among grey wolves, *Canis lupus*, coyotes, *Canis latrans*, black-backed jackals, *Canis mesomelas*, and red foxes, *Vulpes vulpes*, adult males maintain territories and provide food to young and nursing females (Fritts & Mech 1981; Moehlman 1989; Zabel & Taggart 1989; Gese 1998). Consequently, after the death of adult males, litters failed among black-backed jackals (Moehlman 1989) and red foxes (Zabel & Taggart 1989), and breeding females dispersed among grey wolves (Fritts & Mech 1981), black-backed jackals (Moehlman 1989) and coyotes (Gese 1998). This indicates that food provisioning by males was necessary for the survival of young, and males themselves were important to the territory maintenance and social stability of family groups.

Among small and insectivorous canid species, however, the importance of males within family groups appears to be reduced. For example, female bat-eared foxes, *Otocyon megalotis*, are known to maintain solitary territories and rear litters in the absence of males (Maas 1993). Similarly, male Blanford's foxes, *Vulpes cana*, do not provide food to young, although they are often associated with the pups (Geffen & Macdonald 1992). However, whether the decreased importance of males among these species has any effects on family structure and social organization is unknown.

The swift fox is a small canid (2–3 kg) that occurs in the western grasslands of North America. Its diet varies

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seasonally, with a predominance (>80%) of insects during summer (Kitchen et al. 1999; Lemons 2001; Harrison 2003). Swift foxes are primarily nocturnal and are one of the most den-dependent canid species in North America (Egoscue 1979). Research on swift foxes has increased recently because of concerns over reductions in their numbers and distribution (Kitchen et al. 1999; Harrison 2003; Kamler et al. 2003), although details of their social organization are lacking. Populations of swift foxes in Colorado, New Mexico and Texas suffer high mortalities caused by predation from coyotes (Kitchen et al. 1999; Harrison 2003; Kamler et al. 2003); this provides a unique opportunity to examine the impacts of adult deaths on family structures. We analysed data from three independent research projects on swift foxes in the western United States to help elucidate the importance of both sexes to the social organization of this small and insectivorous canid species.

METHODS

Data presented here are from three research teams that conducted separate studies of swift foxes from 1997 to 2001 in Colorado (E.M.G., S.K.), New Mexico (R.L.H.) and Texas (J.F.K., W.B.B., K.M.). Detailed descriptions of study sites can be found in Kitchen et al. (1999) for Colorado, Harrison (2003) for New Mexico and Kamler et al. (2003) for Texas. Because swift foxes are secretive and nocturnal, radiotelemetry was used to obtain information on their ecology and social behaviour. Our research and handling protocols were approved by the Institutional Animal Care and Use Committees at Texas Tech University, University of New Mexico, Utah State University, and the National Wildlife Research Center.

Swift foxes were captured in wire boxtraps baited with road-killed prey species, such as rabbits (*Sylvilagus* spp.), or store-bought beef, chicken and fish scraps. Water was not provided in traps because swift foxes are adapted to semiarid environments and are not limited in their distribution by free-standing water, water was present in the bait, and foxes were in traps only at night. To ensure that foxes were not in traps for long periods, traps were baited and opened each day just before sunset, and were closed after being checked at sunrise. Traps were not opened during adverse weather (e.g. rain or snow), and trapping occurred only from August to March to avoid late pregnancy and early pup-rearing periods. Recaptured foxes and foxes weighing less than 1.5 kg were released without further procedures; thus only new adults and large juveniles close to adult size were processed. Foxes captured in New Mexico and Texas were immobilized with an intramuscular injection of ketamine hydrochloride or tiletamine (10 mg/kg). Immobilized foxes were removed from traps and standard measurements and ectoparasite samples were taken. Foxes were then fitted with radiocollars (30–50 g; <3% of body mass) equipped with mortality sensors, placed back into the traps, monitored until they recovered fully from the effects of the drugs (1–3 h), and released at the capture site. Although some female foxes captured in March were in early pregnancy, these foxes were all recaptures; thus anaesthesia was never given to pregnant or nursing foxes, and all successfully reared litters. Foxes captured in Colorado were processed by personnel wearing thick leather gloves and no anaesthesia was used (all other procedures were similar). Neither type of processing appeared to have adverse effects, as no foxes were injured during trapping procedures, foxes were often recaptured the following night after initial processing, and many foxes remained trap-happy throughout the study. Similarly, radiocollars did not seem to affect fox survival or susceptibility to predation, and the foxes did not behave abnormally (e.g. none left their territories immediately after capture). Radiocollars were removed from the foxes at the conclusion of the study in New Mexico, and research is continuing in both Colorado and Texas.

