

**Swift Fox (*Vulpes velox*):
A Technical Conservation Assessment**

**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

January 21, 2005

Robert M. Stephens and Stanley H. Anderson, Ph.D.
Wyoming Cooperative Fish and Wildlife Research Unit
University of Wyoming
Laramie, Wyoming

Stephens, R.M. and S.H. Anderson. (2005, January 21). Swift Fox (*Vulpes velox*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: <http://www.fs.fed.us/r2/projects/scp/assessments/swiftfox.pdf> [date of access].

AUTHORS' BIOGRAPHIES

Robert M. Stephens is the Grassland Ecologist with the Wyoming Game and Fish Department in Laramie, Wyoming. He received a Master of Science degree in Zoology and Physiology from the University of Wyoming in 2001 for investigation of the winter ecology of northern goshawks (*Accipiter gentilis*). He received a B.S. in Wildlife Biology from Colorado State University in 1993. Other raptor studies with which he has participated include the investigation of foraging habitat used by goshawks during the breeding season and the investigation of lead-toxicity in raptors in relation to scavenging shot prairie dogs. Additionally, he has studied elk and mule deer, and he has worked internationally in New Zealand with several endangered bird species.

Stanley H. Anderson is the leader of the Wyoming Cooperative Fish and Wildlife Research Unit. He received a Ph.D. from Oregon State University in 1970 and a B.S. from the University of Redlands in 1961. During his career at Kenyon College, Oak Ridge National Laboratories, Patuxent Research Center, and the Wyoming Cooperative Fish and Wildlife Research Unit, he has worked extensively on wildlife habitat, publishing as author or co-author more than 230 scientific articles. Stan has done extensive work on raptors throughout the United States, South America, and Australia. He has worked with nearly 100 graduate students at the Co-op and presented courses in ornithology and wildlife management. Throughout his career he has served on many national and international wildlife committees that focused on the protection of declining species.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE SWIFT FOX

The swift fox (*Vulpes velox*) was classified in 1995 as a candidate for listing under the Endangered Species Act (Federal Register 1995). However, its 12-month finding, the U.S. Fish and Wildlife Service concluded that swift fox populations are likely to remain viable into the foreseeable future based on current threats, and removed it from the Candidate list (Federal Register 2001). Data appear to indicate that populations in the core of the current occupied range of the swift fox (eastern Colorado, eastern New Mexico, far western Kansas, and southeastern Wyoming) are viable and stable at this time. However, populations have contracted substantially from large areas of the Great Plains where native grasslands have been heavily converted to agricultural uses, including much of Nebraska, the Dakotas, and Montana. Only small populations remain in southwestern South Dakota and western Nebraska.

Swift fox populations plummeted during the last half of the 18th century and the early 19th century as a consequence of widespread and indiscriminate poisoning that targeted wolves (*Canis lupus*). Trapping and shooting likely also took a heavy toll on fox. With the eradication of wolves, the imposition of regulatory control over the use of poisons, and state regulation of trapping, these catastrophic impacts to swift fox populations were substantially reduced. Today, secondary poisoning of rodents (especially prairie dogs) may have localized effects, but it probably is not a major influence on rangewide viability. More important today are the continued, albeit slower, loss and fragmentation of native prairie habitat, and increased interspecific competition with coyotes (*C. latrans*).

Interspecific competition with coyotes is thought to be one of the greatest threats currently affecting swift fox. This threat is the result of changes in the canid community over the past century due to human eradication of wolves and alteration of native habitats in a way that favors canid generalists. Gray wolves, unlike coyotes, apparently paid little attention to the smaller swift fox, and wolves likely kept the number of coyotes significantly depressed (Johnson and Sargeant 1977). Studies have documented coyotes as the main cause of mortality for the swift fox (Sovada et al. 1998, Olson and Lindzey 2002).

Habitat loss and fragmentation, due to agriculture and urbanization, also have played a major role in the reduction in swift fox range and are thought to threaten swift fox viability in some parts of its range today. The discovery of swift fox using landscapes fragmented by agriculture in Kansas has ignited debate over habitat flexibility in the species. However, data from these altered landscapes are short-term and may not reflect long-term downward trends. Clearly, the pattern of range retraction demonstrates limits in species adaptability to fragmented landscapes. The intensity and type of agriculture and the level of fragmentation in these altered landscapes are factors that probably influence habitat suitability for swift foxes.

Given swift fox vulnerability to habitat fragmentation and competition from other canid species, conservation will probably need to focus on minimizing these adverse influences. The perpetuation or restoration of expansive areas of shortgrass, mixed-grass, and shrub-grass prairies across the species' range is likely a critical factor in the maintenance of viable, well-distributed populations of swift fox. Given that agriculture is a permanent influence on the Great Plains, agricultural practices that take swift foxes into consideration may be crucial in maintaining habitat suitability for the species. Swift fox may be able to persist in landscapes with limited agriculture that maintain characteristics compatible with swift fox occupancy. Such characteristics will likely include dryland crop production, low vegetation height (such as winter wheat) with considerable open ground, and cultivation and husbandry practices that accommodate swift fox denning, while not conducive to the expansion of red fox (*Vulpes vulpes*) occupancy. Those agricultural methods and practices that are consistent with the natural landscape rather than those that drastically alter it (e.g., irrigated cultivation) will most likely accommodate the continued occupancy of swift fox.

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EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). Swift foxes are the focus of an assessment because they were listed as a sensitive species in Region 2 in March 1993. The USFS defines a sensitive species as a plant or animal species whose population viability is identified as a concern by a regional forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (www.fs.fed.us/im/directives/field/r2/fsm/2600/2670_2671.doc). A sensitive species may require special management, so knowledge of its biology and ecology is critical. This assessment addresses the biology, ecology, conservation, and management of swift foxes throughout their range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation status, conservation needs, and management considerations of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop prescriptive management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it cites management recommendations proposed elsewhere, and when these have been implemented, the assessment examines their success.

Scope

The swift fox conservation assessment examines the biology, ecology, conservation, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although some of the literature on the species may originate from field investigations outside the region, this document places that literature in the ecological and social contexts of the central

and southern Rockies. Similarly, this assessment is concerned with the biology and ecology of swift foxes in the context of the current environment. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current context.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on swift foxes are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when refereed information was unavailable elsewhere, but these were regarded with greater skepticism. Unpublished data (e.g., Natural Heritage Program records and Swift Fox Conservation Team reports) were important in estimating the geographic distribution of the swift fox. These data required special attention because of the diversity of persons and methods used in collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate. More specifically, when dealing with uncertainty in this assessment, we always noted when inferences were made, and we used phrases such as ‘is likely to’, ‘is probable that’, and ‘might be’ when the strength of evidence for particular ideas was not certain.

Application and Interpretation Limits of this Assessment

Most of the data presented in this assessment are from site-specific studies. An important limitation of this assessment is its applicability to areas beyond where

the data were collected. While some characteristics remain similar throughout the range of the swift fox, community assemblages become increasingly different as the distance between sites increases. Therefore, the ability to predict the response of swift foxes to various factors becomes increasingly difficult and uncertain as the distance between inference communities increases. Thus, the information should be interpreted generally and applied generally where conservation plans are being developed by inference.

Publication of Assessment on the World Wide Web

To facilitate their use, species conservation assessments are being published on the USFS Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. Peer review was designed to improve the quality of communication and to

increase the rigor of the assessment. Peer review of this assessment was administered by the Society for Conservation Biology, using two recognized experts in this or closely related taxa.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The swift fox was proposed for listing under the Endangered Species Act in 1992. In 1995, the U. S. Fish and Wildlife Service (USFWS) determined that its listing was “warranted but precluded by listing actions of higher priority” (Federal Register 1995). However, studies revealed that, “the swift fox is more abundant and widely distributed than previously thought, and the species is more flexible in its habitat requirements than originally believed” (Federal Register 2001). Therefore, in 2001, the USFWS reported, “We find that the petitioned action is not warranted and are removing the swift fox from the candidate list” (Federal Register 2001). As a result, the primary regulatory and management authority rests with the states. The status of swift foxes in the states of USFS Region 2 ranges from endangered to harvested furbearer (**Table 1**). They are classified as a sensitive species by USFS Region 2 (http://roadless.fs.fed.us/documents/feis/data/sheets/summspd/tes_supp/tes_supp.shtml). The Nature

Table 1. Status of the swift fox in the USDA Forest Service Rocky Mountain Region states (NatureServe Explorer 2002, <http://www.state.sd.us/gfp/Diversity/TES.htm#KEY>, <http://www.kdwp.state.ks.us/hunting/hunting.html>, <http://www.ngpc.state.ne.us/wildlife/ngthreat.html>, <http://wildlife.state.co.us/T&E/list.asp>, <http://uwadmnweb.uwyo.edu/wyndd/>).

State	The Nature Conservancy Rank^a	Classification by State Wildlife Management Agencies
Colorado	S3	Special Concern (not a statutory category)
Kansas	S3	Furbearer – Legally hunted and trapped
Nebraska	S2	Endangered
South Dakota	S1	Threatened
Wyoming	S2S3	Species of Special Concern 3 ^b

^aS – State rank.

1 — Critically imperiled in because of extreme rarity (5 or fewer occurrences or less than 1000 individuals) or because of extreme vulnerability to extinction due to some natural or man-made factor.

2 — Imperiled because of rarity (6 to 20 occurrences or less than 3000 individuals) or because of vulnerability to extinction due to some natural or man-made factor.

3 — Either rare or local throughout its range or found locally in a restricted range (usually known from 21 to 100 occurrences or less than 10,000 individuals).

^bSpecies of Special Concern 3 — Species in which (1) habitat is not restricted, but populations are greatly restricted or declining (extirpation appears possible); or (2) habitat is restricted or vulnerable (but no recent or significant loss has occurred) and populations are declining or restricted in numbers or distribution (but extirpation is not imminent); or (3) significant habitat loss is on-going but the species is widely distributed and population trends are thought to be stable.

Conservancy classifies the swift fox as N3 (vulnerable to extirpation) in the United States and N1N2 (critically imperiled/imperiled) in Canada (NatureServe 2002). Swift fox were officially designated as extirpated from the Canadian Prairies in 1978 (Committee on the Status of Endangered Wildlife in Canada 1978 *in* Pruss 1999).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The primary management authority of swift foxes within Region 2 belongs to each state's wildlife management agency. In Colorado, the swift fox is classified as a species of "State Special Concern", which is not a statutory category. The Colorado Trappers Association petitioned the Colorado Division of Wildlife (CDOW) in 2001 to reopen the swift fox season, which closed in 1991 (Pusateri 2002). While the CDOW commented that the take of up to 500 swift foxes would have little or no effect on overall populations, they decided not to reopen the season due to the amount of public outcry that would likely follow (Pusateri 2002). In Wyoming, it is classified as a "Native Species of Special Concern 3". This is a species in which (1) habitat is not restricted, but populations are greatly restricted or declining (extirpation appears possible); or (2) habitat is restricted or vulnerable (but no recent or significant loss has occurred), and populations are declining or restricted in numbers or distribution (but extirpation is not imminent); or (3) significant habitat loss is on-going but the species is widely distributed, and population trends are thought to be stable (NatureServe 2002). In South Dakota, it has been classified as a state threatened species since 1978 (Kruse et al. 1995). Nebraska classified the swift fox as a state endangered species in 1972 (Andelt 1995). In Kansas, it is classified as a furbearer that can be legally hunted and trapped. Any swift fox taken in Kansas must be presented to the Kansas Department of Wildlife and Parks for tagging within seven days of the close of the season. Between the 1994-95 and 2001-02 furbearer seasons, 181 swift fox were taken by 38 fur harvesters in Kansas (Peek 2002a).

The Swift Fox Conservation Team (SFCT) developed the most broad-scale conservation strategy for the swift fox. The SFCT was established in 1994 after the USFWS was petitioned to list the swift fox in 1992 under the Endangered Species Act. The goal of the SFCT was to obtain information on swift fox populations throughout their range in an attempt to head off a federally mandated recovery effort. Monitoring efforts included a distribution survey in Colorado

(Finley 1999, Pusateri 2002), annual monitoring initiated in Wyoming in 2001 (Grenier and Van Fleet 2002), record-keeping of tagged pelts (Peek 2002a) and several years of track surveys in Kansas (Roy 2000), surveys in portions of South Dakota (Peterson 2000, Stokely 2002), and the development and initiation of suitable survey techniques in western Nebraska in 2001 (Bischof 2002). While these efforts are not yet able to establish a trend, preliminary data indicate that swift foxes are more abundant and widespread than originally thought. As a result of the efforts and data gathered by the SFCT, the USFWS removed the swift fox from the Candidate list (Federal Register 2001).

While the above-mentioned strategies contributed to removing the swift fox from the Candidate List, few fundamental changes actually occurred on the ground to enhance conservation of swift fox populations and their habitat until recently. Private landowners own most of the grassland habitats where swift fox occur. Programs such as the Landowner Incentive Program and Private Stewardship Grants Program, which are administered by the USFWS, provide funds for activities directed at the conservation of habitats occupied by endangered, threatened, petitioned, or declining species on private lands. These funds have been used to obtain conservation easements on ranches in the short-grass prairie of eastern Colorado that are threatened with the pressures of urban sprawl. In Nebraska, these funds have been used for restoration activities in grassland habitats such as the removal of exotic species, grazing deferrals, and improved fencing systems.

Conservation strategies in South Dakota include the reintroduction of swift foxes into parts of their historic range. In 2002, swift foxes were reintroduced to the Bad River Ranch, located near Ft. Pierre, South Dakota. Managers at this site are also attempting to control coyote populations to aid swift fox recovery. Other reintroductions were planned in Buffalo Gap National Grassland and Badlands National Park of South Dakota in late 2003 or early 2004.

