TEETERING ON THE EDGE OF SUITABLE CLIMATE:

KIT FOX (*VULPES MACROTIS*) RANGE LIMIT DYNAMICS IN

EAST-CENTRAL UTAH AND WEST-CENTRAL COLORADO, 1983 TO 2009

by

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Teetering on the Edge of Suitable Climate: Kit Fox (*Vulpes macrotis*) Range Limit Dynamics in East-central Utah and West-central Colorado, 1983 to 2009

Thesis directed by Associate Professor Robert P. Guralnick

Although it is acknowledged that species' occupancy at geographic range edges is likely dynamic and driven by shorter or longer-term extreme climate events, quantitative approaches that integrate spatiotemporal environmental dynamics with patterns in species' occupancy have been lacking. Here I show the utility of such integration. In this study I utilize data on climatic variability, previous records of occurrence, results from field surveys, and modeled spatial projections of climate suitability through time to make inferences about range edge dynamics for kit fox (*Vulpes macrotis*) at the north and east-most extent of the species' distribution in east-central Utah and west-central Colorado for the 27-year period, 1983 to 2009. My results elucidate the roles of mean climate suitability, spatial gradients in climate, and interannual weather variation on range limit formation and occupancy persistence. From spatio-temporal distribution modeling results, a paucity of historic records, a documented extirpation, and survey results, it is apparent that a soft range edge occurs 80 km farther west than an abrupt edge predicted solely by the occurrence of suitable mean climate for kit fox in the study area over the past 27 years. Results indicate that kit fox occupancy likely is on average low or intermittent east of this functional range edge. The novel approach used here is relevant to studies of population and range limit dynamics elsewhere.

CONTENTS

INTRODUCTION **1**

Study Species 2

MATERIALS AND METHODS **6**

Study Area 6

Field Survey Methods 7

- Detection Stations 8
- Sampling Protocol 12
- Sites Surveyed 14
- Sample Periods and Survey Checks 20
- Bait 20
- Evaluations of Detection Data 21
- Efficacy of Detection Station Designs 22

Spatio-temporal Distribution Modeling 22

- Occurrence Records 23
- Climate Variables 24
- Model Building 26
- Model Performance Evaluation 26
- Projecting Distributions of Suitable Climate Though Time 28
- Predictive Distribution Mapping 28
- Suitable Mean Climate Distribution Map 29
- Mapping Spatio-temporal Variability in Suitable Climate 29
- Analysis of Climate Variable Importance 30
- Spatial Gradients in Mean Climate Conditions Across the Range Edge 31

RESULTS **32**

Field Surveys 32

- Test of Two-in-one Hair Snare/Track-plate Detection Station 32
- Kit Fox Detections 33
- Efficacy of Detection Station Designs 36
- Non-target Species Detected 38

Spatio-temporal Distribution Modeling 39
Model Performance 39
Evaluation of Projection Clamping 40
Threshold Evaluation 41
Suitable Mean Climate Distribution Map 41
Heterogeneity in Spatio-temporal Variability in Suitable Climate 41
Climate Variable Importance 46
Spatial Gradients in Mean Climate Conditions Across the Range Edge 46
DISCUSSION 50
Current Extent of Occupancy 50
Distribution of Suitable Mean Climate 51
Legacy of Interannual Variation in Occurrence of Suitable Mean Climate 52
Spatial Gradients in Mean Climate Conditions Across the Range Edge 54
Research Needs 56
CONCLUSION 56
REFERENCES 58

TABLES

Table

1. Locations of test points in east-central Utah, 2008……………………………………12
2. Kit fox sampling site locations in west-central Colorado in 2008 and east-central Utah in 2009……………………………………………………………………………....14
3. Kit fox detections during test in east-central Utah, 2008……………………..…….32
4. Kit fox detections in west-central Colorado in 2008 and east-central Utah in 2009…..34
5. Unique kit fox detections, detection rate, and detection success in west-central Colorado in 2008 and east-central Utah in 2009………………………………………36
6. Non-target carnivore species detections in west-central Colorado in 2008 and east central Utah in 2009…………………………………………………………….....38
7. Locations of non-target carnivore species detected in west-central Colorado in 2008 and east-central Utah in 2009……………………………………............................39

FIGURES

Figure

1. A juvenile kit fox (*Vulpes macrotis*) photographed during study 11 October 2009 in Grand County, Utah……………………………………………………………………..3
2. Map of study area in east-central Utah and west-central Colorado, USA………………7
3. Kit fox detection stations……………………………………………………………….9
4. Kit fox survey locations, 2008–2009…………………………………………………..19
5. Spatio-temporal distribution modeling extent……………………………………….25
6. Kit fox survey locations and detections, 2008–2009………………………….…….35
7. Kit fox print obtained on track-plate and hair captured by a brush inside a two-in-one detection station……………………………………………………………………..36
8. Total unique kit fox detections, detections by station type, and detection rates………37
9. AUC results for test data from all partitions of the occurrence data for the 20 replicate models……………………………………………………………………………….40
10. Predicted distribution of suitable mean climate for kit fox……………….…………42
11. Predicted distribution of suitable mean climate for kit fox and locations of detections 2008–2009…………………………………………………………………………..43
12. Predicted distribution of suitable mean climate for kit fox and extent of private lands within the study area……………………………………………………….……….44
13. Spatio-temporal variation in occurrence of mean suitable climate conditions for kit fox..45
14. Results for jackknife tests of variable importance……………………………………..47
15. Extents used for climate gradient analysis…………………………………….…….48
16. Gradients in mean climate conditions……………………………………….……49

INTRODUCTION

Climate variables are widely considered to be the most important environmental factors influencing the geographic distribution of species (Gaston 2003; Kearney and Porter 2009; Sexton et al. 2009). Geographic ranges are temporally dynamic, expanding, contracting, and shifting in space over time, often in response to climate (Gaston 2003). Climate is known to affect species directly and indirectly via influences on physiology and behavior of individuals and demographic processes of populations (Gaston 2003). Populations at range margins may be particularly vulnerable to fluctuations in climate where local mean conditions may already be near the environmental tolerance limits of the species (Zimmerman et al. 2009). High temporal variance in demographic properties in these marginal environments may lead to elevated extinction risk and range limit maintenance (Holt et al. 2005; Maurer and Taper 2002). Though localized extinctions at range margins are commonly attributed to extreme weather events, few investigators have evaluated the role of climatic variability in determining species' distributions (Gaston 2009) and to my knowledge none have examined impacts on long-term stability of peripheral populations.

Arid lands of the southwestern United States are characterized by extreme interannual and interdecadal climate variability (Sheppard et al. 2002). These dynamic landscapes provide a unique opportunity to evaluate the role of climatic variability in species' range limit formation. In this study, I examine the effects and legacy of interannual climate variation on the current extent of occupancy and predicted distribution of suitable habitat for kit fox (*Vulpes macrotis*) near the north and eastern-most range edge in east-central Utah and west-central Colorado for the 27-year period, 1983 to 2009. This species and study area were selected for analysis because kit fox ecology is intimately tied to climate, the species is of conservation concern in the region, and its current and potential distributions are not known. To accomplish this work I used an approach combining previous records of occurrence, results from field surveys, and modeled spatial projections of climate suitability through time to make inferences about range edge dynamics and probabilities of occupancy persistence.

Given the behavioral ecology and unique morphological and physiological adaptations of the species, I predict that climatic variables, especially those pertaining to precipitation and summer and winter temperatures, will be good predictors of records of occurrence and the potential geographic range of kit fox. I also predict the occurrence of a gradient in mean climate and interannual variability across the study area and a legacy of past climate conditions on the present distribution and functional range edge of the species.

Study Species

Kit fox ecology and population dynamics reflect the climatic regimes experienced across the species' geographic range. The kit fox (Fig. 1) is the smallest fox in North America and is uniquely adapted for life in hot, dry deserts characterized by highly variable precipitation (Cypher 2003). Kit foxes occur in arid and semiarid grasslands and shrublands across much of the southwestern United States, west of the Rocky Mountains and in Baja, California and northern Mexico (Hall 1981; McGrew 1979). Behavioral adaptations that reduce heat loads and conserve water, thus promoting survival in these environments, include diurnal den use and nocturnal activity (Cypher 2003). Morphological adaptations include stiff tufts of protective hair between toe pads that insulate soles of feet from hot ground surfaces (Grinnell et al. 1937). Physiological adaptations permit efficient and adequate water intake from prey, precluding the necessity for open water (Golightly and Ohmart 1983). Water conservation is furthered by minimal use of evaporative heat loss. Instead, kit foxes use thermal conductance and passive heat dissipation mainly via vasodilation and increased blood flow through the head, large ears, lower legs, and paws (Golightly and Ohmart 1983; Klir and Heath 1992).

Figure 1. A juvenile kit fox (*Vulpes macrotis*) photographed during study 11 October 2009 in Grand County, Utah.

Life history traits, including age of reproductive maturity, adult longevity, and large annual litters, predict a relatively high reproductive potential and promote population persistence in landscapes plagued with temporal variability in climate suitability (Cypher 2003). Numerous multiyear studies have documented high frequency, high amplitude fluctuations in kit fox populations, with sizes varying five-fold or more from year to year (Cypher and Scrivner 1992; Cypher and Spencer 1998; Egoscue 1975; White and Garrott 1997; White and Ralls 1993: White et al. 1996). These population fluctuations have been attributed to shifts in primary prey availability, with most resulting from changes in annual precipitation. The highly variable precipitation common to deserts results in boom and bust periods in plant primary production and feast or famine conditions for animals (Polis et al. 2005; Ralls and Eberhart 1997; White and Garrott 1997, 1999; White and Ralls 1993). Periods of prey scarcity resulting from poor weather or population cycles contribute to episodes of increase in the number of female kit foxes who do not successfully reproduce, a reduction in litter size, and ultimately population declines the following year (Egoscue 1975; White and Garrott 1997; White and Garrott 1999; White and Ralls 1993). When prey abundance is low, elevated interspecific exploitative and interference competition with coyotes and red foxes also has an additive and powerful effect on population regulation for kit foxes (Cypher and Spencer 1998; Ralls and White 1996; White et al. 2000; White and Garrott 1997; White and Garrott 1999). On the other hand, periods with favorable weather promote high densities of prey, kit foxes reproduce at their biotic potential, and populations irrupt (O'Farrell 1987; Ralls and White 1995; White and Garrott 1999). In any given year, kit fox populations regulated by prey abundance may reflect cumulative precipitation of the previous two or three years (Cypher et al. 2000; Dennis and Otten 2000). Though marked year to year fluctuations in numbers may be common, high reproductive potential permits rapid recovery from crashes with no overall decreases in otherwise stable populations, as evidenced by 24 years of observations at the Carrizo Plain Natural Area in California (J. Lidberg, pers. comm. cited in Ralls and White 1995).

Kit fox populations are thought to be stable throughout most of the species' geographic range, although localized declines and extirpations have been documented (Cypher 2003). Populations in Mexico and the San Joaquin Valley in California are severely imperiled (Cypher 2003; Moehrenschlager et al. 2004; O'Farrell 1987). Degradation, loss, and fragmentation of habitat, human-caused mortality, and exploitative and interference competition with larger canids are driving these declines (Moehrenschlager et al. 2004). Recent observations of kit foxes at the northern range periphery in Oregon, Idaho, and Colorado are few, but reasons for rarity and long-term trends there are not presently understood (O'Farrell 1987; Seglund and Garner 2007).

Knowledge of occupancy in the northern- and eastern-most limits of the range in east-central Utah and west-central Colorado comes from a small number of historic records dating from 1959 in the Cisco Desert in Grand County, Utah and extreme western Mesa County, Colorado. More recent spotlight surveys were performed 2005 to 2009 in Grand County, Utah and an intensive survey was carried out to assess the distribution and status of the species in western Colorado 1992 to 1996. Follow up surveys were also performed 1997 to 2000 and in 2007. During the period of study from 1992 to 1996, a population of fewer than 50 kit foxes was discovered and monitored (Fitzgerald 1996). Although a small number of kit foxes found were residents of the Grand and Lower Gunnison River valleys in Mesa County, the core of this population existed in the Uncompaghre Valley in Montrose County. Fitzgerald (1996) speculated that, given the small population size and very high levels of mortality among all age groups, the kit fox population in western Colorado would not be self-sustaining. To track the status of the population, kit fox dens were monitored 1997 to 2000. During this time frame, a complete collapse of the population was documented with no evidence of kit fox occupancy in the Uncompaghre Valley by 2000 (Beck 1997, 1998, 1999, 2000). Previously occupied areas of the valley were resurveyed in 2007 to assess natural recovery of the species. This survey yielded only one questionable track detection of kit fox (Seglund and Garner 2007). Because adequate population data are lacking to understand the long-term dynamics and trends of the species near the north and eastern-most range edge, I seek to elucidate the potential role of climate in limiting the extent and distribution of suitable habitat and occupancy of the species over time in east-central Utah and west-central Colorado.

Materials and Methods

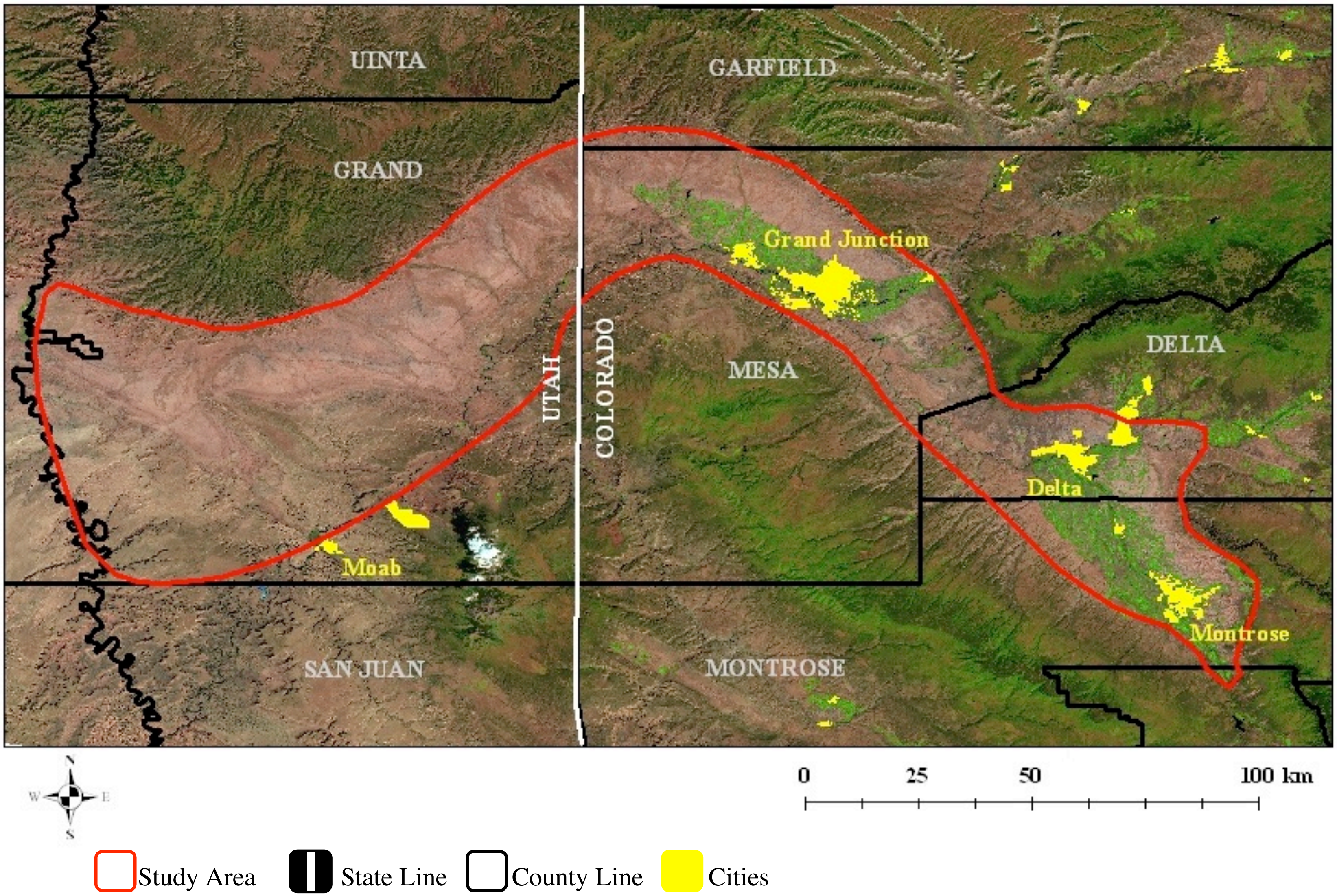
Study Area

The study area occurs within the Colorado Plateau Province and primarily encompasses broad desert valleys bordered by mesas and plateaus in east-central Utah and west-central Colorado (Fig. 2). The study area is approximately 250 km long and extends from the Green River at the western edge of Grand County, Utah, east and south to the town of Montrose, Montrose County, Colorado. Width of the study area varies from roughly 60 km, at its widest in western Grand County, to less than 15 km near the town of Delta, Delta County, Colorado, where lowland habitats constrict. Dominant lowland plant communities include mat saltbush shrubland, salt desert scrub, black brush-Mormon tea shrubland, and greasewood flat.

