Den Ecology of Swift, Kit and Arctic Foxes: A Review

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Abstract: The availability and use of denning sites are important aspects of the ecology of most canids. Swift, kit and arctic foxes are closely related genetically, are similar in size, and share a number of behavioral and ecological traits. Yet, there are many differences between the species, which can be used in comparative studies. In this review, we examine differences and similarities in the den ecology of these species, in order to analyze the relationship between den use and other ecological parameters. We also discuss implications for the management of these foxes. We have found 2 different den ecology strategies, where swift and kit foxes have small litters and regularly change dens during the breeding season, while arctic foxes have large litters in large dens. The primary function of a breeding den is most likely to provide protection against predators. Sufficient escape routes can be achieved either by having several small satellite dens within each home range or by having large dens with many openings. These different den ecology strategies also involve territoriality, and are related to differences in a number of ecological parameters, such as predation rates, availability of dens, food resources and litter sizes. Identification and classification of den sites is a means of making surveys and population estimates more effective, especially for the arctic fox. An analysis of den sites is important for habitat protection and as a preparatory task for re-introduction programs for all 3 species.

Species which are closely related and share many characteristics while differing in others, can provide useful comparisons for ecological or evolutionary studies and for management purposes. Three of the smaller foxes make strong candidates for such a comparison, viz. the swift fox (*Vulpes velox*) of the shortgrass prairies, the kit fox (*V. macrotis*) of the desert, and the arctic fox (*Alopex lagopus*) of the tundra. The former 2 are restricted to North America, while the arctic fox has a circumpolar distribution. Despite differences in geographic range, habitat and physiology, there are striking similarities between the 3 species in genetics, behavior and ecology.

For example, swift, kit and arctic foxes share a strong dependence on good denning sites for breeding. They all live in open habitats and are subject to harsh climatic conditions. Furthermore, they live sympatrically with larger mammalian carnivores that often act as predators or competitors. Underground dens provide shelter for these small foxes, especially during breeding. The young are born blind and are dependent on their parents for approximately 2 months. Their den dependence has become a useful tool for ecologists, as den surveys can give good estimates of reproductive success in a population. For arctic foxes, it is a widely used method for population estimates (e.g., Elton 1924, Macpherson 1969, Angerbjörn et al. 1995, Tannerfeldt 1997). This den dependence has also been used in extermination campaigns (Hersteinsson 1984, Bailey 1992). For swift and kit foxes, den surveys lead to assessments of breeding frequency and litter sizes, which serve as indicators of reproductive success between years and regions (Egoscue 1975, Covell 1992, White and Ralls 1993, White and Garrott 1997).

This paper reviews and compares the den ecology of swift, kit and arctic foxes. It is essential to have an understanding of how availability and distribution of dens affect fox life histories and population dynamics. For example, increasing agricultural and industrial land use in sensitive areas might interfere with fox management and conservation goals. We will thus examine the den as a resource for these small foxes. Our interest was in factors that determine the distribution of dens, their structure and how they are used. How important are den sites to these foxes and what are the relationships between dens, reproductive output and other ecological parameters? Finally, we will try to determine the implications of our results for the management of these species.

The Species

Recent research suggests that the arctic fox should be included in the genus *Vulpes* to form a monophyletic group, and that arctic, kit and swift foxes are very closely related (Martin 1989, Geffen et al. 1992, Mercure et al. 1994). This genetic similarity is the closest that exists between any of the *Vulpes*-like species (Wayne and O'Brien 1987). They share an ancestor possibly adapted to an open desert and prairie habitat. From this, the arctic fox evolved into an exclusively tundra-dwelling species. Recent studies recognize only 3 subspecies of the arctic fox, 2 of which are indigenous to the isolated Commander Islands (Ginsberg and Macdonald 1990). The taxonomy of swift and kit foxes has been intensively debated. Based on protein-electrophoretic methods, Dragoo et al. (1990) concluded that swift and kit foxes were the same species but they argued that morphological differences warranted classification into separate subspecies. More recent mitochondrial DNA analyses, however, suggest that swift and kit foxes should be considered as separate species, namely *Vulpes velox* and *V. macrotis* (Mercure et al. 1994).

Swift and Kit Foxes

Swift and kit foxes are located in topographically flat, arid regions of North America. Historically, swift foxes occupied the Great Plains ranging north-south from central Alberta to central Texas and east-west from eastern North Dakota to central Colorado (Allardyce and Sovada 2003). Swift foxes are separated from kit foxes by the Rocky Mountains but interbreeding does occur within a limited hybridization zone in New Mexico (Rohwer and Kilgore 1973, Mercure et al. 1994). Kit foxes range from southern Idaho and Oregon in the United States to Durango, Zacatecas, and Nuevo in northern Mexico (O'Farrell et al. 1986, List 1998). The San Joaquin kit fox (*Vulpes macrotis mutica*) in southern California is topographically isolated from the main kit fox continuum.

Swift and kit foxes share common ecological requirements and similar threats to their persistence. Comparisons of the northern and southern peripheries of the swift/kit fox complex illustrate that habitat requirements are broadly similar throughout the range (O'Farrell 1987; Scott-Brown et al. 1987). Swift and kit foxes are morphologically similar although kit foxes have slightly longer ears (Dragoo et al. 1990) and smaller body weights than swift foxes (Moehrenschlager 2000). Along with the Fennec fox (*Fennecus zerda*) and Blanford's fox (*Vulpes cana*), these species are amongst the smallest of canids (Ginsberg and Macdonald 1990). Although the individual prey types differ between areas, both fox species primarily consume rodents, lagomorphs, birds, and insects (O'Farrell 1987, Scott-Brown et al. 1987). The species live in arid conditions which typically receive less than 400 mm of precipitation (Moehrenschlager and List 1996), although the San Joaquin kit fox obtains up to 1500 mm of precipitation which primarily falls between November and April (O'Farrell et al. 1986). While home range sizes can be highly variable within species, swift fox home ranges are generally larger than those of kit foxes (Hines and Case 1991, Zoellick and Smith 1992, List 1998, Kitchen et al. 1999, Moehrenschlager 2000).

The current distribution of swift foxes may represent only 38–41 % of its historical range (Sovada and Scheick 2000). The remaining core areas exist in Wyoming, Colorado, and Kansas where foxes appear to be abundant and populations are contiguous (Kahn and Beck 1996). A petition to list swift foxes as endangered was deemed as "warranted but precluded" in the United States, but has recently been overturned (Federal Register 1995). In Canada, this species was extirpated in the 1930's (Herrero et al. 1986), until reintroduction releases began in 1983. A small and apparently stable population has now been established (Cotterill 1997, Moehrenschlager and Moehrenschlager 1999, Moehrenschlager and Moehrenschlager 2001). Kit foxes are declared as threatened in Mexico (List 1998) and the San Joaquin kit fox is endangered (Cypher and Spencer 1998).