The foxes were aged by tooth wear, body size and reproductive condition. Foxes were considered to be juvenile until the breeding season following their birth, whereas all other foxes were considered adults. Female foxes were considered breeders if they were pregnant when captured, or showed evidence of nursing during or after the pup-rearing period. Male foxes were considered breeders if they were associated with a breeding female. Foxes were considered to belong to the same family group (e.g. adult breeders and offspring) if they used the same area and dens concurrently (Kitchen et al. 1999).

To determine the importance of adult breeders to the family structure and social organization, we analysed movements of breeders after the death of their mate. We classified a movement as emigration if a fox permanently left the area that it had used for at least the previous 3 months. We also determined the fate of litters after the death of breeding adults. We classified a litter as having survived if more than one pup survived until 6 months of age, after which time pups were independent from adults.

RESULTS

Adult males and females emigrated at different rates after the death of their mates (Yates-corrected chi-square test: $\chi^2_1 = 10.59$, $P = 0.001$; Table 1). Among the three studies, 14 adult breeding males were monitored after the death of an associated adult breeding female. Twelve of these males emigrated 1–8 weeks after the female died (Table 1): two of these males died, five left the study areas, and five paired with solitary females that had already established

Table 1. Movements of adult swift foxes after their mates died

	Number stayed	Mean time (weeks) alone in territory	Number emigrated	Mean time (weeks) of emigration after mate's death
Males ($N = 14$)	2	5.5 (5–6)	12	4.8 (1–8)
Females ($N = 10$)	9	22.0 (2–56)	1	5.5

Ranges are given in parentheses.

territories in other parts of the study areas. Within 5–6 weeks transient females occupied the territory of the two males that did not emigrate, and these males then paired with the new females (Table 1).

Ten adult breeding females were monitored after the death of an associated adult breeding male. One female then emigrated and nine stayed within their territory (Table 1). Females maintained solitary territories for 2–56 weeks, after which time a new adult male became associated with them. One adult female maintained a solitary territory through a reproductive season during which she did not breed.

Six litters were monitored after the death of one parent. In two cases in which the adult female died, the adult males emigrated and abandoned the litters (approximately 2.5 and 7 weeks old, respectively) and no young survived. The first male left the study site and the second died 3 months after emigrating. In four cases in which the adult male died, all adult females remained with their litters and the young survived until at least 6 months of age. Two of these litters were unborn at the time of male deaths (e.g. females were pregnant), whereas the other two litters were approximately 7 and 8 weeks old, respectively.

DISCUSSION

The swift foxes' social organization was based on female territories: females maintained territories in the absence of males, whereas adult males tended to emigrate in the absence of females. This is the first evidence of a female-based social organization among any canid species. We hypothesize that this social system evolved because of the reduced importance of food provisioning and territorial defence by males. Although males often shared dens with young in our studies, we did not know whether they provided food, although Pruss (1994) found that male swift foxes did bring prey items back to den areas. In addition, we observed remains of small mammals at natal den entrances, suggesting that parents sometimes brought mammalian prey items back to the den. However, when male swift foxes died, females successfully reared litters alone, indicating that food provisioning by males was not necessary for pup survival. Swift foxes are primarily insectivorous (Kitchen et al. 1999; Lemons 2001; Harrison 2003), especially during summer when young are weaned. Thus, insects are probably readily available to pups as they begin to forage for themselves. Insects are generally not large enough to be worth carrying back to the den by adults (Geffen & Macdonald 1992), and swift foxes, like most other fox species (Geffen & Macdonald 1992), are not known to regurgitate further indicating that food provisioning by males is greatly reduced in this species.