Field surveys for the species within the study area were focused in areas presumed to have the greatest potential of supporting kit foxes. I resurveyed sites where Fitzgerald (1996) located kit foxes and adjacent lowland grassland, shrubland and badlands habitats in the Grand, Lower Gunnison, and Uncompaghre valleys of Mesa, Delta, and Montrose counties, Colorado. Surveys were also performed where kit foxes have been detected during spot-light surveys in recent years in Grand County, Utah (A. Wright, pers. comm.).

For modeling purposes, the study area was widened to the entire state of Utah and the western one-half of Colorado to capture a broader range of environmental conditions experienced by kit fox in the northern part of their geographic range, to reduce regional overfitting of the model, and to permit predictions across the greatest extent of lowland habitats immediately west of the foothills of the Rocky Mountains.

Figure 2. Map of study area in east-central Utah and west-central Colorado, USA.



Field Survey Methods

To assess the current distribution of kit fox near the north and eastern-most range edge, I conducted extensive field surveys for the species. Kit foxes are considered to be easily detected by live trapping and non-invasive sampling methods (B. Cypher, pers. comm.; McGrew 1979). Following a recommendation from Fitzgerald (1996) to minimize disturbance to kit foxes, only non-invasive sampling methods were used in this survey. In order to improve confidence in survey data, two complementary detection methods, track-plates housed in boxes and hair snare/track-plate detection stations ("two-in-one") were used (Fig. 3). Carnivore tracks obtained with track-plates are often rapidly identified, providing almost immediate verification of species' presence. Precipitation and wind scouring, however, may impede operability of the plates, so I chose to deploy the two-in-one hair snare/track-plate detection stations as well. The hair snare function is not impacted by precipitation events and hair typically may be identified to species with high confidence. Surveys were conducted late summer and fall in 2008 and 2009. Detection rates for kit foxes tend to be highest during this part of the year when adult animals are less sedentary and young of the year are dispersing (Egoscue 1956; Fitzgerald 1996; Sargeant et al. 2003). Surveys were conducted 30 August to 23 November 2008 in Colorado and 19 September to 31October 2009 in Utah.

Detection Stations

track-plate boxes

Track-plates housed in boxes (henceforth referred to as "track-plate boxes") (Fig. 3) are known to be effective at assessing non-invasively the presence of small to medium size carnivores including swift fox (*Vulpes velox*) and kit fox (A. Seglund, pers. comm.; Seglund and

Figure 3. Kit fox detection stations. Track-plate box (left). Two-in-one hair snare/track-plate detection station (right).

Garner 2007; Uresk et al. 2003). Track-plates 31 cm wide x 81 cm long were constructed from 0.063 gauge aluminum sheeting. Plates were sooted with an acetylene gas flame from a welding torch. A 30 cm long strip of white contact paper was affixed, sticky surface up, to the center of the sooted track-plate. This promotes the transfer of a distinguishable track made when the animal steps from the sooted portion of the plate onto the sticky contact paper. Contact paper found with tracks, were labeled with the date and location obtained and archived for future identification and reference. Digital copies of carnivore tracks are archived at the University of Colorado Museum of Natural History, Boulder, Colorado.

The track-plate was placed in a plywood box to protect it from precipitation and other inclement weather. The 83 cm long x 31 cm wide x 33 cm high box was constructed from low-grade plywood. One end of the plywood box was left open for the animal to enter and walk across the plate. Bait was placed at the rear of the box to lure the animal to enter.

Seglund and Garner (2007) used the track-plate boxes described above in a survey for kit foxes in Colorado in 2007. To be certain of the station's ability to detect kit foxes, they tested the boxes in east-central Grand County, Utah, in 2007. Detections were made during the test at four of nine track-plate boxes with 44% trap success (detections/sampling locations).

two-in-one hair snare/track-plate detection stations

The two-in-one hair snare/track-plate detection stations (Fig. 3) used in this study were triangular "cubbies" with only one entrance, or "tunnels" with two openings. The stations were fitted with track-plates identical to the ones described above and gun brushes which served as hair snares. Hairs intercepted by snares were identified to species on the basis of color or cuticular scale pattern. Identifications were made by comparison to reference hairs obtained from specimens at the University of Colorado Museum of Natural History and published dichotomous keys (Debelica and Thies 2009; Mayer 1952; Moore et al. 1997). The hair snare design used in this study is known to be effective at censusing marten (*Martes americana*) and fisher (*Martes pennanti*) (Kendall and McKelvey 2008; M. Schwartz, pers. comm.), but had not been used to detect kit foxes prior to this study.

The triangular detection stations were 81 cm long. Each side of the triangle measured 30.5 cm. Each station was folded into size from one sheet of 4 mm thick corrugated plastic (*Coroplast*: Colorado Plastic Products, Inc., Boulder, Colorado) measuring 122 x 83 cm. The sheet was held in its triangular shape by two large binder clips on each end. Backs for the cubbies were made with black sunshade cloth. Three zip ties attached the 30.5 cm triangular piece of fabric to the station. Each cubby housed one track-plate and two 30-caliber brass gun brushes at the opening. During year two of the study, the backs were removed from one-half of the stations. These tunnel-like stations had two openings with two brushes at each entrance.

Brushes were connected to a bolt on the stations using electrical fasteners. Because dorsal guard hairs are preferred, the brushes were attached at the centers of opposite walls of the triangle approximately 15 cm from the opening. Brushes were bent 90 degrees at the base so that they could be directed inwards, opposite station openings. In this position, brushes offer less resistance to animals entering the station. Bait was placed at the back of cubbies and in the center of tunnels to lure the animal past the hair snare brushes and across the track-plate. Brushes collected from stations were placed in labeled resealable bags. In a controlled environment hairs were removed from brushes, counted, and placed in 5 x 5 cm resealable bags for storage. Hair samples collected were deposited at the University of Colorado Museum of Natural History, Boulder, Colorado. Brushes were cleaned after each use with a flame from a hand-held propane torch and reused.

Because kit foxes are extremely rare in Colorado and their status and distribution there was not known, it was essential the station design be tested at locations known to support the species in the recent past. I chose, therefore, to test the new hair snare stations informally against track-plate boxes (used by Seglund and Garner (2007) and in this study) in east-central Grand County, Utah. Twenty-two experimental stations, each consisting of one track-plate box and one hair snare station tested alongside one another, were established on two transects in Grand County, Utah. Test surveys occurred 1–29 August 2008. Sampling point locations are listed in Table 1. Experimental stations were in place for two weeks. The hair snare stations tested on one transect in the first survey were tunnels and did not include track-plates. For the second transect and second survey, hair snare stations were modified with the addition of a back and track-plate.

Experimental stations were placed 0.8–1.6 km apart, approximately 50 m from roads. Fresh chicken was used as bait to lure animals into stations.

Table 1. Locations of test points in east-central Utah, 2008.

Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	End Date
1	12	640725	4311569	1-Aug-08	15-Aug-08
2	12	641429	4311810	1-Aug-08	15-Aug-08
3	12	642576	4312098	1-Aug-08	15-Aug-08
4	12	643016	4311485	1-Aug-08	15-Aug-08
5	12	643443	4310667	1-Aug-08	15-Aug-08
6	12	643765	4310095	1-Aug-08	15-Aug-08
7	12	644453	4309151	1-Aug-08	15-Aug-08
8	12	645216	4307968	1-Aug-08	15-Aug-08
9	12	645683	4307460	1-Aug-08	15-Aug-08
10	12	646259	4306933	1-Aug-08	15-Aug-08
11	12	646464	4306121	1-Aug-08	15-Aug-08
12	12	621016	4309943	16-Aug-08	29-Aug-08
13	12	621457	4309337	16-Aug-08	29-Aug-08
14	12	621926	4308702	16-Aug-08	29-Aug-08
15	12	622403	4308058	16-Aug-08	29-Aug-08
16	12	622881	4307408	16-Aug-08	29-Aug-08
17	12	623349	4306768	16-Aug-08	29-Aug-08
18	12	623811	4306141	16-Aug-08	29-Aug-08
19	12	624289	4305495	16-Aug-08	29-Aug-08
20	12	625233	4304224	16-Aug-08	29-Aug-08
21	12	625676	4303548	16-Aug-08	29-Aug-08
22	12	625813	4302778	16-Aug-08	29-Aug-08

Sampling Protocol

To maximize survey effort given the time and budgetary constraints of this study, three sampling points per 5 km^2 hypothetical home range patch were established. This was deemed an appropriate level of effort as Long and Zielinski (2008) recommend placing a minimum of two detection stations per potential home range for mammalian carnivore species and because one detection station per hypothetical home range-sized patch is probably sufficient to detect kit foxes when present (B. Cypher, pers. comm.). Average kit fox home range size in good habitat is 5 km^2 (Cypher 2003). Home ranges may be much larger in suboptimal habitat.

Because of logistical constraints, all sampling occurred along roads. Studies of the effects of roads on kit foxes show minimal impacts on demography, ecology, and behavior (Bjurlin 2004; Bjurlin et al. 2005; Cypher et al. 2005; Cypher et al. 2009). Thus, roads routinely and conveniently function as transects for occupancy surveys for the species (B. Cypher, pers. comm.) (e.g. Fitzgerald 1996; Seglund and Garner 2007; Sargeant et al. 2003; Warrick and Harris 2001; A. Wright, pers. comm.).

Transects through hypothetical home ranges were 5 km long. Each transect had three sampling points placed 1.7 km apart. One track-plate box and one two-in-one hair snare/track-plate detection station were placed on opposite sides of the road from one another, 20–50 m from the road at each sampling point. Though some transects in the vicinity of previously occupied sites were more closely spaced, most transects in the eastern half of the study area were 3–5 km apart. In the western half of the study area transects were spaced 3–20 km apart.

The sampling protocol following questionable kit fox detections was to double the density of detection stations around sampling points where detections occurred and extend the sample period for the transect by two weeks. In addition, if available, an infrared motion-triggered camera was to be placed at the site of the questionable detection to capture a photo of the animal upon its return. This protocol was selected because foxes are commonly considered to be “trap happy;” that is, they generally visit multiple traps and detection stations within their home range and often return to them repeatedly (B. Cypher, pers. comm.; A. Seglund, pers. comm.). Therefore, there is a good probability of detecting an animal more than once and hopefully acquiring a more diagnostic print, hair, or photograph of the animal for correct species identification.

Sites Surveyed

Surveys for kit fox occurred in previously occupied sites, in the vicinity of reported observations of the species, and in adjacent grassland, shrubland, and badland habitats on public lands in portions of Delta, Garfield, Mesa, and Montrose counties, Colorado, and in Grand County, Utah. Survey effort was greatest in the eastern half of the study area in west-central Colorado where the population crash occurred in the last half of the 1990's. Forty-five transects and 136 sampling points were surveyed with track-plate boxes and two-in-one detection stations in Colorado in 2008. Twenty-seven transects in west-central Colorado could not be surveyed because of private road-blocks, poor road conditions, or very high levels of vehicular traffic or recreation. Twenty transects and 60 sampling points were surveyed in Utah in 2009. Table 2 lists the UTM coordinates of sampling points and Fig. 4 shows their locations.

Table 2. Kit fox sampling site locations in west-central Colorado, 2008 and east-central Utah, 2009.

Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	Check Date	End Date
Colorado 2008						
1A	12	670991	4345972	12-Oct-08	17-Oct-08	24-Oct-08
1B	12	670164	4347457	12-Oct-08	17-Oct-08	24-Oct-08
1C	12	669266	4348989	12-Oct-08	17-Oct-08	24-Oct-08
2A	12	671542	4350124	12-Oct-08	17-Oct-08	24-Oct-08
2B	12	671514	4351828	12-Oct-08	17-Oct-08	24-Oct-08
2C	12	671011	4353449	12-Oct-08	17-Oct-08	24-Oct-08
3A	12	670731	4356216	12-Oct-08	17-Oct-08	24-Oct-08
3B	12	670144	4357809	12-Oct-08	17-Oct-08	24-Oct-08
3C	12	668915	4359011	12-Oct-08	17-Oct-08	24-Oct-08
4A	12	678054	4353072	12-Oct-08	17-Oct-08, 24-Oct-08	10-Nov-08
4B	12	678054	4354777	12-Oct-08	17-Oct-08, 24-Oct-08	10-Nov-08
4C	12	677970	4356482	12-Oct-08	17-Oct-08, 24-Oct-08	10-Nov-08
5A	12	678230	4353628	24-Oct-08	30-Oct-08	10-Nov-08
5B	12	677507	4353937	24-Oct-08	30-Oct-08	10-Nov-08
5C	12	678332	4355309	24-Oct-08	30-Oct-08	10-Nov-08
5D	12	677874	4355469	24-Oct-08	30-Oct-08	10-Nov-08
6A	12	675054	4351325	12-Oct-08	17-Oct-08	24-Oct-08