The reasons suggested for the decline in swift and kit fox numbers has been habitat loss and fragmentation (O'Farrell et al. 1986; Scott-Brown et al. 1987). Moreover, both species were susceptible to intensive poisoning programs which were primarily aimed at larger predators (Scott-Brown et al. 1987, Ginsberg and Macdonald 1990). The ecosystem perturbation that resulted from such predator control programs caused a significant shift in the canid community composition. The extirpation of the wolf (*Canis lupus*) allowed for the expansion of coyotes (*C. latrans*) (Schmidt 1991) which are now the primary mortality factor of swift and kit foxes in all telemetry studies (Ralls and White 1995, White and Garrott 1997, Sovada et al. 1998, Kitchen et al. 1999, Moehrenschlager 2000).

The Arctic Fox

The arctic fox inhabits most Arctic land areas above the timber line, including polar deserts and islands far away from the mainland (Preble and McAtee 1923, Lavrov 1932, Chesemore 1975, Hersteinsson 1984, Prestrud 1992a). The arctic fox has many physical adaptations to the Arctic environment, including the best insulative fur of all mammals (Prestrud 1991, Klir and Heath 1992). In the Holarctic range of the arctic fox, productivity is generally low, but food resources can be extremely abundant in small patches and during short time periods. The dominant pattern in these resource fluctuations is determined by rodent population fluctuations. In continental areas, the main prey species in summer are lemmings, (*Lemmus* and *Dicrostonyx* spp.), but also voles, (*Microtus* and *Clethrionomys* spp.) and carcasses of reindeer (*Rangifer tarandus*). In winter, the most important food resources are reindeer carcasses and ptarmigans (*Lagopus mutus* and *L. lagopus*; Macpherson 1969, Kaikusalo and Angerbjörn 1995, Elmhagen et al. 2000). In other areas, arctic fox populations are sustained on more stable summer food resources, mostly at bird cliffs and along shore lines, where food is washed up by the sea at regular intervals (Hersteinsson and Macdonald 1982, Prestrud 1992c, Hersteinsson and Macdonald 1996).

For the arctic fox, the world population is in the order of several hundred thousand individuals (Tannerfeldt 1997), but the species is endangered in some areas. On the Commander Islands (Russia), the threat is a result of an introduced disease (Kruchenkova and Formozov 1995). On the Fennoscandian peninsula (Norway, Sweden, Finland), arctic fox numbers have not recovered from a drastic population decline caused by over-hunting more than 80 years ago (Angerbjörn et al. 1995, Frafjord 1998, Löfgren and Angerbjörn 1998). This population is partly isolated from the Siberian mainland, and the lack of recovery can be explained by the combination of very low fox numbers (below 100 individuals), a lack of large predators leaving carcasses, and an absence of lemming population peaks.

Methods

We have compiled data from a large number of studies on the den ecology of these 3 fox species. Of these, more than 50 studies contained quantitative data which we have used in our analyses (Table 1). We focused our comparisons on parameters which were studied by many authors and for which data were collected in a comparable manner. Estimates of litter size have been accepted only for populations with a sample size larger than 5 and when collected around the time of weaning. Estimates of home range is the mean range given for resident (denning) animals during the breeding season. Juvenile mortality is the percentage of young which were reported to have died before the age of 2 months. We have also included unpublished or reanalyzed data from our own research in the Swedish Arctic Fox Project (see Angerbjörn et al. 1991, Tannerfeldt 1997) and the Canadian Swift Fox Reintroduction Program (see Moehrenschlager 2000).

Results and Discussion

Structure and Location of Dens

SWIFT FOX DENS. Swift fox dens are generally found in elevated areas with well-drained soils, but den sites will differ depending on their function. Extensive natal dens will have numerous entrances whereas dens that are utilized for escape from predators may frequently only have 1 opening (Kilgore 1969; A. Moehrenschlager, personal observation). Swift foxes frequently use or expand the burrows of ground squirrels (*Spermophilus* spp.), prairie dogs (*Cynomys* spp.), or badgers (*Taxidea taxus*), but they can readily dig their own dens (Cutter 1958, Kilgore 1969). Den entrances have a diameter of approximately 20 cm (Cutter 1958, Pruss 1999). The dens are normally situated near the tops of gently sloping hills (Cutter 1958, Uresk and Sharps 1986, Moehrenschlager 2000). Swift foxes primarily den in shortgrass prairie habitat, but also in midgrass prairie (Uresk and Sharps 1986) and cultivated areas (Sovada et al. 1998). In Kansas, the number of den entrances did not differ between cultivated and rangeland sites (Jackson and Choate 2000), while Kilgore (1969) determined that agricultural sites harbored relatively few den entrances in Oklahoma. Rangeland dens in Kansas were characterized by higher and denser vegetation, more rolling topography, smoother den surfaces, and more extensive burrow tailings than dens in cultivated habitats (Jackson and Choate 2000). Excavated dens in shortgrass areas had more and longer branches and extended to a greater depth than those in cultivated sites (Cutter 1958, Kilgore 1969). Swift fox dens can have as many as 17 branches and up to 2 chambers at depths extending to 1 meter (Kilgore 1969). In Nebraska, den entrances primarily had eastern or western exposures (Hines and Case 1991), while in Colorado and Alberta they were randomly oriented (Rongstad et al. 1989, Pruss 1999). Swift fox dens are frequently located in anthropogenic areas such as near roads, in culverts, pipes and buildings (Kilgore 1969, Hines and Case 1991, Zimmerman and Giddings 1997, Pruss 1999, Moehrenschlager 2000). Since coyotes avoid human habitation, such den sites can offer additional protection for swift foxes. However, they may induce additional costs as adults, and pups in particular, are frequently killed by cars and occasionally taken by domestic dogs (*Canis familiaris*; Sovada et al. 1998, Moehrenschlager 2000).

KIT FOX DENS. Kit fox dens are strikingly similar to those of swift foxes. Kit fox dens can also be variable in size and dens utilized for pup-rearing have more entrances than those used for other purposes (Morrell 1972). Like swift foxes, kit fox dens are normally only occupied by the natal pair or family groups (Morrell 1972, Egoscue 1975). Kit foxes frequently utilize or expand the burrows of other animals such as prairie dogs, kangaroo rats (*Dipodomys* spp.), and badgers (O'Neal et al. 1987, List 1998). While some authors consider the digging ability of kit foxes to be poor, others believe it is excellent (O'Neal et al. 1987). Most likely, digging frequency depends on the need and possibility to do so. In areas where numerous holes have been created by other species or where soils are not well drained, foxes may dig only rarely. Kit fox dens in Utah are situated in well-drained areas (O'Neal et al. 1987). Two excavated kit fox dens had grass-lined food and sleeping chambers which were as deep as 2.5 m below the surface (O'Neal et al. 1987). Dens of San Joaquin kit foxes at Camp Roberts had openings with an average height of 20 cm and an average width of 21 cm. Most dens had 2 to 5 entrances and 36% showed signs of fox activity (Reese et al.1992). More frequently than expected, this fox population had dens in grassland and low to medium density woodland, while medium to high density oak woodlands were avoided. Kit foxes were primarily found in well-drained soils and the average slope of occupied hillsides was 19 degrees (Reese et al. 1992). Kit foxes in Mexico's Chihuahuan desert preferred creosote habitat and Mimbres-Tome soil, which is well drained. Steep slopes of 5% to 20% were avoided. Dens were primarily found on slopes oriented to the northwest, and den openings were primarily oriented towards the southeast or northwest (Rodrick and Mathews 1999).

