Historical Range, Current Distribution, and Conservation Status of the Swift Fox, *Vulpes velox,* in North America

MARSHA A. SOVADA, ROBERT O. WOODWARD, and LAWRENCE D. IGL

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

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The Swift Fox (*Vulpes velox*) was once common in the shortgrass and mixed-grass prairies of the Great Plains of North America. The species' abundance declined and its distribution retracted following European settlement of the plains. By the late 1800s, the species had been largely extirpated from the northern portion of its historical range, and its populations were acutely depleted elsewhere. Swift Fox populations have naturally recovered somewhat since the 1950s, but overall abundance and distribution remain below historical levels. In a 1995 assessment of the species' status under the US Endangered Species Act, the US Fish and Wildlife Service concluded that a designation of threatened or endangered was warranted, but the species was "precluded from listing by higher listing priorities." A major revelation of the 1995 assessment was the recognition that information useful for determining population status was limited. Fundamental information was missing, including an accurate estimate of the species' distribution before European settlement and an estimate of the species' current distribution and trends. The objectives of this paper are to fill those gaps in knowledge. Historical records were compiled and, in combination with knowledge of the habitat requirements of the species, the historical range of the Swift Fox is estimated to be approximately 1.5 million km^2. Using data collected between 2001 and 2006, the species' current distribution is estimated to be about 44% of its historical range in the United States and 3% in Canada. Under current land use, approximately 39% of the species' historical range contains grassland habitats with very good potential for Swift Fox occupation and another 10% supports grasslands with characteristics that are less preferred (e.g., a sparse shrub component or taller stature) but still suitable. Additionally, land use on at least 25% of the historical range supports dryland farming, which can be suitable for Swift Fox occupation. In the United States, approximately 52% of highest quality habitats currently available are occupied by Swift Foxes.

Key Words: Swift Fox, *Vulpes velox*, historical and current distribution, status, Great Plains.

The adaptations of canid species to environmental constraints and their generalist attributes allow canids to occupy a variety of habitats; thus, many canid species have relatively broad distributions that span a variety of environmental conditions. Historically in North America, the Red Fox (*Vulpes vulpes*) and Gray Wolf (*Canis lupus*) were found throughout most of the continent (see Hall 1981). Other canid species, such as the Arctic Fox (*Alopex lagopus*), Kit Fox (*Vulpes macrotis*), and Swift Fox (*Vulpes velox*), were largely confined to specific biomes (i.e., arctic tundra, western arid and semiarid deserts, and temperate grasslands, respectively). The distributions of most North American canids have been dynamic, with expansions and contractions occurring through time in response to a variety of factors (Johnson and Sargeant 1977; Johnson et al. 1996; Laliberte and Ripple 2004). Climatic influences (e.g., Hersteinsson and Macdonald 1992), competition from larger canid species (e.g., Johnson and Sargeant 1977; Dekker 1989; Hersteinsson and Macdonald 1992), and human persecution (e.g., Young and Goldman 1944; Johnson and Sargeant 1977; Thiel and Ream 1995) are among acknowledged causes of wide-scale changes to or limits in distributions among canid species.

Based on Swift Fox behaviors, habitat use, and historical records, many biologists believe that the pre-settlement range of the Swift Fox was influenced by, and largely restricted to, the expanse of shortgrass and mixed-grass prairies of North America (see Kahn et al. 1997*). Reasoning behind this belief is that Swift Foxes prefer habitats with short vegetation structure, which provides good mobility and visibility for easier detection and evasion of potential predators (Kilgore 1969; Hines 1980; Carbyn et al. 1994). Results from recent studies strongly demonstrated this implicit preference for landscapes that are open and level or gently rolling to landscapes that are rugged or with tall grasses or shrubs (Kitchen et al. 1999; Olson and Lindzey 2002; Kamler et al. 2003; Sovada et al. 2003).

Monitoring species' distributions and populations over time is an important tool for the management of wildlife species, especially for species of special conservation concern, such as the Swift Fox (Ruggiero et al. 1994). The ability to detect changes in a species' distribution or relative abundance allows a managing agency to respond to potential threats to the health of populations. Estimates of density are preferred to monitoring distributions, but population measures beyond distribution typically are more difficult to obtain. Sampling procedures sufficient to attain accurate density estimates, however, can be costly, and such estimates may not be needed for management purposes (Caughley 1977). The proportion of historical range

that is occupied by a species often is one factor considered when the status is being assessed under the US Endangered Species Act (Scott et al. 2006).

Historical Range

There are challenges in delineating the historical geographic range for the Swift Fox because verified records are sparse and many observational accounts are vague (Kahn et al. 1997*), but mainly because the extent of habitat that was suitable for occupation by Swift Foxes was dynamic over time. A fossil record (Holocene period) from eastern Missouri (Parmalee et al. 1969), which is considerably east of the species' range at the time of settlement, exemplifies the spatial and temporal changes in the species' distribution and extent of suitable habitats. In more recent history, the boundaries of the short-stature grasslands preferred by Swift Foxes have been in flux due to climatic, edaphic, and biotic influences (e.g., grazing by American Bison [*Bison bison*]; Küchler 1972; Risser et al. 1981; Küchler 1985; Weaver et al. 1996). The eastern boundary of short-stature grasslands is particularly ambiguous because of the adaptive response of native grasses to spatial and temporal variation in precipitation. Fluctuations in precipitation and concomitant unpredictability of resources are characteristics of mixed-grass prairie regions. In mixed-grass prairies, when rain is abundant, tall-structured grasses dominate; when dry conditions persist, short grasses dominate (Küchler 1972). Given the Swift Fox's preference for short-stature grasslands, it is ecologically reasonable to assume that its distribution repositioned with climatic variation over time.

Another factor that confounds efforts to define the boundaries of the historical range of the Swift Fox is misidentification of specimens or records, which, in some instances, overextended the Swift Fox historical distribution. For example, a Kit Fox (*Vulpes macrotis*) that was collected in northwestern New Mexico (Bernalillo County), well outside the range of the Swift Fox, was mistakenly recorded as a Swift Fox in museum records (Museum of Southwestern Biology, University of New Mexico record #101289). In some cases, the collection location for a museum specimen was erroneously recorded as the fur-trading post rather than the actual point of collection. More problematically, there was often a lack of data points necessary to improve precision when the extent of the species' range was being plotted.

From the mid-1800s to the early 1900s, the Swift Fox suffered a dramatic contraction in distribution and a population decline directly or indirectly linked to human activities (Allardyce and Sovada 2003). Intense trapping efforts directly contributed to these declines; records from the Hudson's Bay Company showed that 117 025 Swift Fox pelts were sold in London, England, between 1853 and 1877 (Rand 1948). One of the most important causes of population decline was arguably the inadvertent poisoning of Swift Foxes with strychnine-laced baits, which were widely used to control wolves. Swift Foxes readily consumed poisoned baits and reportedly died by the thousands (Bailey 1926; Young and Goldman 1944; Allardyce and Sovada 2003). By 1885, the wolf population had been largely decimated in the plains (Hampton 1997), and the Swift Fox population suffered a similar demise. Poisoning subsided by the late-1800s, but trapping and hunting of wolves and Coyotes (*Canis latrans*) continued, with bounties being used as an incentive. By the early 1900s, the Swift Fox was considered extirpated from Montana, North Dakota, Nebraska, Kansas, and Oklahoma and acutely depleted elsewhere in the United States (i.e., South Dakota, Wyoming, Colorado, New Mexico, Texas); it was also extirpated from Canada (Baker 1889; Fowler 1937; Allardyce and Sovada 2003).

Simultaneous with the campaigns to eradicate wolves were changes in the landscape that curtailed any potential for recovery of Swift Fox populations once poisoning and other pressures subsided. Large expanses of mixed-grass prairies were converted to cropland (Samson and Knopf 1994; Samson et al. 1998). The drier shortgrass prairie was less suitable for grain farming but was amply suited to livestock production; native grazers, such as the American Bison and prairie dogs (*Cynomys* spp.), were largely replaced by domestic cattle, which have different grazing behaviors (Schwartz and Ellis 1981). It is not clear how these changes affected Swift Foxes with regard to habitat requirements, but it is likely that these changes indirectly influenced Swift Fox populations by reducing prey populations. Additionally, northern populations of Swift Fox might have relied heavily on carrion, such as American Bison killed by Gray Wolves or dying of natural causes, to survive severe winter conditions (Carbyn 1986; Klausz et al. 1996). This substantial food source was no longer available once wolves and bison were eradicated or had retreated from the region. Other scavengers, such as the Turkey Vulture (*Cathartes aura*), Black-billed Magpie (*Pica hudsonia*), and Common Raven (*Corvus corax*), experienced similar range contractions and population declines in the prairies, ostensibly with the disappearance of the American Bison (Houston 1977; Tallman et al. 2002).

Beginning in the late 1950s, Swift Fox populations showed signs of natural recovery in the United States as observations were being reported with increasing frequency in core areas of the species' historical range (e.g., Martin and Sternberg 1955; Glass 1956; Anderson and Nelson 1958; Andersen and Fleharty 1964; Long 1965). This trend has continued in some parts of the species' range (Sovada and Scheick 1999*). Today, Swift Foxes are thriving in the plains of Colorado, Kansas, Oklahoma, New Mexico, and Wyoming. Small native populations of Swift Foxes occur in Nebraska, South Dakota, and Texas but are isolated from core populations, as are reintroduced (but expanding) populations in Canada, Montana, and South

TABLE 1. Source (museum or published record) of historical Swift Fox locations near the margins of the species' range. Individual locations are mapped on Figure 1 and identified by the Map ID in this table.