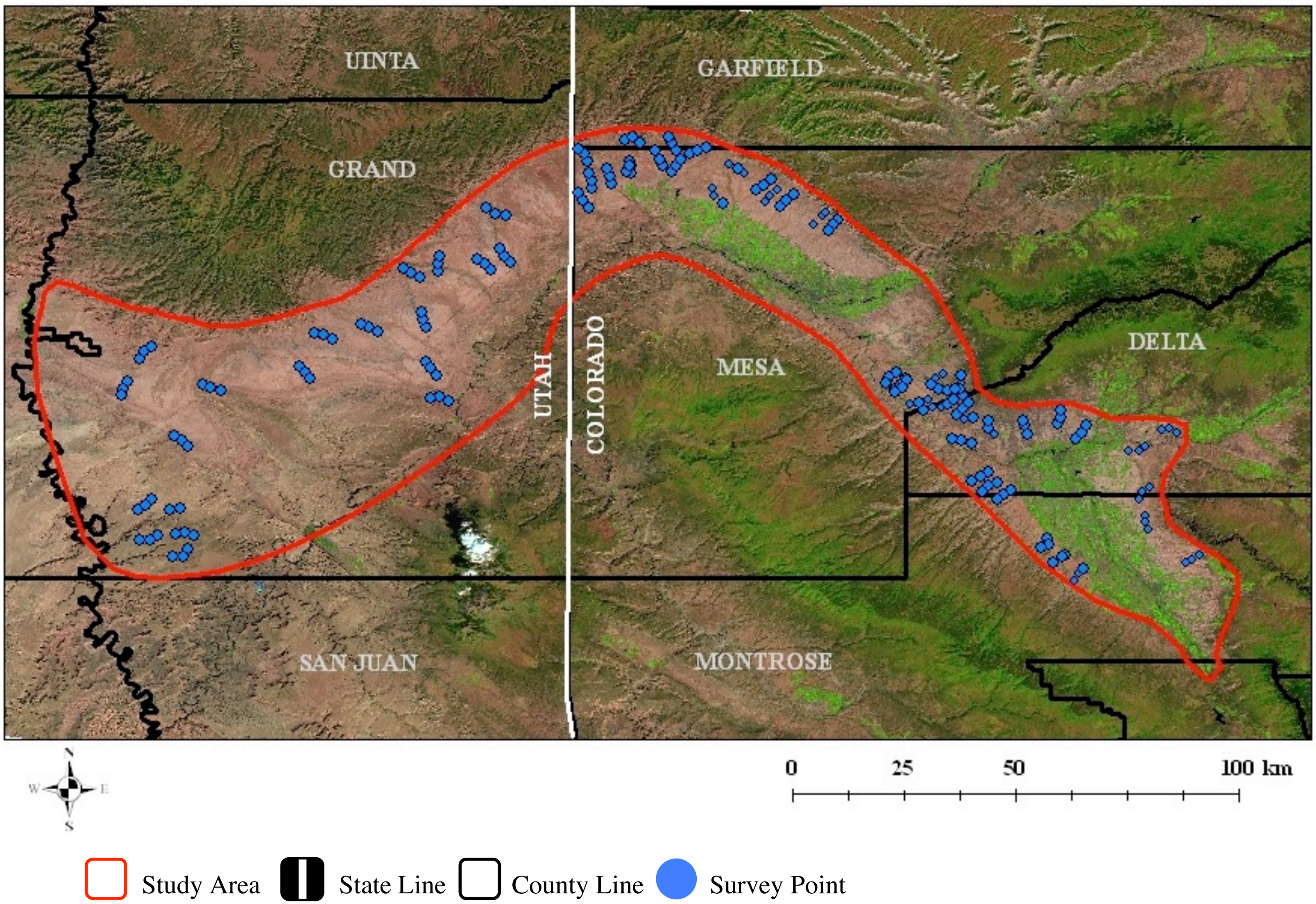
Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	Check Date	End Date
6B	12	674718	4353039	12-Oct-08	17-Oct-08	24-Oct-08
6C	12	674122	4354642	12-Oct-08	17-Oct-08	24-Oct-08
7A	12	677141	4361144	12-Oct-08	17-Oct-08	24-Oct-08
7B	12	678420	4361762	12-Oct-08	17-Oct-08	24-Oct-08
7C	12	679749	4360419	12-Oct-08	17-Oct-08	24-Oct-08
8A	12	683644	4355400	12-Oct-08	17-Oct-08	24-Oct-08
8B	12	683223	4356959	12-Oct-08	17-Oct-08	24-Oct-08
8C	12	682323	4358753	12-Oct-08	17-Oct-08	24-Oct-08
9A	12	685364	4354182	12-Oct-08	17-Oct-08	24-Oct-08
9B	12	686047	4355641	12-Oct-08	17-Oct-08	24-Oct-08
9C	12	686763	4356941	12-Oct-08	17-Oct-08	24-Oct-08
10A	12	686015	4359114	12-Oct-08	17-Oct-08	24-Oct-08
10B	12	685244	4360628	12-Oct-08	17-Oct-08	24-Oct-08
10C	12	684589	4361878	12-Oct-08	17-Oct-08	24-Oct-08
11A	12	688297	4358204	12-Oct-08	17-Oct-08	24-Oct-08
11B	12	689710	4359147	12-Oct-08	17-Oct-08	24-Oct-08
11C	12	691317	4359661	12-Oct-08	17-Oct-08	24-Oct-08
12A	13	178217	4360430	25-Oct-08	1-Nov-08	8-Nov-08
12B	12	696978	4355288	25-Oct-08	1-Nov-08	8-Nov-08
12C	13	180573	4358118	25-Oct-08	1-Nov-08	8-Nov-08
13A	12	694355	4347228	25-Oct-08	1-Nov-08	8-Nov-08
13B	13	175299	4353446	25-Oct-08	1-Nov-08	8-Nov-08
13C	13	174924	4355100	25-Oct-08	1-Nov-08	8-Nov-08
14A	12	700155	4350405	28-Oct-08	8-Nov-08	23-Nov-08
14B	12	701530	4351572	28-Oct-08	8-Nov-08	23-Nov-08
14C	12	702713	4352848	28-Oct-08	8-Nov-08	23-Nov-08
15A	13	183995	4351715	30-Oct-08	8-Nov-08	23-Nov-08
15B	13	185031	4353060	30-Oct-08	8-Nov-08	23-Nov-08
15C	13	186317	4354185	30-Oct-08	8-Nov-08	23-Nov-08
16A	12	704434	4347034	30-Oct-08	8-Nov-08	23-Nov-08
16B	12	705404	4348453	30-Oct-08	8-Nov-08	23-Nov-08
16C	12	706801	4349873	30-Oct-08	8-Nov-08	23-Nov-08
17A	13	192270	4346443	26-Oct-08		23-Nov-08
17B	13	193846	4348318	26-Oct-08		23-Nov-08
17C	13	194606	4349016	26-Oct-08		23-Nov-08
18A	12	714620	4344198	23-Oct-08	1-Nov-08	9-Nov-08
18B	12	713826	4343114	23-Oct-08	1-Nov-08	9-Nov-08
18C	12	712872	4341602	23-Oct-08	1-Nov-08	9-Nov-08
19A	12	757512	4296428	30-Aug-08	9-Sep-08	12-Sep-08
19B	12	758522	4297990	30-Aug-08	9-Sep-08	12-Sep-08
19C	12	759446	4299420	30-Aug-08	9-Sep-08	12-Sep-08
20A	12	754361	4299831	30-Aug-08	9-Sep-08	12-Sep-08
20B	12	754778	4301073	30-Aug-08	9-Sep-08	12-Sep-08
20C	12	754679	4302709	30-Aug-08	9-Sep-08	12-Sep-08
21A	12	749061	4297233	12-Sep-08	19-Sep-08	26-Sep-08
21B	12	748579	4299104	12-Sep-08	19-Sep-08	26-Sep-08
21C	12	748109	4300363	12-Sep-08	19-Sep-08	26-Sep-08

Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	Check Date	End Date
22A	13	222027	4298255	12-Sep-08	19-Sep-08	26-Sep-08
22B	12	742137	4298445	12-Sep-08	19-Sep-08	26-Sep-08
22C	12	742108	4299897	12-Sep-08	19-Sep-08	26-Sep-08
23A	13	216944	4301583	30-Aug-08	9-Sep-08	12-Sep-08
23B	13	218598	4302051	30-Aug-08	9-Sep-08	12-Sep-08
23C	12	739525	4300755	30-Aug-08	9-Sep-08	12-Sep-08
24A	12	736553	4301374	12-Sep-08	19-Sep-09	26-Sep-08
24B	12	737664	4302627	12-Sep-08	19-Sep-09	26-Sep-08
24C	12	738458	4304149	12-Sep-08	19-Sep-09	26-Sep-08
25A	12	734824	4303443	13-Sep-08	19-Sep-09	26-Sep-08
25B	12	736012	4304677	13-Sep-08	19-Sep-09	26-Sep-08
25C	12	737568	4305505	13-Sep-08	19-Sep-09	26-Sep-08
26A	12	736960	4310132	27-Sep-08	3-Oct-08	10-Oct-08
26B	13	216748	4309945	27-Sep-08	3-Oct-08	10-Oct-08
26C	12	736803	4306908	27-Sep-08	3-Oct-08	10-Oct-08
27A	12	733265	4306716	19-Sep-08	27-Sep-08	3-Oct-08
27B	12	734938	4306472	19-Sep-08	27-Sep-08	3-Oct-08
27C	12	736006	4307083	19-Sep-08	27-Sep-08	10-Oct-08
28A	12	731931	4307682	19-Sep-08	27-Sep-08	3-Oct-08
28B	13	212308	4311040	19-Sep-08	27-Sep-08	3-Oct-08
28C	13	213684	4312040	19-Sep-08	27-Sep-08	3-Oct-08
29A	12	746662	4284627	30-Aug-08	9-Sep-08	12-Sep-08
29B	12	745250	4283648	30-Aug-08	9-Sep-08	12-Sep-08
29C	12	744314	4282491	30-Aug-08	9-Sep-08	12-Sep-08
30A	12	744216	4286193	30-Aug-08	9-Sep-08	12-Sep-08
30B	12	742706	4285473	30-Aug-08	9-Sep-08	12-Sep-08
30C	12	741477	4284297	30-Aug-08	9-Sep-08	12-Sep-08
31A	12	742552	4288474	30-Aug-08	9-Sep-08	12-Sep-08
31B	12	741164	4287459	30-Aug-08	9-Sep-08	12-Sep-08
31C	12	739727	4286543	30-Aug-08	9-Sep-08	12-Sep-08
32A	12	739254	4295028	30-Aug-08	9-Sep-08	12-Sep-08
32B	12	737509	4295406	30-Aug-08	9-Sep-08	12-Sep-08
32C	12	736031	4295897	30-Aug-08	9-Sep-08	12-Sep-08
33A	13	213230	4304476	28-Sep-08	3-Oct-08	10-Oct-08
33B	13	211547	4304741	28-Sep-08	3-Oct-08	10-Oct-08
33C	12	730712	4302184	28-Sep-08	3-Oct-08	10-Oct-08
34A	13	207529	4305478	28-Sep-08	3-Oct-08	10-Oct-08
34B	12	729835	4303837	28-Sep-08	3-Oct-08	10-Oct-08
34C	13	210811	4306340	28-Sep-08	3-Oct-08	10-Oct-08
35A	12	725623	4306721	27-Sep-08		10-Oct-08
35B	12	726722	4307533	27-Sep-08		10-Oct-08
35C	12	727460	4308937	27-Sep-08		10-Oct-08
36A	12	727655	4308645	30-Aug-08		12-Sep-08
36B	12	726938	4306879	30-Aug-08		12-Sep-08
36C	12	725506	4305884	30-Aug-08		12-Sep-08
37A	12	725670	4310527	30-Aug-08		12-Sep-08
37B	12	724408	4309216	30-Aug-08		12-Sep-08

Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	Check Date	End Date
37C	12	723932	4307874	30-Aug-08		12-Sep-08
38A	13	245667	4293793	26-Sep-08	3-Oct-08	10-Oct-08
38B	13	247338	4293532	26-Sep-08	3-Oct-08	10-Oct-08
38C	13	248566	4294578	26-Sep-08	3-Oct-08	10-Oct-08
39A	13	249016	4285404	26-Sep-08	3-Oct-08	10-Oct-08
39B	13	247672	4284361	26-Sep-08	3-Oct-08	10-Oct-08
39C	13	247068	4282687	26-Sep-08	3-Oct-08	10-Oct-08
40A	13	248028	4279230	26-Sep-08	3-Oct-08	10-Oct-08
40B	13	247929	4277566	26-Sep-08	3-Oct-08	10-Oct-08
40C	13	248394	4276069	26-Sep-08	3-Oct-08	10-Oct-08
41A	12	759737	4267598	13-Sep-08	19-Sep-08	26-Sep-08
41B	13	235892	4266481	13-Sep-08	19-Sep-08	26-Sep-08
41C	13	235012	4265077	13-Sep-08	19-Sep-08	26-Sep-08
42A	12	756489	4270443	13-Sep-08	19-Sep-08	26-Sep-08
42B	12	756034	4269904	13-Sep-08	19-Sep-08	26-Sep-08
42C	12	754558	4268826	13-Sep-08	19-Sep-08	26-Sep-08
43A	12	753263	4274146	13-Sep-08	19-Sep-08	26-Sep-08
43B	12	753708	4272822	13-Sep-08	19-Sep-08	26-Sep-08
43C	12	752301	4272068	13-Sep-08	19-Sep-08	26-Sep-08
44A	13	257265	4269920	26-Sep-08	3-Oct-08	10-Oct-08
44B	13	255895	4268910	26-Sep-08	3-Oct-08	10-Oct-08
44C	13	254907	4268358	26-Sep-08	3-Oct-08	10-Oct-08
45A	13	252753	4298645	3-Oct-08		20-Oct-08
45B	13	251392	4298131	3-Oct-08		20-Oct-08
45C	13	254079	4297458	3-Oct-08		20-Oct-08
Utah 2009						
46A	12	653289	4345330	17-Oct-09	24-Oct-09	31-Oct-09
46B	12	654855	4344283	17-Oct-09	24-Oct-09	31-Oct-09
46C	12	656796	4343862	17-Oct-09	24-Oct-09	31-Oct-09
47A	12	657644	4333508	17-Oct-09	24-Oct-09	31-Oct-09
47B	12	656615	4334837	17-Oct-09	24-Oct-09	31-Oct-09
47C	12	655800	4336296	17-Oct-09	24-Oct-09	31-Oct-09
48A	12	654357	4331664	17-Oct-09	24-Oct-09	31-Oct-09
48B	12	653265	4332979	17-Oct-09	24-Oct-09	31-Oct-09
48C	12	651816	4333892	17-Oct-09	24-Oct-09	31-Oct-09
49A	12	645063	4330973	17-Oct-09	24-Oct-09	31-Oct-09
49B	12	645191	4332899	17-Oct-09	24-Oct-09	31-Oct-09
49C	12	645457	4334586	17-Oct-09	24-Oct-09	31-Oct-09
50A	12	641921	4329792	17-Oct-09	24-Oct-09	31-Oct-09
50B	12	640539	4330750	17-Oct-09	24-Oct-09	31-Oct-09
50C	12	639113	4331708	17-Oct-09	24-Oct-09	31-Oct-09
51A	12	643178	4318618	19-Sep-09	26-Sep-09	3-Oct-09
51B	12	642694	4320258	19-Sep-09	26-Sep-09	3-Oct-09
51C	12	642345	4321925	19-Sep-09	26-Sep-09	3-Oct-09
52A	12	634871	4317482	19-Sep-09	26-Sep-09	3-Oct-09
52B	12	633385	4318381	19-Sep-09	26-Sep-09	3-Oct-09
52C	12	631895	4319137	19-Sep-09	26-Sep-09	3-Oct-09

Sampling Point	NAD 83 Zone	Easting	Northing	Start Date	Check Date	End Date
53A	12	623773	4316774	19-Sep-09	26-Sep-09	3-Oct-09
53B	12	625491	4316505	19-Sep-09	26-Sep-09	3-Oct-09
53C	12	626887	4315539	19-Sep-09	26-Sep-09	3-Oct-09
54A	12	621288	4309563	26-Sep-09	3-Oct-09	9-Oct-09
54B	12	622272	4308174	26-Sep-09	3-Oct-09	9-Oct-09
54C	12	623285	4306814	26-Sep-09	3-Oct-09	9-Oct-09
55A	12	643432	4310741	19-Sep-09	26-Sep-09	3-Oct-09
55B	12	644302	4309421	19-Sep-09	26-Sep-09	3-Oct-09
55C	12	645255	4307830	19-Sep-09	26-Sep-09	3-Oct-09
56A	12	647419	4301967	19-Sep-09	26-Sep-09	3-Oct-09
56B	12	646038	4302929	19-Sep-09	26-Sep-09	3-Oct-09
56C	12	644380	4302871	19-Sep-09	26-Sep-09	3-Oct-09
57A	12	593359	4310740	10-Oct-09	18-Oct-09	24-Oct-09
57B	12	594063	4312300	10-Oct-09	18-Oct-09	24-Oct-09
57C	12	595422	4313515	10-Oct-09	18-Oct-09	24-Oct-09
58A	12	604396	4305082	27-Sep-09	3-Oct-09	9-Oct-09
58B	12	605902	4304437	27-Sep-09	3-Oct-09	9-Oct-09
58C	12	607517	4303845	27-Sep-09	3-Oct-09	9-Oct-09
59A	12	591201	4305487	10-Oct-09	18-Oct-09	24-Oct-09
59B	12	590492	4303944	10-Oct-09	18-Oct-09	24-Oct-09
59C	12	590205	4302564	10-Oct-09	18-Oct-09	24-Oct-09
60A	12	602004	4291138	10-Oct-09	18-Oct-09	24-Oct-09
60B	12	600920	4292473	10-Oct-09	18-Oct-09	24-Oct-09
60C	12	599627	4293599	10-Oct-09	18-Oct-09	24-Oct-09
61A	12	593357	4277013	10-Oct-09	18-Oct-09	24-Oct-09
61B	12	594752	4277983	10-Oct-09	18-Oct-09	24-Oct-09
61C	12	595703	4279491	10-Oct-09	18-Oct-09	24-Oct-09
62A	12	602384	277737	10-Oct-09	18-Oct-09	24-Oct-09
62B	12	600742	4277384	10-Oct-09	18-Oct-09	24-Oct-09
62C	12	599012	4277014	10-Oct-09	18-Oct-09	24-Oct-09
63A	12	603367	4271240	26-Sep-09	3-Oct-09	9-Oct-09
63B	12	601769	4271919	26-Sep-09	3-Oct-09	9-Oct-09
63C	12	600029	4271759	26-Sep-09	3-Oct-09	9-Oct-09
64A	12	597009	4271443	26-Sep-09	3-Oct-09	9-Oct-09
64B	12	595632	4270379	26-Sep-09	3-Oct-09	9-Oct-09
64C	12	593902	4270210	26-Sep-09	3-Oct-09	9-Oct-09
65A	12	602335	4268191	26-Sep-09	3-Oct-09	9-Oct-09
65B	12	601479	4266617	26-Sep-09	3-Oct-09	9-Oct-09
65C	12	599717	4266714	26-Sep-09	3-Oct-09	9-Oct-09

Figure 4. Kit fox survey locations, 2008–2009.