ARCTIC FOX DENS. Arctic fox dens can be impressive geographical features, with a hundred entrances in a mound or ridge and lush green vegetation contrasting the barren tundra. Arctic fox dens have therefore been monitored through aerial surveys, in some areas with good results (e.g., Macpherson 1969, Garrott et al. 1983, Ericson 1984,

Table 1. Data from 43 different populations of small foxes: kit fox *Vulpes macrotis*, swift fox *V. velox* and arctic fox *Alopex lagopus*. Given are the means for each parameter ± SE, with sample sizes in italics and range (in parentheses). Maximum and mean litter sizes are at the time of weaning. Home ranges are given in km^2 to nearest integer by Minimum Convex Polygon method, unless otherwise stated.

Species	Main Food Resources	Site	Litter size max / n	Litter size mean / n	Max no. dens in breeding season	Reference	Home range (km^2) in breeding season / n	Annual adult mortality	Annual juvenile mortality
V macrotis		Naval Petr. Res., California	6/*101*	3.8/*101*		(Cypher et al. 2000)		0.56	0.86 first 9.5 months
V macrotis	Fluctuating rodents	Carrizo Plain, California	3/*4*	2/*4*	>50 [1] 4	(Ralls et al. 1990; White and Ralls 1993)	pairs: 11 ± 1.2	(0.36-0.45)	(0.46-0.60)
V macrotis	Rodents, rabbits	Sonoran Desert, Arizona			16	(Zoellick and Smith 1992; Zoellick et al. 1989)	grid-cell method: 11 ± 1/7		
V macrotis	Rodents	Camp Roberts, California			50 [2]	(Reese et al. 1992)			
V macrotis	Jackrabbits and cottontails	Naval Petr. Res., California		4.3/*84*		(O'Farrell et al. 1986)			
V macrotis	Fluctuating jackrabbits	Western Utah	6/*17*	3.8/*17*		(Egoscue 1975)			
V macrotis	Rodents, rabbits, birds	Kern County, California	5/*5*	4/*5*	5	(Morrell 1972)			
V macrotis	Rodents, rabbits, birds	Desert Exp. Range, Utah			17	(O'Neal et al. 1987)			
V velox	Rodents, insects	Northern Montana	7/*3*			(Zimmerman and Giddings 1997)			
V velox		SE Colorado		pairs: 2.4/*13* trios: 4.2/*5*		(Covell 1992)		0.47 +/- 0.05	0.87 +/- 0.13
V velox	Rodents, birds, rabbits	Beaver County, Oklahoma	6/*4*	4.3/*4*		(Kilgore 1969)			
V velox	Mammals, birds, insects	Las Animas County, Colorado	5/*5*	3.4/*5*	20+	(Rongstad et al. 1989)		048	0.95
V velox		Alberta/Saskatchewan	7/*12*	4.2/*12*		(Brechtel et al. 1993; Carbyn et al. 1994)		(0.33-0.50)	
V velox	Rodents, birds, rabbits	Alberta/Saskatchewan	8/*29*	3.9/*29*	22	(Moehrenschlager 2000)	fixed kernel estimate: 24/*18*	(0.46-0.64)	
A lagopus	Fluctuating rodents	Hudson Bay, NWT	12/*9*	7.6/*9*		(Hall 1989)			
A lagopus	Fluctuating rodents	Keewatin, Aberdeen Lake, NWT	14/*38*	6.5/*38*		(Macpherson 1969; Speller 1972)			
A lagopus	Fluctuating rodents	Kildin Island, Russia	13/*48*	6.5/*48*		(Lavrov 1932)			
A lagopus	Fluctuating rodents	Prudhoe Bay and Colville River Delta, USA		4.8/*11*		(Burgess 1980; Eberhardt et al. 1983; Fine 1980; Garrott and Eberhardt 1982)	21/*2* and 21 ± 6/*4*		dead pups in 19% of 79 litters
A lagopus	Fluctuating rodents	Snøhetta, Norway				(Landa et al. 1998)	21/*21* (6-60) males: 27/*7* females 18/*14*		
A lagopus	Fluctuating rodents	Norrbotten county, Lapland, Sweden	14/*60*	6.4/*60*		(Angerbjörn et al. 1995)			
A lagopus	Fluctuating rodents	Västerbotten county, Lapland, Sweden	15/*88*	6.1/*88*	2	(Angerbjörn et al. 1997; Angerbjörn et al. 1995; Tannerfeldt et al. 1994)	21/*5* (15 - 36)	(33.3 - 60.0)	(0.08-1.00)
A lagopus	Fluctuating rodents	Jämtland county, Lapland, Sweden	16/*67*	6.4/*67*		(Angerbjörn et al. 1995)			
A lagopus	Fluctuating rodents	Wrangel Island, Russia	18/*53*	6.5/*53*		(Chernyevski and Dorogoi 1981; Dorogoi 1987)			(0.23 - 0.62)
A lagopus	Fluctuating rodents	Yamal, Russia				(Smirnov 1968)			(0.32 - 0.99)
A lagopus	Fluctuating rodents	Yugov Peninsula, Russia	16/*117*	7.8/*117*		(Nasimovich and Isakov 1985)			
A lagopus	Birds and fluctuating rodents	Kokechik Bay, Yukon-Kuskokwim delta, USA				(Anthony 1996; Anthony 1997)	7 ± 2/*26* males: 10 ± 6, females: 5 ± 2		
A lagopus	Sea birds, ptarmigan, littoral	Iceland	10/*309*	4.2/*309*		(Hersteinsson 1984; Hersteinsson and Macdonald 1982)	16/*3* (9 - 19)		
A lagopus	Sea birds, littoral	Bering Island, Russia	9/*12*	5.5/*12*		(Frafjord and Kruchenkova 1995)			
A lagopus	Sea birds, littoral	Mednyi Island, Russia	10/*17* 8/*9*	6.4/*17* 4.5/*9*		(Barabash-Nikiforov 1938; Frafjord and Kruchenkova 1995)			
A lagopus	Sea birds, littoral	Pribilof Islands, USA	11/*22*			(Preble and McAtee 1923)			
A lagopus	Sea birds, littoral	Rat Islands, USA	5/*16*	2.8/*16*		(Berns 1969)			
A lagopus	Sea birds, littoral	Svalbard (Spitzbergen), Norway	8/*35* 8/*5*	5.3/*35* 5.8/*5*		(Frafjord and Prestrud 1992; Prestrud 1992b; Prestrud 1992c; Prestrud 1992d)	54/*7* (10 - 125) females: 48 ± 9/*3* (36 - 50)		
A lagopus	Sea birds, littoral	W Greenland				(Birks and Penford 1990)	non-breeding females: 12/*2* (18 - 24)		

[1] 3–6 unique dens every month over 500 day study period.
[2] In 365–400 day study period.