Biology and Ecology

Systematics and description

Swift foxes are arid-land foxes that stand approximately 30 cm in height at the shoulder, are 60 to 80 cm in length including the tail, and weight between 1.4 and 2.7 kg (Whitaker 1988). They are buff-yellowish above and whitish below; they have black patches on each side of the muzzle and a black-tipped tail (Jones et al. 1985, Whitaker 1988). Males are about 8 percent

heavier than females (Egoscue 1979). Merriam (1902) originally described two subspecies of the swift fox: the northern swift fox (*Vulpes velox hebes*) and the southern swift fox (*V. v. velox*). A subspecies distinction is no longer recognized (Stromberg and Boyce 1986).

Swift foxes can be distinguished from other North American foxes, except the kit fox (*Vulpes macrotis*), by their small size and black-tipped tail (Egoscue 1979). Based on morphometric and genic data, Dragoo et al. (1990) suggested that the swift fox and the kit fox pertain to one species that should be recognized as subspecies, *V. v. velox* and *V. v. macrotis*. Nonetheless, they are currently recognized as distinct species (Thornton and Creel 1975, Egoscue 1979, Jones et al. 1997). Among differences used by Thornton and Creel (1975) to separate adult kit fox from swift fox were (1) longer ears (90.7 to 85.1 mm) with ear bases close to the midline of the skull of kit fox, as opposed to shorter (58.3 to 67.5 mm) and more widely spaced ears of swift fox; (2) head of the kit fox comparatively broader between the eyes and with a narrower snout, compared with the “more rounded and dog-like head” of the swift fox; and (3) length of tail (expressed as percentage of length of body) significantly longer for kit fox (average 62 percent) than the swift fox (average 52 percent). There was no overlap in ear measurements and almost no overlap in the tail to body ratio. Additionally, mitochondrial DNA analysis indicates that swift foxes and kit foxes are two separate species (Mercure et al. 1993).

Distribution and abundance

The swift fox is native to the grassland prairies of the Great Plains region of North America (Kahn et al. 1997). The original range of this species was influenced primarily by the extent of the shortgrass and mid-grass prairie ecosystems (Kahn et al. 1997). Prior to European settlement of the Great Plains, their range reached its northern limits in the prairie provinces of central Canada including Alberta, Saskatchewan, Manitoba, and possibly extreme southeastern British Columbia (Egoscue 1979). In the United States, they occurred east of the Rocky Mountains from Montana to extreme western Minnesota and south to west-central Texas and southeastern New Mexico (Egoscue 1979).

A dramatic range reduction occurred in the United States and Canada in the early 1800s and continued until the mid-1900s as a result of human-related activities (especially predator poisoning campaigns, trapping and shooting, and agricultural development) associated with settlement and development of the prairies (Kahn et al.

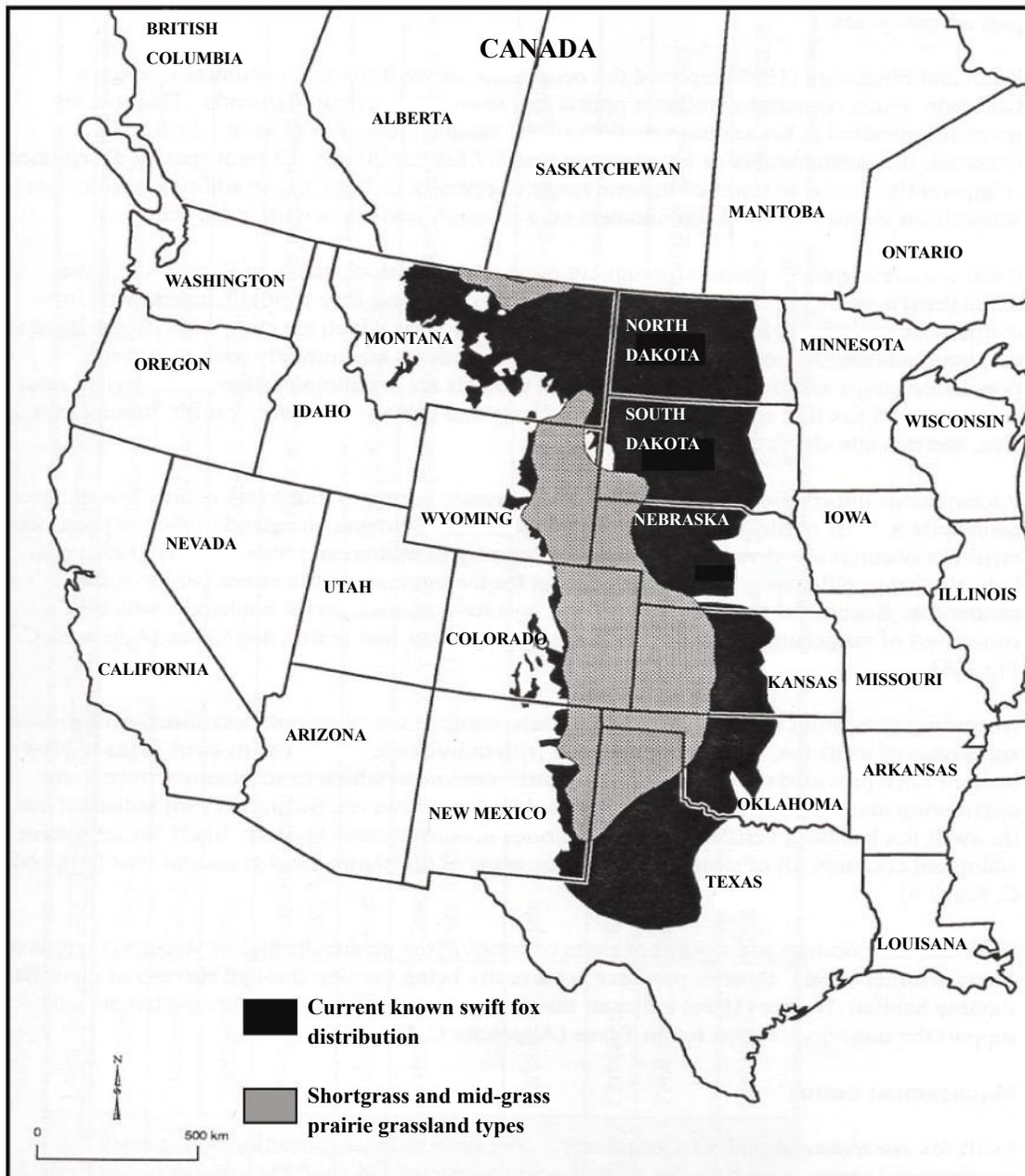
1997). Swift fox populations in the United States began to recover during the 1950s and 1960s (Egoscue 1979). Specimens were found in Kansas in the mid-1950s, where the species was thought to be extinct; in South Dakota after a 60 year absence; in Nebraska, where the first specimens since 1900 were collected in the 1950s; and in Wyoming, with an interval of over 50 years between reported specimens (Egoscue 1979).

The distribution of swift foxes in the United States is relatively widespread although they remain limited to only a portion of their original range (Kahn et al. 1997). Current known swift fox distribution is about 25 percent of its historic range from the literature or approximately 40 percent of the suggested historic range based on vegetation classification mapping of the shortgrass and mid-grass prairie grassland types in the central United States (**Figure 1**). Distributions and associated densities appear highly variable among the occupied states (Kahn et al. 1997).

The present known range is constricted and somewhat disjunct, with an identified population core present in the states of southeastern Wyoming (**Figure 2**), eastern Colorado (**Figure 3**), and western Kansas (**Figure 4**) (Kahn et al. 1997). Swift foxes are currently present throughout their historic range in New Mexico (Harrison and Schmitt 1997) and Oklahoma (Hoagland 1999). Their distributions are restricted in South Dakota (**Figure 5**) and Montana (Kahn et al. 1997), and in Nebraska (**Figure 6**) and Texas they are still undetermined. Swift foxes are apparently absent in North Dakota (Gerads 2000).

Population trend

Settlement of the prairies led to declines in swift fox numbers, with the species being rare throughout much of its range by 1900 (Hillman and Sharps 1978). Many factors contributed to the decline, including inadvertent poisoning aimed at gray wolves, intense trapping, competition with coyotes and red foxes, habitat changes due to agriculture, and rodent control programs (Scott-Brown et al. 1987). Sovada et al. (1998) suggested that the biggest threat currently affecting swift foxes is the change in the canid community within their historic range. Swift foxes apparently thrived in the region when the canid community was dominated by gray wolves (Johnson and Sargeant 1977). Gray wolves killed coyotes, which are the primary competitor of the swift fox; wolves apparently paid little attention to the smaller fox. Additionally, chances of swift fox encounters with wolves probably were less than with coyotes because of the larger home range size and



^aThis map incorrectly depicts the range of swift foxes in Texas. Swift foxes only occur in the northernmost three counties bordering Oklahoma. Swift foxes also occur in Alberta and Saskatchewan near the Montana border.

Figure 1. Current known swift fox distribution^a in the United States (Allen et al. 1995) and classification of shortgrass and mid-grass prairie grassland types in the central United States as modified from Lauenroth (1996 in Kahn et al. 1997).

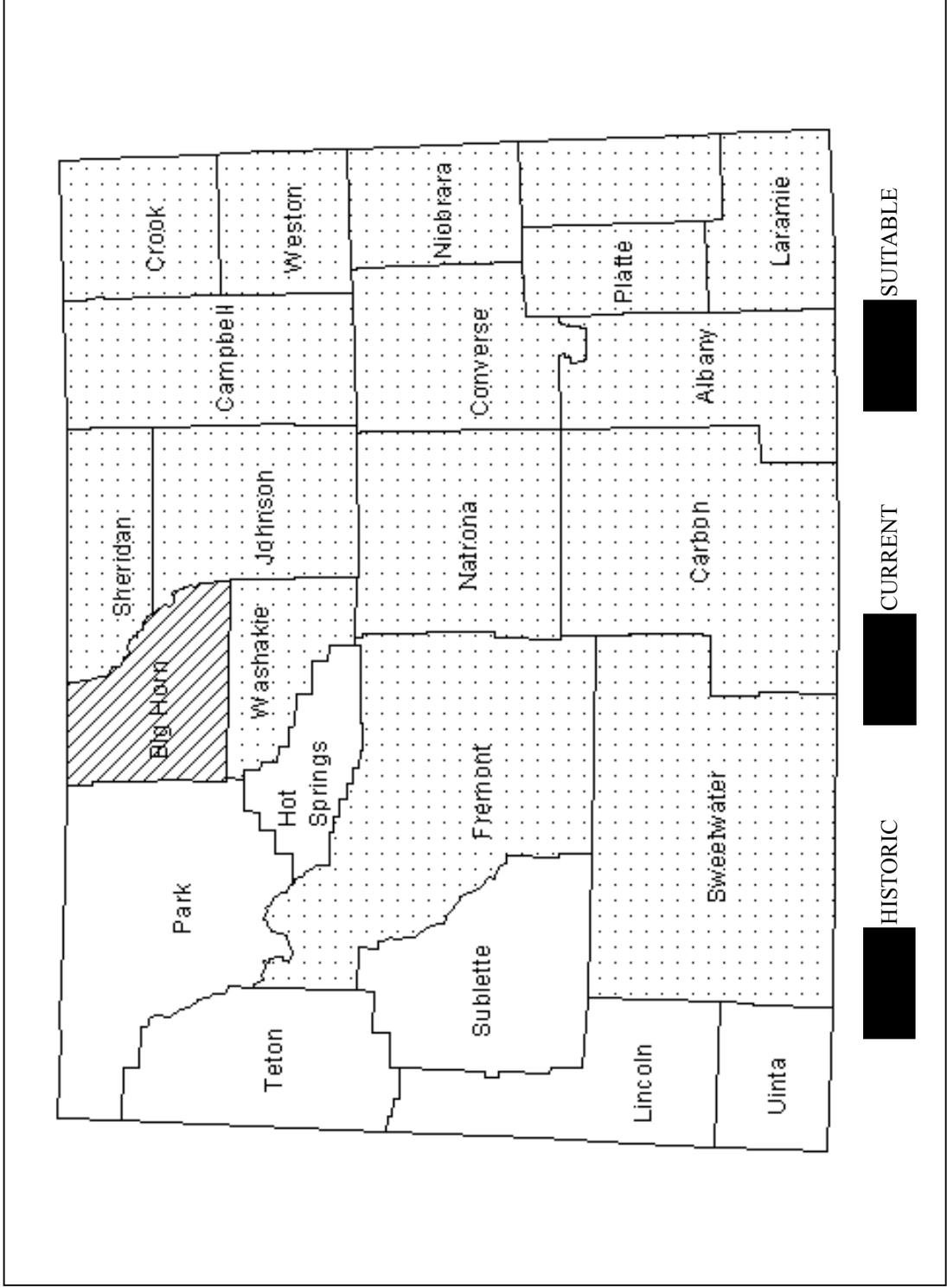


Figure 2. Historic swift fox range, current known species distribution, and potentially suitable habitat in Wyoming.