Sample Periods and Survey Checks

Sample periods (the duration that detection stations are left at the same location) were two weeks. This sample period was deemed sufficient because kit fox detections generally occur within the first few days of a survey or not at all (B. Cypher, pers. comm.). Four transects (9% of Colorado transects) surveyed in 2008 were in place for 3–4 weeks (Table 2). The 2008 survey resulted in more than 3,800 survey nights in Colorado between 30 August and 23 November. The 2009 survey resulted in 1,680 survey nights in Utah between 9 September and 31 October.

Due to time and budget constraints, detection stations were checked and rebaited one time approximately one week into each two week survey, resulting in two sample occasions per station per sample period. According to expert opinion, this should be sufficient effort to detect kit foxes (B. Cypher, pers. comm.). For various reasons, five Colorado transects (11% of Colorado transects) did not receive a mid-survey check and consequently had only one sample occasion (Table 2). Five hundred forty sample occasions in Colorado in 2008 and 240 in Utah in 2009 occurred during the study. Only track-plates with obvious carnivore tracks and non-functioning plates were replaced during mid-survey checks. Brushes were pulled and replaced with clean brushes during the first sample occasion only when hairs were visible or when carnivore tracks were obtained. All brushes were removed and processed following the final sample occasion.

Bait

The bait used to lure animals into stations varied throughout the study, but all are considered to be effective attractants for kit foxes (B. Cypher, pers. comm.). Fresh chicken was used during the first sample period in 2008. Use of this bait was discontinued because the chicken produced oil slicks on the track-plates rendering them less effective and difficult to clean and re-soot. Canned chicken and canned tuna were used during sample periods 2–5 and 6–10, respectively in 2008 and canned mackerel was used in stations on two transects in the vicinity of the sampling point where the probable detection occurred during sample periods 7–8 in 2008. In 2009 all stations were initially baited with canned tuna and rebaited with canned mackerel.

Evaluations of Detection Data

Survey results were evaluated by differences in detection rates and detection success observed across the study area. Kit fox detection rates, defined as the number of detections divided by number of sample occasions, were calculated for all stations and sample occasions combined. Though detection rates do not provide a direct measure of abundance, they have been found to track changes in kit fox and swift fox abundance over time (Schauster et al. 2002; Warrick and Harris 2001). Differences in detection rates across space may also correspond to differences in abundance.

Following a recommendation by Sargeant et al. (1998), I also compared differences in detection success measured as percent of transects with detections. This statistic is favored over detection rate when detection stations and sampling points within clusters are not independent. Sargeant et al. (1998) found that, for generalist mammalian carnivores, sampling points within 2 km of one another were not independent. Data collected from paired track-plate boxes and two-in-one detection stations are undoubtedly dependent as the stations were run simultaneously in close proximity at each sampling point. Adjacent sampling points on transects were spaced 1.7 km and may also be spatially auto-correlated. Data collected during this study from stations on the same transect may therefore not be independent.

Percent of total detections by sample occasion and bait type were calculated though latency to detection and bait preference cannot be separated.

Efficacy of Detection Station Designs

Detection rates for each of the three detection station types were calculated to assess differences in efficacy. For these two calculations, only one detection (track or hair but not both) was used for two-in-one detection stations. The ratio of hair to track detections from two-in-one detection stations and number of detections from cubbies and tunnels were calculated to further assess effectiveness.

Spatio-temporal Distribution Modeling

Distribution modeling was performed with Maxent version 3.3.2 (http://www.cs.princeton.edu/~schapire/maxent/) (Philips et al. 2006). Maxent is a GIS-based modeling technique that uses species' occurrence records and environmental data layers, contrasting them with background data sampled from the remainder of the study area, to output a continuous probability value as an indicator of relative suitability for the species. Maxent is considered to be a reliable and robust distribution modeling approach known to outperform other algorithms (Elith et al. 2006, Hernandez et al. 2006). Because the program only requires presence data, it may be used to make predictions or inferences about habitat suitability and potential distributions in unsampled areas or times (Phillips et al. 2006). I used Maxent to model and characterize the climate niche for kit fox near the northeastern edge of its geographic range. Niche predictions were extrapolated and projected into space to generate an average suitable climate distribution map for the study area and to model shifts in the distribution of suitable climate over the 27-year time period, 1983 to 2009.

The four-step process for spatio-temporal distribution modeling for kit fox near the north and east-most range edge required: 1) acquisition of occurrence records and environmental predictor variables, 2) ecological niche modeling to quantify the relationships between occurrence records and associated climatic conditions, 3) projecting the distribution of suitable environmental conditions in space through time for the 27-year time period, and 4) probability thresholding to generate mean and annual binary suitable climate distribution maps.

Occurrence Records

Because models built with edge data from marginal sites predict suitability skewed away from the optimum (Braunisch et al. 2008), and because it is presently unclear whether past records of kit fox presence in west-central Colorado came from “sink” habitat, I elected to only use records of occurrence from Utah for modeling purposes. In searching for records for kit fox, I surveyed wildlife biologists, professional reports and published data, the Utah Conservation Data Center, and networked biodiversity information systems of natural history collection data collated from multiple repositories and institutions (e.g. MaNIS and other DiGIR providers; Stein and Wieczorek 2004). For greater temporal congruence given the Worldclim dataset (which spans 1960–2000), I used records dating from 1950 to 2009. Of these records, only georeferenced occurrence records with geographic uncertainty of less than 5 km were used (Wieczorek et al. 2004). The total number of records found meeting these criteria was 1,675 observations. The vast majority of these records came from the Utah Conservation Data Center. A small number of the records represent primary vouchers while the majority are observations made by wildlife professionals. After removing duplicates, random subsampling was performed to reduce spatial autocorrelation and to achieve a more even spread and concentration of points across the modeling extent. Minimum distance between points was 1 km. Following subsampling, 191 records remained for model building and testing purposes. Records of occurrence obtained from field surveys were used to evaluate the mean modeled distribution of suitable mean climate for kit fox and to assess the role of interannual variability in climate on kit fox occupancy.

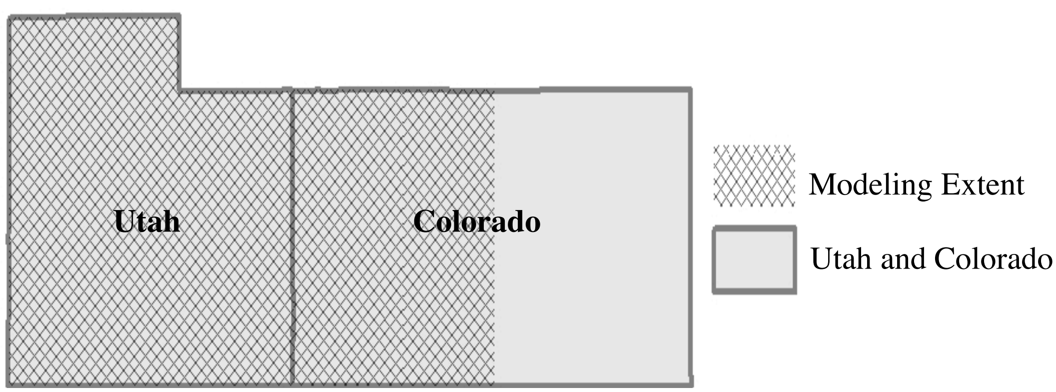
Climate Variables

The set of 17 annual and seasonal climate predictor variables used for building and projecting models of habitat suitability were derived from gridded monthly minimum and maximum temperature and precipitation data acquired from Worldclim (http://www.worldclim.org/) and the PRISM climate group (http://www.prism.oregonstate.edu/). The 17 variables were annual precipitation; seasonal precipitation for spring, summer, fall, and winter; mean temperature for each season; and mean minimum and mean maximum temperature for each season.

Worldclim data are monthly average values for the 40-year time period, 1960 to 2000. The climate variables derived from Worldclim data were used to fit the ecological niche models and to generate a contemporary, suitable mean climate habitat distribution map for kit fox. Monthly climate data for 27 individual years, 1983 through 2009, were obtained from the PRISM climate group. These data were used to project the annual distribution of mean suitable climate for kit fox through space and time.

The spatial resolution of original Worldclim data was 30 arc seconds (~800 m^2) whereas the original PRISM data had a spatial resolution of 2.5 arc minutes (~4 km^2). Because the niche modeling software used requires that all data layers have the same resolution, the PRISM data cells were rescaled to 30 arc seconds using nearest neighbor resampling with ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA). I choose to normalize the datasets by resizing the PRISM cells rather than coarsening and altering the Worldclim data to avoid losing resolution and data desired for initial model training. PRISM data also required unit normalizing to mirror Worldclim data. PRISM precipitation and temperature values were originally expressed as mm*100 and °C*100 respectively, so their cell values were divided by 100 and 10 respectively. All data layers were clipped to the decimal degree extent of 42.004 N, 36.992 S, -105.504 E, and -114.058 W (Fig. 5) and projected to the geographic coordinate system NAD 83. This modeling extent encompasses all of Utah and the western half of Colorado. This modeling extent was chosen to encompass the entire northeastern range limit for kit fox, as well as a portion of the core of the geographic range, represented by a large number of occurrence records dating from 1950 to present.

Figure 5. Spatio-temporal distribution modeling extent.



After clipping data to the desired modeling extent, monthly minimum and maximum temperature and precipitation grid layers were used to derive 17 annual and seasonal predictor variables with the ArcGis 9.3 spatial analyst extension raster calculator (Environmental Systems Research Institute, Redlands, CA). Spring is defined as March, April, May; summer is June, July, August; fall is September, October, November; and winter is December, January, February. Annual precipitation is the sum of precipitation amounts for all months January through December. Seasonal precipitation amounts were calculated by summing the data for the appropriate months. Seasonal mean minimum and mean maximum temperatures were calculated by averaging the mean minimum or maximum temperatures, respectively, for the three appropriate months. Mean seasonal temperatures were calculated by averaging mean minimum and mean maximum temperatures for the three months of each season.

Model Building

Models were built with the 17 climate variables described above and a unique random seed of training data representing 75% of occurrence records (n=144) selected via subsampling for each model. The subsamples comprising the remaining 25% of records (n=47) and presence records obtained from field surveys (n=14) were withheld for testing each resultant model. Because model performance can vary depending on the particular subset of data withheld from training for testing, twenty models, or replicates, were built and averaged with Maxent. The models were run in batch mode with the following auto features: number of background points = 10,142, regularization multiplier =1, maximum iterations = 500, and convergence threshold = 0.00001. "Logistic output format" was selected for predicted distributions.

Model Performance Evaluation

Model performance was assessed by visual inspection and by formal evaluation via receiver operating characteristic (ROC) analysis. The ROC analysis was used to evaluate how well models compared to random predictions. The ROC curve is obtained by plotting sensitivity on the y-axis and the false positive rate on the x-axis for all possible thresholds. Sensitivity, also referred to as the true positive rate, represents absence of omission error or the fraction of all occurrence records (positive instances) that are classified as suitable by the model. The false positive rate, or rate of commission error, is equal to 1-specificity. Specificity represents the fraction of a random sample of background points (negative instances) not predicted suitable. The area under the ROC function, or area under the curve (AUC), represents the probability that a random positive instance and a random negative instance are correctly identified. The AUC provides a single measure of overall model accuracy which may be used as an index of performance (Yost et al. 2008). The AUC value is typically between 0.5 and 1.0 (Yost et al. 2008). A value of 0.85, for instance, indicates that for 85% of the time, a random selection from the occurrence data, either training or testing, will have a score greater than a random selection from the background points. A value of 0.5 indicates that the model is no better than a random prediction. It is important to note that when the ROC analysis is used on presence-only data, as is the case here with Maxent, the maximum AUC is less than one (Wiley et al. 2003). The AUC value may also be smaller for wider ranging or generalist species (Yost et al. 2008) because for these species it is more likely that a larger portion of randomly selected background points, treated as negative instances, will be predicted by the model, thus driving specificity down.

Lastly, model success was evaluated by visual inspection to determine how well the probability values in the output grid fit with the records of occurrence including those obtained during field surveys (Yost et al. 2008). Output grids are generated from application of the Maxent model predictions to the set of GIS grids representing the environmental predictor variables. A good model should produce regions of high probability of suitability over the majority of presence records whereas areas of low probability should contain few to no occurrence points (Yost et al. 2008). I define low probability for this evaluation as less than 50%.

Projecting Distributions of Suitable Climate Though Time

After replicate models based on occurrence data and the 40-year mean climate Worldclim dataset were run, the average niche was projected to annual climate PRISM datasets for the years 1983 to 2009 to extrapolate habitat suitability through space and time. Prior to further processing of annual projections, results from the clamping operations selected during model setup were reviewed. Clamping treats environmental variable conditions not present within the original modeling extent as outside or at the limit of the training range, and omits them from the projection extent. The clamp grid shows the difference between the clamped and non-clamped outputs for each cell, and may be visually inspected to evaluate the potential impact of novel climate conditions on projection reliability. Clamp grids for all projections for all years and models were examined.

Predictive Distribution Mapping

The mean predicted probability distribution built with the Worldclim dataset and the mean projected probability distributions for the 27 years, derived by Maxent from the 20 replicate models, were thresholded to generate a binary geographic suitable mean climate distribution map and annual suitable climate distribution maps. Maxent produces spatial predictions of environmental suitability from 0 (not suitable) to 1 (most suitable). A thresholding rule may be applied to transform the probability predictions of the model to a binary prediction. I applied the equal training sensitivity and specificity logistic threshold. This threshold has been found to produce realistic predictions of species distributions and is automatically reported by Maxent. Appropriateness of this threshold for kit fox was evaluated by training and test omission rates calculated by Maxent for the resultant mean suitable climate distribution map.

Suitable Mean Climate Distribution Map

The suitable mean climate distribution map identifies areas where mean climate is suitable for kit fox. This distribution was examined for congruence with historic records of occurrence and records obtained during field surveys to assess my a priori predictions. Because little doubt remains that geographic range limits are often significantly associated with aspects of climate (Gaston 2003, Kearney and Porter 2009) and because kit foxes exhibit high vagility as evidenced by movement studies (Cypher 2003, Fitzgerald 1996), I predicted this map to be a good estimate of the realized distribution of kit fox across the study area. This prediction was assessed by the degree of coincidence of the projected distribution of suitable mean climate with previous records of kit fox occurrence and records obtained from field surveys in 2008 and 2009. I also predicted that large areas that had been previously surveyed and with no detections would lie beyond the limit of the projected distribution, even if previous records exist for the area.

Mapping Spatio-temporal Variability in Suitable Climate

To visualize spatial heterogeneity in temporal variability in the occurrence of mean suitable climate for kit fox and to evaulate its potential effect on occupancy and persistence, binary annual projections were stacked and summed. Cell values are equivalent to the number of years with mean suitable climate and therefore may reflect the relative likelihood of kit fox occupancy, persistence, and population stability. Here I define mean suitable climate as those condictions identified by Maxent as describing the mean climate niche of the species during model building. Cell values in this summed map are expected to reflect overall longer-term suitablity for kit fox, because levels of species occupancy and local population density at any given time will be a function not only of the contemporary or mean environmental conditions but also of the cumulative number or duration of periods of suitability permitting recruitment events after initial colonization (Jackson et al. 2009). Consequently, I predicted a legacy of recent climatic variation on kit fox occupancy in the study area. Specifically, I hypothesized that areas with the greatest number of cells previously occupied by kit fox in proximity to sites with kit fox detections in 2008 or 2009 would be projected as suitable more frequently (having higher cell values) than patches with previously occupied cells but few to no detections of kit fox in 2008 or 2009. Lastly, I studied the summed map to identify any spatial gradient in overall climate suitablity for the time period, 1983 through 2009.