State/ Province County	Map ID	Year and nearest named location	Museum catalog number or published source
Montana			
Glacier	6	1806, Two Medicine Creek	Lewis and Clark *in* Burroughs (1961)
		1901–1906, near Blackfoot and Kipp (42 specimens collected)	National Museum of Natural History 108260, 108318-9, 116560-1, 130059, 133091-4, 135129, 136566, 139185-7, 145874-7, 146226-8, 146311-25, 146372-3, 146563-4, 147597, 147767
		ca. 1918, no location	Bailey and Bailey (1918)
Cascade	8	1805, Great Falls	Lewis and Clark *in* Burroughs (1961)
Pondera	7	1894, no location	National Museum of Natural History 67599
Big Horn	9	1879, Fort Custer	McChesney (1879*) *in* Knowles et al. (2003)
Wyoming			
Carbon	10	1898, Aurora Lake	American Museum of Natural History 14499-14503
		1856, Bridger Pass	National Museum of Natural History 1871
Laramie	11	1870, Cheyenne	Yale Peabody Museum YPM37
Colorado			
Boulder	13	1903, Boulder	Cary (1911)
Adams	14	1914, Brighten	Denver Museum of Nature and Science
		1916, Simpson	Denver Museum of Nature and Science (9 specimens)
Denver	15	1878, Denver	American Museum of Natural History 24419
El Paso	16	1878, Colorado Springs	American Museum of Natural History 24420
		1933, no location	University of Colorado 10797
		1957, Security	University of Colorado 7187
Jackson	a	1893, location not described	Cary (1911), but Armstrong (1972) was skeptical of record
Pueblo	17	No date, location not described	National Museum of Natural History *in* Armstrong (1972)
Otero	18	1848, Bent's Fort	Emory (1848*)
Weld	12	1910, Cornish	University of Colorado 230-231
New Mexico			
Union	19	1893, Clayton	Seton (1929)
San Miguel	20	1879, Cobra Springs	National Museum of Natural History 16240
Texas			
Martin	21	1902, Stanton	National Museum of Natural History 126222
Midland	22	1905, no location	Bailey (1905)
North Dakota			
Cavalier	23	ca. 1801, no location	Swanson et al. (1945)
South Dakota			
Hughes	24	1917, no location	National Museum of Natural History 300300
Nebraska			
Antelope	25	1900, north part of county	Cary manuscript (ca. 1905) *in* Jones (1964)
Kearney	27	1853, Fort Kearney	National Museum of Natural History A1343-A1348
Saline	b	ca. 1900, no location	Cary manuscript (ca. 1905) *in* Jones (1964), but record was questioned by R. Timm, Curator of Mammals, University of Kansas (personal communication)
Madison	26	1900, no location	Cary manuscript (ca. 1905) *in* Jones (1964)
Kansas			
Trego	28	1880s, no location	National Museum of Natural History A 21663
Ness	30	no date, "Schoharie" historical town	American Museum of Natural History 16609, New York Zoological Society
Kingman	31	1860s, C(S)hikaskia	National Museum of Natural History 8538
Rush	29	1861, Walnut Creek	Grinnell (1914)
Canada			
Alberta	1	1897, Buffalo Lake	Museum of Comparative Zoology B7719
	2	Pre-1928, High River	Anthony (1928)
	3	1904, Lethbridge	Royal Ontario Museum 21578
	4	1894, Medicine Hat	National Museum of Natural History 69460-69463
	5	ca. 1900, Cardston	Soper (1964)

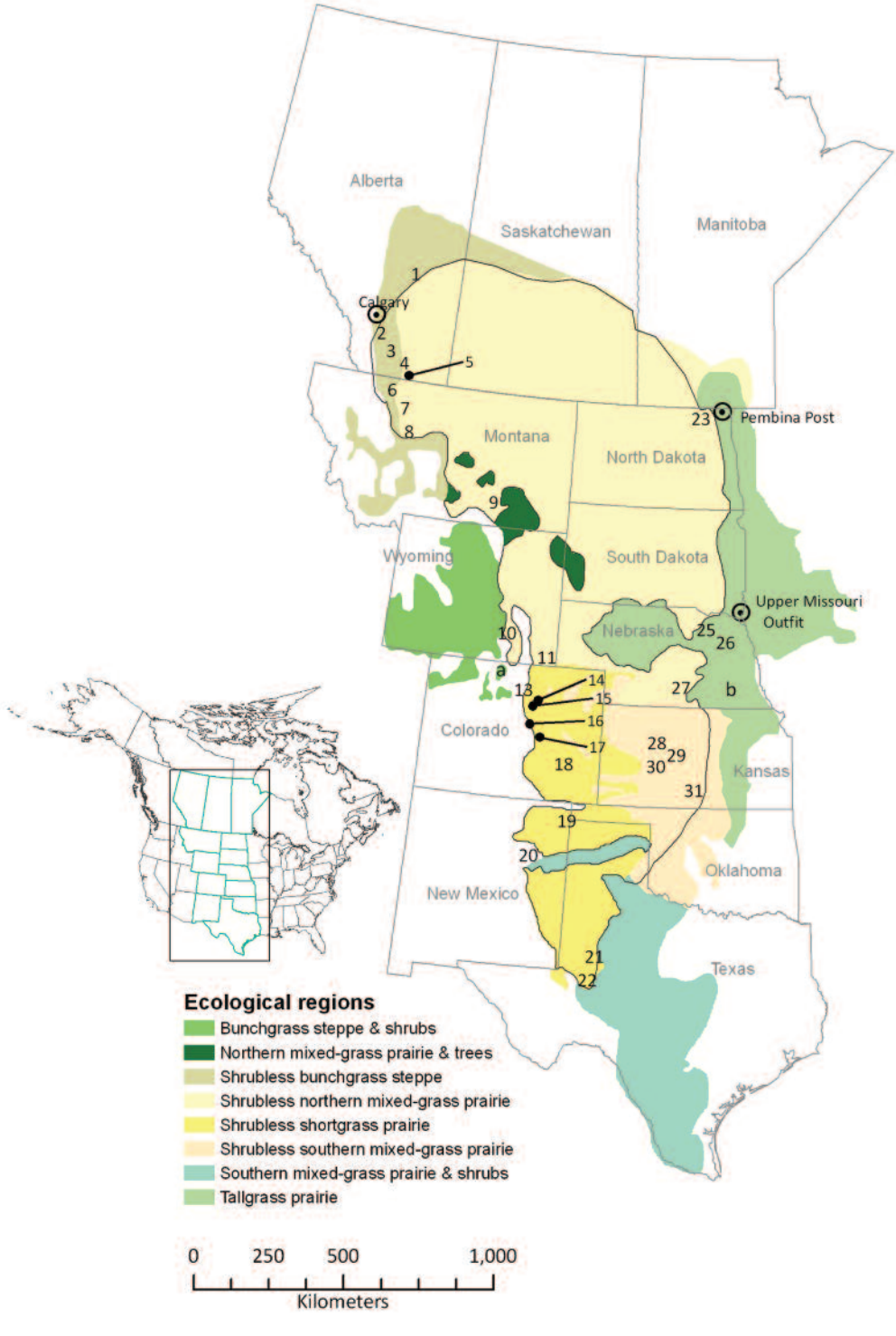

FIGURE 1. Ecological regions modified from Risser et al. (1981) and boundary (black line) of the estimated historical range of the Swift Fox in the United States and Canada. Numbers and letters indicate locations of Swift Foxes from historical records listed in Table 1.

Dakota (Allardyce and Sovada 2003). The species remains absent from large parts of its historical range (e.g., North Dakota, parts of Canada, and Texas).

Administrative status and conservation

In Canada, the first formal recognition of the tenuous status of the Swift Fox occurred in 1978, when the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the Swift Fox as extirpated (Saskatchewan Department of Tourism and Renewable Resources 1978*; Brechtel et al. 1996*). The species' status in Canada was changed to endangered in 1999 subsequent to reintroduction of Swift Foxes at sites in southern Alberta and southern Saskatchewan (Carbyn 1998*; Moehrenschlager and Sovada 2004). The Swift Fox Recovery Team was established in Canada in 1989 to guide conservation and recovery efforts for the species (Carbyn 1995).

In the United States, the US Fish and Wildlife Service (USFWS) received a petition in 1992 to list the Swift Fox under the US Endangered Species Act. Following this review, the USFWS concluded that listing of the Swift Fox was "warranted but precluded by higher listing priorities" (USFWS 1995). The published finding stated that the Swift Fox had been extirpated from approximately 80% of its historical range and that remaining populations existed in scattered, isolated pockets of remnant shortgrass and mixed-grass prairie habitats. The USFWS estimated that approximately 45% of the Swift Fox's habitat throughout its historical range within the United States had been lost as a result of prairie conversion, based on US Department of Agriculture data from 1989 (USFWS 1995). Remaining native prairies often were fragmented into smaller and more isolated grasslands, reducing available habitat and prey. In response to the petition for listing, wildlife management agencies from the 10 affected states (i.e., those located within the historical range of the Swift Fox)—and, later, interested cooperators (federal agencies, conservation organizations, representatives from Canada, the American Zoological Association, tribal entities)—formed the Swift Fox Conservation Team (Dowd Stukel et al. 2003). Because large areas of suitable habitats were not occupied by the species, experts believed that the Swift Fox was a species with potential to expand its distribution. Recent successes of reintroductions (see Discussion section below) substantiated this assumption.

