Conservation Genetics of Kit Foxes (*Vulpes macrotis*) and Coyotes (*Canis latrans*): Using Noninvasive Genetic Sampling to Investigate Two Sympatric Carnivores in the Great Basin Desert

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by

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Authorization to Submit Dissertation

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Abstract

Resource managers worldwide are challenged to protect sensitive species. The status of many species remains ambiguous, in part due to the difficulty in developing cost-efficient monitoring programs. We used noninvasive genetic sampling (NGS) to investigate two sympatric carnivores in the Great Basin Desert: kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*). We developed a conceptual model to optimize NGS design for capture-recapture analyses. We compared statistical classification approaches to field identification (ID) of carnivore scats, and evaluated rates of scat removal to inform noninvasive surveys. To improve efficiency, we developed the ConGenR script to facilitate the determination of consensus genotypes, amplification and genotyping error rates, and genotype matching. We combined NGS with capture-recapture (NGS-CR) analyses to compare likelihood-based abundance estimators. Finally, we combined NGS and occupancy modeling to evaluate coyote and kit fox spatial dynamics. Our results suggested that temporal NGS-CR designs that balanced DNA degradation and sample accumulation reduced costs. Field based scat ID was misleading, but statistical classification provided high accuracy in the absence of molecular ID. Scat removal rates were significantly inflated and influenced survey results at even low levels of disturbance. The choice of estimator and sampling design significantly influenced abundance estimates, and the relationship between estimators varied by species. Occupancy of coyotes and kit foxes were positively and negatively associated with shrubland and woodland cover, respectively. Kit fox probability of local extinction was positively related to coyote activity, yet within an occupied unit, kit foxes were more likely to use areas with greater coyote activity. Collectively, our results demonstrate that NGS can be used to inform conservation and management and explore the relationships between elusive species.

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Dedication

For my wife and my family.

Your patience, support, love, and kindness have allowed me to chase my passions and dreams without restraint. For that, I will forever be grateful.

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Chapter 1: Balancing Sample Accumulation and DNA Degradation Rates to Optimize Noninvasive Genetic Sampling of Sympatric Carnivores

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Abstract

Noninvasive genetic sampling, or noninvasive DNA sampling (NDS), can be an effective monitoring approach for elusive, wide-ranging species at low densities. However, few studies have attempted to maximize sampling efficiency. We present a model for combining sample accumulation and DNA degradation to identify the most efficient (i.e., minimal cost per successful sample) NDS temporal design for capture-recapture analyses. We use scat accumulation and faecal DNA degradation rates for two sympatric carnivores, kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) across two seasons (summer and winter) in Utah, USA, to demonstrate implementation of this approach. We estimated scat accumulation rates by clearing and surveying transects for scats. We evaluated mitochondrial (mtDNA) and nuclear (nDNA) DNA amplification success for fecal DNA samples under natural field conditions for 20 fresh scats/species/season from <1–112 days. Mean accumulation rates were nearly three times greater for coyotes (0.076 scats/km/day) than foxes (0.029 scats/km/day) across seasons. Across species and seasons, mtDNA amplification success was ≥95% through day 21. Fox nDNA amplification success was ≥70% through day 21 across seasons. Coyote nDNA success was ≥70% through day 21 in winter, but declined to <50% by day 7 in summer. We identified a common temporal sampling frame of ~14 days that allowed species to be monitored simultaneously, further reducing time, survey effort and costs. Our results suggest that when conducting repeated surveys for capture-recapture analyses, overall cost-efficiency for NDS may be improved with a temporal design that balances field and laboratory costs along with deposition and degradation rates.

Introduction

Noninvasive genetic sampling, or noninvasive DNA sampling (NDS), is increasingly being used to monitor species that are rare, elusive, or otherwise difficult to survey with traditional techniques (Waits and Paetkau 2005). Genetic material obtained from noninvasive sources (e.g., faeces, hair, feathers) can allow for species identification and individual identification, population genetic structure, genetic diversity, connectivity and sex ratios (Beja-Pereira *et al.* 2009). Combining NDS with capture-recapture and occupancy modeling approaches allows researchers to estimate population demographic parameters (Lukacs and Burnham 2005) and patterns of occurrence (Long *et al.* 2011). Many studies have opted for NDS due to logistical and animal welfare considerations, or improved cost-benefits (e.g., Prugh *et al.* 2005; Brøseth *et al.* 2010; Stenglein *et al.* 2010b).

DNA degradation and genotyping errors can influence NDS results (Taberlet *et al.* 1999; Waits and Paetkau 2005; Beja-Pereira *et al.* 2009). Accordingly, researchers have expended considerable effort to understand how factors such as sample age (Piggott 2004; Murphy *et al.* 2007; Santini *et al.* 2007), environmental conditions (Piggott 2004; Murphy *et al.* 2007; Santini *et al.* 2007; DeMay *et al.* 2013), diet (Murphy *et al.* 2003; Panasci *et al.* 2011), sample collection and storage techniques (Murphy *et al.* 2002; Palomares *et al.* 2002; Piggott and Taylor 2003; Stenglein *et al.* 2010a; Panasci *et al.* 2011), locus length (Buchan *et al.* 2005; DeMay *et al.* 2013) and species-specific differences (Piggott and Taylor 2003, Buchan *et al.* 2005) influence the degradation of DNA. Collectively these studies indicate DNA degradation and genotyping errors vary among species and environmental conditions. General recommendations to reduce degradation and genotyping errors included sampling

the freshest scats and conducting surveys during the driest and/or coldest seasons (Murphy *et al.* 2007; Santini *et al.* 2007).