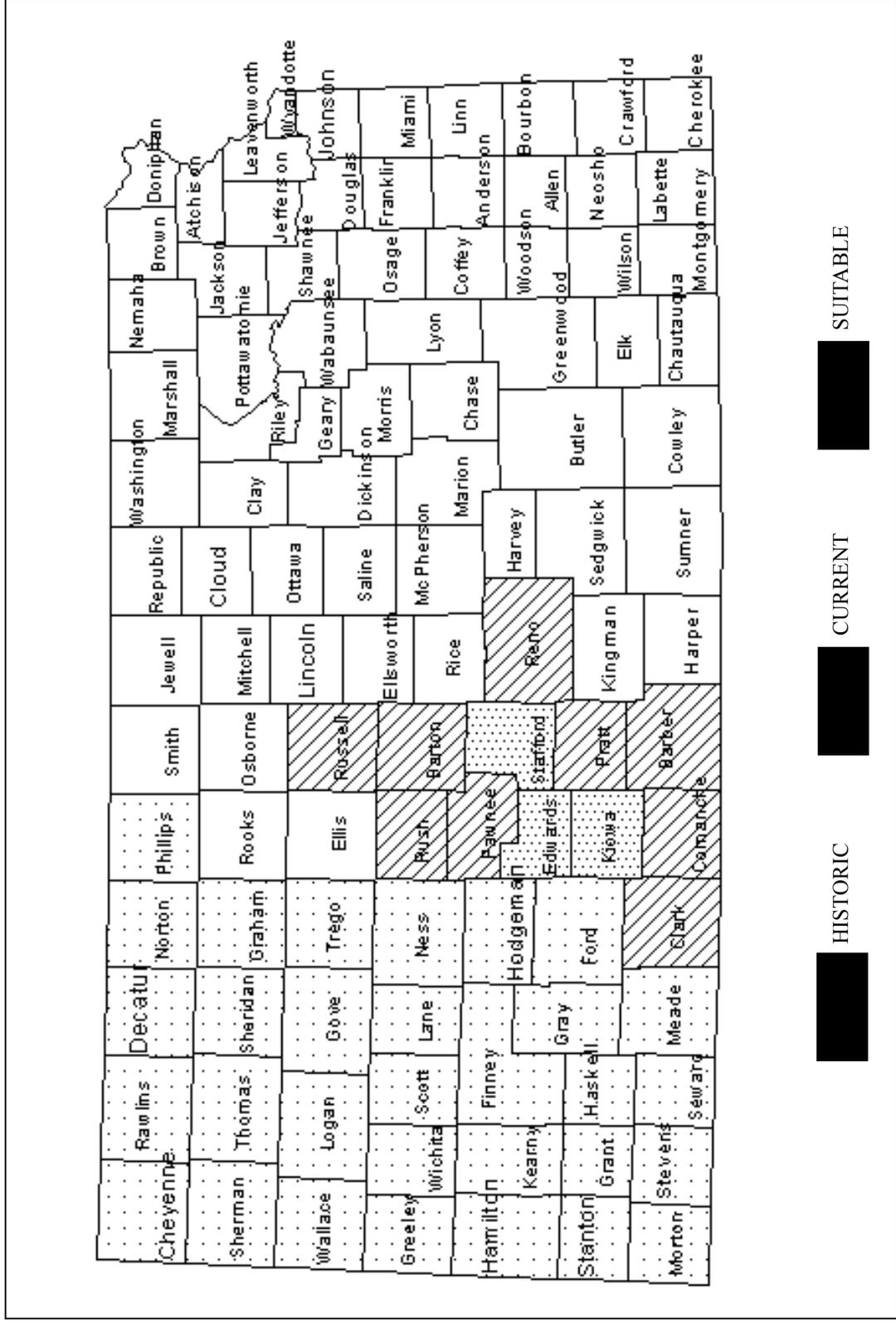


Figure 4. Historic swift fox range, current known species distribution, and potentially suitable habitat in Kansas.

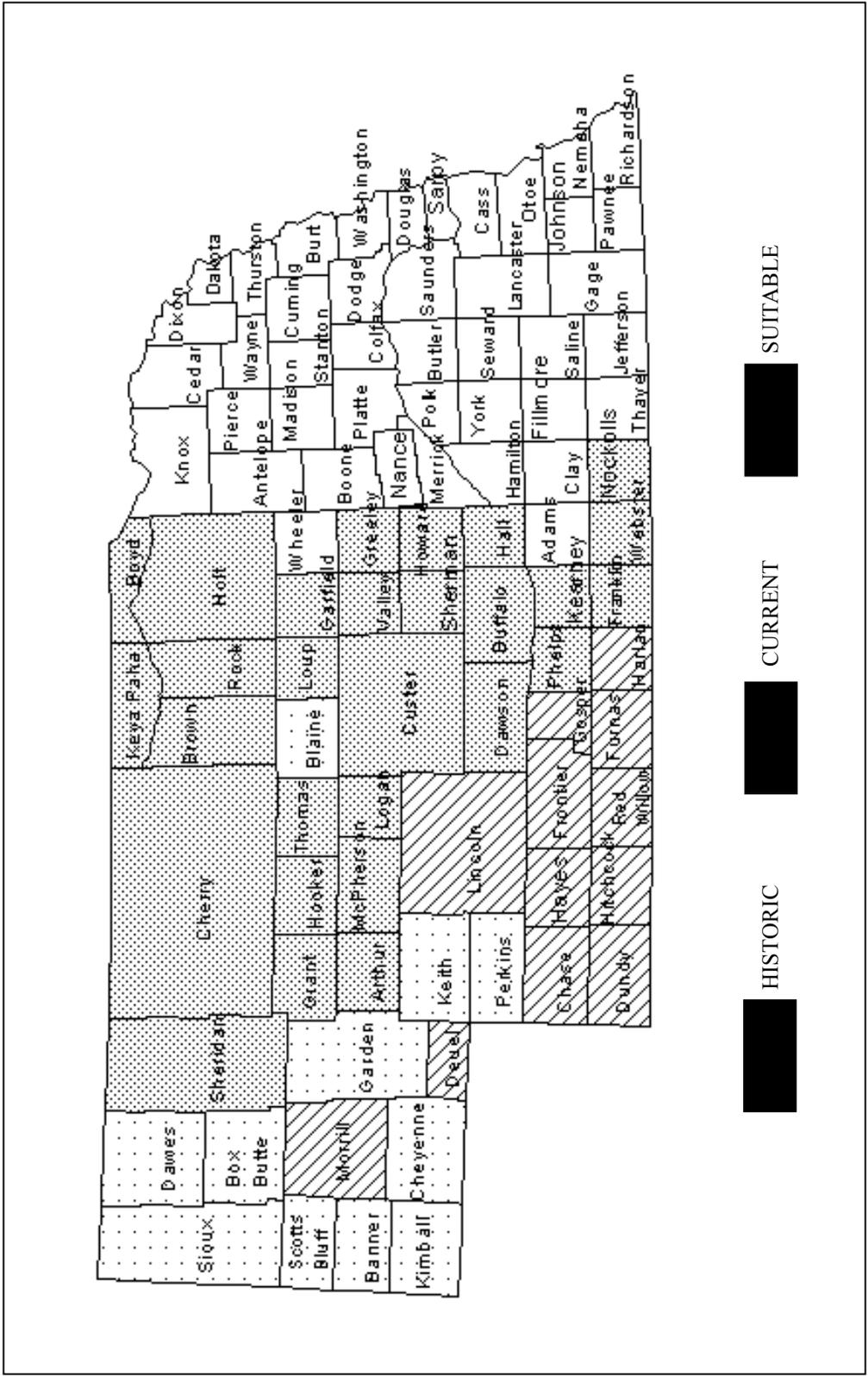


Figure 6. Historic swift fox range, current known species distribution, and potentially suitable habitat in Nebraska.

lower overall density of wolves compared to coyotes (Johnson and Sargeant 1977). More importantly, wolves likely kept the number of coyotes significantly depressed (Johnson and Sargeant 1977). There is considerable evidence that interspecific competition, often as interference competition, acts as a mechanism regulating spatial distribution and population size among canid species (Carbyn 1982, Rudzinski et al. 1982, Sargeant et al. 1987, Bailey 1992, Ralls and White 1995).

Swift fox populations in the United States began to recover during the 1950s and 1960s (Egoscue 1979). Recovery during this period is probably related to the eradication of gray wolves, resulting in the decreased use of indiscriminate poisons. Currently though, it is not possible to assess swift fox population trends in Region 2 since monitoring has only recently begun. The best indicator we presently have of the status swift fox populations in Region 2 is distribution information, which indicates that the species is present throughout much of its historical distribution in Wyoming, Kansas, and Colorado. However, the swift fox is apparently absent from much of its historical distribution in South Dakota and Nebraska.

Activity pattern and movements

Activity periods of swift foxes typically commence at sunset and cease at sunrise (Hines and Case 1991). Diurnal activity of females without pups and males usually consists of lying near den entrances (Hines and Case 1991). Females with pups may make short daytime forages in search of food, with the pups remaining at the den (Hines and Case 1991). Hines and Case (1991) reported that swift foxes in Nebraska traveled an average of 13.1 ± 0.7 km per night and 1.2 ± 0 km per hour. Resting periods during the night were few and varied in length. Swift foxes probably hunt throughout the night and rest only during the day.

Until recently, relatively little was known about the timing and pattern of swift fox dispersal. Schauster et al. (2002) reported information on the dispersal of 13 swift foxes during a two-year study in eastern Colorado. Of six adults (2 males; 4 females), five began dispersal movements during the breeding/gestation season (15 December - 14 April), whereas one adult female dispersed during the dispersal season (15 August - 14 December). Total distance moved during dispersal was 11.9 ± 8.8 km (range = 5.0 - 29.0 km), and the total number of days spent dispersing before a new area of use was established was 28.3 ± 20.8 (range = 6 - 67 days). All dispersing adults remained alive and

established new denning and foraging areas. In contrast, only three (37.5 percent) of eight dispersing juveniles (6 males; 2 females) remained alive and established new denning and foraging areas. For juvenile dispersers, the total distance moved was 12.6 ± 3.2 km (range = 8.4 - 15.9 km) while the total number of days spent dispersing was 32.1 ± 13.7 (range = 15 - 50 days). The furthest dispersal distance we found in the literature of a wild-born swift fox was a yearling female that was found dead 67 km from its capture site (Olsen 2000).

Covell (1992) studied the dispersal of swift fox pups at Pinon Canyon Maneuver Site in Colorado. Most pup dispersal (79 percent) occurred in September and October, with October accounting for more than half of all dispersal events. Mean dispersal distances for male and female swift foxes were 9.4 ± 1.7 km and 2.1 ± 0.2 km, respectively. Three of nine females (dispersal = 4.4 ± 0.5 km) and three of six males (dispersal = 17.1 ± 2.8 km) were considered to have dispersed from parental home ranges (≥ 2.4 km). The six males that remained in their parental home ranges were significantly farther from the natal den than were the remaining six females (males = 1.7 ± 0.1 km, females = 0.9 ± 0.1 km; $t = 3.414$, $P = 0.01$).

The only other dispersal information we found was on the dispersal distance of reintroduced swift foxes. The mean dispersal distance of swift foxes reintroduced into the Canadian prairie was 12.8 km (Carbyn et al. 1994). Dispersal of captive-raised swift foxes reintroduced into South Dakota ranged from 14 to 203 km (Sharps 1984).

Habitat

Swift foxes occur in the Great Plains in a variety of habitats including shortgrass and mid-grass prairies, plowed fields and fencerows, and sagebrush (Egoscue 1979, Jones et al. 1985, Uresk and Sharps 1986, Sovada et al. 1998, Olson and Lindzey 2002). They select habitat with low-growing vegetation and relatively flat terrain, friable soils and high den availability, and areas near roads. Low-growing vegetation and flat terrain allow swift foxes to scan large areas for potential predators such as coyotes, their main cause of mortality (Sovada et al. 1998, Olson and Lindzey 2002). Swift foxes are the most burrow-dependent canid in North America, (Jackson and Choate 2000), using them for predator avoidance and pup rearing (Herrero et al. 1986). The importance of den sites for predator avoidance has been documented in studies (Olsen 2000) that observed higher probabilities of swift fox mortality on the edge or outside of its territory (a defended area).

This might indicate that foxes are more susceptible to predation in less familiar areas, possibly because they do not know the location of dens that could provide refuge (Sovada et al. 1998, Kitchen 1999, Olson and Lindzey 2002). Friable soils are important because den site availability is higher in areas with this type of soil due to easier construction (Kilgore 1969, Jackson and Choate 2000). Several studies have also reported that swift foxes select habitat adjacent to roads (Hillman and Sharps 1978, Hines and Case 1991, Pruss 1999, Olsen 2000). Habitat selection for areas adjacent to roads might be because (1) coyotes avoid areas with human activity, limiting competition pressures on swift foxes in roadside habitats, (2) roads are convenient travel corridors, and (3) vehicle-killed carrion is available as a food source.

Shortgrass prairie

Shortgrass prairie is the common habitat type used by swift foxes. Vegetation is typically dominated by buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), needle and thread (*Stipa comata*), sagebrush (*Artemisia* spp.), snakeweed (*Gutierrezia* spp.) and saltbush (*Atriplex canescens*). A typical description of swift fox habitat in the shortgrass prairie from southwestern South Dakota is, "The landscape was a broad flood plain with gently sloping to undulating upland prairie. The dominant vegetation consists of buffalograss, needleleaf sedge, blue grama, and western wheatgrass, and the soil types are primarily clayey to sandy-clay-loams" (Uresk and Sharps 1986). Habitat at another South Dakota site was described as, "gently undulating hills with the grasses mentioned above present, numerous livestock watering ponds, and the soil type consisting primarily of clay to clay-loams" (Uresk and Sharps 1986).

Sagebrush steppe/shortgrass prairie

Swift foxes in the Shirley Basin of southeastern Wyoming occupy areas that are not the typical swift fox habitat (Hoagland 1997). They occur in a transition zone between shortgrass prairie and sagebrush-steppe plant communities (Knight 1994). Olson (2000) described swift fox habitat use in this area. At the second order of selection (Johnson 1980), swift foxes selected against creek drainages. At the third order of selection (Johnson 1980), swift foxes generally used the vegetation types available in proportion to their abundance regardless of prey abundance or security rankings. However, foxes used only sagebrush, sagebrush/grassland, and grassland vegetation types on flat (<3 percent slope)

topography. They did not den in greasewood (*Sarcobatus vermiculatus*), playa lake, bare/rocky terrain, riparian, and saltbush vegetation types. Pup rearing was the only period in which habitat selection was detected. Foxes used sagebrush vegetation less than expected in the 1998 pup-rearing period and playa lakes less in the 1999 pup-rearing period. It is somewhat surprising that swift foxes used shrub habitats in proportion to their availability throughout most of the year as these shrubs limit visibility. However, it should be noted that mean sagebrush height was lower than swift fox eye level.