Analysis of Climate Variable Importance

The jackknife test of variable importance was used to evaluate the strengths of each predictor variable for training and testing data in the model. A separate model for the jackknife test was performed by Maxent for each of the 20 replicate models. During runs of the model, each variable is excluded one at a time, while a model is created with the remaining variables. Then a model is created using each variable in isolation. Lastly, a model is created using all variables. Variable importance is measured by the level of gain increase for a variable when used alone and by the drop in gain when omitted from the full model. The variable with highest gain has the most useful information by itself and the variable inducing the greatest drop in gain when omitted has the most important information not present in other variables. The test was performed on training gain, test gain, and the AUC. The training and test gain plots generated with data from the test show which variables are the best fit to the training and test data respectively. The AUC plot shows which variables are the most effective for predicting the distribution of the occurrence data set aside for testing, when predictive performance is measured using AUC. The top four predictor variables revealed by the mean jackknife results were used for subsequent analyses of datasets to identify and describe any gradient in mean climate conditions across the study area and predicted range edge, and to evaluate spatial variation in the frequency of fluctuations beyond mean suitable climate conditions. Given the physiology, behavior, and ecology of the species, I predicted the most important climate variables to be those pertaining to precipitation and summer and winter temperatures.

Spatial Gradients in Mean Climate Conditions Across the Range Edge

To identify any possible spatial gradient in mean climate suitability across the study area I explored differences in the 40-year mean climate conditions for the three most important predictor variables. Mean conditions for the predictor variables for the 40-year time period were calculated for three extents spanning the study area. The three extents were the predicted distributions of suitable mean climate for Grand County, Utah, and Mesa County, Colorado, and the Gunnison and Uncompaghre valleys in Delta and Montrose counties, Colorado. These regions were extracted from the total modeling extent and 40-year means were calculated from the Worldclim dataset with ArcGIS 9.3. Collectively, these data may provide a foundation for interpreting interannual variability in climate suitability across space, because environmental conditions near the range edge often are near the ecological tolerance limit of species. Theory predicts and field observations confirm that climate conditions for many species commonly fluctuate beyond suitable more frequently near range edges than in the core of ranges (Gaston 2003).

Results

Field Surveys

Test of Two-in-one Hair Snare/Track-plate Detection Station

One of the two test transects produced one track detection of kit fox in a track-plate box and two hair detections in two two-in-one detection stations. The observed detection rate for this transect was 13.6% (3 detections/22 sample occasions). The second transect did not have any detections of kit fox. The combined detection rate for both transects was 6.8% (3 detections/44 sample occasions). Locations of kit fox detections are listed in Table 3. The only non-target species detected on test transects (by hairs on brushes) was American badger (*Taxidea taxus*). This species also was detected in track-plate boxes as were western spotted skunk (*Spilogale gracilis*), white-tailed prairie dog (*Cynomys leucurus*), desert cottontail (*Sylvilagus audubonii*), and "deer mice" (probably *Peromyscus* sp.). Because sample sizes were insufficient to assess experimentally the relative effectiveness of the two detection methods, both track-plate boxes and two-in-one detection stations were used in the surveys for kit fox in Colorado in 2008 and in Utah in 2009.

Table 3. Kit fox detections during test in east-central Utah, 2008.

Sampling Point	Number of Detections	Type	NAD 83 Zone	Easting	Northing	Date
4	1	hair	12	643016	4311485	15-Aug-08
5	1	track	12	643443	4310667	15-Aug-08
7	1	hair	12	644453	4309151	15-Aug-08

Kit Fox Detections

Results from surveys in the eastern half of the study area in west-central Colorado and the western half of the study area in east-central Utah differed significantly. The results, therefore, are presented separately for the two areas. With more than 3,800 survey nights, between 30 August and 23 November 2008 at 136 sampling points on 45 transects, this survey resulted in only one questionable but probable track detection of kit fox in Colorado. Following this questionable kit fox detection, sampling effort there was extended one sample period and was doubled with the addition of four new sampling points within 0.8 km of the detection site. A motion-triggered camera was set at the station where the detection occurred. The camera remained in place for one sample period. No additional detections of foxes occurred. Thus, in Colorado, probable kit fox presence was recorded at only one of 45, or 2.2% of transects and the observed detection rate was less than 0.2% (1 detection/540 sample occasions).

In Utah, 1,560 survey nights 19 September to 31 October 2009, at 60 sampling points on 20 transects yielded 30 unique confirmed detections of kit fox (only one possible detection per two-in-one detection station per sample occasion counted for this measure). The combined detection rate for the survey in Utah was 12.5% (30 detections/240 sample occasions). Kit foxes were confirmed present with track-plate boxes and/or two-in-one detection stations at 14 sampling points on 10 of 20, or 50% of transects in Utah. Detections were split equally between sample occasions one and two. The locations and dates of confirmed kit fox detections in Utah and the one probable detection in Colorado are listed and shown in Table 4 and Fig. 6 respectively. Table 5 shows the number of unique kit fox detections, detection rate, and detection success observed in Colorado and Utah. Figure 7 shows a diagnostic kit fox track obtained on a track-plate and a hair sample obtained with a brush.

Table 4. Kit fox detections in west-central Colorado in 2008 and east-central Utah in 2009.

Sampling Point	Track-plate Box Detections	Two-in-one Detections	NAD 83 Zone	Easting	Northing	Date
Questionable Detection Colorado 2008						
4B		1 track	12	678054	4354777	17-Oct-08
Confirmed Detections Utah 2009						
46B	1 track		12	654855	4344283	31-Oct-09
47A	1 track		12	657644	4333508	31-Oct-09
50B	2 track	2 track 2 hair	12	640539	4330750	24-Oct-09 31-Oct-09
50C	2 track	2 track 2 hair	12	639113	4331708	24-Oct-09 31-Oct-09
52B		1 track 1 hair	12	633385	4318381	26-Sep-09
54A	1 track	2 track 2 hair	12	621288	4309563	3-Oct-09 9-Oct-09
54B		1 track 1 hair	12	622272	4308174	3-Oct-09 9-Oct-09
54C	1 track	1 track 1 hair	12	623285	4306814	3-Oct-09
55A	1 track		12	643432	4310741	3-Oct-09
55B	1 track	2 track	12	644302	4309421	2-Oct-09 3-Oct-09
60B	1 track	1 hair	12	600920	4292473	24-Oct-09
61C		1 track 1 hair	12	595703	4279491	18-Oct-09
63A	1 track	2 track 2 hair	12	603367	4271240	3-Oct-09 9-Oct-09
65A		1 track 1 hair	12	602335	4268191	3-Oct-09 9-Oct-09

Figure 6. Kit fox survey locations and detections, 2008–2009.

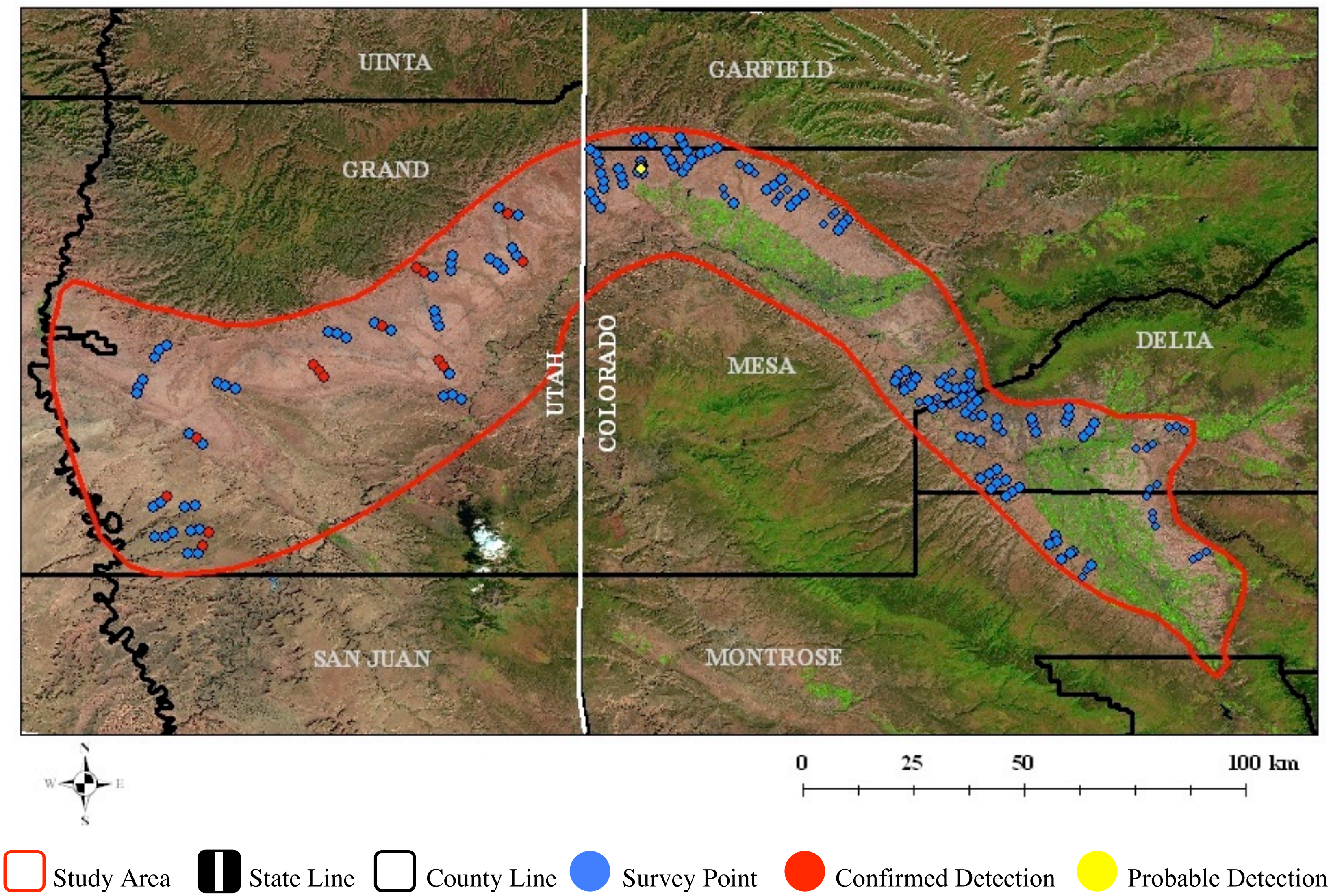
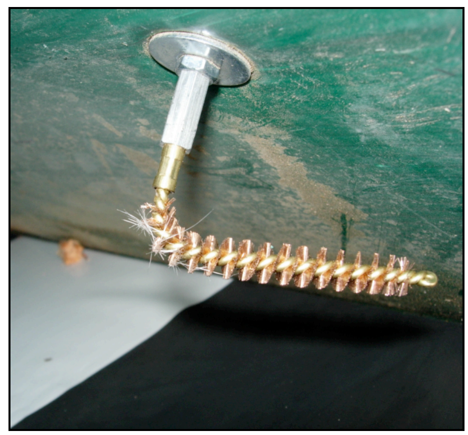


Table 5. Unique kit fox detections, detection rate, and detection success in west-central Colorado in 2008 and east-central Utah in 2009.

Common Name	Scientific Name	Number of Unique Detections	Detection Rate (detections/checks)	Detection Success (% of transects)
Colorado 2008				
kit fox	*Vulpes macrotis*	1-probable	0.02%	2.2%
Utah 2009				
kit fox	*Vulpes macrotis*	30-confirmed	12.5%	50%

Figure 7. Kit fox print obtained on track-plate (left) and hair captured by a brush inside a two-in-one detection station (right).

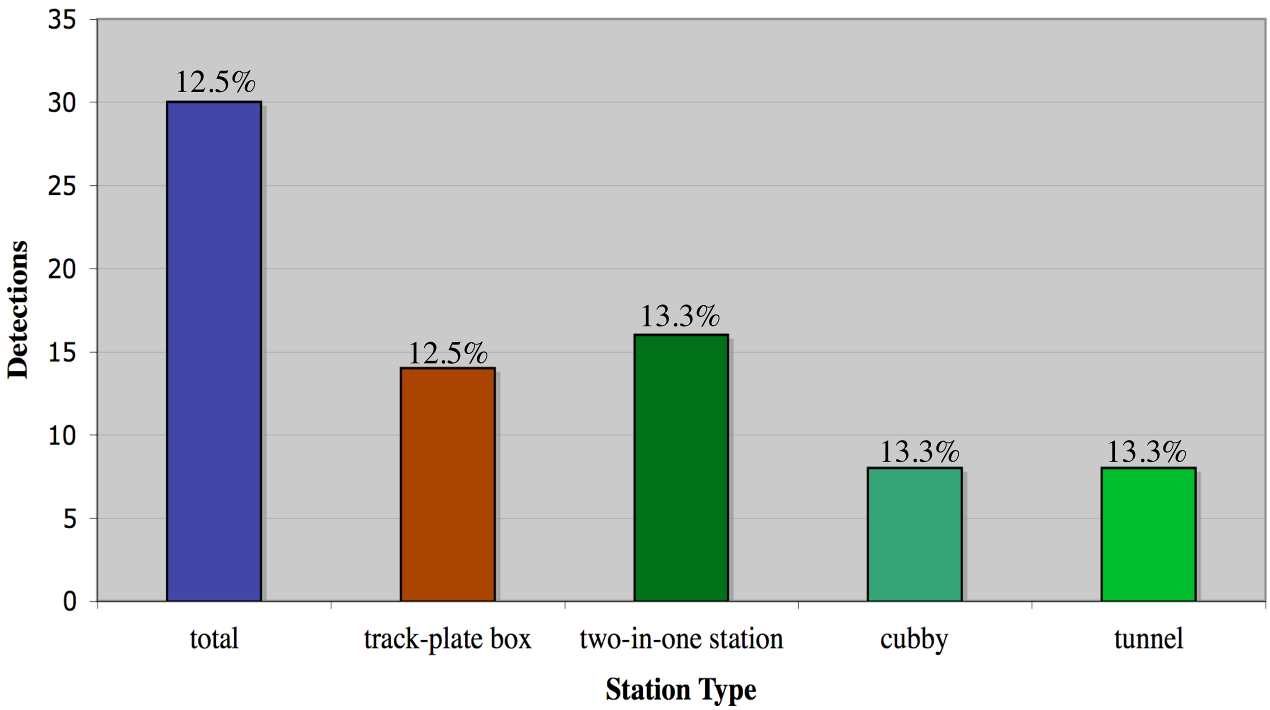


Efficacy of Detection Station Designs

Detection results from the Utah survey indicate that the performance or efficacy of all three detection station designs were nearly proportional in this study. Fourteen of the 30 confirmed detections came from track-plate boxes and 16 came from two-in-one detection stations. The detection rates for track-plate boxes and two-in-one detection stations were 11.7% (14 detections/120 sample occasions) and 13.3% (16 detections/120 sample occasions), respectively. The two two-in-one hair snare/track-plate detection station designs performed equally well on three accounts. Cubbies and tunnels each produced eight detections with an equal detection rate of 13.3% (8 detections/60 sample occasions). Neither the cubby nor the tunnel outperformed the other in detecting kit foxes by the hair snare or track-plate components.

And hair to track detections within two-in-one detection stations were one to one with 15 confirmed hair detections and 15 confirmed track detections. Questionable but probable detections of kit fox occurred on another five transects. The number of confirmed detections and detection rate for each station type are shown in Fig. 8.

Figure 8. Total unique kit fox detections and detections by station type. Numbers above bars are detection rates (number of detections/sample occasions). Only one detection counted per two-in-one station per sample occasion for calculations.



Precipitation or high wind events disrupted operability of a large number of detection stations during four of eight weeks of surveys by splattering soot or blowing dust and sand across track-plates. Though track-plates in two-in-one detection stations were occasionally rendered nonfunctional by wind or rain, this problem was more common in track-plate boxes as they are taller and more open. The true impact of wind on hair sample retention on brushes in two-in-one detection stations is not known but hair samples were found in some stations that had been "sandblasted."