While previous efforts to optimize NDS have focused on ways to minimize DNA degradation and genotyping errors, they have not explicitly incorporated sample accumulation rates. Understanding sample accumulation rates (i.e., the rate at which noninvasive genetic samples accrue and can be obtained) is critical to designing efficient sampling and may influence the optimal temporal sampling frame. Faecal DNA is a common source of noninvasive genetic samples, but sample accumulation rate is likely affected by diet, behavior, physiology and environmental conditions. For example, seasonal variation in diet, behavior and space use by carnivores can influence scat deposition rates and patterns (Andelt and Andelt 1984; Ralls *et al.* 2010). Additionally, heavy rain or winds can remove scats, as can conspecifics (Livingston *et al.* 2005).

The temporal sampling design of NDS can be optimized to maximize laboratory success while minimizing overall cost per successful sample. Laboratory costs are driven by the number of samples collected, polymerase chain reaction (PCR) success rates and genotyping error rates (Fig. 1.1). Scat accumulation rates, survey effort (spatial coverage), desired sample size (number of samples required to achieve objectives) and the number of sampling events (temporal frequency) necessary to achieve the desired sample size influence field costs (Fig. 1.1). Thus, to optimize the temporal design for NDS, pilot studies should consider both laboratory and field costs by incorporating DNA degradation and sample accumulation rates for each species, season and study site.

Here, we present a model for combining information on sample accumulation and DNA degradation to optimize (i.e., identify the most cost-effective) temporal sampling

design for capture-recapture studies employing NDS. We use scat accumulation rates and faecal DNA degradation rates for two sympatric carnivores, kit foxes (*Vulpes macrotis*; hereafter foxes) and coyotes (*Canis latrans*), across two seasons in the Great Basin desert of Utah, USA, to demonstrate how this approach can be implemented. In regards to scat accumulation, we hypothesized that (1) scat accumulation would be greater for coyotes than foxes due to their more omnivorous diet and higher abundance and (2) seasonal variation in diets would result in higher accumulation rates in summer than winter for both species (Andelt and Andelt 1984; Arjo *et al.* 2007; Kozlowski *et al.* 2008). Regarding DNA degradation, we hypothesized that (1) due to its higher relative abundance mitochondrial DNA (mtDNA) would have higher PCR (or amplification) success rates than nuclear DNA (nDNA), (2) amplification success would decrease over time for both nDNA and mtDNA, (3) amplification success would decrease more precipitously for nDNA than mtDNA and (4) amplification success for nDNA would be higher for shorter microsatellite loci than longer loci (Buchan *et al.* 2005; DeMay *et al.* 2013).

Materials and Methods

Study Area

Our investigation took place on the U.S. Army Dugway Proving Ground (DPG), in western Utah. Located within the Great Basin, DPG is characterized by basin and range formations with elevations from 1228–2154 m (Arjo *et al.* 2007). The site experiences cold winters and moderate summers; coldest and warmest months are January (mean high = 3.3°C, mean low = -8.8°C) and July (mean high = 34.7°C, mean low = 16.3°C), respectively. Mean annual precipitation is approximately 20 cm with the greatest rainfall occurring in spring (Arjo *et al.* 2007). Sampling seasons corresponded to periods preceding breeding

(January and February) and juvenile dispersal (July and August) for target species and aligned with periods of reduced precipitation in the region (Arjo *et al.* 2007).

Sample Accumulation Surveys

Scat accumulation surveys in which transects are cleared and surveyed ~14 days later are commonly used to estimate relative abundances of canids (Gese 2001; Schauster *et al.* 2002). Using this approach, we conducted scat accumulation surveys between September 2010 and July 2012. Scat surveys were originally initiated to evaluate relative abundance of foxes and coyotes and therefore data was available not only for our winter and summer sampling seasons, but also for spring. Fifteen 5 km transects along dirt or gravel roads were cleared and surveyed for carnivore scats ~14 days later (mean = 13.9 ± 0.51 *SD*, range = 13–16). Each 5 km transect was surveyed during two summers (2010, 2011), two springs (2011, 2012) and one winter (2011). Additionally, to expand the spatial coverage and ensure that standardized accumulation rates (scats/km/day) were similar between sampling intervals of different durations, we evaluated scat accumulation along eight shorter transects during one summer (2012), using a random starting point, direction and length (mean = 2.6 ± 0.85 *SD*, range = 1–3.5 km) and surveying seven days after clearing. We determined species for each carnivore scat detected during accumulation surveys based on overall appearance, size and shape (Kozlowski *et al.* 2012).