The Swift Fox Conservation Team developed the *Conservation Assessment and Conservation Strategy* (Kahn et al. 1997*), to be implemented *in lieu* of applying the Endangered Species Act as a means of conserving the species (Dowd Stukel et al. 2003). The document outlines short- and long-range goals, objectives, and strategies for management of the Swift Fox throughout its range in the US. The Strategy is considered a working document that is modified periodically based on the accomplishments of the Swift Fox Conservation Team, new information, and data needs. That is, objectives and strategies are prioritized and accomplishment dates are set, based, in part, on the USFWS's recommendations and suggestions to the Team; accomplishments are reviewed and reported on an annual basis. One recommendation presented in the Strategy was that Swift Fox distribution be re-evaluated every five years. Over time, population declines or increases and contractions or expansion of areas occupied by Swift Foxes can be detected; marked declines or range contractions should trigger action by the Team. The Strategy also identifies criteria for evaluating the success of the conservation strategy, including having the United States population of Swift Foxes occupy a minimum of 50% of the suitable habitat that is available (Conservation Assessment and Conservation Strategy, page vii). Therefore, to assess species status, the USFWS requires a sensible estimate of the historical range as well as the current distribution.

In this paper, we present an estimate of the historical range of the Swift Fox based on an integration of available records (e.g., museum records, accounts by early explorers) with physiographic habitat types (Risser et al. 1981) that have been identified by experts as suitable for occupation by Swift Foxes. Also presented is an estimate of the current distribution of the Swift Fox, based on presence/absence survey data collected between 2001 and 2006. Finally, the area of potential occupation (i.e., predicted distribution) within the historical range is estimated, based on current apportionment of suitable habitats. The range boundaries should be considered tentative and dynamic rather than distinct, and some areas within this geographic range are not occupied or may be unsuitable for occupation.

Methods

The historical range of the Swift Fox was estimated by compiling published information, museum records, university records, state agency records, fur-trade records, and accounts of early naturalists and explorers. Available records were limited and fragmentary and, by themselves, were insufficient to delineate the entire historical range of the Swift Fox. Gaps were reconciled with knowledge of the historical extent of suitable habitat once available for Swift Fox occupation. This was appropriate, because there is compelling evidence (Kilgore 1969; Hines 1980; Kamler et al. 2003; Sovada et al. 2003) and agreement among biologists knowledgeable about Swift Foxes (Swift Fox Conservation Team members; Kahn et al. 1997*) that short-stature grasslands are preferred to taller vegetation (Harrison and Whitaker-Hoagland 2003; Moehrenschlager and Sovada 2004). Thus, shortgrass and mixed-grass prairies (Risser et al. 1981; Figure 1, Table 1) were considered the starting base map for the species' historical range. If a record of a Swift Fox location was outside the shortgrass or mixed-grass prairies, or if locations seemed spurious, the validity of those records was closely examined. Conversely, if

there were historical records that conspicuously omitted mention of Swift Foxes among detailed and complete mammal accounts, this too was considered when the historical range was being delineated. Once the outer boundary of the historical range had been defined, the area of the range was calculated. Large forested, shrub-dominated, or montane areas within the short-grass and mixed-grass prairies were not included in the range area estimate; however, many smaller areas of unsuitable habitats (e.g., see Hoffmann and Jones 1970) remained in the calculation of areas. Ultimately, the historical range is a liberal estimate of the extent of plains once occupied by Swift Foxes.

The current distribution of the Swift Fox in the United States was estimated with data provided by members of the Swift Fox Conservation Team and cooperators from each of the 10 states located within the historical range of the Swift Fox. Data were compiled from a variety of survey methods (e.g., track surveys, night-lighting, trapping surveys; see the 2001–2006 annual reports of the Swift Fox Conservation Team for details of methods used by state agencies, found at http://wildlife.state.co.us/WildlifeSpecies/GrasslandSpecies/SwiftFoxConservationTeam.htm) and other observations (e.g., fur-harvest records, verified sightings, research studies, reintroductions, etc.) of Swift Foxes during 2001–2006. Most states do not conduct annual surveys (e.g., Kansas completes the survey over a three-year period and the survey cycles every five years); therefore, the five-year period of data collection is inclusive among the state agencies conducting the surveys. In the United States, the smallest sample unit that could be consistently applied across the range of the Swift Fox was at the county level. The metric used was occurrence (i.e., presence or absence). For Canada, the distribution of Swift Foxes was based on published surveys (Moehrenschlager and Moehrenschlager 2006*). The sample units in Canada were blocks of 93 km^2, but not all blocks in the region of study were surveyed. An unsurveyed block was considered occupied by Swift Foxes if the unsurveyed block abutted at least two blocks that were occupied. Historical and current distribution boundaries were reviewed for accuracy by a state agency representative of the Swift Fox Conservation Team. The proportion of the historical range still occupied by Swift Foxes, based on the survey results, was calculated.

Several caveats should be considered in interpreting the map depicted herein of the current distribution of the Swift Fox. First, surveys used to generate this map were not all-inclusive of the Swift Fox historical range, and areas that were surveyed were not searched with equal intensity among states and provinces. Management agencies made knowledge-based decisions on the extent of the surveys, limiting their efforts to appropriate areas or habitats within the constraints of resources available for surveys. A county with a single Swift Fox observation was weighted equally to a county with multiple and widespread observations; thus, inference to numbers of Swift Foxes would be erroneous. Differences among survey methodologies and temporal variation across the range were not measured.

To predict areas with the potential for reoccupation by the Swift Fox under current landscape conditions, land-cover data from GAP analyses (US Geological Survey National GAP Analysis Program, http://gapanalysis.nbii.gov/portal/server.pt) and the National Land and Water Information Service (Government of Canada 2008*) were used. Because of discrepancies among individual states and Canada in vegetative variables used to define land-cover categories, suitability of habitats was considered state by state and for Canada based on the expert opinion of members of the Swift Fox Conservation Team and knowledgeable biologists. Predicted suitability of habitats was categorically ranked as high, medium, or low quality (see Appendix). The high-quality habitats included low to medium structured grassland without a shrub component. Medium-quality habitats included grasslands with a minor shrub component and croplands that could be identified as dominated by dryland cropping methods (crop/fallow rotation). Low-quality habitats included areas dominated by cropland (not identified as dryland) with a mix of grassland in the landscape. In Kansas, Conservation Reserve Program (CRP) fields were delineated in the GAP analysis. Unlike other states in the historical range of the Swift Fox, CRP fields in Kansas are often planted to tallgrass species that are seldom used by Swift Foxes (Sovada et al. 2003), therefore, CRP fields in Kansas were considered low-quality habitat. Land cover was bounded by the species' historical range, and then suitable habitats and habitat features were identified and the area calculated by habitat quality categories.

Results

Historical Records

Information on Swift Fox distribution from literature, historical records, and national, regional, and university museums in the United States and Canada was sparse. Historical locations of Swift Fox observations were patchy and often unverifiable. Figure 1 shows historical locations of Swift Foxes nearest to the estimated boundaries of the species' distribution, based on published accounts and museum records. A more extensive list (i.e., core and marginal records) of historical records is included in Sovada and Scheick (1999*). Allardyce and Sovada (2003) reviewed historical literature and records of Swift Foxes in the United States; the following updates that review and include historical accounts from Canada, with a focus on marginal records.

North Dakota – The first published record of the Swift Fox was in Alexander Henry's fur shipment records from the Pembina Post of the Northwest Company's Red River District (see Reid and Gannon 1928). The main post was located at the junction of

the Pembina and Red rivers in what is now northeastern North Dakota, with branch posts to the west in the "Hair Hills" (Pembina Hills) and the mouth of the Red River in Canada. Henry wrote that 117 "kit" foxes were taken between 1800 and 1806, and 120 foxes were received from the Hudson's Bay Company at Pembina in 1805-1806 (note that some early accounts referred to the Swift Fox as Kit Fox). Henry's journals do not identify the specific trapping locations of individual Swift Foxes but rather likely indicate the nearest location where fox pelts were traded. The small number taken in the seven years of records suggests Swift Foxes were not common in the vicinity of northeastern North Dakota during the operation of the Pembina Post. This post was likely near the northeasternmost boundary of the Swift Fox's historical range. Similarly, Reid and Gannon (1928: 188) suggested that Swift Foxes likely were not common in northeastern North Dakota and indicated that "…being a plains animal it is quite probable they were more common farther west." However, Bailey (1926) quoted Charles Cavileer from "A Story of '53" describing the fur trade in Walhalla, as obtaining 400–600 "kit foxes" each year from the Pembina Hills region during a period before the American Bison disappeared.

South Dakota – The entire state of South Dakota was generally considered to be within the historical range of the Swift Fox in most published descriptions (Over and Churchill 1941; Hall and Kelson 1959; Egoscue 1979; Hall 1981). However, E. Birney (Bell Museum of Natural History, University of Minnesota, personal communication) and J. K. Jones (Texas Tech University, Lubbock) found no record of Swift Foxes in the easternmost counties (tallgrass prairie) of South Dakota when they were conducting research for their book, *Handbook of Mammals of the North-Central States* (Jones and Birney 1988). Swift Fox remains were found at archeological sites along the Missouri River in four counties, including Walworth (Mobridge site ca. 1650–1700 and Walth Bay site ca. 1550–1600), Buffalo (Medicine Crow site ca. 1700–1750), Sully (Sully site ca. occupied within last 500 years), and Hughes (Pierre Indian Learning Center site ca. 1620–1750) counties (K. Lippincott, South Dakota Archeological Consultant, personal communication). Many Swift Fox pelts were traded at the American Fur Company's Upper Missouri Outfit near the confluence of the Big Sioux and Missouri rivers during 1825–1838 (Johnson 1969). The easternmost historical record for South Dakota was a museum specimen (National Museum of Natural History [NMNH] #300300) collected in 1917, northwest of Pierre in Hughes County.