Swift foxes typically use relatively open shortgrass prairie habitats with high visibility (Kilgore 1969), which is likely related to predator avoidance. Swift foxes killed by predators were found in sagebrush vegetation more than expected; this suggests that the risk of death was greater in sagebrush than other vegetation types. This appears to be balanced out by higher recruitment in home ranges with a larger proportion of sagebrush as these foxes were observed with bigger litters. Olson (2000) concluded that low-growing (<30 cm), low-density (16 percent cover) sagebrush vegetation should be considered suitable swift fox habitat.

Selection for soil types was more consistent than selection for vegetation types. Foxes selected loamy soils (selection ratio 1.21; $P < 0.001$) at den sites, and they generally avoided impervious clay (selection ratio 0.27; $P \leq 0.001$), saline loamy (selection ratio 0.32; $P \leq 0.001$), and sandy (selection ratio 0.47; $P \leq 0.003$) soils. Loamy soils contain moderate amounts of sand, silt, and clay that allow for easier burrowing than clayey soils yet provide adequate stability after construction (as opposed to sandy soils). Soil type can be a better indicator of suitability of an area for swift fox dens than vegetation type because 81 percent of dens were found in loamy soil at one site.

Foxes also were found in closer proximity to water sources during the pup-rearing periods, indicating a need for free water. Nearly all water sources on one study area were man-made (windmills, stock ponds). The availability of water at man-made sources may be an important factor for persistence of swift fox populations during dry years (Olson 2000).

Agricultural landscapes

Swift foxes are also known to inhabit some landscapes that have been partially converted for agriculture. Sovada et al. (1998) classified habitat at two sites in western Kansas as cropland and rangeland. The

cropland area was relatively flat and highly fragmented into cropland fields (approximately 76 percent of the area in cultivated fields), primarily a dryland winter wheat-fallow rotation, but with corn, milo, sunflowers, and sorghum. The rangeland area was one of rolling hills and largely contiguous native grassland, and it was moderately to heavily grazed. Dens and den sites found in cropland and rangeland in Kansas were nearly identical in most respects (Jackson and Choate 2000). Based on observations from several studies, it has been suggested that swift fox are able to persist in some agricultural areas (M. Sovada personal communication). The characteristics that most likely limit the persistence of swift fox populations in areas converted for dryland agriculture are vegetation height, competition with coyote and red fox, and direct human causes such as trapping and poisoning. Irrigated agriculture may eliminate suitable denning sites.

Den sites

Swift foxes may modify and use the burrows of other mammals such as prairie dogs, badgers (*Taxidea taxus*), and ground squirrels, or they may dig their own (Kilgore 1969). Dens are used year round, but swift foxes often shift from one den to another, possibly due to external parasite infestations (Kilgore 1969, Hillman and Sharps 1978). Swift foxes usually den in areas of scant vegetation and low slopes that provide a clear view of the surrounding area (Kilgore 1969). Uresk and Sharps (1986) reported that swift fox dens found in South Dakota were generally located on or near the tops of hills on the undulating prairie, in pastures receiving moderate to heavy cattle use. Soil types are variable, ranging from loam, clay-loam, and sandy-clay-loam to mostly clay (Uresk and Sharps 1986, Hines and Case 1991). However, most dens are found in soils that are loamy in nature. Positioning of dens on hills is thought to benefit survival by increasing the amount of time available to swift foxes to detect predators and to retreat into their underground refuges (Pruss 1999).

Hillman and Sharps (1978) reported that the dimensions of den openings average 19 cm wide by 22 cm high. The number of den openings is variable, natal dens having more openings on average than non-natal dens (Kilgore 1969, Hillman and Sharps 1978, Hines 1980). Most den openings have been reported to be within 3.5 m of each other, with the distance between openings increasing as the number of openings increases (Jackson and Choate 2000). Foxes may have as many as six different dens (Pechacek et al. 2000). In southeastern Wyoming, 75.1 ± 27.2 percent ($n = 24$) of dens belonging to an individual fox were located within

its core area (50 percent utilization distribution) and paired foxes ($n = 3$) shared most dens (males: 70.3 ± 26.3 percent, females: 81.9 ± 18.8 percent) (Pechacek et al. 2000).

Pruss (1999) compared the characteristics of occupied ($n = 32$) and unoccupied ($n = 33$) den sites in Canada. Two-sample t tests and Mann-Whitney U tests indicated that occupied sites were located on the tops of hills ($P < 0.01$), closer to roads (occupied sites = 266.8 ± 88.9 m; unoccupied sites = 418.5 ± 89.9 cm, $P < 0.01$), and in places where old grass was significantly higher than at unoccupied sites (occupied sites = 27.1 ± 1.3 cm; unoccupied sites = 22.1 ± 1.5 cm, $P < 0.05$). A stepwise discriminant function analysis identified den position on a hill as the variable that most strongly discriminated between occupied and unoccupied sites (Partial $r^2 = 0.315$, $F = 28.93$, $P < 0.0001$).

Roads

Several studies have documented the tendency of swift foxes to select habitat adjacent to roads (Hillman and Sharps 1978, Hines and Case 1991, Pruss 1999, Olsen 2000). Hines and Case (1991) suggested that proximity to roads appeared to be the predominant factor in den selection when otherwise suitable habitat was available. Dens averaged 418 ± 105 m from roads; 68 percent were within 230 m. Hillman and Sharps (1978) found all swift fox dens within 1.6 km of roads. Pruss (1999) reported that the mean distance of occupied dens ($n = 32$) from roads was 267 ± 89 m. Olsen (2000) reported that dens were located closer ($t = 4.42$, $df = 312$, $P < 0.001$) to roads ($\bar{X} = 204$ m, $SE = 11$, $n = 196$) than random points ($\bar{X} = 304$ m, $SE = 19$, $n = 196$). Hines and Case (1991) evaluated the possibility of high visibility of swift foxes near roads biasing this theory of den selection near roads and concluded that bias was unlikely as searches for foxes in remote areas proved futile. Additionally, analysis of fox movements indicated selection for areas near roads as 66 percent of telemetry locations were of foxes traveling within 1 km of roads while only 30 percent of the study area was within 1 km of roads (Hines and Case 1991).

Water

Whether swift foxes need permanent water sources near their den sites has not been established (Scott-Brown et al. 1987). Olsen (2000) reported that dens were located closer ($t = 3.30$, $df = 284$, $P = 0.001$) to water sources ($\bar{X} = 1,053$ m, $SE = 34$, $n = 196$) than random points ($\bar{X} = 1309$ m, $SE = 70$, $n = 196$). Hillman and Sharps (1978) reported that all known den sites

were within 1.6 km of water. However, even though Pruss (1999) did not detect a significant difference, burrows occupied by swift foxes were located farther from water than unoccupied burrows (occupied sites = $1,013 \pm 74$ m, $n = 32$; unoccupied sites = 870 ± 83 cm, $n = 33$; $P > 0.20$).

Food habits

Swift foxes hunt primarily at night (Miller et al. 1998). They are opportunistic feeders, eating seeds, berries, grass, insects, amphibians, reptiles, small animals, birds, and carrion (Uresk and Sharps 1986, Hines and Case 1991, Olson 2000, Zimmerman et al. *in press*). The number of food items in swift fox diets identified by individual studies ranges from 18 to 24, but it is likely to be higher (Kilgore 1969, Zumbaugh et al. 1985, Hines and Case 1991). Swift fox diets vary seasonally and geographically. Small mammals, then insects, typically make up the major proportion of foods eaten by swift fox (Cutter 1958a, Kilgore 1969, Uresk and Sharps 1986, Rongstad et al. 1989, Kitchen et al. 1999). Birds and plant material are less commonly consumed (Uresk and Sharps 1986). Mammals are consistently used throughout the year while birds and invertebrates are consumed seasonally as available (Olson 2000, Harrison 2001).

In South Dakota, the most frequent items in swift fox scats were mammals (49 percent), followed by insects (27 percent), plants (13 percent), and birds (6 percent) (Uresk and Sharps 1986). Even though

percentages differed, foods were consumed in the same relative ranking during the three years of the study (Uresk and Sharps 1986). Black-tailed prairie dogs (*Cynomys ludovicianus*) were the most common mammalian prey item, and insect prey items included Orthoptera (grasshoppers) and Coleoptera (beetles). Swift fox diets included 13 mammalian prey species and six avian prey species (**Table 2**).

Swift fox diets are variable throughout the year with no apparent focus on any particular prey items (Kitchen et al. 1999, Olson 2000). In southeastern Wyoming, swift fox diets reflected the relative abundance of each species throughout the year, indicating opportunistic foraging (Olson 2000). Percent occurrence of mammalian prey was highest during the pair formation period (December - March) when availability of non-mammalian prey types was most reduced. Occurrence of pronghorn (*Antilocapra americana*) in scats peaked in the dispersal (September - November) and pair formation periods, when pronghorn that died during the hunting season and winter were most available as carrion. Diets included at least eight species of rodents (Sciuridae, Geomyidae, Cricetidae, and Heteromyidae), shrews (Soricidae), rabbits and hares (Leporidae), pronghorn, birds, reptiles, beetles, grasshoppers, bees and wasps (Hymenoptera), and fleas (Siphonaptera) (Olson 2000).

The differences in species composition of swift fox diets across their geographical range are likely due to variation in distribution of potential prey species (Hines

Table 2. Mammalian and avian prey of swift foxes in South Dakota (Uresk and Sharps 1986).

Mammalian prey	black-tailed prairie dogs (<i>Cynomys ludovicianus</i>) hispid pocket mouse (<i>Perognathus hispidus</i>) northern pocket gopher (<i>Thomomys talpoides</i>) deer mouse (<i>Peromyscus maniculatus</i>) thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>) northern grasshopper mouse (<i>Onychomys leucogaster</i>) western harvest mouse (<i>Reithrodontomys megalotis</i>) eastern cottontail (<i>Sylvilagus floridanus</i>) white-tailed jackrabbit (<i>Lepus townsendi</i>) voles (<i>Microtus</i> spp.) shrews (<i>Sorex</i> spp.) undetermined Mustelidae.
Avian prey	western meadowlark (<i>Sturnella neglecta</i>) chestnut-collared longspur (<i>Calcarius ornatus</i>) mourning dove (<i>Zenaidura macroura</i>) horned larks (<i>Eremophila alpestris</i>) lark bunting (<i>Calamospiza melanocorys</i>) red-winged blackbirds (<i>Agelaius phoeniceus</i>).

1980). For example, studies in Texas, Utah, Oklahoma, and Kansas (Cutter 1958a, Egoscue 1962, Kilgore 1969, Zumbaugh et al. 1985) reported lagomorphs as principal items in the diet. However, studies in Colorado and Wyoming reported that swift fox diets were more variable and did not detect lagomorphs as principal prey items (Rongstad et al. 1989, Olson 2000).

Breeding biology

Breeding occurs from December to February depending on latitude (Kilgore 1969, Hines 1980, Covell 1992). Gestation is approximately 51 days (Kahn et al. 1997). Average litter sizes, based on counts of pups at natal dens, are 3.3 to 5.0, with a range of one to eight (**Table 3**; Scott-Brown et al. 1987, Sovada et al. 1998). The pup's eyes and ears open about day 10 to 15 days after birth (Kilgore 1969). Pups are reared in dens with den sites possibly being changed several times during the pup-rearing period (Kahn et al. 1997). Under certain circumstances, litters from different fox pairs might share the same natal dens. Olson (2000) observed two instances in which an adult female lost her mate and moved her litter to the natal den of another fox pair. Whelps are nutritionally weaned about six to seven weeks postpartum (Kilgore 1969). At four or five months, the young foxes are almost fully grown and difficult to distinguish from adults (Kahn et al. 1997). Though little is known about pup-dispersal, it begins during September and October (Kahn et al. 1997).

Swift foxes are monestrous, apparently monogamous. They will form pair bonds in early winter, and these may last several years (Kahn et al. 1997). They pair and breed the first breeding season following birth, as Olson (2000) observed seven of 10 year-old females with young. Following the death of a mate, swift foxes rapidly find new mates (Olson 2000). In Wyoming, 21 percent of the foxes studied had more than one mate, and two male foxes had three different mates (Olson 2000). If a fox lost its mate, it typically switched home ranges after a new mate was found (Olson 2000).

Demography

In general, swift foxes are short-lived carnivores with relatively high reproductive potential. They pair and breed the first breeding season following birth (Olson and Lindzey 2002). Average litter sizes, based on counts of pups at natal dens, are 3.3 to 5.0 (range = 1 - 8; Scott-Brown et al. 1987, Sovada et al. 1998). It appears that most fox pairs reproduce as 19 of 24 (79 percent) swift fox pairs were observed with young over a three-year study in Wyoming (Olson and Lindzey 2002).

While swift foxes can live to be greater than seven years old, most die at a much younger age. At any given point in time, the majority of swift foxes present in a population are likely to be under three years old. Matlack et al. (2000) recovered 22 dead swift foxes on their Kansas study area and estimated their ages by examination of cementum annuli (Dimmick and Pelton 1994) as follows: <1 year - 5 individuals (22.7 percent); 1 year - 7 individuals (31.8 percent); 2 years - 4 individuals (18.2 percent); 3 years - 2 individuals (9.1 percent); 5 years - 1 individual (4.5 percent); 6 years - 2 individuals (9.1 percent); and 7 years - 1 individual (4.5 percent). In Colorado, Schauster et al. (2002) recovered 30 swift fox carcasses and reported that 43.3 percent were <3 years old (n = 13), 23.3 percent were 3 to 5 years old (n = 8), and 26.6 percent were 5 to 7 years old (n = 7 percent).