Table 2. Distribution and physical characteristics of arctic fox dens in North America, Siberia, Svalbard, Greenland and Scandinavia. Based on Dalerum et al. (2001). Values in parentheses indicate total range.

Area	Site	Habitat	Geographic Region	Den Type	Latitude	No. of Dens	Density (dens/km^2)	Den openings[a]	Den area[a] (m^2)	Source
Northern Alaska	Prudhoe Bay and Colville River Delta	Coastal tundra	Arctic	Burrows	70°N	38–50	1/12 and 1/34	33 (1-85)	256 (1-625)	Garrott et al. 1983, Eberhardt et al. 1983
Northern Alaska	Teshekpuk lake area	Coastal tundra	Arctic	Burrows	70°N	50		4 (1-26)	30 (1-100)	Chesemore 1969
Northern Canada	Herschel Island	Coastal tundra	Arctic	Burrows	69°N	17	1/3	20 ± 14	123 ± 122	Smits et al. 1988
Northern Canada	Yukon coastal plain	Coastal tundra	Arctic	Burrows	69°N	25	1/102	19 ± 9	130 ± 116	Smits et al. 1988
Western Alaska	Yukon-Kuskokwim delta	Coastal tundra	Sub-arctic	Burrows	61°N	11	1/5	5 ± 3 (2-10)		Anthony 1996
Northern Siberia	Wrangel Island	Coastal tundra	Arctic	Burrows	70°N	41		31 (5-67)	70 (15-220)	Dorogoi 1987
Svalbard	Nordenskiöldland	Coastal area	Arctic	Combined rock/burrows	77°N	59	1/13	10 ± 9 (1-35)	52 ± 76 (2-630)	Prestrud 1992d
West Greenland	Disko Island	Coastal area	Arctic	Combined rock/burrows	69°N	17		18 ± 18 (1-63)	196 (3–1134)	Nielsen 1994
Norway	Hardangervidda	Mountain tundra	Sub-arctic	Burrows	60°N	31		(1-40)	(10-50000)[b]	Østbye et al. 1978
Sweden	Vindelfjällen	Mountain tundra	Sub-arctic	Burrows	66°N	69	1/21	27 ± 22 (2-89)	277 ± 237 (20-1085)	Dalerum et al. 2001

[a] Mean ± sd.
[b] Includes "den complexes," presumably with several dens.

Anthony 1996). The most important limitation to denning in the Arctic is permafrost, which often lies less than 50 cm below ground. Therefore, productive arctic fox dens are usually situated on elevated mounds, ridges, eskers, pingos, or river banks. The common characteristic of good denning sites is that they lie above the permafrost layer, accumulate comparatively little winter snow and are sun-exposed, often facing south (Macpherson 1969, Bannikov 1970, Østbye et al. 1978, Underwood and Mosher 1982, Anthony et al. 1985; Prestrud 1992d, Dalerum et al. 2001). Dens have also been found to face away from dominant summer winds (Nielsen et al. 1994). Preferred soil materials are glacifluvial sand and silt (Chesemore 1969, Østbye et al. 1978, Nielsen et al. 1994, Dalerum et al. 2001). Dens are gradually excavated deeper and deeper, as the permafrost table gradually drops due to increased air ventilation and water drainage. The thawing depth beneath a den can be twice the normal depth (Skrobov 1960, Chesemore 1969). The construction process thus takes many years, and large arctic fox dens have been described as active for hundreds of years (Lönnberg 1927, Zetterberg 1945, Macpherson 1969). Macpherson (1969) suggested an average life-span of 330 years for each den. Good den sites are limited (Smits and Slough 1993) and new arctic fox dens are constructed mainly in peak population years (Dorogoi 1987). In permafrost areas, dens are often quickly eroded and thus remain small. If necessary, dens can also be placed under large rocks and boulders (Prestrud 1992d). In some areas, artificial structures are used for denning (Eberhardt et al. 1983). In 9 studies covering a total of 539 arctic fox dens, the mean number of openings per den varied from 4 to 44 and mean den area varied from 30 to 277 m^2 (summarized in Table 2, see Dalerum et al. 2001). In Sweden, where little permafrost exists, there are dens with 147 openings, and den areas covering up to 1085 m^2 (mean=44 openings and 277 m^2, N=77; Dalerum et al. 2001). In such large dens, there is often a succession of burrows from freshly dug to completely collapsed openings (Macpherson 1969).

The openings of arctic fox dens in soft ground are round or slightly oval, 15–20 cm in diameter (Smits et al. 1988). Usually, there is little bare ground outside them, as the dug-out material is spread rather thinly, allowing the vegetation to sprout through (Chesemore 1969). The arctic fox is not as "messy" as, for instance, the red fox (*Vulpes vulpes*), and normally leaves few food remains outside the den. Even old bones and dry skin are cached in or near the den, except when food is extremely abundant (M. Tannerfeldt and A. Angerbjörn, personal observation). In rocky areas, dens are therefore difficult to find. The best signs of a whelping den are strong fox odor in the openings, extensive trampling in the vegetation between openings, and small scats. In addition, arctic fox pups often bark from below ground when approached by a human.

The excavation of arctic fox dens have consequences on plants. Poaceae and *Dryas* thrive on many sites, which are nutrient rich from fox droppings and food remains, have a warmer soil, better drainage, lower permafrost and better airing than the surrounding ground (Chesemore 1969, Macpherson 1969, Garrott et al. 1983, Smits et al. 1988, Anthony 1996). Due to the comparatively high productivity, arctic fox dens can also locally be important to grazers such as reindeer/caribou and small rodents. On the Yamal Peninsula in Siberia, there are about 24,000 dens covering on average of 250 m^2, totaling 6 km^2 of lush "arctic fox meadow" (Skrobov 1960). In other habitats, arctic fox dens may be small, ephemeral and difficult to find. This mainly occurs in areas of extensive permafrost, flooded areas (Skrobov 1960, Anthony 1996) and in rocky arctic deserts (Prestrud 1992d).

Despite their prominence in the landscape, there is little information on what arctic fox dens look like below ground. According to Skrobov (1960), dens occupy larger areas in northern Yamal (around 300 m^2) than in the south (around 100m^2). Den area is directly proportional to the severity of the conditions and especially to the proximity of the upper permafrost horizon (Skrobov 1960). This suggests that arctic fox dens extend horizontally where their downward extension is limited. On Wrangel Island near Bering Strait, a complete den was excavated, revealing a 10 x 8-m tunnel grid connecting 17 openings (Dorogoi 1987). The deepest tunnels were only 64 cm below ground, indicating a 2-dimensional structure. There was 1 widened whelping chamber in the den. Also from the Russian northeast, Nasimovich & Isakov (1985) described a cross-section of a typical den, which followed the ground contour of a slope. The tunnel systems in more complex dens have an intricate, 3-dimensional structure (Høst 1935 *in* Østbye et al. 1978), and foxes can have underground connection between most burrows also in dens with more than 50 active openings (M. Tannerfeldt, personal observation). Boitzov (1937) also excavated dens: "In the nests were found dry grass, moss, feathers and all kinds of bones. However remains of food were also found throughout the whole labyrinth." Non-natal dens, often called satellite dens, are usually smaller than natal dens for arctic foxes (Smits and Slough 1993). Arctic foxes usually have only a few satellite dens within their territory. Satellite dens can be small escape holes or day resting sites, but the category also includes alternative rearing dens.