Faecal DNA Degradation

Faecal DNA degradation was assessed at DPG during two seasons, winter (initiated 8 February 2012) and summer (initiated 11 July 2012), corresponding to proposed field sampling seasons. In each season, 20 fresh scats were collected per species. Fox scats were obtained from live-captured, free-ranging individuals and coyote scats were obtained from

the USDA/NWRC/Predator Research Facility (Millville, UT, USA). Scats were frozen within four hours of collection. On average, fox and coyote scats were stored frozen for 18 months and <1 month, respectively, before being transferred to the study site, thawed and placed in the field and protected from disturbance with a frame covered with wire mesh (25mm openings; 0.7 gauge wire). We collected faecal DNA samples from each scat at days 1, 3, 7, 14, 21, 56 and 112, or until the scat was fully utilized. Day 1 samples were collected just prior to exposure to field conditions. We added a day 5 time point during summer to provide greater resolution, as a recent study detected a significant decline in coyote faecal DNA quality as early as five days post-deposition (Panasci *et al.* 2011). Additionally, a severe wind event during winter buried experimental plots after day 21, so day 56 and 112 time points were only available for summer. Faecal DNA samples were collected from the side of each scat following procedures of Stenglein *et al.* (2010a), and scats were considered fully utilized when no additional samples could be collected in this manner. All samples were stored in 1.4 ml of DET buffer (20% DMSO, 0.25 M EDTA, 100 µM Tris, pH 7.5 and NaCl to saturation; Seutin *et al.* 1991). Due to natural variability in scat sizes, some smaller scats were fully utilized before completion of all time points, resulting in reduced sample sizes at later time points. To maintain more equitable sample sizes among time points during summer, we placed three additional scats for each species out at the start of the degradation study and sampled these scats in place of fully utilized scats at later time points.

DNA Extraction and PCR Amplification

We conducted faecal DNA extraction and PCR amplification in a facility dedicated to low quality DNA. Faecal DNA samples were extracted using the QIAamp DNA Stool Mini Kits (Qiagen, Inc., Valencia, CA, USA) with negative controls to monitor for contamination

(Taberlet and Luikart 1999; Beja-Pereira *et al.* 2009). We performed mtDNA species identification tests by amplifying fragments of the control region (Onorato *et al.* 2006; De Barba *et al.* 2014). Species-specific PCR products lengths were 336–337 base-pairs (bp) for foxes and 115–120 bp and 360–364 bp for coyotes (De Barba *et al.* 2014). Samples that failed to amplify for mtDNA were repeated once to minimize sporadic effects (Murphy *et al.* 2007). For individual identification, we amplified fox and coyote samples with seven and nine nDNA microsatellite loci, respectively (Appendix 1.1). We conducted PCR on a BioRad Tetrad thermocycler (Bio-Rad, Hercules, CA, USA) including negative and positive controls. PCR conditions, including primer concentrations and thermal profiles, are presented in Appendix 1.1. We visualized results using a 3130xl DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and scored allele sizes with Genemapper 3.7 (Applied Biosystems, Foster City, CA, USA). Samples were considered successful for species identification if amplification of ≥1 mtDNA fragment was achieved in either the first or second amplification attempt. We calculated mtDNA success rates as the proportion of successful samples across each time point and season. We calculated nDNA amplification success rates (number of successful amplifications/total possible) and sample success rates (proportion of samples that amplified at ≥50% of the loci) for each time point and species.

Genotyping Error Rates

We combined replicates for each scat (i.e., all replicates across time points with successful nDNA amplification) to establish consensus genotypes (Taberlet *et al.* 1999; Pompanon *et al.* 2005). To achieve a consensus genotype we required that heterozygote and homozygote alleles be observed in two and three independent replicates, respectively. Following the methods of Broquet and Petit (2004), we classified the observation of an allele

not present in the consensus genotype as a false allele (FA) and the amplification of only one allele in a heterozygous consensus genotype as allelic dropout (ADO).

Data Analysis

Scat accumulation results were standardized across transects and species as daily accumulation rates (scats accumulated/days since clearing = scats/km/day). We employed a generalized linear model to test effects of season and species on scat accumulation (O'Hara and Kotze 2010). We considered a Poisson regression model with a log link function, but residuals indicated under-dispersion so we based inferences on quasi-likelihood with a free dispersion parameter. We used a likelihood ratio test to compare models with and without interactions. We compared the influence of main effects and factor levels with contrast analysis (R package contrast; Kuhn *et al.* 2011; R Core Team 2014).

We evaluated PCR success, FA and ADO as binary response variables with mixed-effects logistic regression models to assess DNA degradation rates, with sample included as a random effect to resolve pseudoreplication effects due to multiple observations per sample with SAS 9.3 (SAS Institute Inc. 2011). We included time since the scat was placed in the field (log transformed), DNA type (mtDNA vs. nDNA), species (fox vs. coyote), season (winter vs. summer) and locus length as fixed effects in the model for PCR success. We excluded DNA type from models for FA and ADO as these pertain only to nDNA. We categorized nDNA locus lengths based on the mid-length of alleles per locus by species (range: 90–275 bp).