The relatively high reproductive rates of swift foxes are necessary to balance out low survival rates, especially of juveniles. Estimates of adult swift fox survivorship range from 0.40 to 0.75 (**Table 4**; Fitzgerald 1997, Kitchen et al. 1999, Olson and Lindzey 2002). Estimates of juvenile survival range from 0.05 to 0.33 (Rongstad et al. 1989, Sovada et al. 1998). Sex ratios and survival rates between the sexes are similar (Jackson and Choate 2000, Matlack et al. 2000, Olson and Lindzey 2002, Schauster et al. 2002). Sovada et al. (1998) reported that adult survival varied throughout the year with mortality significantly highest during the spring ($P < 0.01$; spring = 0.33 ± 0.08 [$\bar{X} \pm SE$], summer

Table 3. Mean litter size of swift foxes.

Location	Mean Litter Size	Study
Kansas	3.25 ± 0.34 (n = 8)	Sovada et al. (1998)
Oklahoma	5 (n = 4, range = 3-6)	Kilgore (1969)
South Dakota	4 (n = 5, range = 3 - 5)	Hillman and Sharps (1978)
Wyoming	4.6 (n = 25, SE = 0.36, 95% CI = 3.8, 5.3)	Olson and Lindzey (2002)

Table 4. Survival rates of swift foxes.

Location	Survivorship	Period	Study
Colorado	0.64	1 year	Kitchen et al. (1999)
Colorado	0.57	1 year –1995	Fitzgerald (1997)
	0.75	1 year –1996	
Colorado	0.53	1 year	Covell (1992)
Colorado	0.52 – Adult	1 year	Rongstad et al. (1989)
	0.05 – Juvenile	1 year	
Kansas	0.45 ^a – Adult	11 months	Sovada et al. (1998)
	0.33 ^a – Juvenile	6 months	
Montana	0.46	1 year	Zimmerman et al. (<i>in press</i>)
Wyoming	0.69	1 year –1996	Olson and Lindzey (2002)
	0.4	1 year –1997	
	0.66	1 year –1998	

^aModified from mortality data (Survivorship = 1 – Mortality rate).

= 0.22 ± 0.08, fall = 0.05 ± 0.05, winter = 0.10 ± 0.07). However, Olson and Lindzey (2002) reported that the likelihood of dying did not appear to be greater during any particular biological period.

Reported mortality rates of kit fox, the species most similar to swift fox, are also high. Ralls and White (1995) reported an annual mortality rate of 0.42 for a kit fox population on the Carrizo Plain Natural Area in California. Cypher and Scrivner (1992) reported annual estimates of 0.53 (1980-94) and 0.68 (1985-90) for kit foxes on the Naval Petroleum Reserves in California. Disney and Spiegel (1992) reported annual mortality rates of 0.60 (1990) and 0.32 (1991) for kit foxes in Kern County, California.

The reported estimates of swift fox home range size vary from 3.7 to 32.3 km² (**Table 5**). It is difficult

to make meaningful comparisons between the different studies due to differences in data collection and home range estimation methods. Home range sizes of males and females appear to be similar. In southeastern Wyoming, Pechacek et al. (2000) estimated the home ranges of males to be 13.0 ± 4.7 km² and females to be 9.8 ± 2.6 km², but the difference was not significant (*t*-test; *t* = -1.2, *df* = 8, *P* = 0.257). Kitchen et al. (1999) also reported that the seasonal home range sizes of foxes did not differ significantly between males (5.4 ± 0.4 km²) and females (5.3 ± 0.5 km²) (*t* = 0.11, *df* = 53, *P* >0.05). Home ranges are smallest during the pup-rearing period (May - August) and largest during the dispersal period (September - November) (Kitchen et al. 1999, Olson 2000).

Home range overlap of paired foxes appears to be greater than range overlap of unpaired animals as

Table 5. Home range size of swift foxes.

Location	Mean Home Range (km ²)	Method	Study
Colorado	7.6 ± 0.5 ($\bar{X} \pm SE$)	?	Kitchen et al. (1999)
Colorado	11.0 – Males 6.6 – Females	?	Fitzgerald (1997)
Colorado	20 – 30 (Range)	Minimum perimeter polygon	Rongstad et al. (1989)
Nebraska	32.3	Minimum perimeter polygon	Hines and Case (1991)
Wyoming ^a	10.7 – 14.8 (Range) 14.8 – 16.6 3.7 – 6.9	95% utilization distribution in Ranges V	Olson (2000)
Wyoming	11.7 ± 1.3 ($\bar{X} \pm SE$) 7.7 ± 1.1	95% Adaptive kernel 100% Minimum convex polygon	Pechacek et al. (2000)

^aEstimates were of home ranges during three biological periods: (1) pair formation (December - March), (2) dispersal (September – November), (3) pup-rearing (May – August).

Pechacek et al. (2000) reported that home range overlap of paired foxes (95 percent adaptive kernel: 59.6 ± 7.9 percent; $n = 8$ combinations) was significantly greater than range overlap of unpaired animals (95 percent adaptive kernel: 9.9 ± 2.8 percent; $n = 18$ combinations). Olson (2000) also confirmed this trend as he observed that home range overlap between pair members throughout the year ranged from 51 to 91 percent while overlap between adjacent fox pairs averaged only 11.9 percent ($n = 20$; $SE = 2.3$; 95 percent $CI = 6.9, 16.9$). Therefore, while others (Hines 1980, Cameron 1984, Carbyn et al. 1994) did not consider swift foxes territorial, Olson (2000) suggested that the low incidence of home range overlap between adjacent fox pairs and the exclusive use of core areas by pairs were likely due to territorial behavior on his study area.

The population size of swift foxes in the shortgrass prairie habitats of eastern Colorado has been estimated between 7,000 and 10,000 with even more animals in mixed agricultural/prairie habitats (Pusateri 2002). At a site in eastern Colorado, Fitzgerald (1997) estimated the swift fox population density to be 0.19 per km^2 . Taking temporal differences into account, Schauster et al. (2002) reported that swift fox density varied seasonally from 0.18 ± 0.10 per km^2 during the 1997 pup-rearing season to 0.30 ± 0.18 per km^2 during the 1998 dispersal season. Swift fox density has been reported to be negatively associated with both coyote and lagomorph abundance but positively correlated with rodent abundance (Schauster et al. 2002). At a 228 km^2 -study area in New Mexico, the swift fox population

density was between 0.07 and 0.11 foxes per km^2 from 1999 to 2001 (Harrison et al. 2002).

Lifecycle graph and model development

We formulated a lifecycle graph for swift fox that comprised two stages (censused as young of the year and as “adults” - yearlings or older). Adult survival of 57.5 percent was used since it is the median of the mean survival values from several studies (Fitzgerald 1997, Kitchen et al. 1999, Olson and Lindzey 2002). We also used the approximate midpoint of a range of litter sizes given by Scott-Brown et al. (1987) and Sovada et al. (1998), counting only the female offspring. We further assumed considerably lower survival in the first year, a value for which we solved by assuming the population growth rate, λ , was very close to 1.0 (1.005). This “missing element” method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. We did not assume any change in fertility with age, though such changes are common in many species. From the resulting lifecycle graph (Figure 7), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one year census interval (McDonald and Caswell 1993, Caswell 2001).

Here, we present a summary of our model results and direct readers to [Appendix](#) for the complete methodological considerations and technical analyses. Our first exercise was to conduct a sensitivity analysis.

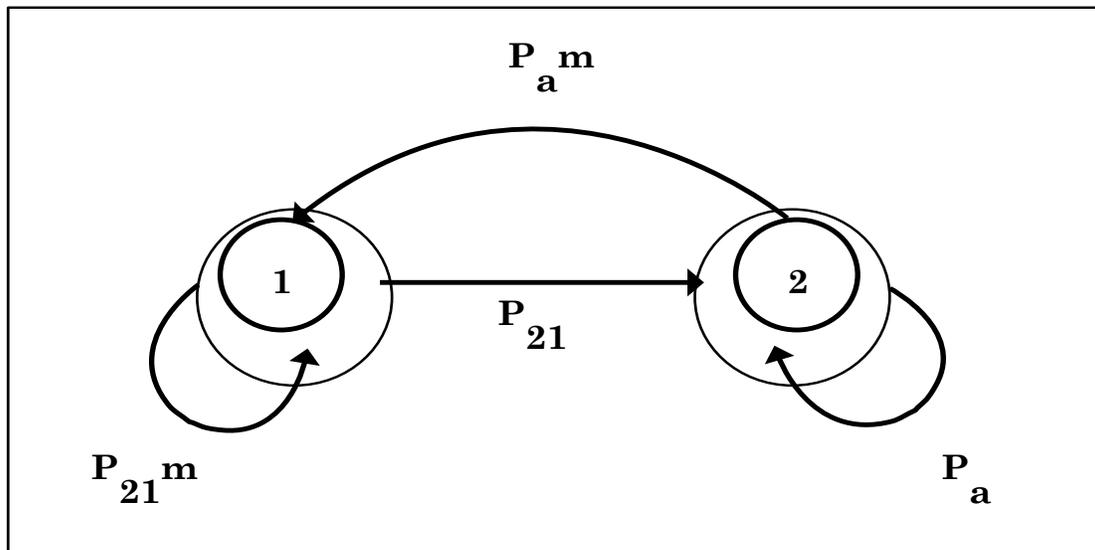


Figure 7. Lifecycle graph for swift fox. The numbered circles (“nodes”) represent the three stages (first-year birds, second-year birds and “older adults”). The arrows (“arcs”) connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ij}) or fertility (F_{ij} ; the arcs pointing back toward the first node).

Sensitivity is the effect on λ of an absolute change in the vital rates (i.e., survival and fertility). The vital rate to which λ was most sensitive for the swift fox was first-year survival. Thus, our major conclusion from the sensitivity analysis is that survival rates, especially first-year survival rates, are most important to population viability.

Next, we conducted the elasticity analysis. Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivity analysis. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. The elasticities have the useful property of summing to 1.0. Elasticity analyses for the Brewer's sparrow indicate λ was most elastic to changes in "adult" survival ($e_{22} = 32.7$ percent of total elasticity). Next most elastic were first-year survival and "adult" reproduction ($e_{21} = e_{12} = 24.9$ percent of total elasticity). First-year reproduction was less important ($e_{11} = 18.3$ percent of total elasticity). The sensitivities and elasticities for swift fox were generally consistent in emphasizing survival transitions. Thus, survival rates are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis

Finally, we constructed a stochastic model to simulate the effect of environmental variation on λ . The stochastic model produced two major results. First, stochastic fluctuations in survival transitions had appreciably greater detrimental effects than did varying fertility transitions. Stochastic fluctuations in first-year and "adult" survival resulted in extinctions, whereas stochastic fluctuations in fertility did not. Second, the level of the stochastic fluctuations greatly affected the strength of the detrimental effects (Case 2 vs. Case 4; 8 extinctions vs. 0 extinctions). These results indicate that populations of swift fox are vulnerable to stochastic fluctuations in survival (due, for example, to variations in winter weather), especially when the magnitude of fluctuations is high. Nevertheless, the importance of "adult" survival to the life cycle of swift foxes and the relatively even distribution of elasticity values may, to some extent, help to buffer them against environmental stochasticity. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Swift fox may, therefore,

have responded evolutionarily by reducing factors that would lead to variability in "adult" survival.

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in any demographic analysis. The most important "missing data elements" in the life history for swift fox are for survival, which emerge as vital rates to which λ is sensitive as well as elastic. Better data on "adult" survival rates and their variability would also be useful. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on our "uncorrelated" assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models:

- ❖ Survival accounts for 73 percent of the total "possible" sensitivity, with first-year survival as the most important (49 percent of total) followed by "adult" survival (24 percent of total). Any absolute changes in survival rates will have major impacts on population dynamics.
- ❖ "Adult" survival ($e_{22} = 33$ percent) and, to a lesser extent, first-year survival and "adult" reproduction ($e_{21} = e_{12} = 25$ percent) account for the great majority of the total elasticity. Proportional changes in survival rates will have a major impact on population dynamics.
- ❖ The reproductive value of "older" females is considerably higher than that of offspring. Thus "adult" females may act as a reservoir of population dynamics, and a buffer against environmental stochasticity, under the model formulated here.