Reduced importance of food provisioning by males has also been found among other insectivorous fox species. For example, female bat-eared foxes den communally (Nel et al. 1984; Malcolm 1986) and successfully rear litters in the absence of males (Maas 1993), indicating that food provisioning by males is not necessary for pup survival. Male Blanford's foxes do not provide any food to nursing females or young, and pups depend on their mother's milk until they begin to forage for themselves (Geffen & Macdonald 1992); however, males do accompany young (Geffen & Macdonald 1992), as we observed for swift foxes. Whether a female-based social organization occurs among these, or other, insectivorous fox species is unknown, but deserves further investigation.

Under the social organization of swift foxes, adult females appeared to be the limiting factor, whereas adult males were needed only for reproduction and possibly protection of young. Family groups of swift foxes were often female biased, because in addition to solitary breeding females, some family groups were polygynous, denned communally (e.g. two breeding females and one adult male) and had nonreproductive yearling females (Kamler 2002). Thus, reproductive groups were influenced more by the number of adult females than by the number of adult males. However, swift foxes, like other small canids, are limited primarily by predation from larger canids (Cavallini 1996; Kamler et al. 2003). Thus, the presence of males might be beneficial to young, as extra adults can help warn and protect young from potential predators (Moehlman 1989). This may explain why adult males are often associated with young, although this hypothesis needs to be tested.

Interspecific variation in social organization among canid species has been related to body size, where small species tend to have female-biased sex ratios and large species male-biased sex ratios (Moehlman 1989). Among larger canids, extreme forms of a male-biased social organization have been reported among African hunting dogs, *Lycaon pictus*, and Ethiopian wolves, *Canis simensis*, where groups of males maintain territories and family structure, and females emigrate from family groups (Sillero-Zubiri et al. 1996; Creel & Creel 2002). Under these social systems, groups of males are probably the limiting factor, because they are necessary to provide food to pups and maintain pack territories (Malcolm 1980; Sillero-Zubiri & Gottelli 1995). Only one or a few females are needed per family group to reproduce and nurse pups (Sillero-Zubiri et al. 1996; Creel & Creel 2002).

These findings, together with our results, indicate that extreme variations in social systems among canid species are influenced not only by body size, but also by the importance of food provisioning and territorial defence by males. For example, African hunting dogs, one of the largest canid species, consume the largest prey and consequently have the most male-biased social organization, as males are the primary food provider for large litters. Ethiopian wolves prey primarily on small rodents, but rodent biomass and habitat richness vary greatly throughout their range (Sillero-Zubiri & Gottelli 1995). This unevenly distributed but stable food resource probably necessitates the defence of stable home ranges (i.e. resource defence) by groups of males in high-density areas, as larger groups of canids are better able to defend optimal resources than smaller ones (Macdonald 1983). In contrast, swift foxes, and possibly other insectivorous foxes, consume small prey (insects) that tend to occur evenly across relatively homogeneous habitats (e.g. grasslands). Therefore, swift foxes have the most female-biased social organization, as food acquisition by males is not required for pup survival, and rigid territorial and resource

defence by males is not necessary. However, most canid species fall in between the above extremes: both sexes necessarily acquire food and defend territories and consequently share the importance of group stability and social organization.

Finally, canids also vary in social organization and group structure within species (Moehlman 1989). Even African wild dogs and Ethiopian wolves have been found to have group structures that were less dominated by males than in other areas of their distribution (Sillero-Zubiri & Gottelli 1995; Creel & Creel 2002). Thus, group structures of swift foxes might be more influenced by males in other areas of their range, possibly related to differences in food resources or other factors. Our study areas were in the southern part of the distribution of swift foxes, thus influences of both sexes on group structures should be investigated in other parts of their range.

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