Optimization of NDS Temporal Design

Our goal was to optimize a NDS temporal design that could be employed within a capture-recapture framework for foxes and coyotes. To this end, we derived a total cost per

successful sample (i.e., sample that achieves a consensus genotype for individual identification) at sampling intervals from 1 to 56 days, where the interval represented the number of days between clearing and survey, or between sequential surveys.

Both spatial survey effort and desired sample size must be selected by the researcher, but may be informed by previous research, power analyses and/or simulations (Williams *et al.* 2002). We selected a survey effort of 150 km, a length of transect which we felt provided reasonable coverage of our study site and encompasses 1350 km^2 within 2.5 km of transects, the radius of the average fox home range at DPG (Dempsey 2013). We identified desired sample sizes of 200 fox and 400 coyote samples, values approximately three times the number of individuals expected to be in our study area (Solberg *et al.* 2006).

We determined the number of samples accumulated and available for collection at each potential sampling interval (1–56 days, hereafter interval), by calculating the product of the daily accumulation rate (scats/km/day), the number of kilometers surveyed (effort) and the number of days in the interval. We combined the number of samples accumulated at each interval with our model-predicted PCR success rates to calculate the number of successful samples for each interval, considering that each interval contained scats of varying ages and levels of degradation. For example, for an interval of three days, we assumed that 33.3% of the scats were one, two and three days old, and that each age class was characterized by its model-predicted PCR success.

Noninvasive samples commonly suffer from genotyping errors (Pompanon *et al.* 2005), which can influence costs. For each interval, we summed the model-predicted FA and ADO rates to determine the overall predicted genotyping error rate. We then calculated the number of genotyping errors expected for samples on each day as the entrywise product of

the number of successful samples and the predicted genotyping error rate for that day. The total number of samples with a genotyping error within a given interval then, was the sum of the number of samples with a genotyping error across all days contributing to the interval. The cumulative genotyping error rate for an interval was determined as the proportion of successful samples with a genotyping error.

As genotyping errors increase, additional replicates are required to reconcile differences among genotypes (Pompanon *et al.* 2005). Within a capture-recapture framework, errors in multilocus genotypes can result in overestimates of abundance and bias survival estimates (Lukacs and Burnham 2005). Consequently, we set a goal of maintaining a probability of error ≤2% in our dataset. We assumed genotyping error rate was similar across loci and replicates were independent. We calculated the probability of having an error in the consensus genotype at a given interval as the cumulative genotyping error rate raised to the number of replicates, then multiplied by the number of loci. We estimated our laboratory costs to be approximately $60/sample (including labor and supplies for extraction, four independent amplifications and finalization of the consensus genotype), based on current laboratory expenses, with a 25% increase in cost for each additional pair of replicates. Thus, when the number of replicates required to maintain our goal of ≤2% error exceeded four, we increased the number of replicates incrementally by two until the goal was achieved or eight replicates were reached. We estimated our hourly field costs to be $10/hour/technician (including labor and fuel) and we could survey 150 km of transects in 160 hours (e.g., two technicians working 40 hours/week for two weeks or four technicians working 40 hours/week for one week). For each interval, we divided the desired sample size by the total number of successful samples to determine the number of sampling events required.

We standardized cost as cost per successful sample at each interval. Thus the total laboratory cost and field cost for each interval were each divided by the number of successful samples. We then combined these costs to obtain an overall cost per successful sample and identified the optimal intervals as those that minimized the overall cost per successful sample. Additionally, to estimate savings obtained from monitoring species concurrently, we calculated the average annual cost per successful sample by dividing the field costs in half (i.e., split between species for each given sampling event) and averaging winter and summer estimates of cost per successful sample for each species.

Results

Scat Accumulation

Scat accumulation surveys were conducted along 170.5 km, 150 km and 75 km of transects in summer, spring and winter, respectively. Rates of scat accumulation were higher for coyotes (mean = 0.076 scats/km/day ± 0.009 *SE*) than foxes (mean = 0.029 scats/km/day ± 0.007 *SE*) across seasons (Fig. 1.2). The likelihood ratio test comparing models with and without interactions was not significant ($P = 0.673$) and therefore we report results for the model with main effects only. Species had a significant effect on scat accumulation when controlling for season (contrast, $z = -9.09$, $P < 0.001$; Table 1.1). Season contrasts controlling for species indicated that spring accumulation rates were significantly different from summer (contrast, $z = 5.99$, $P < 0.001$) and winter (contrast, $z = -3.16$, $P = 0.002$), but that summer and winter differed only marginally (contrast, $z = 1.89$, $P = 0.059$; Table 1.1; Fig. 1.2).