Distribution and Use of Dens

SWIFT FOXES. Swift fox dens are usually clustered (Cutter 1958, Hines and Case 1991). Two successively used swift fox dens in Oklahoma were only 200 m apart (Kilgore 1969). Pruss (1994) found that den shifts maximally spanned 500 m. Moehrenschlager (2000) found that most movements reflected this pattern, but 1 fox pair moved 7 pups across a highway for a total distance of 1.9 km. Swift foxes use larger dens during the pup-rearing season than at other times of the year (Kilgore 1969). In southeastern Wyoming, 75.1% of dens were located within the core area of individual swift fox home ranges and common core areas of 4 fox pairs contained 84.6% of shared dens (Pechacek et al. 2000).

KIT FOXES. Kit fox dens are also clustered. O'Neal et al. (1987) found that 7–17 dens which were no more than 100 m apart formed clusters that were smaller than 2 km^2. Egoscue (1975) noted that natal dens of neighboring kit foxes were at least 3.2 km apart. Kit foxes in Arizona utilized 3–16 dens per individual and den sites were further from riparian habitat than expected (Zoellick et al. 1989). The mean movement distance between successive San Joaquin kit fox dens in California was 711 m and some foxes utilized over 50 different dens (Ralls et al. 1990).

Kit foxes use numerous dens and change between them frequently. In Utah, kit foxes changed dens as often as 33 times in 1 breeding season (O'Neal et al. 1987). Morrell (1972) found that San Joaquin kit foxes used up to 4–5 dens per month, that dens were switched most commonly during the dispersal period, and that larger dens were used during the breeding season than at other times of the year. Ralls (1990) found that San Joaquin kit foxes switched den sites after a mean period of 3.1 days and that approximately half of the dens were only utilized for 1 day at a time. Foxes infrequently reused the same sites and individuals used 3–6 unique dens per month. The rate of den switching can differ between seasons and age classes. Adults and juveniles tended to remain in the same den longest during April and September. Within each month, adults used approximately 1 more den than juveniles (Ralls et al. 1990). San Joaquin kit foxes used an average of 11.8 dens/year; the largest number of dens was used during the dispersal season whereas few were utilized during breeding and pup-rearing. Individual dens were only used for an average of 10.0% of the year, and an average of 46.6% of dens used annually had not been used by the same fox in the previous year (Koopman et al. 1998). In contrast, kit foxes in the Chihuahuan desert of Mexico used more dens during breeding and pup-rearing seasons than at other times of the year. Natal dens and satellite dens were similar, although natal dens had taller den entrances and fewer cactus species surrounding the den than non-natal sites (Rodrick and Mathews 1999).

ARCTIC FOXES. Arctic foxes maintain territories during the breeding season, sometimes all year round. Territory size and shape are determined by food availability (Hersteinsson 1984, Angerbjörn et al. 1997). There is little overlap between territories and the borders are strongly defended, although trespassing occurs when the territory owners are out of sight (Eberhardt et al. 1983, Hersteinsson 1984, Prestrud 1992b). Within each territory, there are usually 2–3 potential natal dens and several small non-natal (satellite) dens. Outside the breeding season, arctic foxes keep only a few holes open in the snow, also in large dens (M. Tannerfeldt, personal observation). Most authors agree that landscape features, substrate properties and food dispersion govern the distribution of arctic fox denning sites. Den distribution is therefore sometimes random (Fine 1980), sometimes more widely spaced than random (Macpherson 1969, Prestrud 1992b, Dalerum et al. 2001) and sometimes clumped (Prestrud 1992b, Anthony 1996). Successful denning sites on Svalbard were clustered along valley sides and the coast. Within each year, however, breeding dens were more widely spaced than random, as a result of territoriality (Prestrud 1992b). Density of arctic fox dens may vary from 1 den per 3 km^2 to 1 per 102 km^2 (Smits et al. 1988).

The large litters of arctic foxes may be split up between several dens or moved to alternative rearing dens, usually as a result of disturbance. The average distance pups are moved is 1.5–2.2 km (Boitzov 1937, Eberhardt et al. 1983, Prestrud 1992b). However, a 6-week-old arctic fox litter of 9 young moved 6 km, following red fox predation at the natal den (Elmhagen 2001). Pups may also be moved back and forth several times (Prestrud 1992b). Anthony (1996) described 1 litter of 8 which was split into 2 dens, a litter of 9 into 5 dens, and a litter of 10 into 7 dens. On Svalbard, litters were split between 2 dens in 8 cases, and entire litters moved from the primary den in 5 cases (Prestrud 1992b). Eberhardt et al. (1983) suggested that splitting of broods could reduce the risk of losing an entire litter to predation or reduce disease transmission.

Dens for Protection

The smaller canids and the pups of the larger species often run the risk of being killed by raptors and larger mammalian predators, especially when living in open habitats (e.g., Carbyn 1986, Thurber et al. 1992, Lindström et al. 1995, Ralls and White 1995, Palomares and Caro 1999). Swift and kit foxes live in moderately open habitats and are at peril from coyote, red fox, domestic dog, and golden eagle (*Aquila chrysaëtos*) (Covell 1992, Disney and Spiegel 1992, Carbyn et al. 1994, Ralls and White 1995, Moehrenschlager and Moehrenschlager 1999). To our knowledge, every telemetry study on swift or kit foxes has documented coyote-induced mortalities, and coyotes are responsible for up to 87% of fox mortalities (White and Garrott 1997). Survival rates of the latter fox species may depend on a combination of interspecific, resource-dependent home range webs and the availability of dens as escape routes (Moehrenschlager 2000). Arctic foxes live in an extremely open habitat and are killed by red fox, wolf, domestic dog, brown/grizzly bear (*Ursus arctos*), polar bear (*U. maritimus*), wolverine (*Gulo gulo*), snowy owl (*Nyctea scandiaca*) and golden eagle (Lavrov 1932; Bannikov 1970; Garrott and Eberhardt 1982; Frafjord et al. 1989; Menyushina 1994a,b).

There can also be interspecific competition for dens between canids, sometimes accompanied by food competition (e.g., Smits and Slough 1993). If the mere presence of a larger canid can reduce an animals willingness to use an area, it can be excluded from the dens in that area. This might seem to contradict other hypotheses, which state that size differences can permit otherwise similar carnivore species to coexist (e.g., Rosenzweig 1966). But a theoretical model showed that these are not mutually exclusive, but can be 2 cases in a continuous spectrum of situations with varying prey and predator sizes (Wilson 1975). Coyotes have shown interspecific territoriality towards red foxes (Dekker 1983, Voigt and Earle 1983, Sargeant et al. 1987). Similarly, coyotes avoided wolf pack territories and, like white-tailed deer (*Odocoileus virginianus*), lived mainly on wolf territory boundaries (Fuller and Keith 1981). In these situations, it is difficult to distinguish between competition and predation, but the resulting distribution is the same.