Non-target Species Detected

Non-target mammalian carnivores detected in Colorado in 2008 by tracks included red fox, western spotted skunk, raccoon (*Procyon lotor*), house cat (*Felis catus*), and domestic dog (*Canis familiaris*). Dogs also were detected in Colorado by hairs found on brushes. Only two non-target carnivore species, red fox and raccoon, were detected in Utah in 2009. Both were track detections. Desert cottontails were detected in both Colorado and Utah by hair on brushes and by tracks. Numerous track detections of small mammals also were made. Ground squirrels and mice made up the vast majority of these detections. Small mammals detected by tracks were white-tailed prairie dog, rock squirrel (*Spermophilus variegatus*), unknown small ground squirrel species, woodrat (*Neotoma* sp.), Ord's kangaroo rat (*Dipodomys ordii*), and "deer mice" (probably *Peromyscus* sp.). Tracks and scats of black bear (*Ursus americana*), red fox, and coyote were found on or near roads on very few transects. Table 6 shows the number of detections, detection rate, and detection success observed in Colorado and Utah for each of the carnivore species. Locations and dates of observations are listed in Table 7.

Table 6. Non-target carnivore species detections in west-central Colorado in 2008 and east-central Utah in 2009.

Common Name	Scientific Name	Number of Unique Detections	Detection Success (detections/checks)	Detection Success (% of transects)
Colorado 2008				
dog	*Canis familiaris*	5-confirmed	0.9%	4%
house cat	*Felis catus*	2-confirmed	0.4%	4.4%
raccoon	*Procyon lotor*	1-confirmed	0.2%	2.2%
western spotted skunk	*Spilogale gracilis*	2-confirmed 5-probable	1.3%	13.3%
red fox	*Vulpes vulpes*	2-confirmed	0.4%	4.4%
Utah 2009				
raccoon	*Procyon lotor*	1-confirmed	0.4%	5%
red fox	*Vulpes vulpes*	1-confirmed	0.4%	5%

Table 7. Locations of non-target carnivore species detected in west-central Colorado in 2008 and east-central Utah in 2009.

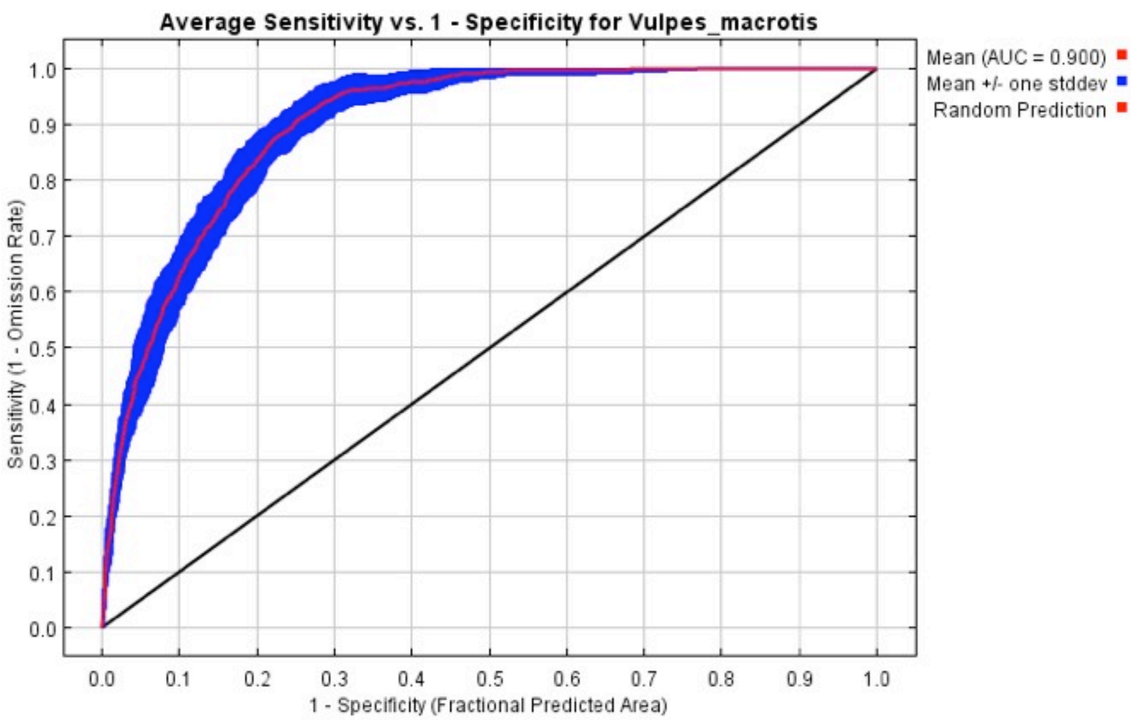
Common Name	Scientific Name	Sampling Point	NAD 83 Zone	Easting	Northing
Colorado 2008					
dog	*Canis familiaris*	15C	13	186317	4354185
		23A	13	216944	4301583
		26B	13	216748	4309945
		42B	12	756034	4269904
		4A	12	678054	4353072
house cat	*Felis catus*	19C	12	759446	4299420
		20B	12	754778	4301073
raccoon	*Procyon lotor*	27B	12	734938	4306472
red fox	*Vulpes vulpes*	19A	12	757512	4296428
		2A	12	671542	4350124
western spotted skunk	*Spilogale gracilis*	21C	12	748109	4300363
		23B	13	218598	4302051
		24A	12	736553	4301374
		32A	12	739254	4295028
		32B	12	737509	4295406
		42A	12	756489	4270443
Utah 2009					
red fox	*Vulpes vulpes*	50B	12	640539	4330750
raccoon	*Procyon lotor*	56A	12	647419	4301967

Spatio-temporal Distribution Modeling

Model Performance

The AUC values for all partitions of the occurrence data for the 20 replicate models were high, thus indicating good predictive power. AUC values ranged from 0.9294 to 0.9405 (mean 0.9352) for training datasets and 0.875 to 0.9298 (mean 0.9) for test datasets (Fig. 9). Visual inspection for congruence between records of occurrence and high probability values in the output grid depicting the model's spatial prediction of climate suitability also revealed a good fit of the model. The vast majority of records of occurrence used for modeling occurred within cells with high probabilities of climate suitability, whereas expanses of cells with probabilities of suitability less than 50% contained very few records. Records from the original dataset withheld from the subsample used for modeling also occurred almost entirely within cells with high probabilities. Records of occurrence obtained during field surveys, however, occurred in cells with probabilities ranging from less than 2% to more than 80%. Six (43%) of the 14 kit fox detections made in Grand County, Utah in 2009 were in cells with probabilities of suitability greater than 70%, two (14%) were in cells with 50–70% suitability, and the remaining six (43%) were in cells with probabilities of suitability less than 50%.

Figure 9. AUC results for test data from all partitions of the occurrence data for the 20 replicate models.



Evaluation of Projection Clamping

Visual inspections of clamp grids for all projections for all years and models identified no to negligible occurrence of novel climate conditions across the modeling extent for the years projected.

Threshold Evaluation

The equal training sensitivity and specificity logistic threshold for the mean prediction resulting from the 20 replicate models was 0.3338. The training omission rate and test omission rate for the mean prediction at this threshold were 0.1458 and 0.2659, respectively.

Suitable Mean Climate Distribution Map

The predicted distribution of suitable mean climate shows high correspondence with historic records of occurrence and records obtained during field surveys in Grand County, Utah (Figs. 10–11). The projection did not encompass one known, small occupied patch in Grand County near the southwest corner of the study area. In the eastern one-half of the study area in west-central Colorado, none of the historically occupied sites were projected suitable and none produced detections of kit fox during field surveys. The predicted extent in east-central Colorado overlaps mostly with private lands with very little habitat predicted on public land (Fig. 12). Consequently, fewer than five of the 45 transects surveyed in this part of the study area occurred within the predicted extent of suitable mean climate. The one and only questionable but probable detection of kit fox in the eastern part of the study area occurred approximately 3 km from the edge of the projected distribution of suitable mean climate.

Heterogeneity in Spatio-temporal Variability in Suitable Climate

The map depicting spatio-temporal variability in occurrence of mean suitable climate for kit fox (Fig. 13) shows congruence between high cell values (>11) and higher numbers of sites previously occupied by kit fox in proximity to sites with detections in 2009 within the Cisco Desert in Grand County, Utah. Though previous records and recent detections of kit foxes were

Figure 10. Predicted distribution of suitable mean climate for kit fox.

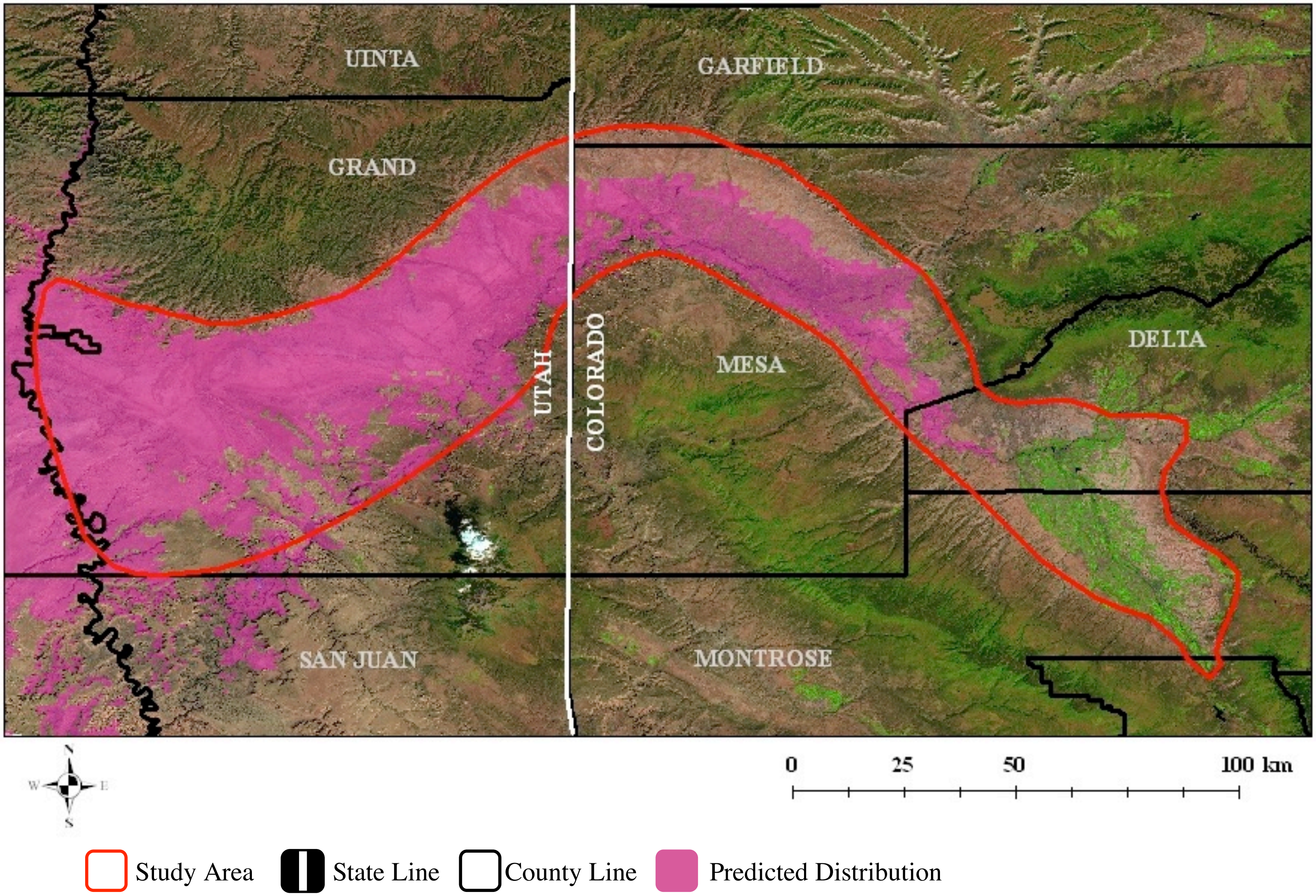


Figure 11. Predicted distribution of suitable mean climate for kit fox and locations of detections 2008–2009.

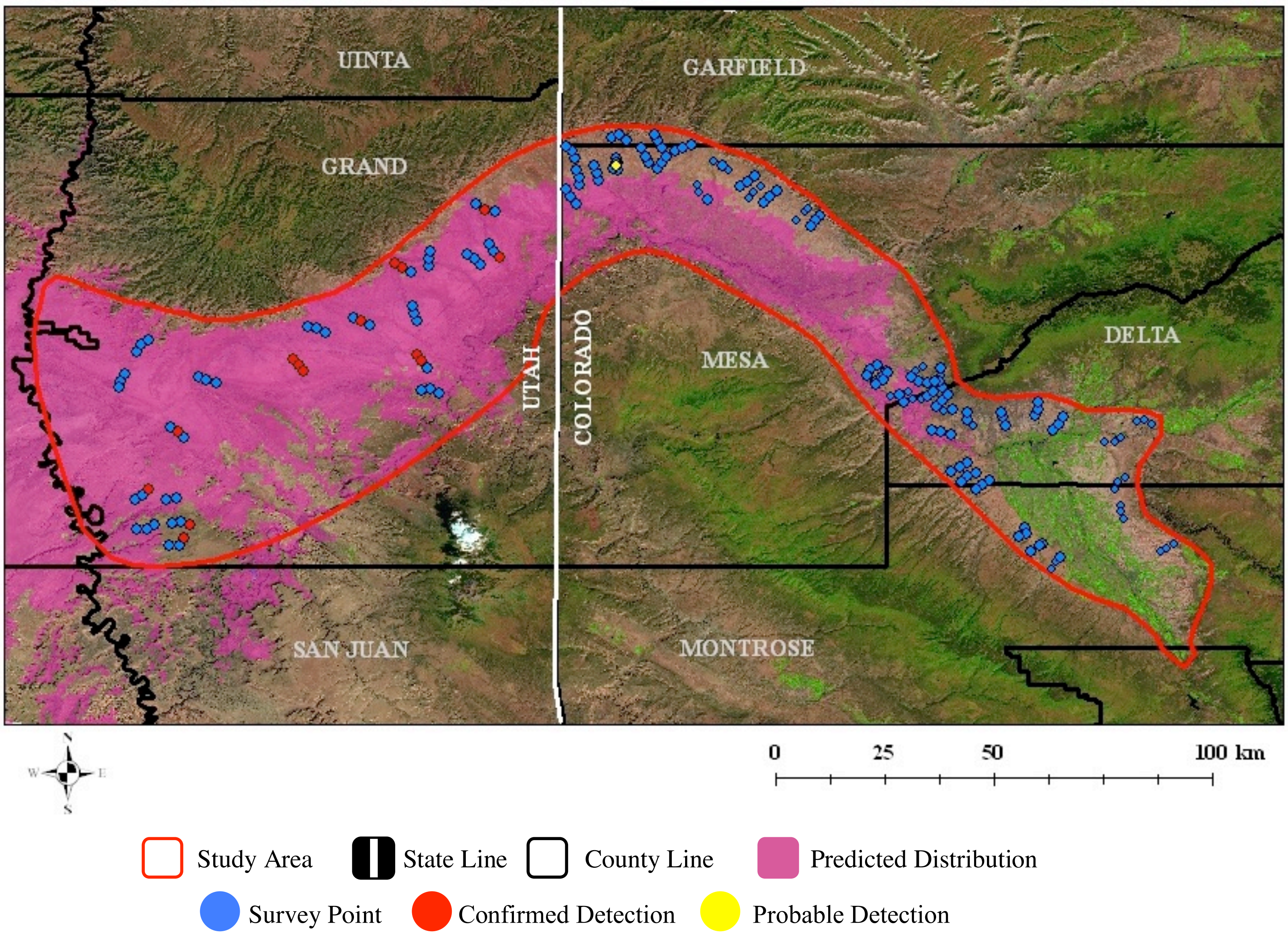


Figure 12. Predicted distribution of suitable mean climate for kit fox and extent of private lands within the study area.