PCR Success Rates

Across time points, 95% ($n = 90$; winter) and 91% ($n = 132$; summer) of fox samples successfully amplified for mtDNA on the first PCR attempt. An additional 5% ($n = 5$) and

3% (*n* = 4) of fox samples successfully amplified for mtDNA on the second PCR attempt, giving overall fox mtDNA success rates of 100% (*n* = 95) and 94% (*n* = 145) in winter and summer, respectively. Overall coyote mtDNA success was 97% (*n* = 100) and 91% (*n* = 157) in winter and summer, respectively, with 89% (*n* = 89; winter) and 87% (*n* = 136; summer) of the samples successfully amplifying for mtDNA on the first PCR attempt and an additional 8% (*n* = 8) and 4% (*n* = 7) amplifying on the second PCR attempt. Both species exhibited high amplification success rates over time with mtDNA success rates ≥95% through 21 days in both seasons (Fig. 1.S1).

Across time points, fox nDNA amplification success rates (number of successful amplifications/total possible) were 75% (*n* = 665) and 72% (*n* = 1015) in winter and summer, respectively, compared to success rates of only 68% (*n* = 900) and 45% (*n* = 1413) for coyotes. Fox nDNA sample success rates (proportion of samples successful at ≥50% of the loci) were ≥95% through day 3 (winter) and day 7 (summer), ≥70% through day 21 in both seasons and declined to <30% by day 56 (summer; Fig. 1.S1). Coyote nDNA sample success rates ranged from 80% to 90% through day 5 in both seasons, remained ≥70% through day 21 in winter, but declined in summer to <50% by day 7 and <25% by day 56 (Fig. 1.S1).

Models indicated that all the main effects significantly influenced PCR success (Table 1.2). Mitochondrial DNA had higher success than nDNA and success for both DNA types decreased over time (Fig. 1.3). Locus length significantly influenced nDNA PCR success, with longer loci having lower success (Fig. 1.3). PCR success was significantly influenced by season, with higher success in winter than summer. A significant effect of species was also detected (Fig. 1.3). Significant interactions among fixed effects reveal the complex nature of DNA degradation (Table 1.2). We detected significant interactions

between the fixed effects of time and both season and locus length. PCR success for mtDNA and nDNA declined more slowly in winter than summer and nDNA success declined more precipitously for longer loci than shorter loci (Fig. 1.3). Significant interactions were detected between species and both time and locus length (Table 1.2).

Genotyping Error Rates

Overall genotyping error rates varied between species (Fig. 1.S2); across seasons and sampling periods, overall ADO was lower for foxes (18%) than coyotes (25%), while overall FA rate was slightly higher for foxes (5%) than coyotes (2%). Winter samples of both species had lower genotyping error rates on average than summer samples. Fox winter ADO rates ranged from 4% to 36%, whereas fox summer ADO rates ranged from 15% to 42% (Fig. 1.S2). Coyote ADO rates ranged from 10% to 29% in winter and 15% to 56% in summer (Fig. 1.S2). In both seasons, FA rates were low for both species (Fig. 1.S2). Models for ADO and FA suggested that season and species, respectively, were the only main effects influencing each model (Table 1.2). Model results for ADO were influenced by a significant interaction between time and species, while model results for FA were influenced by significant interactions of time with season and species, and locus length with species (Table 1.2). Model-predicted cumulative genotyping error rates (combined ADO and FA rates across loci and intervals) were lower for foxes (winter mean = 20.9% ± 0.6% *SE*; summer mean = 25.1% ± 0.6% *SE*) than coyotes (winter mean = 31.5% ± 0.6% *SE*; summer mean = 37.4% ± 0.5% *SE*) and higher in summer than winter for both species.

Optimization of NDS Temporal Design

For fox, the predicted number of samples accumulated ranged from 4.1 (interval = 1 day) to 226.8 (interval = 56 days) in winter and 6.2 (interval = 1 day) to 345.0 (interval = 56

days) in summer. The predicted number of coyote samples accumulated ranged from 12.5 (interval = 1 day) to 697.2 (interval = 56 days) in winter and 13.5 (interval = 1 day) to 756.0 (interval = 56 days) in summer. For both species, the number of samples predicted to fail for nDNA microsatellite amplification, however, increased as interval length increased (Fig. 1.S3). Across seasons and time points, a greater proportion of accumulated coyote samples were predicted to fail than fox samples (Fig. 1.S3).

Based on model-predicted genotyping error rates, our goal of ≤2% probability of error in the dataset could be achieved for fox with five or fewer replicates at all intervals, with four replicates being sufficient up to 34 days in winter and 16 days in summer. To achieve this goal for coyotes up to seven replicates were required. In winter, five replicates were required for intervals of three to 16 days, six replicates for intervals of 17 to 49 days and seven replicates for intervals ≥50 days. For summer coyote samples, the minimum number of replicates required was five (one to three days). Six replicates were required for intervals of four to 17 days and seven replicates for intervals of ≥18 days.

The number of sampling events necessary to obtain desired sample sizes was initially high due to the low number of samples accumulating over shorter intervals, but declined precipitously (Fig. 1.4). The number of sampling events was higher initially in winter than summer for both species due to seasonal differences in accumulation. The number of sampling events required was typically greater for foxes than coyotes despite the smaller desired sample size; this difference was greater in summer than winter (Fig. 1.4).