WEB				CENTRUM
4	3	2	1	

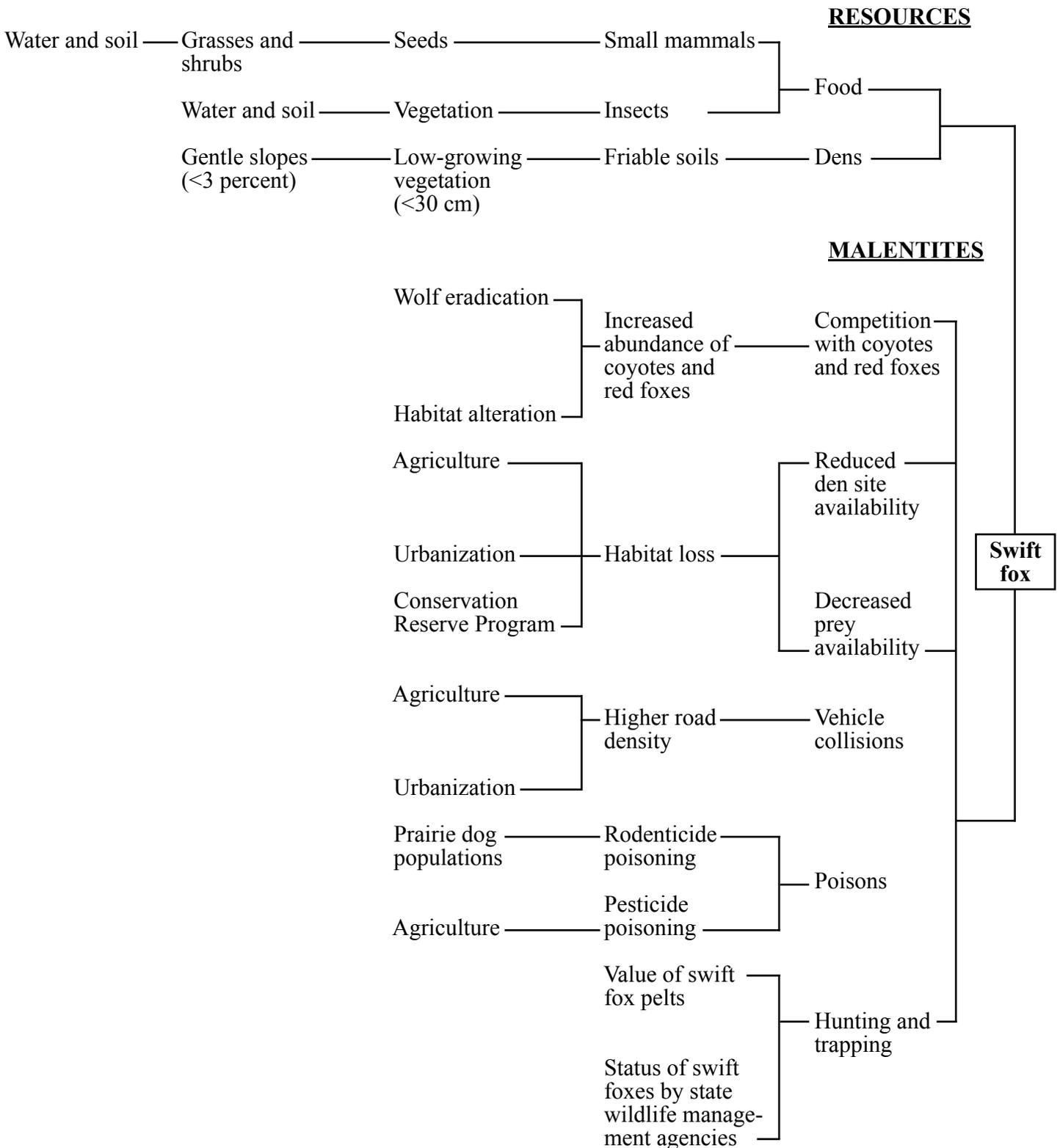


Figure 8. Envirogram representing the web of linkages between swift fox and the ecosystem in which they occur.

- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival rates to population dynamics. Swift foxes appear fairly vulnerable to environmental stochasticity that would affect “adult” survival.

Community ecology

In this section, we discuss interactions between the swift fox, their competitors, predators, and the relationship of these interactions to habitat use (**Figure 8**). Additionally, parasites and disease, and symbiotic and mutualistic interactions are discussed.

Coyotes are generally regarded as the primary cause of swift fox mortality (Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Matlack et al. 2000, Olson and Lindzey 2002). Olson and Lindzey (2002) reported that coyote-caused mortality accounted for 73 percent of known-cause deaths. Of the 14 coyote-killed foxes for which home ranges were estimated, seven were found dead outside of their home range, one was on the home range edge, and six were found dead well within their home range. This trend has emerged in several studies, suggesting that foxes might be more vulnerable to coyotes in less familiar areas, presumably due to decreased knowledge of proximate den locations (Sovada et al. 1998, Kitchen 1999, Olson and Lindzey 2002).

Numerous studies have documented that competitively dominant carnivores can limit the distribution and abundance of smaller carnivore species. For example, red foxes have restricted ranges when they are sympatric with coyotes (Voigt and Earle 1983, Sargeant et al. 1987), and coyotes are killed by wolves and will often avoid areas of high wolf abundance (Fuller and Keith 1981, Carbyn 1987). Evidence of coyote-caused swift fox mortalities has been reported in several studies and is generally believed to constitute interference competition as opposed to predation, owing to the lack of consumption of the fox carcass by the coyote (Rongstad et al. 1989, Sargeant and Allen 1989, Cypher and Spencer 1998, Sovada et al. 1998, Kitchen et al. 1999). In one study, interference competition was evident, with 48 percent (n = 25) of swift fox mortalities identified as confirmed or probable coyote-caused deaths. Further evidence of the impact of coyotes on swift fox populations comes from several studies in which increases in fox numbers were reported following coyote-removal or -control programs (Kilgore 1969, Linhart and Robinson 1972, Covell 1992, Henke

1992, Kamler 2002). Thus, coyotes are considered the main competitors of swift foxes.

We did not find any information documenting competition between swift foxes and red foxes but it has been speculated that red foxes could be competitively dominant due to their larger size. Ralls and White (1995) suggested that although coyote predation on kit foxes can be severe, red foxes may pose an even greater threat to kit fox populations because red foxes rapidly expanding into areas occupied by kit foxes appear to be displacing them. This observation of kit fox-red fox relations possibly is a model of the relations between the swift fox and red fox (Sovada et al. 1998). The degree of competition is undocumented between swift and kit foxes but hybridization occurs where their ranges overlap in New Mexico and western Texas (Mercure et al. 1993).

Predation in this document is considered killing for food (Taylor 1984). Known predators of swift foxes include golden eagles (*Aquila chrysaetos*), badgers, bobcats (*Lynx rufus*), and domestic dogs (*Canis familiaris*) (Kahn et al. 1997). Potential predators include red foxes, large hawks, and great horned owls (*Bubo virginianus*) (Sovada et al. 1998).

Miller et al. (1998) described the parasites found on swift foxes. One coccidian, one cestode, and six nematode species were identified from 14 foxes. These parasites could lead to debilitating pathology of the gastrointestinal tract, asymptomatic urinary tract infections, gastrointestinal hemorrhaging contributing to morbidity, and respiratory infections that could increase the risk of mortality due to predation, as well as decrease foraging efficiency. Two tick and one flea species were collected from 22 foxes. None of the 15 foxes sampled had evidence of *Dirofilaria immitis* microfilaremia, but this does not exclude the potential for heartworm infections to occur.

Understanding the role of disease in swift fox ecology is especially important in areas where they are considered threatened or recovering, as exposure to pathogens could threaten population recovery efforts (Miller et al. 2000). After conducting a serologic survey for selected infectious disease agents in swift and kit foxes, Miller et al. (2000) reported that prevalence rates were 30 percent for canine parvovirus, 13 percent for canine distemper virus, 20 percent for vesicular stomatitis New Jersey, 14 percent for vesicular stomatitis Indiana, 5 percent for Cache Valley virus, 4 percent for Jamestown Canyon virus, 1 percent for

rabies virus, 1 percent for Colorado tick fever virus, and 1 percent for western equine encephalitis virus. In addition, antibodies were not found to *Yersinia pestis*, *Francisella tularensis*, and *Borrelia burgdorferi* in serum from 25 Colorado swift foxes (Miller et al. 2000). Olson (2000) reported that 81 percent of swift foxes at a site in southeastern Wyoming had been exposed to canine distemper virus, but only two foxes were known to have died from the virus.

CONSERVATION

Threats

Historically, human activities have presented the greatest threat to the swift fox (Hillman and Sharps 1978). Swift fox are easily trapped, shot, or poisoned, and many times they have become victims of control efforts directed toward rodents and other predators (Uresk and Sharps 1986). While these forms of mortality are now considerably less common, they still occur (Kahn et al. 1997). Competition with coyotes and red fox may now be the most significant conservation threat to swift fox, although it is likely that habitat loss from agricultural conversion also continues to effect swift fox viability (Kahn et al. 1997). The threshold at which agriculture impacts swift fox is debatable, however, as studies have reported that relative abundance and survival of swift fox in mixed agricultural-use areas were similar to those of foxes in rangeland areas (Jackson and Choate 2000, Matlack et al 2000). Data from these studies, however, are short-term and do not permit assessment of long-term stability and viability of swift fox in landscapes that are heavily fragmented by agriculture. Vehicle-caused mortality along highways and secondary roads constitutes another threat to swift fox populations (Kahn et al. 1997, Sovada et al. 1998).

Competition with coyotes and red foxes

See above discussion in the Community ecology section.

Agriculture

The known negative impacts of agriculture to swift foxes include the loss and fragmentation of habitat, changes in the canid community leading to increased competition, decreased prey abundance, and dens being collapsed by farm machinery. However, the threshold at which landscape conversion for agricultural uses negatively affects the sustainability of swift fox populations is uncertain. Some have hypothesized that the conversion of shortgrass prairie to agricultural

lands was responsible, at least partially, for reduction of the swift fox in the northern Great Plains (Hillman and Sharps 1978, Egoscue 1979). Indeed, the intensity of agriculture and fragmentation are high within many parts of the historic ranges of swift fox where they have not become re-established. There also are vast tracts of shortgrass prairie not reoccupied by swift foxes, indicating that other factors may be responsible. However, such tracts are primarily on the periphery of swift fox range. There also are areas where the conversion of shortgrass prairie for dryland agriculture has altered the landscape, yet swift fox populations persist. The long-term effects on population viability in these highly altered landscapes are unknown. The effects of different intensities and various types of agriculture on swift fox viability clearly need more research.

Studies (Sovada et al. 1998, Matlack et al. 2000) have reported that swift fox in rangeland and cropland sites in Kansas had similarities in some demographic parameters. Matlack et al. (2000) reported that relative abundance was similar between rangelands (1.75 adults per 100 trap-nights) and croplands (2.27 adults per 100 trap-nights; $X^2 = 0.55$, $df = 1s$, $P = 0.47$). Survival was also similar between habitats ($F_{1,31} = 0.02$, $P = 0.89$), but the cause of mortality varied between habitats (Matlack et al. 2000). Foxes in rangelands were killed more frequently by coyotes, which might be due to a preference of coyotes for areas with low human disturbance (Sargeant et al. 1987). Foxes in rangelands were also killed more frequently by vehicles than were foxes in the croplands (Matlack et al. 2000). Swift foxes in croplands were more likely to die from non-traumatic causes (70 percent vs. 18 percent), which might be a result of foxes in rangelands being healthier (Matlack et al. 2000). Adult foxes in rangelands averaged 6 to 7 percent larger than those in croplands, suggesting that abundance and availability of prey was lower in croplands (Matlack et al. 2000). Therefore, foxes in cropland sites might have been more prone to starvation or disease, but actual causes were unknown. Even though some differences were detected, Matlack et al. (2000) suggests that certain farming practices provide sufficient, if not optimal, conditions for the swift fox. Sovada et al. (1998) also reported that swift foxes in Kansas had similar survival rates in both habitats. However, coyote predation was the main form of mortality at both sites, and foxes in croplands were killed more frequently by vehicles, in contrast to the results of Matlack et al. (2000). A key parameter missing from both studies is the reproductive success of swift foxes in rangelands and croplands. Without these data, it is impossible to make inferences about population viability.

Jackson and Choate (2000) reported that swift foxes were able to find suitable habitat for denning in agricultural landscapes. They reported that nine of 15 dens found in croplands were in fallow wheat fields, three were in winter wheat, one was in fallow milo, one was in fallow sunflowers, and one was in dryland corn. Fallow fields and fields with winter wheat were likely used because swift foxes need sites with unobstructed views for their den sites. Thus, these sites would likely be the best available denning habitat. On several occasions, dens that were disturbed by farm implements were reopened and utilized immediately following disturbance. No dens were found in irrigated fields. An important distinction to make here is the differences between dryland agriculture and irrigated agriculture. Dryland agriculture relies on rainfall and uses land much less intensively than irrigated agriculture. For example, in irrigated areas, crops grow and are harvested more quickly, and soils are subject to flooding or heavy application of water. Thus, irrigated areas are much less suitable for swift foxes, and swift foxes are rarely found there. Based on observations from several studies, it has been suggested that swift fox are able to persist in some dryland agricultural areas (M. Sovada personal communication).

Vehicle collisions

Sovada et al. (1998) observed that 22 percent of swift fox mortality in western Kansas was caused by vehicle collisions. Additionally, juvenile swift foxes in cropland areas were more prone to vehicle collisions than juveniles in rangeland areas (Sovada et al. 1998). This may be attributed to 90 percent more roads in the cropland area. All vehicle casualties occurred between 29 August and 9 October (Sovada et al. 1998). Matlack et al. (2000) reported that vehicle collisions accounted for 24 percent of swift fox mortalities of 22 radio-collared swift foxes at a site in western Kansas. In this study, however, swift foxes in rangeland areas were more prone to vehicle collisions than swift foxes in cropland areas (Matlack et al. 2000).

Poisoning

Poisoning has probably been the most deleterious influence upon swift fox populations in the Great Plains (Scott-Brown et al. 1987). "Perhaps the most important (factor contributing to swift fox decline) was inadvertent poisoning from strychnine-laced baits placed by professional 'wolfers' and ranchers. There was an unwritten law of the Old West that no cowhand should pass a carcass without lacing it with strychnine sulphate in the hope of killing one more wolf. Swift foxes died

in the thousands, as they were generally the first to take the poisoned meat" (Young 1944 in Scott-Brown et al. 1987). With the advent of regulatory controls over the use of such poisons, poisoning impacts on swift fox populations are substantially reduced. Nonetheless, localized poisoning of swift foxes has been documented and still occurs. Four adult swift foxes in Kansas died of organophosphate toxicosis caused by the pesticide Thimet, also known as Phorate (Sovada et al. 1998). Thimet is an organophosphorus insecticide that is registered for use on several types of crops, but primarily corn. Miller et al. (1994) suggested primary or secondary poisoning may affect local swift fox populations, especially where rodenticides are used to control prairie dogs, a continuing common practice.