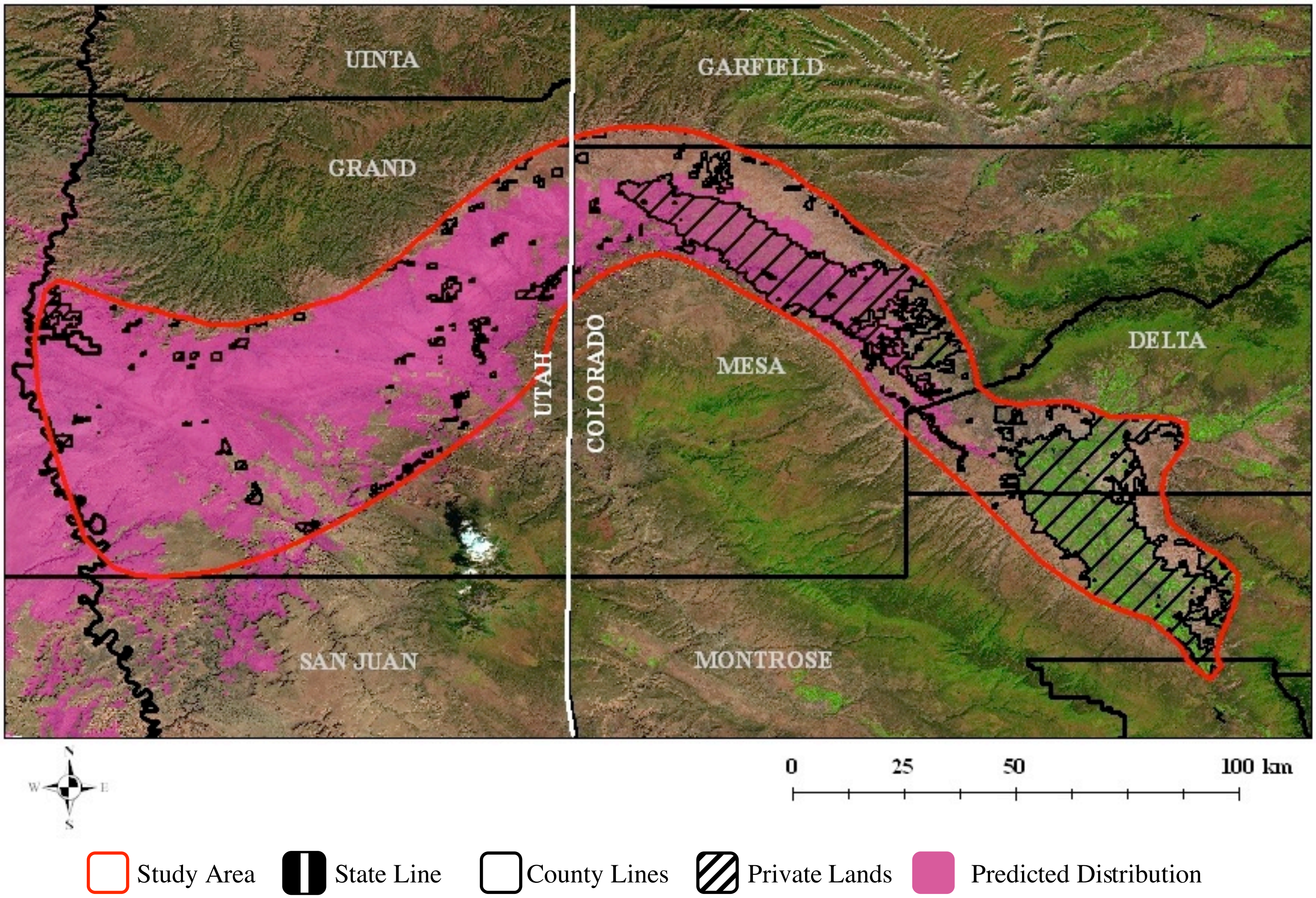
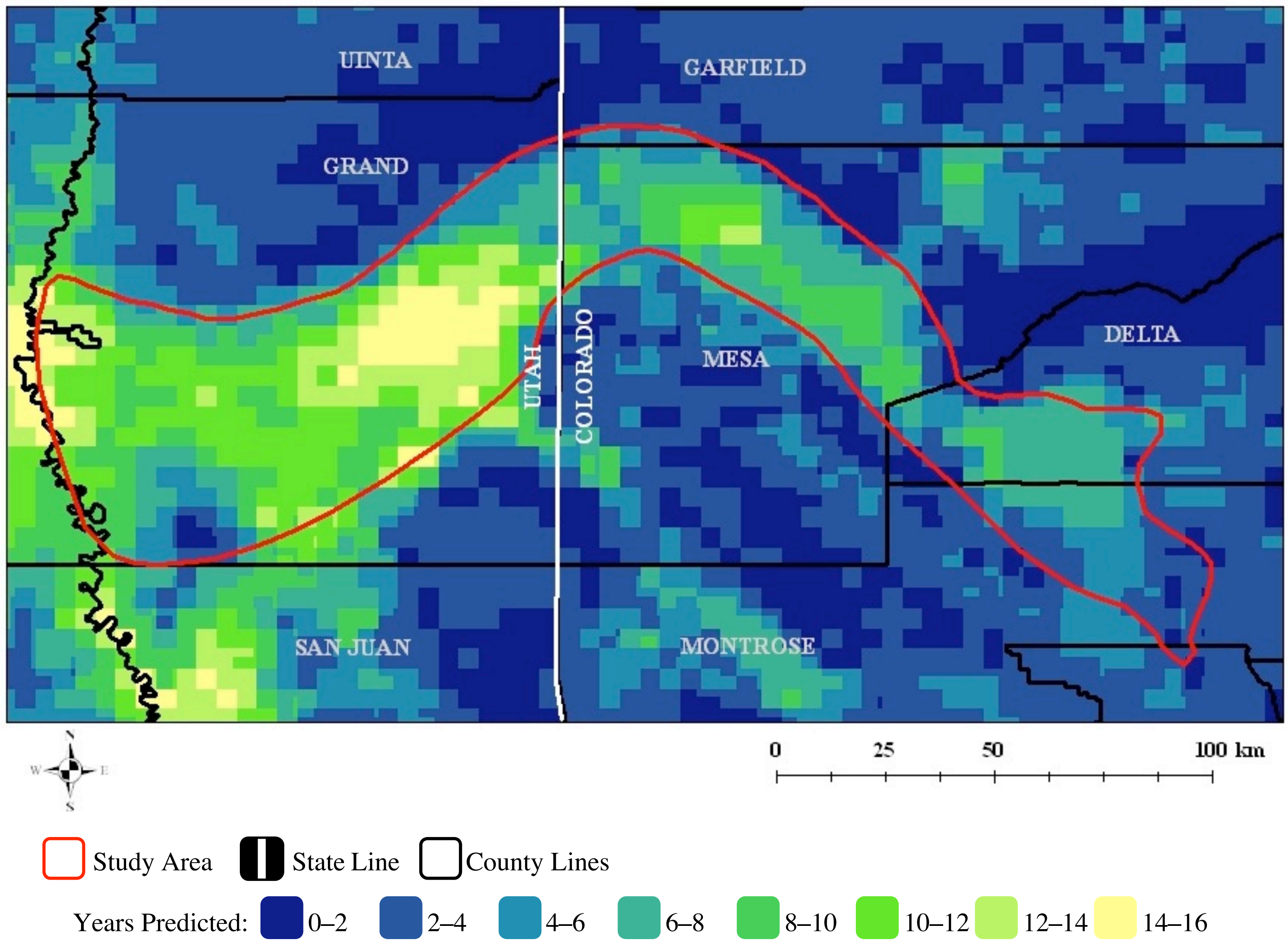


Figure 13. Spatio-temporal variation in occurrence of mean suitable climate conditions for kit fox. Map cell values represent the total number of years projected, 1983–2009.



concentrated in patches of cells with higher values, some did occur in patches of cells with low values (<9) indicating occurrence of mean suitable conditions in fewer than one-third of the years 1983 to 2009. Despite this observation, a west-to-east gradient of rapidly decreasing overall suitability identified by cell values is evident throughout the length of the study area. Areas previously occupied by kit fox in the eastern half of the study area in Mesa, Delta, and Montrose counties, Colorado as indicated above, yielded no detections of the species in 2008. All of these areas have low cell values (<7) reflecting mean suitable conditions there in fewer than 25% of years. Areas of highest cell values in the eastern half of the study area are small, and limited entirely to private lands (which were not surveyed).

Climate Variable Importance

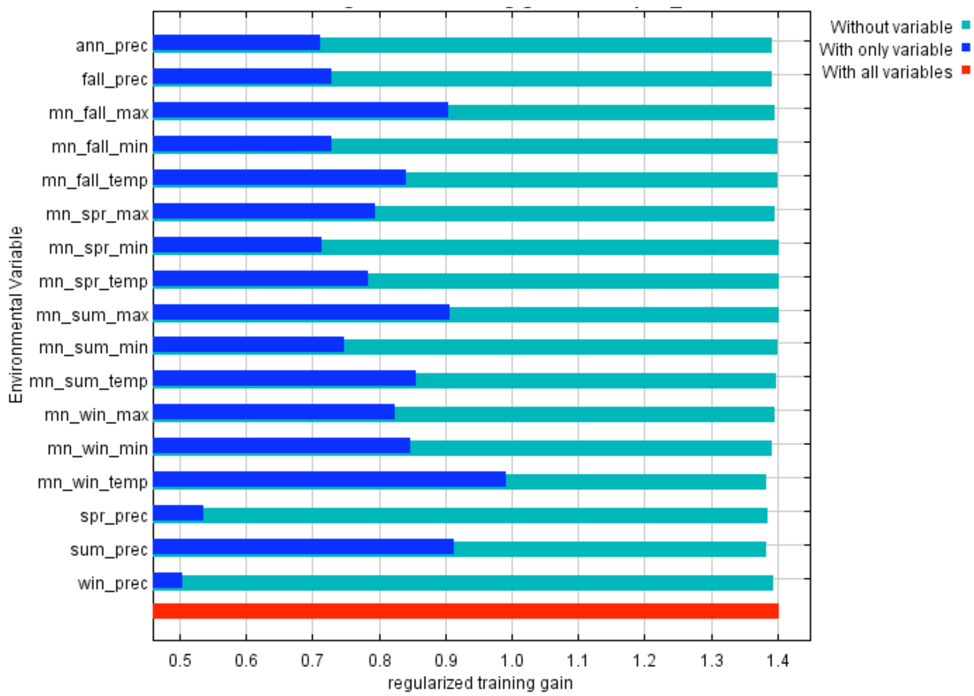
Jackknife test results show consistency in importance of the four most important predictor variables (Figs. 14a–b). Across all tests, the environmental variable with highest gain when used in isolation was mean winter temperature. Mean summer maximum temperature, mean fall maximum temperature, and summer precipitation also contributed greatly to the gain of the models. No variable altered the models more than any other when omitted.

Spatial Gradients in Mean Climate Conditions Across the Range Edge

Gradients in mean winter temperature, mean summer maximum temperature, and summer precipitation are evident across the length of the study area. Fig. 15 shows the three extents for which means were calculated as described above. Figures 16a–c show mean values for each of the variables for each of these extents. Mean summer maximum temperature (33.05°C, *SE* 0.43) is warmest in the predicted extent of Grand County, Utah, the west-most

Figure 14. Results for jackknife tests of variable importance; (a) jackknife of regularized training gain, (b) jackknife of regularized test gain.

(a) Jackknife of Regularized Training Gain



(b) Jackknife of Regularized Test Gain

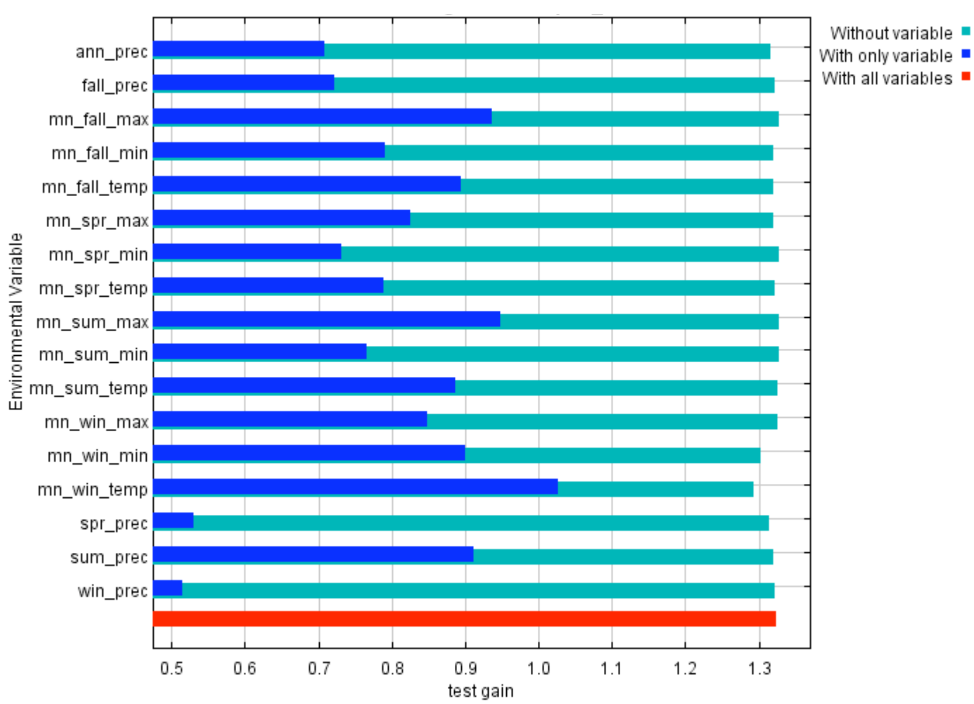
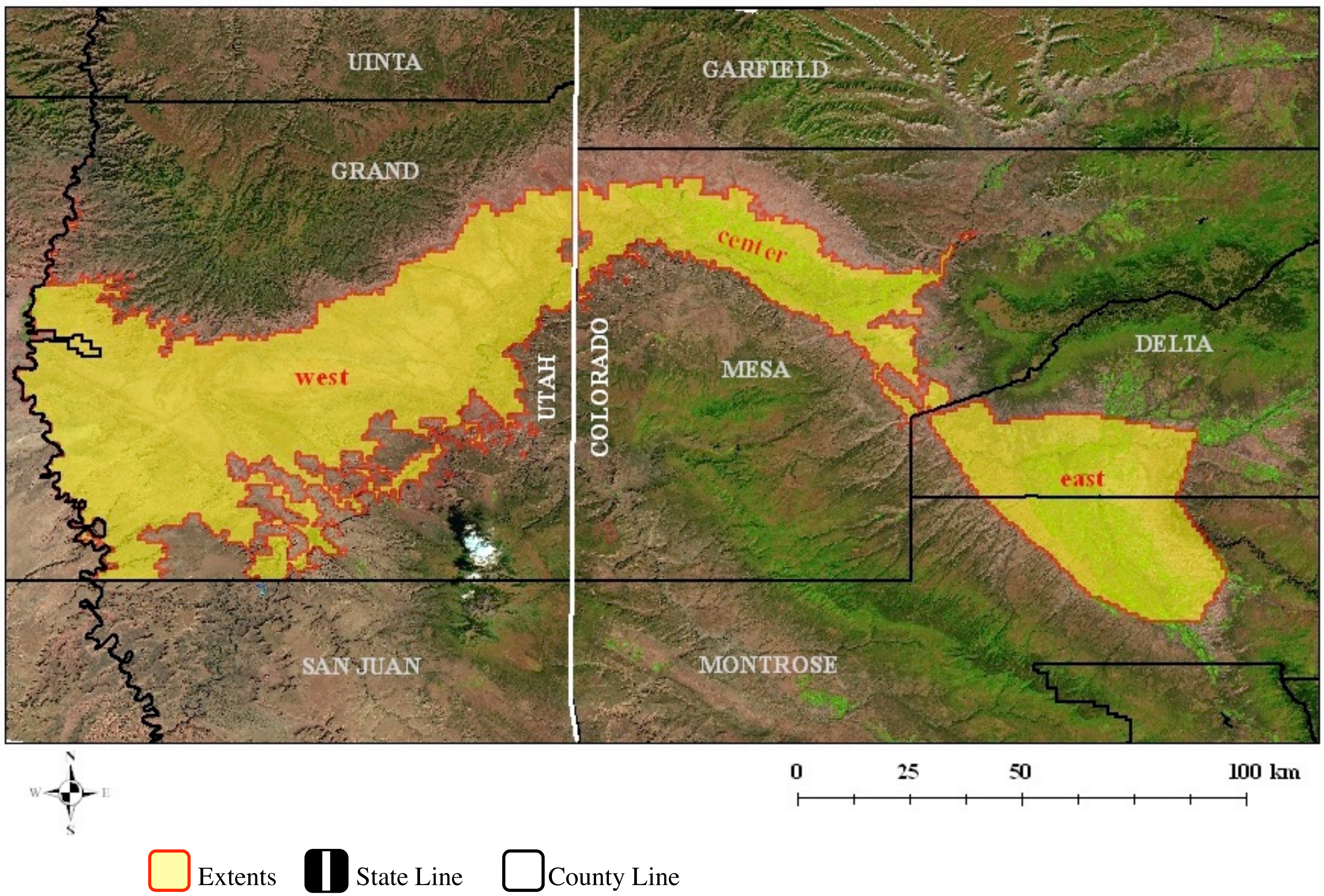


Figure 15. Extents used for climate gradient analysis. The west extent is the predicted distribution of suitable mean climate in Grand County, UT. The center extent is the predicted distribution in Mesa County, CO. The east extent is the east-most third of study area – Gunnison and Uncompahgre valleys.