Overall cost per successful sample showed a similar pattern across species and seasons, but with differences in the magnitude and timing of changes. Cost per successful sample was highest for both species and seasons at the shortest intervals and was higher for

foxes (Fig. 1.4a) than coyotes (Fig. 1.4b) at shorter intervals. For both species, cost per successful sample was higher in winter than summer at short intervals. Summer cost per successful sample surpassed winter costs at seven days for coyotes and 16 days for foxes. Costs per successful sample declined as the number of required sampling events reduced field costs, until genotyping errors were sufficiently high to require additional replicates, increasing laboratory costs. The overall lower cumulative genotyping error resulted in smaller increases in overall cost for foxes (Fig. 1.4a) relative to coyotes (Fig. 1.4b). Sharp increases in cost associated with additional replicates occurred at a shorter interval for foxes (35 days) than coyotes (50 days) in winter. In summer, sharp increases in cost associated with additional replicates occurred at the same interval (17 days) for both species. When surveying species simultaneously, overall cost per successful sample was reduced (Fig. 1.4c) for each species, due to reduced field costs for each species individually. Average annual cost per successful sample suggested that a temporal sampling frame of ~14 days would reduce costs for each species and allow species to be monitored simultaneously (Fig. 1.4c).

Discussion

Our study is among the first to incorporate DNA degradation and sample accumulation rates to optimize NDS design; a similar approach was recently applied to ungulates (Woodruff *et al.* 2015). Our approach provides a novel method to improve efficiency of NDS and should be transferrable to systems or species where pilot studies can elucidate sample accumulation and DNA degradation rates (Fig. 1.1). By reducing costs, optimization approaches can make NDS an appealing monitoring strategy when funding is limited. Optimization allows NDS practitioners to increase spatial extent, temporal resolution, or the number of species monitored in ongoing studies. Our study evaluated faecal

DNA degradation of two carnivores under the same environmental conditions and over two seasons. Studies evaluating faecal DNA degradation rates have become customary for NDS (Murphy *et al.* 2007; Santini *et al.* 2007; DeMay *et al.* 2013), but only two have evaluated degradation for multiple species simultaneously (Piggott 2004; Nsubuga *et al.* 2004).

Factors Influencing Sample Accumulation

The relative abundance of coyotes was higher than foxes across the study site (Arjo *et al.* 2007) and this difference likely contributed to higher observed accumulation rates for coyotes. Spring accumulation rates were significantly lower than summer and winter (Table 1.1; Fig. 1.2); winter accumulation was marginally lower than summer accumulation (Table 1.1). Coyotes and foxes increase their consumption of plants and insects in summer (Kozlowski *et al.* 2008), which may increase scat deposition rates (Andelt and Andelt 1984). Female foxes spend more time in or near dens during the reproduction season (Ralls *et al.* 2010) and these behavioral changes may contribute to lower accumulation rates in spring. Low spring accumulation rates suggest that from a sample accumulation perspective, summer and winter seasons are more appropriate for NDS.

Factors Influencing Faecal DNA Degradation

Time had a significant influence on PCR success, consistent with other canid studies (Piggott 2004; Santini *et al.* 2007; Panasci *et al.* 2011). Our nDNA amplification success rates were similar to those reported by previous canid studies, including coyotes (Panasci *et al.* 2011), wolves (*Canis lupus*; Santini *et al.* 2007) and red foxes (*Vulpes vulpes*; Piggott 2004). Our fox nDNA amplification success was high relative to other canids, while coyote nDNA success was lower than previously reported (Panasci *et al.* 2011). This disparity

stresses the importance of understanding interspecific and intraspecific seasonal variation in degradation rates.

Similar to other studies (Buchan *et al.* 2005; Scandura *et al.* 2006; DeMay *et al.* 2013), locus length significantly influenced nDNA PCR success, suggesting researchers may be able to improve success by selecting shorter loci. We detected a significant effect of season on degradation with winter samples showing less DNA degradation than summer samples. Piggott (2004) documented higher faecal DNA degradation rates in winter than summer and attributed this to increased moisture during winter. Previous studies indicate that environmental conditions such as temperature, UV exposure and humidity influence DNA degradation rates (Nsubuga *et al.* 2004; Murphy *et al.* 2007, Stenglein *et al.* 2010a). Winters and summers at DPG receive less precipitation than other seasons, but temperatures are significantly different (see *Study area*) and UV exposure is highest in summer. Our study design did not allow investigation of the influence of weather on degradation. We placed all samples in the field on the same day each season and therefore weather and time were confounded. We suspect though, that differences observed between seasons were related to broad differences in environmental conditions.

Our observed ADO and FA rates were similar to those reported in other canid studies (Piggott 2004; Santini *et al.* 2007; Stenglein *et al.* 2010b; Panasci *et al.* 2011). We were unable to detect a significant effect of time on genotyping errors, but this was likely due to small sample sizes associated with ADO and FA models. We observed a discernable, but not statistically significant increase in model-predicted ADO rates over time, but not in FA rates.