Nebraska – Prior to settlement, the Swift Fox likely occurred in western and central Nebraska (Jones 1964; Hall 1981; Hines and Case 1991). Tallgrass prairies were prevalent in the eastern portion and sand hills of Nebraska (Risser et al. 1981) and were inconsistent with habitat that is typically occupied by Swift Foxes. In handwritten notes, Merritt Cary, ca. 1905 (manuscript, USFWS, Washington, D.C., see Jones 1964), described some eastern locations in the state. Cary wrote of foxes in Antelope and Madison counties, but there were no specimens. A record from Saline County (M. Cary, ca. 1905, *in* Jones 1964) is considered questionable (R. Timm, Curator of Mammals, University of Kansas Museum, personal communication). The easternmost verifiable historical records are of four Swift Foxes taken along the Platte River near Fort Kearney, Kearney County, in 1853 (NMNH #A1343–A1348). Historical records from the eastern part of the state largely coincide with the extent of mixed-grass prairie.

Kansas – Zumbaugh and Choate (1985) extensively reviewed historical accounts of the Swift Fox in Kansas and identified the species' historical range in the state as corresponding to the shortgrass and mixed-grass prairie regions, bounded in the east by the tallgrass prairies of the Flint Hills. Three museum specimens date back over 100 years. The easternmost historical record in Kansas is a specimen collected in the 1860s in Kingman County, near Chikaskia (NMNH #8538). Other eastern records include a record from Trego County from the 1880s (NMNH #A21663), a record from Ness County in 1901 (near the historical town of Schoharie; American Museum of Natural History [AMNH] #16609), and an account from Rush County in 1861 (Grinnell 1914). The Swift Fox occurred in at least 36 counties and perhaps as many as 44 counties in Kansas (including verified and unverified records; see Zumbaugh and Choate 1985). There are several published accounts (Allen 1874; Knox 1875; Mead 1899; Lantz 1905; Carter 1939) that indicate that the Swift Fox was abundant historically in the high plains of western Kansas.

Oklahoma – There are several historical accounts of Swift Foxes in Oklahoma that indicate that the species occurred throughout the panhandle region (Cimarron, Texas, and Beaver counties) and the western portions of three adjacent counties (Harper, Woodward, and Ellis counties; Blair and Hubbell 1938; Duck and Fletcher 1945; Hall 1981; Caire et al. 1989). The first specimens of Swift Foxes from Oklahoma were collected in 1888 from the Neutral Strip, Indian Territory (panhandle; Caire et al. 1989). The Swift Fox was notably absent from records of mammals observed during two expeditions to parts of Oklahoma outside the panhandle region (Irving 1835; Marcy 1854*). During the first expedition in 1835, Washington Irving joined a military expedition from Fort Gibson in northeastern Oklahoma to the center of the state. Irving's book, *Tour of the Prairies* (1835), did not include the Swift Fox in its detailed accounting of mammals. In 1852, Captain Randolph B. Marcy explored the Red

River, which defines the present southern border of Oklahoma. The Swift Fox was absent from Marcy's list of encountered mammals (Marcy 1854*). Moreover, several agencies conducted biological explorations of the lands that were opened to settlers during the Oklahoma land runs of 1889 and 1893 without observation of Swift Foxes. These include exploration by the (1) American Museum of Natural History in western Oklahoma, including near Corrumpa and Seneca creeks in the southwestern part of present-day Cimarron County; (2) the Field Museum of Natural History in Chicago in Wood County (Elliot 1899*); and (3) the US Bureau of the Biological Survey expeditions under E. A. Preble, J. H. Gaut, V. Bailey and D. E. Lanz. These absences suggest that the species' historical range in Oklahoma may have been limited to the far western portion of the state, yet the habitat designations in Risser et al. (1981) showed potentially suitable habitats further east. Biotic districts described by Blair and Hubbell (1938) are finer-scaled habitat designations for Oklahoma that show the shortgrass plains district transitioning through sand areas to the mixed-grass plains district. The eastern boundary of the shortgrass plains district in Oklahoma is a distinct and abruptly rising scarp. The historical range for Swift Foxes in Oklahoma may have been somewhat contained by this biotic district.

Texas – Egoscue (1979), Hall (1981), and Jones et al. (1987*) defined the historical range of the Swift Fox in Texas as the panhandle region south into the west-central portion of the state; approximately 78 counties were included. Bailey (1905) provided the first published report of Swift Foxes in Texas; he examined five Swift Foxes from Martin County (one stored at NMNH #126222) and also reported on Swift Foxes from Midland, Oldham, and Armstrong counties. Jones et al. (1987*) indicated that only 28 counties in Texas had reliable records of Swift Foxes, based on the literature, trapping records, and museum specimens. They estimated that half of the historical range, as defined in earlier literature (e.g., Egoscue 1979; Hall 1981), was no longer suitable for the species due to conversion of grassland to intensive agriculture (high plains below the 34th parallel). Certainly, Swift Foxes occurred in other counties lacking recorded observations or specimens, but there is a striking absence of records from the grassland type defined by Risser et al. (1981) as the southern mixed-grass prairie with shrubs (see Sovada and Scheick 1999*). This absence provides further evidence of Swift Fox avoidance of habitats with taller structure. Similar to the shifting nature of the boundary between mixed-grass and tallgrass prairies described above, encroachment of shrubs in the southern mixed-grass prairie (Archer 1994) likely influenced Swift Fox distribution.

New Mexico – In the plains-mesa grasslands of New Mexico, Swift Foxes likely occurred in 12 counties (Dick-Peddie 1993), including Colfax, Union, Mora, Harding, San Miguel, Guadalupe, Quay, De Baca, Curry, Roosevelt, Chaves, and Lea counties (Kahn et al. 1997*). Bailey (1931), Egoscue (1979), and Hall (1981) described the species as occurring east of the Pecos River drainage in the extreme eastern portion of New Mexico. The first record of the Swift Fox in New Mexico was a skull collected in 1879 near Cabra Spring in San Miguel County (NMNH #16240). Seton (1929) reported collecting a Swift Fox near Clayton in Union County (between October 1893 and February 1894; see also Caire et al. 1989). There are no records of Swift Foxes in New Mexico from 1894 to 1952, except for a single report from Santa Rosa labeled *V. macrotis* (i.e., Kit Fox), which Bailey (1931) believed was a Swift Fox. A museum specimen (Museum of Southwest Biology [MSB], University of New Mexico, #BRD101289) identified as *V. velox,* collected in 1928 about 13 km southwest of Albuquerque, which is substantially outside all estimates of the historical range of the Swift Fox, was recently examined and identified as *V. macrotis* (R. Harrison, University of New Mexico, Albuquerque, personal communication). There is range overlap with the Swift Fox's close relative, the Kit Fox, in the Trans-Pecos region of New Mexico, where the two species are known to hybridize (Mercure et al. 1993). Hubbard (1994*: 4) concluded that the hybrid zone for the two species "appeared to be restricted to an area not exceeding 50–60 miles [80.5–96.6 km] in width in the Pecos Basin of New Mexico." It is important to note, as Hubbard (1994*: 5) reported, that the contact zone between Swift and Kit foxes "is as enduring as it is broad", existing for several thousand years, yet abrupt morphological differences between Swift and Kit foxes exist in this zone.

Colorado – The Swift Fox was reported as common in the shortgrass and mixed-grass prairie regions in the eastern half of Colorado (e.g., Cary 1911; Armstrong 1972; Hall 1981). Cary (1911) recounted an 1895 report that indicated that Swift Foxes were rare in the Loveland area of Larimer County in north-central Colorado. Earliest accounts in Colorado included observations of the "prairie fox" near Bent's Fort (Otero County in southeastern Colorado) in notes from a military reconnaissance in 1848 (Emory 1848*). A museum specimen was collected in Bent County in 1889 (NMNH #187994-5). Western historical locations were documented by museum specimens collected in 1878, including one in Denver County (AMNH #24419) and another in El Paso County near Colorado Springs (AMNH #24420). A fox was killed 4.8 km northeast of Boulder (Boulder County) in north-central Colorado in 1903 (Cary 1911). Cary (1911) recounted a report of two Swift Foxes shot near Arapahoe Creek (Jackson County) in 1893, but Armstrong (1972) was skeptical of this account because the habitats seemed unsuitable. Although it is possible that Swift Foxes pioneered into North Park

TABLE 2. The estimated area of Swift Fox historical range, the area of habitats that are currently suitable[a] within that range, and the area of suitable habitats that are occupied by Swift Foxes as determined from surveys conducted 2001–2006.