Trapping and hunting

Trapping pressure may have been another important associated factor in the decline of the swift fox in North America (Scott-Brown et al. 1987). Between 1835 and 1838 the American Fur Company received 10,614 swift fox pelts from their upper Missouri and Sioux trading outfits (Hillman and Sharps 1978). Currently, the impacts of trapping are presumed to be minimal due to regulations prohibiting or regulating trapping harvest in all states, and to the low value of swift fox pelts in states where harvest is still legal.

"The importance of human harvest in limiting or regulating swift fox populations is unknown. There is insufficient information to weigh the impact of harvest on species distribution or population densities. For example, swift fox populations in Colorado have remained widespread despite 55 years of harvest. No noticeable reduction in distribution has occurred in Kansas since the opening of a season on swift fox in 1982. In comparison, swift fox have been protected from harvest in South Dakota, Nebraska, and Oklahoma, with no apparent increase in distribution or population densities during the same period. It must be noted, however, that native prairie habitat in these states has been substantially reduced due to agricultural conversion. Prices for swift fox pelts varied from \$3 to \$10 during 1987 to 1997. Low pelt prices provide some interest but little incentive to actively harvest swift fox. Thus, total estimated harvest of swift foxes has steadily declined since 1982" (Kahn et al. 1997). It is unclear from these results whether swift fox will respond to reduced harvest. In these cited cases, it is likely that other factors are regulating the population.

Isolated cases of lead-toxicity could affect swift foxes as a result of humans hunting the prey of swift

foxes. Zumbaugh et al. (1985) detected the presence of lead shot in the stomach contents of swift foxes, indicating that they prey on crippled or dead animals shot by hunters.

Urbanization

Information on the impacts of urbanization on swift fox populations is scarce. Directly, urbanization causes a loss of habitat. Urbanization is also likely to result in increased roadkills, predation, and competition with dogs. Little is known about the ability of swift foxes to cohabitate with humans. Cutter (1958b) reported three occupied dens within 100 m of human habitation.

Livestock grazing

Olson (2000) suggested that cattle grazing is beneficial to swift foxes, so long as the swift fox prey base is not adversely affected by the grazing regime. Cattle grazing helps to maintain the shorter vegetation that swift foxes prefer and requires development of water sources, which is thought to benefit swift foxes. Moderate to heavy grazing by livestock was common throughout two sites in South Dakota where swift foxes were present (Uresk and Sharps 1986). In Texas, 19 of 25 dens were in heavily grazed pastures (Cutter 1958b).

Conservation Reserve Program

Changes in habitat associated with the Conservation Reserve Program (CRP) could also place swift foxes at risk. Kahn et al. (1997) discussed how the CRP has affected the swift fox. The CRP, established under the 1985 Farm Bill and renewed under that Bill's 1990 extension, has revegetated millions of cropland acres into grass cover. However, in many areas of the shortgrass prairie ecosystem, CRP fields were planted to tallgrass prairie species or taller non-native grasses. When these fields were left ungrazed, unmowed, and unburned, these grasses developed into dense rank stands unsuitable for swift fox. Current management guidelines for CRP-enrolled lands do not appear to provide adequate habitat for swift fox, although these lands are utilized by coyotes and red fox. Ideally, new CRP guidelines should provide incentives for program participants to plant native grass species, particularly in areas that support an existing swift fox population. Under these circumstances, the CRP program may benefit swift fox by returning converted grassland to shortgrass prairie habitat. Even then, the limited term

of CRP program enrollments complicates assessment of long-term effects on swift fox populations.

Conservation Status of the Swift Fox in Region 2

Kahn et al. (1997) described the distribution of swift foxes in the United States as relatively widespread although they occupy only a portion of their original range. "Current known swift fox distribution is apparently about 25 percent of the reported historic range from the literature or approximately 40 percent of the suggested historic range based on vegetation classification mapping of the shortgrass and mid-grass prairie grassland types in the central United States" (Lauenroth 1996 *in* Kahn et al. 1997). We are not aware of any information that would allow us to determine swift fox population trends throughout their range. Most monitoring efforts have been initiated within the past few years and have not collected enough data to establish a trend.

Based on studies that have collected distribution and demographic data, the viability of swift fox populations in Wyoming, Kansas, and Colorado do not appear to be threatened at this time. There is, however, concern for swift fox populations in South Dakota and Nebraska, based on major range contractions that have occurred in each state. The distribution of swift foxes in South Dakota is extremely limited even though suitable shortgrass prairie habitat remains in the southwestern part of the state (Kahn et al. 1997). In Nebraska, swift fox occur only in very limited numbers in the panhandle and southwestern portion of the state (Kahn et al. 1997). The limited distribution of swift foxes in Nebraska and South Dakota appears related to the dearth of shortgrass prairie remaining in each state. Remaining populations are found primarily in those areas of remnant shortgrass prairie.

Swift foxes occupy a variety of habitats in the Great Plains including shortgrass and mid-grass prairies, and sagebrush steppe; they may also use some agricultural areas (e.g., plowed fields and fencerows). Studies indicate that swift fox populations in shortgrass prairie and sagebrush steppe habitat are viable at this time. Data collected in agricultural areas of Kansas do not include data on the reproductive success in rangeland areas compared to agricultural areas, nor are the data long-term. While such data may indicate somewhat greater flexibility in swift fox habitat requirements than was previously thought, they may also be inadequate to reflect long-term downward trends in highly fragmented

landscapes. The substantial contraction of swift fox distribution from much of the Great Plains heavily converted to agricultural production, demonstrates obvious limits to their ability to adapt to an altered landscape. Throughout the historical distribution of the swift fox in Region 2, many of the areas no longer occupied are those most heavily fragmented and disturbed by agriculture.

Distribution data suggest that swift foxes are vulnerable to habitat change in the form of conversion for agricultural purposes. However, the conversion of landscapes for agricultural purposes is occurring at a much slower rate than in previous years (Federal Register 2001). Because of that, the authors do not consider this threat to be a limiting factor within their current distribution. Much of the information gathered from recent studies of swift fox ecology indicates that swift fox viability in Region 2 is sustainable within its remaining core distribution.

Management of the Swift Fox in Region 2

Implications and potential conservation elements

During the last century, changes associated with human settlement of the Great Plains have had significant impacts on swift fox populations. Numerous factors contributed to the decline, including inadvertent but widespread poisoning aimed at gray wolves and rodent control, intense trapping, competition with coyotes and red foxes, and widespread conversion of habitat to agricultural uses (Scott-Brown et al. 1987). Poisoning and intense trapping were probably the factors most responsible for the decline of swift fox populations during the first half of the 1900s. After wolves were eradicated from the Great Plains, the intensity of poisoning efforts decreased, and swift fox populations in the United States began to recover during the 1950s and 1960s (Egoscue 1979). Today, the most limiting factors affecting the return of swift foxes to unoccupied parts of their historic range are probably competition with coyotes and red foxes, and the conversion of shortgrass prairie for agriculture. It has been suggested that the key component in the restoration of swift fox is the provision of suitable habitat where they can obtain prey while avoiding predation (Kahn et al. 1997). To achieve such conditions more information is needed on the response of swift fox to various types and intensities of habitat alteration and fragmentation.

Presented below are the primary goals and objectives delineated by the SFCT (Kahn et al. 1997). The goal was to maintain or to restore swift fox populations within each state to provide the spatial, genetic, and demographic structure throughout at least 50 percent of the available suitable habitat, in order to ensure long-term species viability and to provide species management flexibility. The top two objectives were (1) to establish a SFCT to develop and determine priorities and lead management activities, and (2) to document the present distribution of swift foxes within each state. Secondary objectives were (1) to develop and implement statewide monitoring programs that provide population trend information and detect changes in local distribution, (2) to develop swift fox habitat criteria in order to identify current habitat availability, (3) to identify and delineate existing suitable swift fox habitat within each state, and (4) to provide swift fox distribution and suitable habitat information to other prairie ecosystem mapping efforts through state Natural Heritage Programs and Geographical Information Systems or Gap Analysis activities. Information on these objectives is presented in the reports of the SFCT, which are listed below.

Allen, S.H., J. Whitaker-Hoagland, and E. Dowd Stukel, editors. 1995. Report of the Swift Fox Conservation Team, 1995. North Dakota Game and Fish Department, Bismarck, ND.

Giddings, B., editor. 1997. Swift Fox Conservation Team 1997 Annual Report. Montana Department of Fish, Wildlife, and Parks, Helena, MT.

Luce, B. and F. Lindzey, editors. 1996. Annual Report of the Swift Fox Conservation Team, 1996. Wyoming Game and Fish Department, Lander, WY.

Roy, C.C., editor. 1999. 1998 Swift Fox Conservation Team Annual Report. Kansas Department of Wildlife and Parks, Emporia, KS.

Schmitt, C.G., editor. 2000. Swift Fox Conservation Team 1999 Annual Report. New Mexico Department of Game and Fish, Santa Fe, NM.

Schmitt, C.G. and B. Oakleaf, editors. 2001. 2000 Swift fox conservation team annual report. Santa Fe, New Mexico Department of Game and Fish, NM.

Peek, M., editor. 2002. Swift Fox Conservation Team 2001 Annual Report. Kansas Department of Wildlife and Parks, Emporia, KS.

Tools and practices

Inventory and monitoring

When selecting a technique for monitoring a population, goals need to be well thought-out and determined prior to initiating surveys. A common goal of monitoring is to measure population trends. To accomplish this, a method must be selected that provides power and a variance estimate so that statistically meaningful analyses can be performed.

Various techniques provide information on presence, relative abundance, or absolute abundance. Measures of relative abundance rely upon an index, such as percentage of scent stations visited, to indicate population trends (Harrison et al. 2002). Relative abundance techniques used for swift foxes include trapping (Finley 1999), scent stations (Bischof and Lavelle 2002), tracking plates (Woolley et al. 1995, Mote 1996, Dieni et al. 1997, Olson et al. *in press*), collection of scat (Sovada and Roy 1996, Dieni et al. 1997), track surveys (Roy et al. 1999, Hoagland 2000), calling (Harrison et al. 2002), and spotlighting (Hillman and Sharps 1978, Woolley et al. 1995, Mote 1996, Sovada and Roy 1996, Dieni et al. 1997). Measures of absolute abundance reflect the actual numbers of swift foxes present in a population (Harrison et al. 2002). Absolute abundance techniques used for swift foxes include mark-resight (Roell 1999), mark-recapture (Cotterill 1997), and collection of scats coupled with microsatellite DNA analysis (Harrison et al. 2002).

Surveys of swift fox populations have been initiated by each state in Region 2. In Colorado, biologists monitor swift fox population trends using mark-resight methodologies with cameras every five years (Pusateri 2002). In Wyoming, tracking plate surveys are used annually (Grenier and Van Fleet 2002). In South Dakota, searches for tracks and other swift fox sign were recently conducted, but survey methods have not been firmly established (Stokely et al. 2002). Biologists in Nebraska recently used scent stations to monitor swift fox populations, but a formal survey protocol has not been established (Bischof and Levelle 2002). In Kansas, searches for tracks and other swift fox sign and pelt tagging reports are used (Roy 2000, Peek 2002a). It should be noted that none of the current monitoring activities in Region 2 include the monitoring of ecological factors that may affect swift fox numbers, such as coyote density, precipitation, or prey density. As a result, if a decline in density or range is observed, it will be difficult, at best, to determine the cause.

Olson et al. (*in press*) recommended using tracking plates to detect swift fox trends in persistence over a broad geographical region (i.e., statewide). Tracking plates are relatively inexpensive, easy to use, and tracks left on a hard surface are readily identifiable. When tracking plate transects were placed within swift fox home ranges, the probability of detecting at least one fox from a marked pair was 0.67 (95% CI = 0.35-0.88) and 0.88 (95% CI = 0.52-0.99) during the first (27 June - 3 July 1997) and second (28 August - 3 September 1997) trials, respectively. Olsen et al. (*in press*) suggested that late summer is a preferable time to conduct surveys because the likelihood of detecting a swift fox is increased due to the addition of young-of-year foxes.

Fitzgerald (1997) live-trapped swift foxes in an effort to determine presence at various sites in eastern Colorado. Approximately 44 percent of the foxes available were captured. Capture success was highest during the months of October and November with 10.1 and 8.7 catches per 100 traps, respectively. Estimates of detection were substantially lower than those reported by Olson et al. (*in press*), and the time, energy, and cost of live-trapping are much higher than with tracking plates. Additionally, the greater costs and decreased efficiency associated with live-trapping makes the method impractical for sampling broad geographical areas as is practical with tracking plates.

Various methods have been suggested to predict whether or not habitat is suitable for swift foxes. Pruss (1999) reported that by using a stepwise discriminant function analysis, five potential discriminators of occupied and unoccupied swift fox den sites were position on a hill, height of new grass, distance to water, distance to roads, and slope. Den position was the variable that discriminated most strongly between sites. Based on the five habitat variables, the discriminant function model correctly classified 28 of the 32 occupied sites as being occupied (87.5 percent) and 26 of the 33 unoccupied sites as being unoccupied (78.8 percent). This tool may be useful for survey and census purposes, selecting reintroduction sites, and modifying existing habitat. Olson (2000) suggested that suitable swift fox habitat could be identified by the following three physical features: soil type, vegetation type, and slope. Soils suitable for swift fox denning are those with friable textures that will maintain their structure (i.e., loamy soils). Vegetation should be low growing, preferably lower than swift fox eye level (~30 cm). Types of vegetation may vary from shortgrass prairie to grassland-shrub communities, provided the dominant

shrub component is low-growing. Topography needs to be flat to gently rolling.

In some situations, control of coyotes may enhance distribution and abundance of swift fox populations (Sovada et al. 1998). However, effectiveness of management based on coyote control would be difficult to attain and sustain due to logistics and expenses associated with a necessary ongoing effort. Cypher and Scrivner (1992) evaluated reduction of coyote numbers to increase kit fox survival but were unsuccessful in reducing coyote numbers sufficiently to affect kit fox populations. Fitzgerald (1997) also recommended against coyote control despite considerable coyote mortality at his Colorado study site as the swift fox population appeared to be stable with good survivorship and relatively high reproduction.