(a) Mean Summer Maximum Temperature

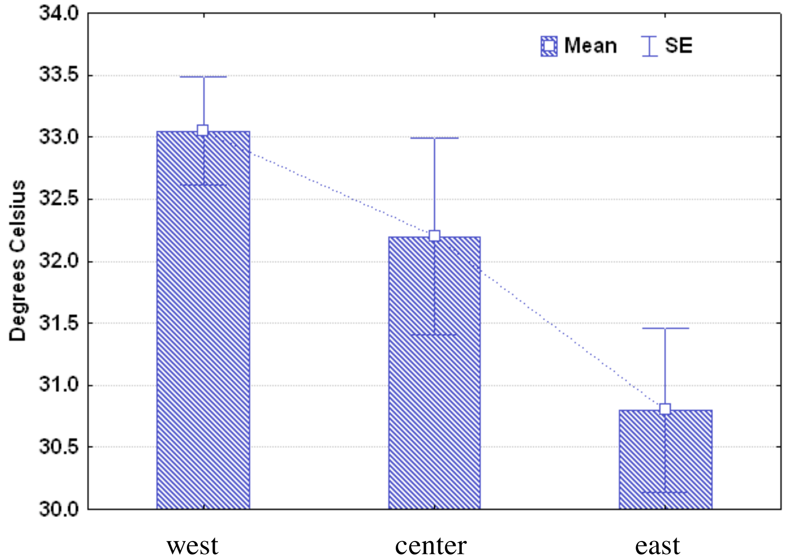
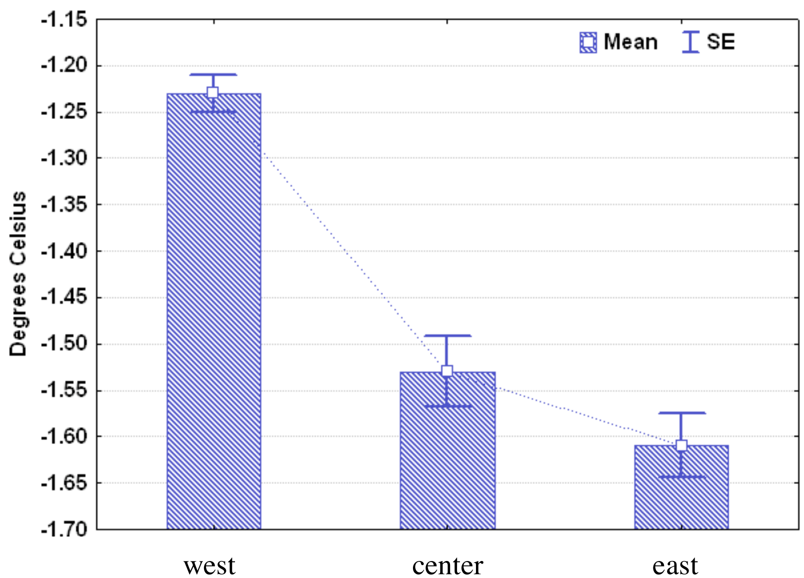
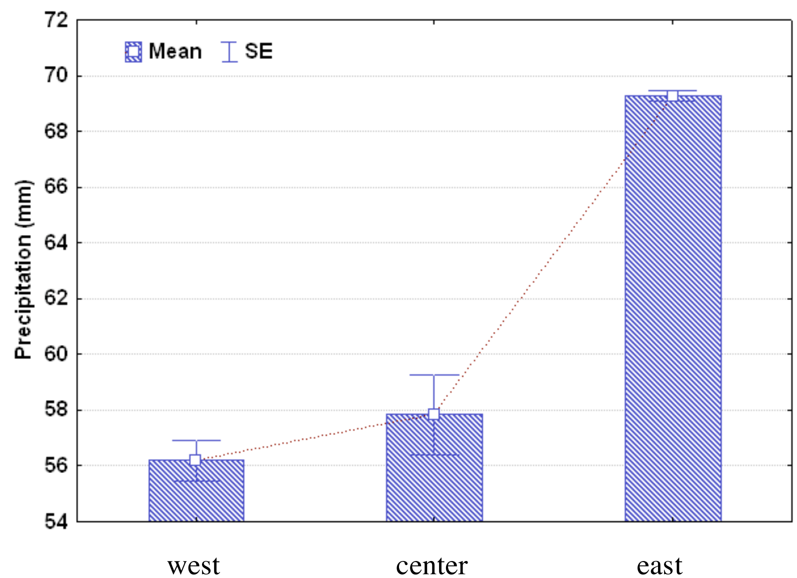


Figure 16. West to east gradients in (a) mean summer maximum temperature, (b) mean winter temperature, and (c) summer precipitation across the study area.
The west extent is the predicted distribution of suitable mean climate in Grand County, UT. The center extent is the predicted distribution in Mesa County, CO. The east extent is the east-most third of study area – Gunnison and Uncompahgre valleys.

(b) Mean Winter Temperature



(c) Summer Precipitation



extent. The eastern-most extent encompassing the Gunnison and Uncompaghre valleys in Delta and Montrose counties has the coolest mean summer maximum temperature (30.8°C, *SE* 0.66). Mean winter temperature in the western-most extent is substantially cooler than the other two extents, with the mildest conditions experienced in the eastern-most extent (-1.23°C, *SE* -0.02). Mean winter temperature in the eastern-most extent is coldest (-1.61°C, *SE* -0.03). Summer precipitation also shows a gradient with the western-most extent receiving substantially less precipitation than the eastern-most extent (56.2 mm, *SE* 0.73; 69.27 mm, *SE* 0.18, respectively).

Discussion

Though biogeography and metapopulation theory predict an important role of high frequency and high amplitude fluctuations in environmental suitability in population stability and the formation of range limits via influences on demographic rates, these phenomena have rarely been studied because the required population and environmental data often are lacking (Gaston 2003; Holt et al. 2005; Zimmermann et al. 2009). In this study I elucidated the roles of mean climate suitability, spatial gradients in climate, and interannual weather variation on range limit formation and occupancy persistence via spatio-temporal distribution modeling for kit fox at the north and east-most extent of the species' distribution, 1983 to 2009. The correlative results shown here, the first derived from field-based data, support classic predictions with evidence of a soft range limit existing along gradients in mean climate suitability and interannual deviation from mean suitable conditions.

Current Extent of Occupancy

Field surveys for kit fox in 2008 and 2009 revealed a dramatic shift in occupancy across the study area with high rates of detection (12.5%) and detection success (50%) in the western half of the study area and only one questionable but probable detection in the eastern half despite a doubled sampling effort there (Table 5; Fig. 6). According to expert opinions, the detection rate observed in Grand County, Utah, is good for kit foxes and likely adequate to detect shifts in abundance (B. Cypher, pers. comm.; S. Townsend, pers. comm.). The results from this survey therefore indicate that there are currently few if any resident kit foxes within the surveyed portions of the study area in west-central Colorado; and it is clear that the species has not recovered from the population crash there at the end of the 1990's. Though sufficient population data are lacking to understand fully the long-term dynamics and trends of the species across the study area, the potential role of climate in limiting the extent and distribution of suitable habitat and incidence of occupancy through time is elucidated by the results of my modeling and climate gradient analyses.

Distribution of Suitable Mean Climate

As predicted, the projected distribution of suitable mean climate (Fig. 10) is a good estimate of the realized distribution of kit fox across the study area, evidenced by the degree of overlap with previous records of kit fox occurrence and records obtained from field surveys in the western half of the study area. This map reveals, however, that sites previously occupied in the eastern half of the study area occur where mean climate is outside the range of suitability. Given results from field surveys indicating the presence of few if any kit foxes and apparent lower incidence of occupancy there, this is not surprising.

In the western half of the study area, the projected distribution encompasses all but one small, occupied patch of habitat near the southwest corner of the study area. It is presently not known whether the foxes known to have resided in the patch for at least the past four years occur in atypical or underrepresented climate conditions or if they exist in a pocket of suitable micro-climate not captured in the resolutions of the climate datasets used for projecting distributions.

Though the suitable mean climate distribution map captures the vast majority of existing occurrence data in the western half of the study area, the map does not in and of itself represent the actual potential distribution of suitable habitat in the eastern part of the study area. Examination of the suitable mean climate distribution map with an overlay of private property ownership (Fig. 12) reveals an abrupt range edge in the center of the study area where mean suitable climate conditions become restricted to private lands. The private lands in this area are composed of developed and agricultural covers. Presence of larger competitors (e.g. coyotes, red foxes, and dogs) on these lands (personal observation) likely diminishes suitability for kit foxes. Observations of kit foxes have not been reported for the area.

Legacy of Interannual Variation in Occurrence of Suitable Mean Climate

The summed map, depicting spatial heterogeneity in interannual variation in the occurrence of mean suitable climate conditions, (Fig. 13) reveals the legacy of recent climatic variation on incidence of kit fox occupancy. Although annual projection results depicted in the summed map do not entirely cohere to my predictions, a general trend in overall suitability decreasing west to east is evident. Consequently, the summed map paints a slightly different picture of the potential distribution of kit fox across the study area through time. Though annual projections show expansions and contractions in the distribution of mean suitable conditions over time, the summed map shows that over the past 27 years, a soft range edge has tended to be on average 80 km farther west than the abrupt edge shown on the map depicting the distribution of suitable mean climate. East of this soft range edge, climate shifts beyond mean suitable conditions more frequently because, as the gradient analyses discussed later reveal, conditions there on average are literally more on the extreme edge of the species' tolerance limit.

From the summed map, a paucity of historic records, a documented extirpation, and survey results, I posit that kit fox occupancy is on average low or intermittent in the eastern half of the study area. It is likely that longer periods of highly favorable conditions across the region result in positive population growth in the western half of the study area. This in turn may drive local population growth in the eastern part of the region by an influx of surplus foxes from the west. During these periods, kit foxes that disperse to the east may establish residency and reproduce, persisting and growing in numbers for some years until climate conditions shift to unsuitable, again causing population decline or extirpation in the eastern part of the study area.

Of interest is why on the summed map, higher cell values do not encompass more records of occurrence in the western part of the study area, especially for areas with previous records of occurrence in close proximity to new records obtained in 2009. A few possible explanations exist. My ecological niche model was built with climate data averaged from 1960 to 2000. The niche described therefore reflects only mean suitable conditions. Though the model likely does not predict unfavorable conditions as suitable, the model cannot capture elevated suitability of short-term weather events with conditions that lie far beyond the mean suitable range of conditions. For example, unusually high levels of annual precipitation may result in great increases in prey populations with corresponding increases in kit fox populations (Ralls and Eberhart 1997; White and Garrott 1997,1999; White and Ralls 1993). Consequently, areas with low-value cells but evidence of a higher incidence of occupancy may not necessarily have truly lower levels of overall suitability through time. Because in some years these areas may not have been projected "suitable" by the model even though conditions may have been favorable at the time. The suitable mean climate distribution map indicates that this is likely the case as this map did capture all but one of the records from the west. Alternative explanations for discrepancies between predictions and omitted records were discussed above. The same explanations for low cell values may hold for some of the annual projections in the eastern half of the study area.

Though the model predicted very few years of mean suitable climate in the eastern half of the study area, more years of favorable conditions might actually have occurred, permitting short-term occupancy in and around the period of study 1992 to 1996, when a small population of kit foxes was known to exist there. As continued monitoring until 2000 documented, the small kit fox population there was eventually extirpated or driven to undetectably low numbers. Results from surveys by Seglund and Garner (2007) and those presented here confirm that the species has not recovered to a detectable level of occupancy. The suitable mean climate distribution map, the summed map, and results from the gradient analyses discussed below indicate that climate suitability in the eastern part of the study area tends to be poor for kit fox.

Spatial Gradients in Mean Climate Conditions Across the Range Edge

As discussed above, the ecological niche modeling results and projections indicate that climate is indeed a good predictor of records of occurrence, with the most important predictor variables being those reflecting the species' unique adaptations. Observed gradients in summer precipitation, mean summer maximum temperature, and mean winter temperature all follow trends with decreasing suitability west to east, with the Cisco Desert in Grand County, Utah experiencing drier and hotter summers and milder winters; and the Lower Gunnison and Uncompaghre valleys in Delta and Montrose counties, Colorado, experiencing wet, mild summers and colder winters (Figs. 13a–c).

Kit foxes are well adapted for life in hot dry deserts so it follows that mean summer maximum temperature and precipitation would be important variables. Many of these traits, however, may be maladaptive in extreme cold. This supposition appears to be supported by the species' affinity for milder winter temperatures. Mildly cold temperatures likely do not pose a challenge to kit foxes, but extreme cold may have several deleterious effects on the animal. Energetic requirements of kit foxes may be particularly high during periods of very low temperatures because of high levels of heat loss through extremities. When temperatures are cool (<23°C), excess heat loss is avoided by reducing blood flow through these regions via vasoconstriction (Klir and Heath 1992). But because these parts of the body are not well insulated with hair or adipose tissue, vasodilation increases blood flow to these areas to prevent freezing during extremely cold temperatures (<-5°C) (Klir and Heath 1992), thereby increasing caloric needs. However, extreme cold may concomitantly reduce total nocturnal prey availability as small mammal species enter torpor, hibernate, or shift activity to warmer times of the day (O'Farrell 1974). Additionally, extreme cold may reduce available foraging time as kit foxes shift periods of activity to avoid the coldest temperatures of the night and to track shifts in activity patterns of prey. Available night foraging time and food availability are known to limit the ranges of some species. The northern range limit of the Indian crested porcupine (*Hystrix indica*) for example is determined by the minimum required hours of nocturnal feeding (Alkon and Saltz 1988) and the northern limit of red fox in North American is determined by prey availability (Hersteinsson and Macdonald 1992).

Because the most important predictor variables show significant trends in suitability west to east and because they likely interact synergistically together and with other variables not evaluated here (e.g. winter precipitation) it is unlikely that kit foxes will ever be very successful for long periods of time in the eastern-most part of the study area—at least in the short-term.

Research Needs

Additional field surveys for kit fox and long-term monitoring will be required to assess the validity of the models presented here. To evaluate whether the model fully captured the realized climate niche of the species in the study area, surveys should be conducted west of the apparent functional soft range edge in the broadest range of climate conditions within potentially suitable vegetation communities. Surveys also should be performed in a manner that will permit evaluation of the predictive power of the summed map. Continued monitoring for presence is also encouraged in the east half of the study area in the most suitable areas of habitat to understand long-term trends more fully.

Conclusion

Although it is well known that occupancy at range edges is likely dynamic and driven by shorter or longer-term extreme climate events, quantitative approaches that integrate spatio-temporal environmental dynamics with patterns in species' occupancy have been lacking. Here I show the utility of such an integration, utilizing data on climatic variability linked with knowledge of species' ecology, and historic and recent records of occurrence and habitat modeling. The findings reported here indicate that a spatio-temporal modeling approach may perform better at predicting a functional range edge for species than using mean climate data projections alone; because at the edge, climate conditions shift beyond the mean suitable state more frequently, resulting in an effective range edge closer to the core of the geographic distribution. My novel approach used to investigate affects of climate variability on range limit formation also are relevant to studies of population and range limit dynamics elsewhere.

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