		Grassland								Cropland							
		High quality				Medium quality				Medium quality				Low quality			
	Area of historical range	Available in historical range		Occupied counties or blocks[b]		Available in historical range		Occupied counties or blocks[b]		Available in historical range		Occupied counties or blocks[b]		Available in historical range		Occupied counties or blocks[b]	
	km^2	km^2	%[c]	km^2	%[d]	km^2	%[c]	km^2	%[d]	km^2	%[c]	km^2	%[d]	km^2	%[c]	km^2	%[d]
United States																	
Colorado	108 244	41 848	39	34 275	82	3 203	3	2 728	85	34 349	32	29 671	86	10 000	9	7 824	78
Kansas	119 952	31 213	26	12 831	41	8 171 [e]	7	4 890	60	45 214	38	22 298	49	22 279	19	10 983	54
Montana	199 520	92 124	46	48 355	52	36 556	18	18 561	51	33 725	17	17 584	52	15 777	8	8 054	51
Nebraska	88 357	37 149	42	10 088	27	677	1	0	0	10 270	12	2 463	24	24 241	27	2 445	10
New Mexico	47 600	32 918	69	30 669	93	5 881	12	4 268	73	1 192	3	310	26	555	1	390	70
North Dakota	167 239	33 484	20	0	0	30 134	18	0	0	0	0	0	0	75 917	45	0	0
Oklahoma	31 459	14 070	45	10 533	75	5 667	18	3 928	69	7	0	7	100	10 212	32	7 699	75
South Dakota	164 338	77 826	47	47 382	61	23 722	14	11 825	50	0	0	0	0	46 232	28	12 645	27
Texas	86 155	33 116	38	3 442	10	9 752	11	714	7	360	0	0	0	25 878	30	1 567	6
Wyoming	72 757	32 366	44	25 205	78	19 725	27	16 507	84	5 909	8	5 569	94	3 590	5	3 126	87
Subtotal	**1 085 621**	**426 114**	**39**	**222 780**	**52**	**143 488**	**13**	**63 421**	**44**	**131 026**	**14**	**77 902**	**59**	**234 681**	**22**	**54 733**	**23**
Canada																	
Alberta	89 118	53 290	60	2 396	4	1 413	2	85	6	39 735	45	60	0	–		–	
Saskatchewan	239 297	76 237	32	4 139	5	4 790	2	83	2	169 266	71	3 176	2	–		–	
Manitoba	34 021	10 284	30	0	0	420	1	0	0	20 019	59	0	0	–		–	
Subtotal	**362 436**	**139 811**	**39**	**6 535**	**5**	**6 623**	**2**	**168**	**3**	**229 020**	**63**	**3 236**	**1**	–		–	
Total U.S. and Canada	**1 448 057**	**565 925**	**39**	**229 315**	**41**	**150 111**	**10**	**63 589**	**42**	**360 046**	**25**	**81 138**	**23**	**234 681**	**16**	**54 733**	**23**

[a] High-quality grassland habitats: short to mid-height perennial grassland habitats.
Medium-quality grassland habitats: mid-height to tall perennial grassland habitats with sparse shrub component.
Medium-quality cropland habitats: suitable agricultural lands, with predominantly dryland cropping practices.
Low-quality cropland habitats: cropland marginally suitable or of unknown suitability.

[b] In the United States, the sample unit is county. In Canada, the sample unit is a block 93 km^2 (see Methods for description).

[c] Percentage of the area of historical range.

[d] Percentage of the habitat available in the historical range.

[e] Conservation Reserve Program lands planted mostly to tallgrass species, which provide low quality perennial grassland habitat for Swift Foxes.

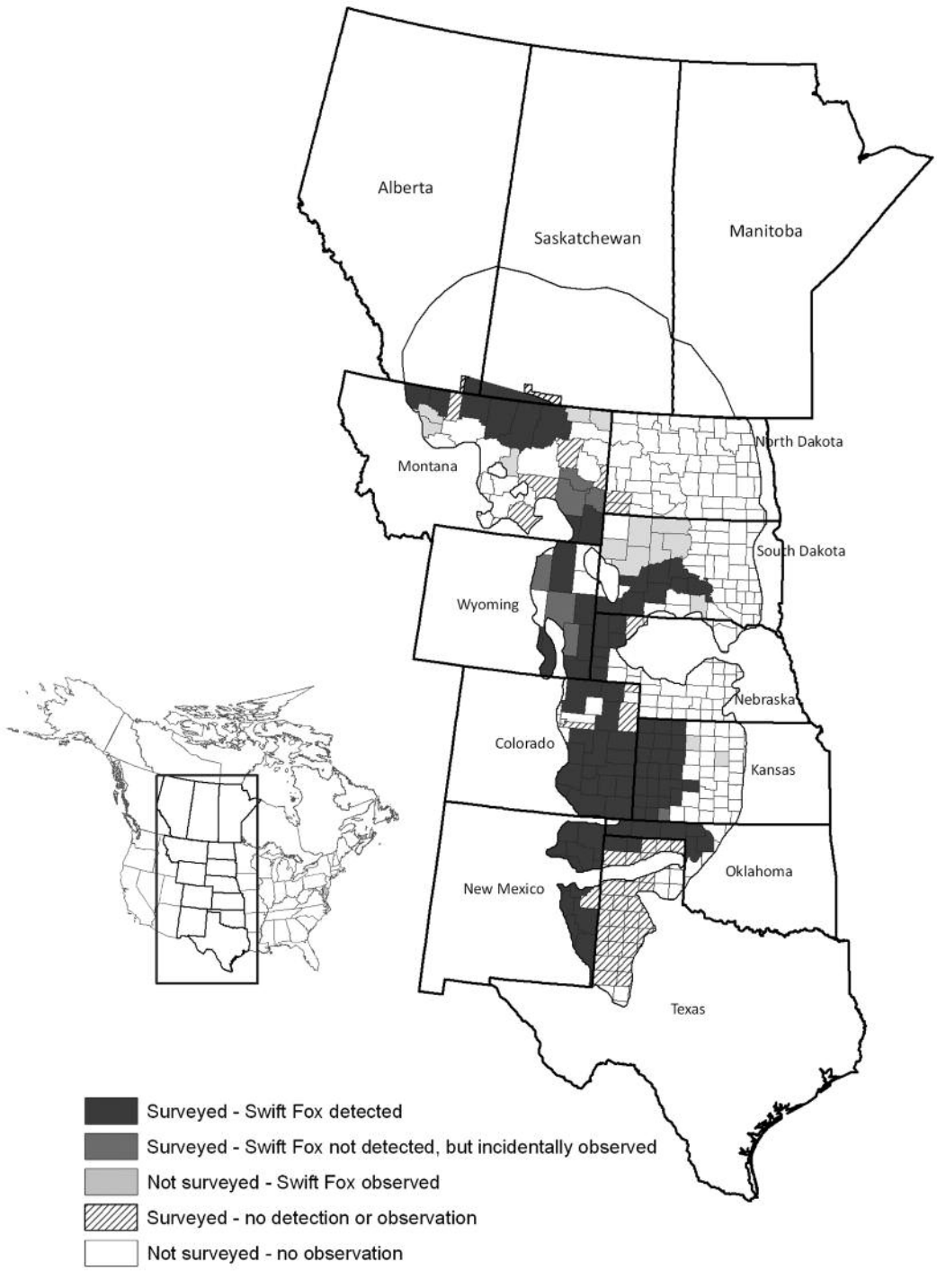

FIGURE 2. Recent occurrences of Swift Fox by county in the United States and the surveyed area in Canada (Moehrenschlager and Moehrenschlager 2006*), bounded by the estimate of the species' historical range. Swift Fox occurrences in the United States are from survey results, confirmed observations, and fur-harvest records, 2001–2006. Swift Fox occurrences in Canada are from live-trap surveys and incidental observations, 2005–2006.

(Colorado basin) from nearby Carbon County in Wyoming, along the North Platte River valley, if Swift Foxes did occur in Jackson County, Colorado, they likely were rare and only occasional occupants on the fringe of the species' distribution.

Wyoming – In Wyoming, published records position the western edge of the species' historical distribution along the eastern portions of Carbon, Johnson, Natrona, and Sheridan counties (Long 1965; Hall 1981; Lindberg 1986). Museum specimens were collected near Cheyenne, Laramie County, in 1870 (Yale Peabody Museum #YPM37); near Fort Laramie, Goshen County, in the 1880s (NMNH #A16460); and near Bridger Pass, Carbon County, in 1856 (NMNH 1871). Five specimens were collected near Aurora Lake, Carbon County, in 1891 (AMNH #14499-14503).

Montana – In Montana, the Swift Fox was once considered common in the shortgrass to mixed-grass prairies east of the Rocky Mountains (Kahn et al. 1997*; Knowles et al. 2003). Meriwether Lewis and William Clark observed Swift Foxes during their expedition along the Marias and Missouri rivers in 1805 and 1806 (Burroughs 1961). In the late 1800s, Coues (1878) reported that Swift Foxes were common between the Milk River in Montana and the Canadian border. There are many other reports of Swift Foxes in Montana in the late 1800s and early 1900s (e.g., Audubon and Bachman 1854; Allen 1874; Grinnell 1875*; McChesney 1879*; see Knowles et al. 2003). Westernmost historical records are from Glacier (1806, Lewis and Clark *in* Knowles et al. 2003), Pondera (1894, NMNH #67599), Toole (1905, NMNH #146372), and Cascade (Lewis and Clark 1805 *in* Knowles et al. 2003) counties. The last historical record of Swift Foxes in Montana was in 1918, when Bailey and Bailey (1918) noted that the Swift Fox commonly occurred on the plains along the eastern edge of Glacier National Park. Hoffman et al. (1969) considered the species extirpated in Montana after a 16-year absence in fur harvest records. The next Swift Fox record was an individual captured in Custer County in 1978 (Moore and Martin 1980).