Swift foxes in Colorado (Kitchen et al. 1999) and in Canada, and kit foxes in Mexico (Moehrenschlager 2000), cannot escape from coyotes through habitat partitioning. Coyote home ranges in Mexico and Canada completely enveloped fox home ranges. However, coyotes moved randomly relative to simultaneously tracked swift foxes (Kitchen et al. 1999), and relative to swift fox or kit fox den sites (Moehrenschlager 2000). Swift and kit fox mortalities in Canada and Mexico, respectively, appear to be a function of interspecific encounter rates. Although coyotes are the main cause of swift and kit fox mortalities, they may be essential to the long-term persistence of these species because they exclude red foxes (Ralls and White 1995).

In Alberta and Saskatchewan, coyotes and swift foxes are sympatric while red foxes are normally peripheral in agricultural habitat. Nevertheless, red foxes can invade swift fox areas and take over swift fox dens (Moehrenschlager 2000). Den characteristics of swift foxes, red foxes and coyotes differed significantly. Red fox dens had significantly greater slopes than swift foxes, and red fox dens were closer to human habitation than those of the other canids. Although swift fox dens were found at all distances, red foxes always denned within 3 km of ranches, whereas all coyote dens were at least 3 km from these sites (Moehrenschlager 2000).

For arctic foxes, the main competitor for dens is the red fox. Being larger, red foxes can chase away or kill arctic foxes (Rudzinski et al. 1982, Frafjord et al. 1989, Hersteinsson et al. 1989, Hersteinsson and Macdonald 1992), thereby excluding them from important parts of their fundamental niche (Elmhagen 2001). High quality arctic fox dens were inhabited less often when red foxes were breeding within an 8-kilometer radius from the dens, than when red foxes were not present (Elmhagen 2001). Also wolves, wolverines and bears can take over arctic fox dens for breeding (Macpherson 1969, Angerbjörn and Isaksson 1995).

The examples of red foxes invading arctic and swift fox den sites illustrate the importance of the den as a crucial resource, especially during the breeding season. If dens are critical, then the intensity of competition should depend upon the availability of these sites. Since dens are more available to swift and kit foxes than to arctic foxes, we hypothesize that arctic foxes are more susceptible to competitive exclusion by red foxes than the smaller *Vulpes* species. Based on the interspecific relationships of swift and red foxes with coyotes in Canada, such pressure on arctic foxes might only be alleviated through the presence of the historic apex canid in the arctic: the wolf.

Litter Sizes

On the population level, reproductive rates are determined by the proportion of breeding females and their litter sizes, both of which are influenced by food availability in Canidae (Macpherson 1969, Bannikov 1970, Englund 1970, Lindström 1989, Hersteinsson and Macdonald 1992, Tannerfeldt et al. 1994, Geffen et al. 1996). Litter sizes of Canadian swift foxes are correlated to breeding season body weights; consequently, winter severity can affect reproductive output in the subsequent year (Moehrenschlager 2000). Among kit foxes, breeding probabilities are closely linked to resource availability (Egoscue 1975, White and Ralls 1993). In Utah, the proportion of breeding individuals and litter size changed in response to the abundance of black-tailed jackrabbits (*Lepus californicus*) (Egoscue 1975). The prey base of kit foxes can be severely impacted by drought, which is directly manifested on the level of fox reproduction (White and Ralls 1993, Warrick and Cypher 1998).

In swift and kit foxes, litter sizes are disproportionately small compared to other canids, and so is total litter weight relative to body size (Geffen et al. 1996). The mean litter size for kit foxes and swift foxes is 3.5 and maximum litter sizes are 6 and 8 foxes, respectively (Table 1). This may be related to the food resources of swift and kit foxes, which are quite stable in comparison with the lemming fluctuations that govern most arctic fox populations, with up to 1000-fold increases in prey density (Krebs 1993). Although prey populations also for kit and swift foxes may undergo temporary crashes (White and Ralls 1993), the comparative diversity of swift and kit fox diets may allow these species to sustain smaller declines than arctic foxes, whose populations are closely tied to lemming population fluctuations.

But litter sizes are not only determined by food availability. In arctic foxes, it has been noted that coastal populations generally have smaller litters than inland foxes. Arctic foxes can have up to 19 young, which is among the largest known litter size in the order Carnivora (Ewer 1973, Ovsyanikov 1993). Also, when total litter weight, controlled for gestation time, is plotted against female weight, the arctic fox has the highest values among the Canidae (Geffen et al. 1996). A review of 16 arctic fox studies showed that unpredictable food resources (i.e., fluctuating lemming populations) were associated with larger litter sizes than more stable food resources were (unpredictable: mean litter sizes 2.8–6.4, maxima 5–11, N=5 studies; stable: mean litter sizes 5.0–11.2, maxima 7–18, N=11 studies; Tannerfeldt and Angerbjörn 1998). There were significant differences also in variances, as well as in placental scar count means. It was therefore suggested that litter size in the arctic fox is determined by adaptive plasticity. In short, according to the jackpot hypothesis, foxes with unpredictable food resources generally will have larger litter sizes at a given food resource level (Tannerfeldt and Angerbjörn 1998).

Dalerum et al. (2001) analyzed reproductive data from 16 years in 31 arctic fox breeding dens. There were 43 (58.1%) unoccupied dens which were not included in the analysis. Within breeding dens, standardized number of arctic fox litters was positively related to den area. Also, arctic fox litter size was positively related to den area. Further, for all 74 arctic fox dens in the area, the number of openings and the area covered by an den were positively related (Fig.1; Dalerum et al. 2001). Also Anthony (1996) found natal dens to be larger than non-natal dens. This confirms the conventional wisdom that large dens are good dens for arctic foxes. Arctic foxes thus chose large dens for breeding, which significantly improves their reproductive output.

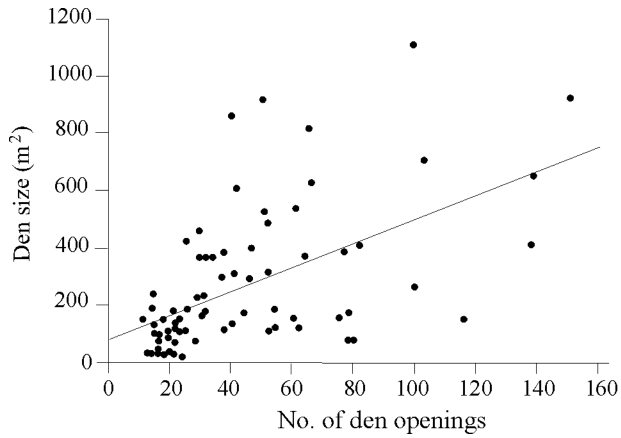

Figure 1. For arctic fox dens, the number of den openings and the area covered by a den are positively related (F (1, 72) = 37.1, R^2 = 0.33, p <0.001, y = 87.8 + 4.30x, n *= 74). From Dalerum et al. (2001).*

Den Quality

As shown in the previous section, there are clearly good and bad dens for arctic foxes. For swift and kit foxes, distinctions into good and bad den sites have not been made. However, den sites will be used several years (Pruss 1994) and specific dens have been used at least 5 consecutive years (A. Moehrenschlager, unpublished data). Yet, Canadian swift foxes during 1995–1998 never used the same den for the birth of different litters (A. Moehrenschlager, unpublished data).