Optimization of NDS Temporal Design

By balancing sample accumulation and DNA degradation, an optimal NDS design can be selected that minimizes cost per successful sample. The optimal interval varies by species and season and is driven by sample collection (field) and processing (laboratory) costs. While the optimal interval is simply the interval that minimizes the cost per successful sample, additional factors should be considered such as the number of target species and interspecific differences in sample accumulation and DNA degradation. Initial costs per successful sample were calculated for sampling species independently (Fig. 1.4a; Fig. 1.4b). If a common interval is selected for foxes and coyotes, both species can be surveyed simultaneously on the same transects and overall field costs can be reduced (Fig. 1.4c). Additionally, selection of the optimal interval should consider downstream analyses. For example, demographic closure assumptions may be difficult to meet at extended intervals and small reductions in the cost per successful sample may be insufficient justification to select extended intervals.

Our results indicate a range of intervals for foxes and coyotes could be selected to improve efficiency and these intervals are shorter in summer than winter. For example, summer cost per successful sample was minimized for foxes at day 14 and coyotes at day 9, but selection of an interval ±2 days from these optimal intervals changed the cost per successful sample by <$1. The range of effective intervals was wider in winter. Winter cost per successful sample was minimized for foxes and coyotes at days 34 and 24, respectively, yet the cost per successful sample changed <$1 for intervals up to eight days shorter (25–33 days) for foxes and for 24 intervals surrounding (16–40 days) the optimal interval for coyotes. We were interested in selecting a common interval that was effective for both

species and consistent across seasons. Summer cost per successful sample limited the upper bound of the common interval, as cost increased sharply for both species after day 17. We thus identified an interval of 14 days as the common interval within our system (Fig. 1.4c). At 14 days, winter cost per successful sample was reduced and continuing to decline slowly for both species and the number of sampling events was small enough to conduct sampling over a single season.

Based on these results, we recommend NDS efforts account for sample accumulation and DNA degradation during the design phase (Fig. 1.1). Previous studies have recommended sampling the freshest scats possible (Murphy *et al.* 2007; Santini *et al.* 2007; DeMay *et al.* 2013). Our results show that when sampling over time within a capture-recapture framework, short intervals may be cost-prohibitive if a substantial sample size is required. Thus, we recommend sampling designs consider cost per successful sample and minimize violations of assumptions for downstream analyses.

Limitations and Implications for Research

Collection of fresh samples (e.g., samples known to be ≤1 day old) to evaluate DNA degradation is logistically prohibitive, particularly when species are rare, elusive, or difficult to capture. Consequently, many studies comparing PCR success (e.g., between species, under environmental variations, over time) have relied on samples from captive populations (Murphy *et al.* 2002; Murphy *et al.* 2003, Piggott 2004; Murphy *et al.* 2007; Santini et al. 2007; DeMay *et al.* 2013). In our study, scats used to evaluate DNA degradation varied between species in origin and length of storage. We obtained fresh scats from free-ranging foxes during live-capture, but fresh scats from free-ranging coyotes were unavailable. Consequently, fresh coyote scats were obtained from a captive population. Although scats

were frozen upon collection, stored for variable lengths of time and thawed prior to placement in the field, we do not feel that storage time or the freeze-thaw cycle significantly impacted PCR success. While we did not explicitly test the influence of freezing during this study, we previously evaluated PCR success of canid scats stored in a standard freezer and found no decline in PCR success for samples frozen for up to one year, when the study ended (unpublished data). Our results support this conclusion. On average, fox and coyote scats were stored frozen 18 months and <1 month, respectively. Despite the longer storage time of fox scats, observed PCR success rates were the same (mtDNA) or higher (nDNA) for foxes in both seasons and scats of both species produced high PCR success at the earliest time points (Fig. 1.S1). Additionally, winter temperatures at our site fluctuate from below to above freezing (night vs day temperatures) and scats naturally experience repeated freeze-thaw cycles, yet in this experiment we observed higher PCR success rates for both species in winter relative to summer, suggesting that freeze-thaw cycles were not the driving cause of DNA degradation.

Variation in diets between captive and free-ranging coyotes may also influence the generalization of results to the wild population. Differences in diet could influence the rate of intestinal cell shedding or the amount of inhibitors in fecal samples. However, we do not believe that using captive coyote scats substantially influenced our results. We have data on success rates for free-ranging coyote samples collected in winter and summer 2013, and results are comparable to model-predicted results from our degradation experiment. For example, for a 14 day interval our model predicted mean nDNA success rates for coyote scats of 64.6% (winter; range 46.5–80.7%; Fig. 1.3) and 47.7% (summer; range 24.9–71.2%;

Fig. 1.3), and success rates for free-ranging coyotes sampled with a 14 day interval were 78% (winter) and 55% (summer).