Canada – The Swift Fox was once a common species in the southern prairie regions of Canada, but by the 1930s, it was considered nearly extinct (Anthony 1928) or extinct (Stewart 1974; Carbyn et al. 1994). The historical distribution of the species in Canada corresponds to the shortgrass or mixed-grass prairie regions of southwestern Manitoba, southern Saskatchewan, and southeastern Alberta (Soper 1964; Banfield 1974; Carbyn et al. 1994). Soper (1964) bounded the northern- and westernmost distribution in Alberta along the 53rd parallel and west to the foothills of the Rocky Mountains. In Saskatchewan, its northern distribution extended to the Saskatchewan River (also near the 53rd parallel; Carbyn et al. 1994). There are no verified records of Swift Foxes in Manitoba, but it is likely that the species occasionally occurred in the southwestern corner based on fur harvest records from northeastern North Dakota (Carbyn et al. 1994). Several publications (e.g., Anthony 1928; Anderson 1946; Miller and Kellogg 1955; Hall 1981) indicated that the range of the Swift Fox crossed the mountains of western Montana and extended into southeastern British Columbia, but the authors provided no evidence. This determination was contradicted by Soper (1964) and Hoffmann et al. (1969), who did not list the species as part of British Columbia's fauna; there are no known historical or contemporary records of the Swift Fox in British Columbia (Egoscue 1979). Museum records for Alberta include a Swift Fox collected in 1878 from near Medicine Hat (NMNH #187993); four foxes collected from "Medicine Hat-Assiniboine" in 1894 (NMNH #69460-69462); one collected near Calmalli in 1894 (NMNH #69463); and six collected in the Calgary area in 1900-1901 (NMNH #108255-108259, 108261). The foxes from the Calgary area were collected by W. G. Mackay and G. F. Dippie, owners of a furhouse, and thus the collection location of these specimens is unclear, but likely in the Calgary area. The last confirmed record of Swift Fox in Canada prior to the 1983 reintroduction program (discussed below) was a specimen (Royal Ontario Museum #2803170005) taken in 1928 near Govenlock, Saskatchewan (Carbyn 1998*).

Minnesota and Iowa – It is difficult to assess the historical distribution of the Swift Fox in Minnesota and Iowa based on available information. There are no known records of Swift Foxes in Minnesota (E. Birney, Bell Museum of Natural History, University of Minnesota, personal communication). Nevertheless, several authors have included Minnesota in the historical range of the species (Hall and Kelson 1959; Hawley 1974; Hillman and Sharps 1978; Egoscue 1979; Hazard 1982; Carbyn et al. 1994). The inclusion of Minnesota as part of the historical distribution has been accepted implicitly, but the evidence for this assertion has been elusive. The claim may have been based on speculation by Swanson et al. (1945: 71), who suggested that since the Swift Fox is found throughout North Dakota, it "… occasionally ventured into Minnesota." Despite a complete absence of confirmed or unconfirmed sightings in Minnesota, the speculation by Swanson et al. (1945) clearly has merit, because environmental conditions on the tallgrass prairies of western Minnesota occasionally may have been suitable for Swift Foxes (see Discussion). In Iowa, there are no verified records, although, without stated evidence, Swift Fox occurrence was indicated in a mammal list (Allen 1942 *in* Hines 1980) and in several range maps (Hall and Kelson 1959; Hawley 1974; Hillman and Sharps 1978; Carbyn et al. 1994). Dinsmore (1994) presented a comprehensive account of possible Swift Fox occurrences in Iowa since European settlement, including observations in Sac and Pocahontas

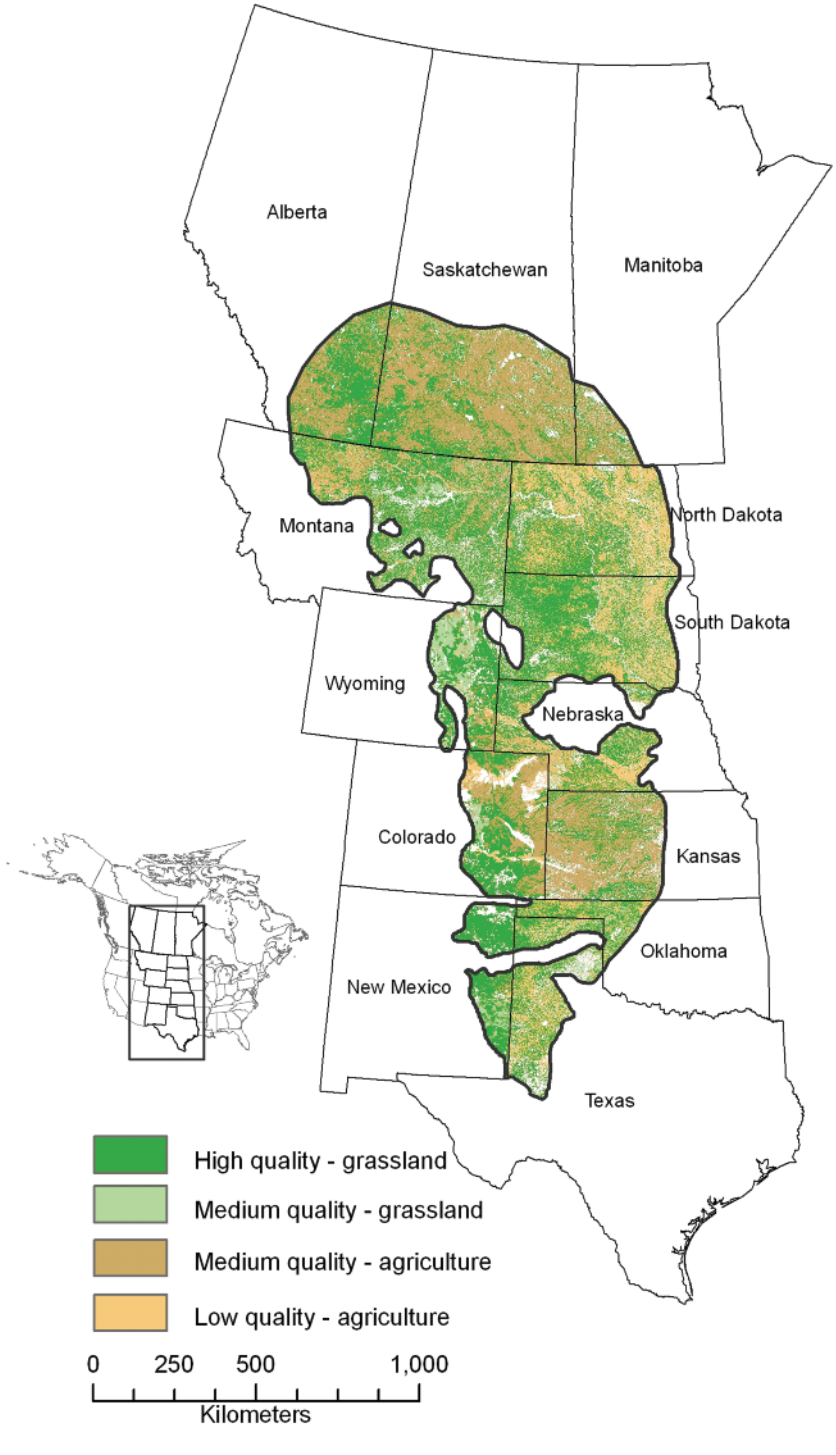

FIGURE 3. Low-, medium-, and high-quality habitats mapped using digital data provided by GAP analysis (http://gapanalysis.nbii.gov/portal/server.pt) in the United States and by the National Land and Water Information Service (Government of Canada 2008*) in Canada. Suitability for Swift Fox occupation is based on information from the literature and expert opinion (see Appendix).

counties in the mid-1800s and Dickinson County in 1882. Descriptions from some of these reports may fit the Swift Fox, but inconsistent use of common names and lack of a specimen contribute to the confusion (Dinsmore 1994). No records of Swift Foxes exist for counties in South Dakota or Nebraska that are adjacent to Iowa. As with Minnesota, Swift Foxes may have occurred intermittently and in low densities in the far western portions of Iowa when habitat conditions were suitable.

Estimates of the Historical, Current, and Potential Distributions

Assimilating the records described above with habitat requisites of the Swift Fox results in an estimate of a historical range that was substantially larger than the current distribution. The estimated area with habitat suitable for Swift Foxes prior to settlement is approximately 1 085 621 km^2 in the United States and 362 436 km^2 in Canada (Appendix). A synthesis of Swift Fox survey data collected during 2001–2006 indicates that the species occupies approximately 44% of its historical range in the United States and 3% in Canada (Figure 2). The area searched for signs of occupancy comprised 48% of the historical range in the United States and 4% in Canada. Parts of the historical range were not surveyed systematically during 2001–2006, largely because it was not economically wise to search areas known to be vacant for many years or areas disconnected from existing populations. Rather, surveys focused on areas of known occupancy and those adjacent to areas of known occupancy. Herein, the assumption is that unsurveyed areas were not occupied by Swift Foxes.

The area within the historical range containing short-structured grasslands most suitable (i.e., high-quality habitat category) for Swift Fox occupancy is 426 115 km^2 in the United States and 139 811 km^2 in Canada, comprising 39% of the historical range overall (Table 2, Figure 3). Grasslands with a short, sparse shrub component (i.e., medium-quality habitat) suitable for use by Swift Foxes occurs in 10% of the historical range, and cropland dominated by dryland agricultural practices with potential for use by Swift Foxes occurs in at least 25% of the historical range. In the United States, approximately 52% of highest quality habitats currently available are occupied by Swift Foxes.

Discussion

The Swift Fox is considered an important indicator species for the former extent of shortgrass and mixed-grass prairies; this reflects the species' strong association with short-structured grasslands (Egoscue 1979). Data on current habitat use and preferences, in conjunction with historical records and published information, support the assertion that the pre-settlement distribution of the Swift Fox was largely limited to the shortgrass and mixed-grass ecosystems. By definition, the Swift Fox should encounter the boundary of its realized niche at the edge of its range, where environmental conditions are less than ideal and habitat quality declines (*sensu* Kanda et al. 2009). Grassland ecosystems, however, are inherently dynamic, and the edges of the historical range of the Swift Fox undoubtedly were pliant and reflected prevailing environmental conditions. When environmental conditions changed along the species' distributional boundary, the suitability of the grassland habitat likely changed as well. Thus, defining the historical range limit of the Swift Fox with any precision may be impossible. Nonetheless, some publications (e.g., Hall 1981; Scott-Brown et al. 1987) probably have overstated the extent of the species' historical range by as much as 20–25% (see Kahn et al. 1997*). Swift Foxes likely occupied areas of the tallgrass prairie during some years or periods, when the vegetation was shorter than average (e.g., during prolonged drought, changes in grazing pressure), but these limited and occasional occupations did not represent areas of sustained occupation, and inclusion in the estimates of the species' historical range is not supported by the species' habitat preferences.