The arctic foxes' preference for specific dens could be used for management purposes. It would be advantageous to be able to identify "hot spots" for breeding, upon which surveys and management actions could focus. Angerbjörn et al. (1995) investigated arctic fox den data collected during 2 decades from an area of approximately 32,500 km^2 in Sweden. Each den was assigned a quality index (QI), based on its rate of occupancy (years producing litters divided by years monitored). As the basic population cycle had a 4-year period, dens which had been monitored less than 4 years were excluded, and the remaining 154 dens were assigned to 1 of the following 4 categories (with percentage of dens in parentheses): Cat1, QI = 0 (38.3%);

Cat2, QI ≤0.25 (38.3%); Cat3, 0.25 <QI ≤0.5 (20.8%); Cat4, QI >0.5 (2.6%). This index was used to check a monitoring program for biases (Angerbjörn et al. 1995). It would also be interesting to test whether this quality index is related to size or other den characteristics.

Macpherson (1969) categorized arctic fox dens from an airplane as either "youthful" (no characteristic vegetation and few burrows), "mature" (well-developed with good mat of vegetation), "old" (large den with many burrows and rich vegetation), or "senile" (not active with collapsed burrows). Strangely enough, however, he reported an occupancy rate of 21.4% for the latter category. The word "senile" suggests that there is a definite end to the use of a particular den. However, if good den sites are valuable to arctic foxes, why abandon them? They may be abandoned when they have been excavated by other animals (Macpherson 1969). Destroyed dens could be brought back into use after the tunnels have fallen in completely and the material on the den site has stabilized. In some large arctic fox dens, 1 side of a hill or ridge has an active den, while the other side contains old and collapsed burrows. This implies that the same den site is used continuously, although specific burrows may be left to collapse. It is also possible that dens are abandoned for a number of years to avoid a heavy parasite load (Butler and Roper 1996). Parasite infestation is an interesting aspect of den ecology, which has received little attention so far.

Social Organization

Within the canid family, helpers and/or communal feeding are reported for at least 10 species (see Kleiman [1977] for a review; also for kit fox see Cutter [1958]; dhole [*Cuon alpinus*] see Johnsingh [1982]; arctic fox see Hersteinsson [1984]). This apparently alloparental behavior is a phenomenon which has generated many theories, models and hypotheses (e.g., Brown 1983; Ferguson et al. 1983; Pyearah 1984; Schantz 1984a,b; Kruuk and Macdonald 1985). But for the smaller Vulpes, there is little evidence of extra adults providing valuable care for non-offspring (e.g., Strand et al. 2000). For several species, the number of helpers is larger when food is more abundant (Harrington et al. 1983). But, assuming that help is given by feeding the pups or the mother, the benefit to the parents should be largest at intermediate levels of food abundance (Hersteinsson 1984). Thus, there can be a conflict between parents and offspring. Taking into consideration the different options open to parents, helpers and offspring in the flexible social systems of canids, the interactions between individual and kin selection become very complex (Emlen 1978). A general model has shown that group sizes are not always of the size that would maximize individual fitness, but larger (Rodman 1981). This, Rodman concluded, is an effect of kin selection.

Swift and kit foxes are mainly monogamous (O'Farrell 1987, Scott-Brown et al. 1987), but more than 2 foxes are frequently seen at den sites. In Colorado, swift fox trios and a quad consisting of a male and accompanying females were observed in a coyote-control area. Litter sizes of groups with multiple females were significantly larger than those of pairs (Covell 1992). In Utah, a yearling female kit fox was a helper (O'Neal et al. 1987). Egoscue (1975) observed 1 polygamous trio which produced pups. Among San Joaquin kit foxes, trios contained either 2 males or 2 females (Ralls et al. 1990). Since these observations were made during a period of resource scarcity which virtually eliminated reproductive output, trio formation is not necessarily linked to abundant resources.

In Wyoming, 70% of dens belonging to mated, male swift foxes and 82% of dens belonging to females were shared with their mates (Pechacek et al. 2000). Females with dens were located with their mates approximately 60% of the time. Koopman et al. (1998) found that San Joaquin kit fox mates denned together for 45% of the year and mated adults denned together less often during dispersal than during the breeding season. Adult males and females denned with their offspring for up to 17 and 18 months, respectively. Den sharing with the yearlings decreased as the next litter was born but returned to previous levels after 2 months. Den sharing by siblings was as common in the second year as in the first, but ceased after 21 months of age.

Similar to red foxes, arctic foxes can increase group size at high population densities, usually by allowing additional adults at breeding dens (Zetterberg 1953; Eberhardt et al. 1983; Macdonald 1983; Schantz 1984a,b; Lindström 1986; Hersteinsson and Macdonald 1992; Strand et al. 2000). The Mednyi Island arctic fox population, however, is an interesting extreme in this respect. The island earlier had a very dense population of several thousand animals, with 5 individuals per km^2 (Boitzov 1937). In this population, arctic fox adults lived in large groups that shared dens. In the 1980's, numbers dropped to a few dozen due to an introduced ear tick (Kruchenkova and Formozov 1995). However, the complex social system remains and in 33 examined dens, the number of adults were as follows: 2 adults 39%, 3 adults 36%, 4 adults 15%, 5 adults 6% and 6 adults 3% (Frafjord and Kruchenkova 1995). In the Mednyi Island population, it is apparently common that related females join their litters (Kruchenkova and Formozov 1995). In Norway, it was confirmed that pups in 1 den suckled from 2 lactating females (Strand et al. 2000). The authors assumed this to be 2 different litters raised together. Two litters in 1 den have also been recorded in red foxes (Macdonald 1980). In Sweden, arctic fox females were observed to join litters with neighbors on 2 occasions. In 1 case, it was a 2-year-old daughter who moved her 2 pups to join her mother and her litter after predation attempts from red foxes at the daughter's den. The next day, 1 of the daughter's pups died as a result of bite wounds from a red fox (Elmhagen 2001).

Concluding Discussion

SIMILARITIES BETWEEN THE SPECIES. Swift, kit and arctic foxes share a number of behavioral and ecological traits, with similarities in their den ecology. The primary function of breeding dens is most likely to provide protection against predators. In addition, dens provide protection for juveniles against harsh weather in open landscapes. For all 3 species, natal dens are larger than satellite dens. Furthermore, arctic foxes choose the largest dens for breeding and reproductive output is positively correlated with den size. This relationship holds true also for dens with more than 100 openings, which indicates that large burrow systems with many escape routes are important. In swift and kit foxes, the importance of predator avoidance is instead manifested through a large number of escape routes in a 'survival sieve' of satellite dens within each home range (Moehrenschlager 2000).