Public education may be important in areas where human-caused mortality other than legal harvest of swift foxes is an issue. In Nebraska, where the swift fox is classified as endangered, the Nebraska Game and Parks Commission publicized the presence of swift foxes in the area so that they would not be mistaken for coyotes (Hines and Case 1991). They also posted swift fox crossing signs along roads frequented by swift fox, identifying them as endangered and increasing public awareness of the presence of the species (Hines and Case 1991).

The reintroduction of swift foxes can be used to establish populations in areas where they were extirpated but suitable habitat remains. Swift foxes have been successfully reintroduced into parts of Canada (Carbyn et al. 1994) and Montana, and recent reintroductions have also occurred in South Dakota. To be effective, reintroductions must be targeted for areas where adequate quality habitat remains, and where the canid community has not changed in a way that might prohibit the establishment of self-sustaining populations. Smeeton and Weagle (2000) prepared a review of reintroduction techniques.

Ultimately, conservation of grassland habitat is likely to be the most important tool for maintaining the viability of swift fox populations over the long term. Threats to the grasslands include urbanization, conversion for agriculture, introduction of noxious weeds, energy development, and the loss of natural disturbances such as fire and intermittent grazing that previously influenced grassland habitat. A challenge to state and federal agencies interested in participating in conservation efforts in these areas is that much swift fox habitat is in private ownership. However, programs such

as the Landowner Incentive Program (LIP) and Private Stewardship Grants Program (PSGP) were created to provide opportunities for state and federal agencies to build partnerships with private landowners interested in conducting conservation activities on their property. LIP and PSGP, which are administered by the USFWS, provide funds for activities directed at the conservation of habitats occupied by endangered, threatened, petitioned, or declining species on private lands. The impacts of these programs within the grasslands have been noticed in the shortgrass prairie of eastern Colorado where these funds have been used to obtain conservation easements on ranches threatened with the pressures of urban sprawl. In Nebraska, these funds have been used for restoration activities in grassland habitats such as the removal of exotic species, grazing deferrals, and improved fencing systems.

Information Needs

Presented below is a list of the information needed to further our knowledge of the swift fox and to better enable managers to manage for sustainable swift fox populations.

1. How does competition with coyotes and red fox limit the distribution and dispersal of swift foxes?
2. How do different agricultural practices affect swift fox? Specifically focus on sizes and juxtaposition of fields, degree of fragmentation, crop-fallow systems, and tilling practices (Jackson and Choate 2000, Matlack et al. 2000). By examining the impacts of different agricultural practices on swift foxes, modifications to present practices might allow greater use of croplands by swift foxes. Additionally, long-term data on the persistence of swift fox in highly fragmented habitats would be valuable.
3. What soil types are important to swift foxes? As Olson (2000) noted, soil type may be the best predictor of habitat suitability for swift foxes.
4. What is the relationship between swift fox population size and precipitation? In a 15-year study, Cypher et al. (2000) found correlations between the previous year's precipitation, prey density, and the population density of kit foxes. Swift fox populations may respond in a similar manner.

5. What is the relationship of swift fox populations to prey density?
6. What are mortality rates and dispersal patterns of pups during the first year (Fitzgerald 1997, Olson 2000)?
7. What are mortality factors of swift fox, especially non-traumatic causes (Sovada et al. 1998)?
8. Can the number of dens be increased by artificial means? Rongstad et al. (1989) hypothesized that survival may be related to the number of dens within a home range. Therefore, they recommended that a study should be conducted within the home ranges of radio-tagged foxes to determine the use of artificially created dens before this management tool is tried.

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APPENDIX

Matrix Model Development for the Swift Fox

Lifecycle graph and model development

We formulated a lifecycle graph for swift fox that comprised two stages (censused as young of the year and as “adults” – yearlings or older). Adult survival of 57.5 percent was used since it is the median of the mean survival values from several studies (Fitzgerald 1997, Kitchen et al. 1999, Olson and Lindzey 2002). We also used the approximate midpoint of a range of litter sizes given by Scott-Brown et al. (1987) and Sovada et al. (1998), counting only the female offspring. We further assumed considerably lower survival in the first year, a value for which we solved by assuming the population growth rate, λ , was very close to 1.0 (1.005). This “missing element” method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. We did not assume any change in fertility with age, though such changes are common in many species. From the resulting lifecycle

graph (**Figure A1**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_{ij} describing survival rates, and m describing number of female offspring per female (**Table A1**). **Figure A2** shows the numeric values for the matrix corresponding to the lifecycle graph of **Figure A1**. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the offspring number used was half the total annual production of offspring, assuming a 1:1 sex ratio. Note also that the fertility terms (F_{ij}) in the top row of the matrix include both a term for offspring production (m_i) and a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later. The population growth rate was 1.005, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

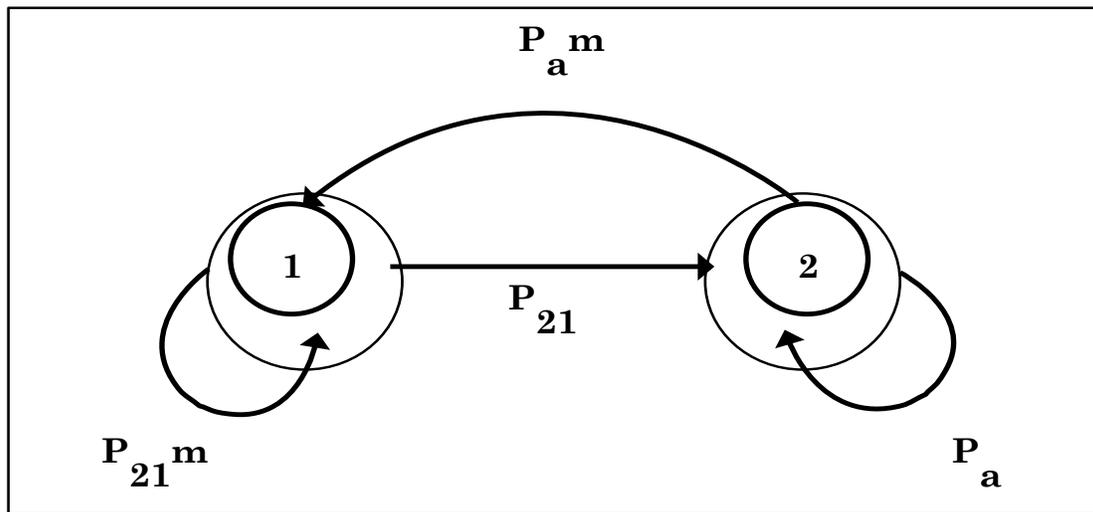


Figure A1. Lifecycle graph for swift fox. The numbered circles (“nodes”) represent the three stages (first-year birds, second-year birds and “older adults”). The arrows (“arcs”) connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ij}) or fertility (F_{ij} ; the arcs pointing back toward the first node).

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for swift fox.

Parameter	Numeric value	Interpretation
M	2.0	Number of female offspring produced by a female
P_{21}	0.215	First-year survival rate
P_a	0.575	Survival rate of “older adults”

	1	2
1	$P_{21}m$	$P_a m$
2	P_{21}	P_a

Figure A2a. Symbolic values for the projection matrix of vital rates, **A** (with cells a_{ij}) corresponding to the swift fox lifecycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1**.

	1	2
1	0.43	1.15
2	0.215	0.575

Figure A2b. Numeric values for the projection matrix of vital rates.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on λ of an **absolute** change in the vital rates (a_{ij} , the arcs in the lifecycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to λ , which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_{ij}) and fertility (F_{ij}) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the “weak links” in the life cycle of a pest. **Figure A3** shows the “possible sensitivities only” matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the biologically impossible sensitivity of λ to the transition from Stage 2 “adult” back to being a Stage 1 first-year animal).

The summed sensitivity of λ to changes in survival (72.8 percent of total sensitivity accounted for

by survival transitions) was greater than the summed sensitivity to fertility changes (27.2 percent of total). The single transition to which λ was most sensitive was first-year survival (48.5 percent of total). The second most important transition was “adult” survival (24.3 percent of total). The major conclusion from the sensitivity analysis is that survival rates, with an emphasis on first-year survival, are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 to 40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs in a fish species). Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_{ij}) and survival (P_{ij}) for a given species. It is important to note

	1	2
1	0.428	0.214
2	1.144	0.572

Figure A3. Possible sensitivities only matrix, S_p (blank cells correspond to zeros in the original matrix, A). The λ of swift fox is most sensitive to changes in first-year survival (Cell $s_{21} = 1.144$) and “adult” survival (Cell $s_{22} = 0.572$).

that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for swift fox are shown in **Figure A4**. λ was most elastic to changes in “adult” survival ($e_{22} = 32.7$ percent of total elasticity). Next most elastic were first-year survival and “adult” reproduction ($e_{21} = e_{12} = 24.9$ percent of total elasticity). First-year reproduction was less important ($e_{11} = 18.3$ percent of total elasticity). The sensitivities and elasticities for swift fox were generally consistent in emphasizing survival transitions, with the elasticities placing a heavy emphasis on “adult” survival. Thus, survival rates are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable stage distribution (SSD, Table A2)** describes the proportion of each stage or age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For swift

	1	2
1	0.183	0.248
2	0.248	0.327

Figure A4. Elasticity matrix, E (remainder of matrix consists of zeros). The elasticities have the property of summing to 1.0. The λ of swift fox is most elastic to changes in “adult” survival ($e_{22} = 0.327$), followed by first-year survival and “adult” fertility ($e_{21} = e_{12} = 0.248$).

Table A2. Stable age distribution (right eigenvector). At the census, two thirds of the individuals in the population should be young of the year. The remaining third will be “older adult” females with a mean age of 2.3 years.

Stage	Description	Proportion	Mean age (\pm SD)
1	Young of the year (to yearling)	0.67	0 \pm 0
2	“Older adult” females	0.33	2.3 \pm 1.8

fox at the time of the post-breeding annual census (just after the end of the breeding season), emergent young of the year represent 67 percent of the population, and “adults” represent 33 percent of the population. **Reproductive values (Table A3)** can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, offspring at emergence) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, 1.0. An “adult” female individual (Stage 2) is “worth” 2.7 offspring. The cohort generation time for this species was 2.4 years (SD = 1.8 years).

Stochastic model

We conducted a stochastic matrix analysis for swift fox. We incorporated stochasticity in several ways (**Table A4**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation we used a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under

Table A3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, offspring at emergence) stage. The reproductive value of the first age-class or stage is, by definition, 1.0.

Stage	Description	Reproductive value
1	First-year females	1.0
2	“Older adult” females	2.7

Table A4. Results of four cases of different stochastic projections for swift fox. Stochastic fluctuations have the greatest effect when acting on both survival transitions (Cases 2 and 3).

	Case 1	Case 2	Case 3	Case 4
<u>Input factors:</u>				
Affected cells	All the F_{ij}	All the P_{ij}	P_{22} only	All the P_{ij}
S.D. of random normal distribution	1/4	1/4	1/4	1/8
<u>Output values:</u>				
Deterministic λ	1.005	1.005	1.005	1.005
# Extinctions/100 trials	0	8	0	0
Mean extinction time	N.a.	1,387	N.a.	N.a.
# Declines/# surviving populations	10/100	53/92	14/100	0/100
Mean ending population size	6.4×10^7	2.7×10^6	$5/7 \times 10^7$	1.4×10^8
S.D.	2.3×10^8	1.2×10^7	4.7×10^8	3.3×10^8
Median ending size	539,645	3,605	183,320	1.8×10^7
Log λ_s	0.0022	-0.0012	0.0013	0.002
λ_s	1.0022	0.9988	1.0013	1.002
Percent reduction in λ	0.28	0.62	0.37	0.13

the deterministic analysis). Under Case 1 we subjected the fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean). Under Case 2 we varied the survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean). Under Case 3 we varied only “adult” survivals (P_{22}) with high levels of stochastic fluctuation. Case 4 resembled Case 2 in varying both survival transitions, but with only half the level of stochastic fluctuation (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) of the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A4**) produced two major results. First, stochastic fluctuations in survival transitions had appreciably greater detrimental effects than did varying fertility transitions. Stochastic fluctuations in first-year and “adult” survival (Case 2)

resulted in extinctions, whereas stochastic fluctuations in fertility did not. Second, the level of the stochastic fluctuations greatly affected the strength of the detrimental effects (Case 2 vs. Case 4; 8 extinctions vs. 0 extinctions). The difference in the effects of which vital rate was most important is predictable largely from the elasticities. λ was most elastic to changes in the survival transitions, especially “adult” survival. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. The extinctions and declines simulated should not be interpreted as estimates of extinction risk — instead they should be viewed as a way to compare the detrimental effects of stochasticity within the bounds of the models. That is, Case 2 (**Table A4**) does not indicate an 8 percent chance of extinction, but does suggest that fluctuations in survival rates will

have much stronger effects on population dynamics than will fluctuations in fertility rates. These results indicate that populations of swift fox are vulnerable to stochastic fluctuations in survival (due, for example, to variations in winter weather), especially when the magnitude of fluctuations is high. Nevertheless, the importance of “adult” survival to the life cycle of swift foxes ($e_{22} = 0.327$ in **Figure A4**), and the relatively even distribution of elasticity values may, to some extent, help buffer them against environmental stochasticity. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Swift fox may, therefore, have responded evolutionarily by reducing factors that would lead to variability in “adult” survival.

Potential refinements of the models

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase

confidence in any demographic analysis. The most important “missing data elements” in the life history for swift fox are for survival, which emerge as vital rates to which λ is sensitive as well as elastic. Better data on “adult” survival rates and their variability would also be useful. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on our “uncorrelated” assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

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