North American grasslands have experienced significant changes since European settlement, and the Swift Fox has survived and adapted to vastly changed land use. The once expansive grasslands in the Swift Fox's historical range are now typically fragmented or degraded. Habitat composition can vary significantly, and suitability for Swift Fox occupation can be difficult to define. Consider, for example, that Swift Foxes are adequately supported in crop-dominated landscapes with a grassland component if the agricultural practices are dryland farming (Kilgore 1969; Hines 1980; Shaughnessy 2003; Sovada et al. 2003). Even though Swift Foxes are considered a hallmark species of short-structured grasslands, the intensity and system of mixed agricultural/rangeland landscape do not necessarily diminish the habitat value. But agricultural cropping practices changing from dryland farming to more irrigation and large monotypic crop fields are more common; such changes likely will not benefit Swift Foxes that presently are able to use fallow fields for foraging and denning.

The species' recovery, which began in the 1950s, proceeded slowly as Swift Foxes dispersed from remnant populations to reoccupy parts of the central and southern portions of the historical range. Early on, this reoccupation was assisted by a decline in the intensity of human-caused mortalities (e.g., poisoning, trapping). Yet, pioneering by Swift Foxes northward in their historical range was not evident, even though suitable habitats were available. Factors limiting or delaying the expansion of Swift Foxes into unoccupied parts of their historical range are unknown and may be key to conservation of this species. Swift Foxes are opportunistic foragers, using a wide variety of food items, including small mammals, birds, insects, reptiles,

and carrion (Kilgore 1969; Scott-Brown et al. 1987). The generalist foraging behaviors of Swift Foxes make food an unlikely limiting factor, and there is no evidence to support food availability as a reason for limiting population expansion.

There are two possible reasons for the inability of Swift Foxes to achieve marked expansion into suitable areas within their historical range. First, Swift Foxes may simply be poor colonizers. Dispersing Swift Foxes are at risk of mortality as they move through unfamiliar areas seeking an area for settlement, and pioneers may have difficulty finding mates in newly colonized areas. Significant changes in landscape (increased agriculture, lack of corridors) may also result in increased risk of predation. Second, interspecific competition with Red Foxes and Coyotes could inhibit pioneering Swift Foxes from going into areas occupied by either of these species, creating an ecological barrier for settlement into new areas. There have been marked changes in the canid community within the historical range of the Swift Fox, lending support to this possibility. When Swift Foxes apparently thrived in the region, the canid community was dominated by wolves; presently it is dominated by Red Foxes and Coyotes (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).

The northward expansion of the Swift Fox into Montana, South Dakota, and southern Canada has been facilitated by reintroduction programs. Four reintroduction programs have been completed and are considered successful (i.e., achieved population growth rate of ≥1 and an index count of ≥100 Swift Foxes). The first was conducted by the Canadian Wildlife Service and cooperators (Carbyn et al. 1994). They released Swift Foxes annually from 1983 until 1997, on privately owned grasslands and community pastures in Alberta and Saskatchewan. Swift Foxes expanded their distribution from these release sites, and they have recolonized areas along the US-Canada border in north-central Montana (Zimmerman et al. 2003; Moehrenschlager and Moehrenschlager 2006*).

The second successful reintroduction effort (1998–2002) occurred on Blackfeet Tribal lands, east of Glacier National Park, in north-central Montana (Ausband and Foresman 2007). This reintroduction effort was followed by reintroductions at two sites in South Dakota, both completed in 2007. The first, funded by the Turner Endangered Species Fund, is located on the Bad River Ranch and surrounding areas in central South Dakota (Honness 2007*; Honness and Phillips 2007*). The second South Dakota effort occurred at Badlands National Park and Buffalo Gap National Grassland, which is approximately 100 km southwest of the Bad River Ranch (Sovada et al. 2006*; Schroeder 2007). The expectation is that, as the two populations grow, they will merge, and westward expansion will result in a merger with an isolated native population near Ardmore, South Dakota. As evidence of this, two male Swift Foxes released on Bad River Ranch have come in contact with Badlands National Park Swift Foxes (G. Schroeder, US National Park Service, personal communication) and one is believed to have mated with a Badlands female fox in the 2006 breeding season. Additionally, a male fox from Badlands National Park dispersed away from the park (approximately 110 km) and was confirmed to have mated with a female fox in the Ardmore area; they raised a litter of pups in 2005 (G. Schroeder, US National Park Service, personal communication). Thus, three populations have begun to intersperse breeding in central to southwestern South Dakota.

There are three ongoing reintroduction efforts for which it is too early to predict their outcomes: (1) Lower Brule Sioux Tribal lands (begun in 2006, South Dakota; Grassel 2007*), (2) Fort Peck Tribal Lands (begun in 2006, Montana; Kunkel et al. 2007*), and (3) Kainai (Blood Tribe) First Nation lands (begun in 2004, Alberta, Canada; Smeeton 2006*).

Determining the current distribution of a native species is less enigmatic than defining its historical range, but such information is, nevertheless, difficult to attain. Yet, a measure of population status and trends has relevance to the conservation of the species. Expansion or contraction in distribution of the species can inform management agencies of trends in a population on a large scale. For the Swift Fox, management agencies of individual states have identified methods for monitoring populations that they can afford to apply within a five-year schedule. Kansas, Montana, and Oklahoma conduct extensive surveys that are relatively inexpensive. These states use townships (93 km^2) as the sample unit, surveying approximately half the townships in the region of the survey (e.g., for Kansas, the region is about one-third of the state). With these data, it is appropriate to apply Markov chain Monte Carlo image restoration analyses to provide an estimate of the underlying distribution rather than just an atlas map of presence or absence (Sargeant et al. 2005). In contrast, North Dakota, a state with no known breeding population of Swift Foxes, relies on less extensive track surveys in areas of expected presence of Swift Foxes dispersing from established nearby populations and incidental observations provided by the general public, trappers, and state agency personnel. Additionally, articles are published in local magazines asking trappers and the public for their cooperation in reporting sightings (e.g., Sovada 2008*). There is marked variation in the intensity and extent of surveys conducted by each agency, yet efforts are appropriate based on resources and the status of the population within an agency's jurisdictions. The sharing of survey results by agencies facilitates the ability of managers to detect

significant change in population status throughout the range.

Although state and provincial management agencies have employed several approaches to monitoring Swift Foxes, the county-level map of occurrence (Figure 2) provides a simple but practical approach across the entire range of the species. With county-level data collected approximately every five years, management agencies can gain information on expansion, contraction, or stability in distribution. Contractions in distribution or isolation of populations would alert the managing agencies to potential threats to the health of populations. In contrast, stable or expanding distribution should reassure agencies that management actions may have been effective.

The first range-wide survey in the United States was conducted by state agencies during 1995–1999 (Sovada and Assenmacher 2005*). These surveys were conducted with the same methods as the 2001–2006 surveys, and results were also reported by county occupancy, as presented herein for the 2001–2006 surveys. Summaries of the 1995–1999 data indicate Swift Foxes occupied 39% of the historical range during that period. Results from the 2001–2006 surveys indicate a 5% increase in the area occupied, suggesting relative stability or an expanding population.

Since the 2001–2006 surveys, evidence of Swift Foxes dispersing into unoccupied areas of their historical range suggests progressive expansion. In South Dakota, Schroeder and Jenks (2008*) reported significant pioneering of Swift Foxes from the reintroduced Badlands population into unoccupied areas in the state. There also is compelling evidence that individuals from the reintroduced populations from South Dakota and Montana are expanding into North Dakota. In the last three years, six Swift Foxes were recovered (killed by vehicles or trapped) in southwestern North Dakota (Bowman [3], Slope [1], Morton [2] counties), one Swift Fox was recovered in north-central North Dakota (Bottineau County), and another was found in 2007 just across the eastern border of North Dakota in western Minnesota (Clay County). This is the first confirmed record of a Swift Fox in Minnesota. Four of the eight recovered Swift Foxes were tagged and linked to reintroduction sites in South Dakota; one of these was a wild-born fox. The remaining four recovered Swift Foxes had not been tagged, indicating dispersal from wild populations or at least one generation post-release from a reintroduced population. The recoveries in North Dakota represent a notable increase in the number of Swift Fox observations in the state; the Swift Fox was not reported in North Dakota between 1915 and 1970, and only four records were recorded between 1970 and 1994. Although there is no evidence of a breeding population in North Dakota, the recent observations in North Dakota and a known breeding pair in adjacent Perkins County, South Dakota (Schroeder and Jenks 2008*) provide support for this species eventually re-establishing a breeding population in North Dakota and perhaps in southeastern Saskatchewan and southwestern Manitoba.