Another similarity between these foxes is that natal dens are exclusively used by resident family groups. There are some exceptions to this, where breeding pairs may share a den. However, this phenomenon seems to be restricted to close relatives, and foxes are normally strongly territorial when breeding. Swift and arctic foxes, and possibly also kit foxes, tend to use den sites with lush vegetation near hilltops. As discussed for the arctic fox, lush vegetation around the den may result from the foxes' own activity. Hilltops are well drained, which reduces the risk of flooding. High sites also allow for better predator detection.

DIFFERENCES BETWEEN THE SPECIES—TWO DEN ECOLOGY STRATEGIES. We have also discussed differences in the den ecology of arctic, kit and swift foxes. Swift and kit foxes depend on dens throughout the year. Apparently, they need dens for protection of both adults and pups. Also arctic foxes may stay in their territory throughout the winter, but often leave their breeding grounds in winter. They may even spend several months as scavengers far out on the pack ice, following polar bears (Chesemore 1968; Pulliainen 1965).

Swift and kit foxes utilize more dens than arctic foxes do. This is probably the result of several factors. In the permafrost areas of arctic foxes, there is often a very limited numbers of potential den sites. Further, it is easier to enlarge small dens than to dig new dens in the Arctic, due to increasing thawing depth. On the lower latitudes of swift and kit foxes, there are many other species that dig dens which can be taken over by foxes (Cutter 1958, Kilgore 1969). When larger denning predators such as red foxes or badgers are common, dens may be taken over and it might be better to have many small dens than to invest time in digging large dens. This might be the reason why the arctic fox has difficulties in coping with an expanding red fox population (Hersteinsson et al. 1989, Hersteinsson and Macdonald 1992), while swift and kit fox populations can persist or even increase despite large numbers of competitors and predators. In undisturbed tundra systems, the only terrestrial predator to seriously compete with the arctic fox for dens is the wolf. The weight ratio between arctic foxes and wolves is around 1:10 (Ginsberg and Macdonald 1990). Their differences in home range sizes and den use are probably so large that competition for dens has been of little importance in shaping arctic fox den ecology. Swift and kit foxes, on the other hand, have evolved in areas with several den dependent competitors, but also with den providers, such as badgers and prairie dogs. Swift and kit foxes should therefore be less vulnerable than arctic foxes to increasing den competition.

Den switching is common among canids, and numerous related factors have been considered as explanations. Ryon (1986) reviewed 5 potential causes: 1) disturbance; 2) flea infestation; 3) leaking dens; 4) shifting towards food sources; and 5) predator avoidance. Although foxes will move in response to some disturbances, swift foxes in Canada utilized the same dens immediately before and after intensive pipeline construction (Moehrenschlager 2000). Swift and kit foxes have heavy flea and tick parasite loads (A. Moehrenschlager, personal observation) compared to arctic foxes, where fleas and ticks are normally not found during handling (Aguirre et al. 2000; M. Tannerfeldt and A. Angerbjörn, personal observation). The frequent, short-distance den changes of swift and kit foxes may thus be the result of parasite avoidance. Changes in food resources and leaking dens can cause den switching (Pruss 1994), but cannot account for the majority of movements. While den shifting in response to food shortages can explain long-distance movements, most consecutively used swift fox dens are close together (Pruss 1994, Moehrenschlager 2000) and short transfers would not provide substantial hunting advantages. In Canada, coyotes or signs from them were seen at 75 inspections of swift fox dens, so den switching may be a response to high predation pressure. However, predator presence does not necessitate den switching and most Canadian swift foxes did not abandon dens after coyote visits. For arctic foxes, den switching and splitting of litters is often related to predation events or human disturbance (Eberhardt et al. 1983, Prestrud 1992b).

We have thus found what could be seen as 2 different den ecology strategies in these fox species. In most areas, the arctic fox has large dens, few satellite dens and seldom move between dens during the breeding season. Swift and kit foxes, on the other hand, have small dens, use many satellite dens and readily move between them. This difference between den ecology strategies is connected to differences in a number of life history traits. The strategies also involve territoriality, and are related to differences in a number of ecological parameters such as predation rates, availability of dens, food resources and litter sizes (Table 3). To cope with fluctuating food resources, arctic foxes

Table 3. Life history traits and ecological parameters related to denning for 3 fox species. The table depicts the most common situation for each species; for the arctic fox, populations feeding in coastal areas are excluded. Data from Table 1 and references therein.

Trait or parameter	Arctic fox	Kit fox	Swift fox
Den size	Large	Small	Small
Satellite dens	Few	Many	Many
Den changes in breeding season	Rare	Very common	Very common
Litter size	Very large	Small	Small
Territory stability (between year)	Strong	Weak	Weak
Territory size	Large	Small	Small
Availability of dens	Low	High	High
Food resources	Fluctuating	Relatively stable	Relatively stable
Predation rate on young	Low-medium	High	High
Main mortality cause for adults	Starvation	Predation	Predation

have developed the ability to produce very large litters (Tannerfeldt and Angerbjörn 1998). This is facilitated by the access to large and relatively safe dens. In contrast, swift and kit foxes have smaller litters than expected by allometric relationships. This is perhaps a necessity when changing dens as often as every 3 days (Ralls et al. 1990).

In conclusion, denning swift and kit foxes often move between a number of small dens, as a result of higher predation risk and stronger competition for dens. Parasite avoidance might also play a role in short-range moves. These foxes have a good availability of already-dug dens. Arctic foxes, in the other hand, live in a less diverse ecosystem with fewer dens, predators and competitors. They have large litters in large dens and mostly stay in 1 den during the breeding season, unless disturbed by humans or predators.

Management Implications

Den ecology is an important aspect of the management of all 3 fox species. Dens are crucial as shelter against harsh weather for the young and for protection against predators for both young and adult foxes. Habitat protection for these foxes should therefore focus on important den sites. For arctic foxes, we have shown that important dens can be identified quite readily. Although there are indications of preferred den sites also for swift foxes (Pruss 1999), both kit and swift foxes move frequently between dens, so their entire home range areas should ideally be protected.

Identification and classification of den sites is a means of making surveys and population estimates more effective, especially for the arctic fox. An analysis of den sites is also an important preparatory task for re-introduction programs, as den availability is a crucial aspect of the suitability of an area for foxes. If necessary, it may also be possible to construct or improve den sites. As pointed out by Pruss (1999), information on preferred den sites could further be used to improve conditions for captive foxes.

There is a large number of studies of fox dens in the literature, but many aspects of foxes' use of dens warrant further investigation. For example, how do foxes utilize their home range and its dens, and how does this change with predation pressure and food availability? Does the minimum density of dens necessary for breeding change with predation pressure, and is this related to the quality of available dens? Swift foxes den successfully in some agricultural areas but not in others; does this depend on the availability of dens? Finally, it is worth considering whether human-made dens in some areas could be a tool to increase survival of endangered populations of arctic, swift or kit foxes.

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