In conclusion, we evaluated the distribution and status of the Swift Fox across its historical range in the United States and Canada. The Swift Fox currently occupies less than one-half of its former range, an area that once covered over 1.5 million km^2 of the mid-continent. Although loss, fragmentation, and degradation of prairie habitats since European settlement have undoubtedly compromised the potential distribution of this species, the Swift Fox currently occupies a greater percentage of its historical range than it did in the mid-1900s. For instance, consider that, during the 20th century, the species was deemed extirpated from Canada (Carbyn et al. 1994) and five states: Kansas and Oklahoma (Cockrum 1952), Nebraska (Jones 1964), Montana (Hoffmann et al. 1969), and North Dakota (Jones and Birney 1988). Several other states lacked observations of Swift Foxes for decades (Texas 1905–1948; Colorado 1916–1941; Wyoming 1898–1958; South Dakota 1914–1966; Sovada and Scheick 1999*). Once poisoning and other significant sources of mortality were suppressed, dispersal and reintroduction into unoccupied but suitable habitats facilitated recovery of the Swift Fox in parts of its former range (Moehrenschlager et al. 2004; Allardyce and Sovada 2003). In particular, the success of Swift Fox reintroductions in the northern parts of the species' range confirm that there are unoccupied areas with adequate resources to support Swift Foxes and that viable populations can be sustained once local populations attain sufficient numbers.

These successes in population growth and reoccupation of former range should not dissuade proactive measures to promote continued conservation and recovery of the species. Grassland habitats continue to be lost, fragmented, and degraded, and extirpation and isolation of local populations remain a concern. Although the Swift Fox tolerates some modification of landscapes, it is not yet known what degree of alteration is tolerable (e.g., ratio of grassland to agriculture, connectivity of grasslands; Moehrenschlager and Sovada 2004). Recovery strategies for this species will depend on integrating actions at the state, national, and continental levels, and wildlife management agencies in the United States and Canada must remain vigilant to ensure the species' population viability and the desired level of recovery established in management plans.

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Appendix

Area (km^2) of Swift Fox historical range and available habitats suitable for Swift Fox occupation within its historical range by state and province. Habitats are those classified in GAP analysis for individual states (USGS National GAP Analysis Program, http://gapanalysis.nbii.gov/portal/server.pt) and, for Canada, the National Land and Water Information Service (Government of Canada 2008*).

Habitat categories[a]	Historical range (total km^2)	Grassland land cover		Agricultural land cover	
		High quality[b]	Medium quality[c]	Medium quality[d]	Low quality[e]
Montana	199 520				
Agricultural lands (dry)				33 725	
Agricultural lands (irrigated)					15 777
Altered herbaceous			8 700		
Very low cover grasslands		8 140			
Low/moderate cover grasslands		73 688			
Moderate/high cover grasslands		9 559			
Mixed xeric shrubs			9 405		
Silver sage		737			
Salt-desert shrub/dry salt flats			1 211		
Sagebrush			10 597		
Mesic shrub-grassland associations			2 006		
Xeric shrub-grassland association			4 637		
Total		**92 124**	**36 556**	**33 725**	**15 777**
North Dakota	167 239				
Cropland					75 917
Planted herbaceous			28 920		
Prairie (mesic tallgrass mix)		2 054			
Prairie (bluestem-needlegrass-wheatgrass)		5 472			
Prairie (wheatgrass)		8 259			
Prairie (needlegrass)		7 392			
Prairie (little bluestem)		4 298			
Prairie (fescue)		444			
Prairie (sand)		4 165			
Prairie (saline)		1 400			
Shrubland sagebrush			903		
Sparse vegetation others			311		
Total		**33 484**	**30 134**	**0**	**75 917**
South Dakota	164 338				
Agriculture					46 232
High cover grassland			13 868		
Low cover grassland		40 157			
Medium cover grassland		19 163			
Sand hills, sparse vegetation			312		
Shale barren slope, sparse vegetation			717		
Xeric shrubland			44		
Mesic shrubland			344		
Deciduous shrubland			33		
Hayland			2 013		
Idle grassland			6 391		
Pastureland		18 506			
Total		**77 826**	**23 722**	**0**	**46 232**
Wyoming	72 757				
Mountain big sagebrush			167		
Grass-dominated riparian			606		
Mixed-grass prairie		32 252			
Irrigated crops					3 590
Wyoming big sagebrush			17 975		
Dryland crops				5 909	
Grass-dominated wetland			6		
Shortgrass prairie		114			
Xeric upland shrub			971		
Total		**32 366**	**19 725**	**5 909**	**3 590**

Appendix *(continued)*

Area (km^2) of Swift Fox historical range and available habitats suitable for Swift Fox occupation within its historical range by state and province. Habitats are those classified in GAP analysis for individual states (USGS National GAP Analysis Program, http://gapanalysis.nbii.gov/portal/server.pt) and, for Canada, the National Land and Water Information Service (Government of Canada 2008*).

Habitat categories[a]	Historical range (total km^2)	Grassland land cover		Agricultural land cover	
		High quality[b]	Medium quality[c]	Medium quality[d]	Low quality[e]
Nebraska	88 357				
Sandsage shrubland			677		
Little bluestem-gramma mixed-grass prairie		21 846			
Western wheatgrass mixed-grass prairie		207			
Western shortgrass prairie		15 096			
Agricultural fields					24 241
Fallow agricultural fields				10 270	
Total		**37 149**	**677**	**10 270**	**24 241**
Colorado	108 244				
Dryland crops				34 349	
Irrigated crops					10 000
Tallgrass prairie			1 897		
Sand dune complex (grassland)			538		
Midgrass prairie		3 412			
Shortgrass prairie		38 436			
Foothill/mountain grassland			767		
Mesic upland shrub			0		
Xeric upland shrub			1		
Total		**41 848**	**3 203**	**34 349**	**10 000**
Kansas	119 952				
Sand prairie		982			
Western wheatgrass prairie		3 132			
Mixed prairie		19 525			
Shortgrass prairie		7 574			
Conservation Reserve Program Land			8 171		
Dryland crops[f]				45 214	
Other cultivated land					22 269
Weedy upland					10
Total		**31 213**	**8 171**	**45 214**	**22 279**
Oklahoma	31 459				
Sandsage prairie		2 218			
Gypsum grasslands			379		
Midgrass sand prairie			3 625		
Midgrass sandsage prairie		985			
Midgrass prairie		4 610			
Grama-buffalograss prairie		6 056			
Agriculture				7	
Crop (warm season)					10 212
Improved/introduced pasture (warm season)		201			
Sandsage savanna			1 663		
Total		**14 070**	**5 667**	**7**	**10 212**
Texas	86 155				
Cropland (irrigated, row, herbaceous, etc.)					25 878
Microphyllous evergreen shrubland			2 712		
Lowland mixed evergreen-drought deciduous shrubland			3 947		
Medium-tall bunch temperate or subpolar grassland		10 701			
Temperate or subpolar grassland with a sparse shrub layer		4 433			
Semipermanently flooded temperate or subpolar grassland			345		
Short sod temperate or subpolar grassland		17 982			
Annual graminoid or forb vegetation				360	
Intermittently flooded temperate or subpolar grassland (e.g., Playa Lakes)			1 341		
Round-crowned temperate or subpolar needle-leaved evergreen woodland			1 295		
Temperate broad-leaved evergreen shrubland			112		
Total		**33 116**	**9 752**	**360**	**25 878**

Appendix *(continued)*

Area (km^2) of Swift Fox historical range and available habitats suitable for Swift Fox occupation within its historical range by state and province. Habitats are those classified in GAP analysis for individual states (USGS National GAP Analysis Program, http://gapanalysis.nbii.gov/portal/server.pt) and, for Canada, the National Land and Water Information Service (Government of Canada 2008*).

Habitat categories[a]	Historical range (total km^2)	Grassland land cover		Agricultural land cover	
		High quality[b]	Medium quality[c]	Medium quality[d]	Low quality[e]
New Mexico	47 600				
Plains-mesa broadleaf sand-scrub			4 713		
Chihuahuan desert scrub			114		
Chihuahuan broadleaf deciduous desert scrub			578		
Shortgrass steppe		17 731			
Mid-grass prairie		15 187			
Chihuahuan desert grassland			402		
Chihuahuan foothill-piedmont desert grassland			74		
Dryland agriculture				1 192	
Irrigated agriculture					555
Basin/playa			0		
Total		**32 918**	**5 881**	**1 192**	**555**
U.S. TOTAL	**1 085 621**	**426 114**	**143 488**	**131 026**	**234 681**
% of historical range		39.25%	13.22%	12.07%	21.62%
Alberta	89 118				
Shrubland			1 413		
Grassland		38 560			
Agriculture (cropland)				39 735	
Agriculture (pasture/forage)		14 730			
Total		**53 290**	**1 413**	**39 735**	
Saskatchewan	239 297				
Shrubland			4 790		
Grassland		39 837			
Agriculture (cropland)				169 266	
Agriculture (pasture/forage)		36 400			
Total		**76 237**	**4 790**	**169 266**	
Manitoba	34 021				
Shrubland			420		
Grassland		7 949			
Agriculture (cropland)				20 019	
Agriculture (pasture/forage)		2 335			
Total		**10 284**	**420**	**20 019**	
CANADA TOTAL	**362 436**	**139 811**	**6 623**	**229 020**	
% of historical range		38.58%	1.83%	63.19%	

[a] Habitats from state GAP analyses (USGS National GPA Analysis Program, http://gapanalysis.nbii.gov/portal/server.pt 2008) and Government of Canada/Agriculture and Agri-Food Canada (2008) with potential for occupation by Swift Foxes.
[b] High-quality grassland habitats: short to mid-height perennial grassland habitats.
[c] Medium-quality grassland habitats: mid-height to tall perennial grassland habitats with sparse shrub component.
[d] Medium-quality cropland habitats: suitable agricultural lands, predominantly with dryland cropping practices.
[e] Low-quality cropland habitats: cropland marginally suitable or of unknown suitability.
[f] Kansas GAP did not separate dryland farming practices from others. This estimate is modified based on the estimate by Rogers et al. (2000*) of 67% dryland crops in western Kansas.