We analyzed winter and summer degradation within the same models for PCR success, ADO and FA to increase sample size and statistical power, but winter samples were only available through day 21. Model-predicted results for winter intervals >21 days assume that trends in predicted values continue in the same way beyond 21 days (i.e., that the log odds of the outcome is linear in the log of time) and consequently, these predictions should be interpreted with caution. Missing winter data points do not affect the inferences ≤21 days and it is during this time that the most substantial changes occurred (Fig. 1.3).

Monitoring and Management Implications

This study presents a conceptual model for optimizing NDS for capture-recapture analysis, which can be extended to any species or system where estimates of sample accumulation (e.g., hair snaring rate, scat accumulation rate) and DNA degradation rates can be quantified. We demonstrate that this novel optimization approach can effectively reduce costs of NDS monitoring programs. By initiating a pilot study to evaluate sample accumulation and DNA degradation rates, NDS monitoring costs can be minimized, allowing monitoring to occur over larger spatial extents and at higher temporal resolutions than would be possible otherwise. Differences observed in sample accumulation and DNA degradation rates between species and across seasons, at the same study site, reiterate the importance of pilot studies for effectively implementing NDS (Taberlet *et al.* 1999; Waits and Paetkau 2005). We recommend that when possible, pilot studies incorporating DNA degradation should use fresh scats collected from target populations. Additionally, practitioners optimizing NDS should compare field collected data to model-predicted results to evaluate

model performance, particularly when samples used during pilot studies have an origin other than the population being monitored.

Kit fox populations are believed to be declining and their contemporary distribution is unclear. High mtDNA success suggests that NDS can be used to explore presence or occupancy of elusive species, such as kit fox, across large spatial areas. When employing NDS for occupancy modeling (or similar approaches), researchers should acknowledge that mtDNA amplifications may incorporate old samples violating closure assumptions and should clear transects before surveying or evaluate sample persistence (MacKenzie and Reardon 2013). Nuclear DNA success rates were sufficient to identify individuals and provide an effective capture-recapture approach to estimate population demographic parameters (Kohn *et al.* 1999; Marucco *et al.* 2011). Both mtDNA and nDNA can be used for monitoring communities or intraguild interactions and provide a cost-effective means to monitor management strategies.

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Data Accessibility

Raw data (.csv) and analysis code for scat accumulation (R script) and models of PCR success, ADO and FA (SAS scripts) available on Dryad, doi:10.5061/dryad.23k27.

Tables

Table 1.1. Generalized linear model and contrast analysis results with standard errors (SE) and lower (LL) and upper (UL) 95% confidence bounds for scat accumulation samples collected from September 2012 to July 2012 at Dugway Proving Ground, Utah. Species levels include coyote (*Canis latrans*) and kit fox (*Vulpes macrotis*). Season levels include spring, summer and winter. Significant (*) p-values for z statistic evaluated at $\alpha = 0.05$.

	Estimate	SE	z-value	*P*-value	LL	UL
Model Parameters						
(Intercept)	-3.07	0.243	-12.37	<0.001*	-3.52	-2.56
Summer	0.66	0.277	2.38	0.019*	0.13	1.22
Winter	0.47	0.349	1.36	0.177	-0.23	1.16
Kit fox	-0.97	0.253	-3.83	<0.001*	-1.49	-0.49
Contrasts						
Coyote vs. Kit fox	-1.08	0.119	-9.09	<0.001*	-1.32	-0.85
Summer vs. Winter	0.26	0.137	1.89	0.059	-0.01	0.53
Summer vs. Spring	0.79	0.131	5.99	<0.001*	0.53	1.04
Spring vs. Winter	-0.53	0.167	-3.16	0.002*	-0.85	-0.19

Table 1.2. Mixed-effects logistic regression model results for PCR success, allelic dropout and false alleles for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) faecal DNA samples collected in 2012 during winter and summer at Dugway Proving Ground, Utah. Reported Chi-square test statistics and *P*-values were generated with Type III tests of fixed effects. Significance (*) was evaluated at $\alpha = 0.05$. Time was log-transformed days since the scat was placed in the field. DNA types included mitochondrial and nuclear DNA. Locus length (LL) was based on the midpoint of each locus (range 90–275 base pairs).

	PCR success		Allelic dropout		False alleles	
Fixed effect	Chi-square	*P*-value	Chi-square	*P*-value	Chi-square	*P*-value
Time	4.93	0.0263*	0.80	0.3706	0.09	0.7678
DNA type	224.03	<0.0001*	--	--	--	--
LL	8.73	0.0031*	0.03	0.8661	1.26	0.2614
Season	4.02	0.0449*	4.11	0.0427*	0.93	0.3337
Species	25.90	<0.0001*	0.64	0.4237	7.95	0.0048*
Time × Season	42.02	<0.0001*	0.28	0.5966	5.91	0.0150*
Time × Species	24.15	<0.0001*	4.09	0.0432*	4.94	0.0262*
Time × LL	13.38	0.0003*	1.03	0.3100	0.04	0.8386
LL × Season	1.57	0.2100	1.22	0.2699	0.15	0.7020
LL × Species	8.36	0.0038*	1.57	0.2098	10.16	0.0014

Figures

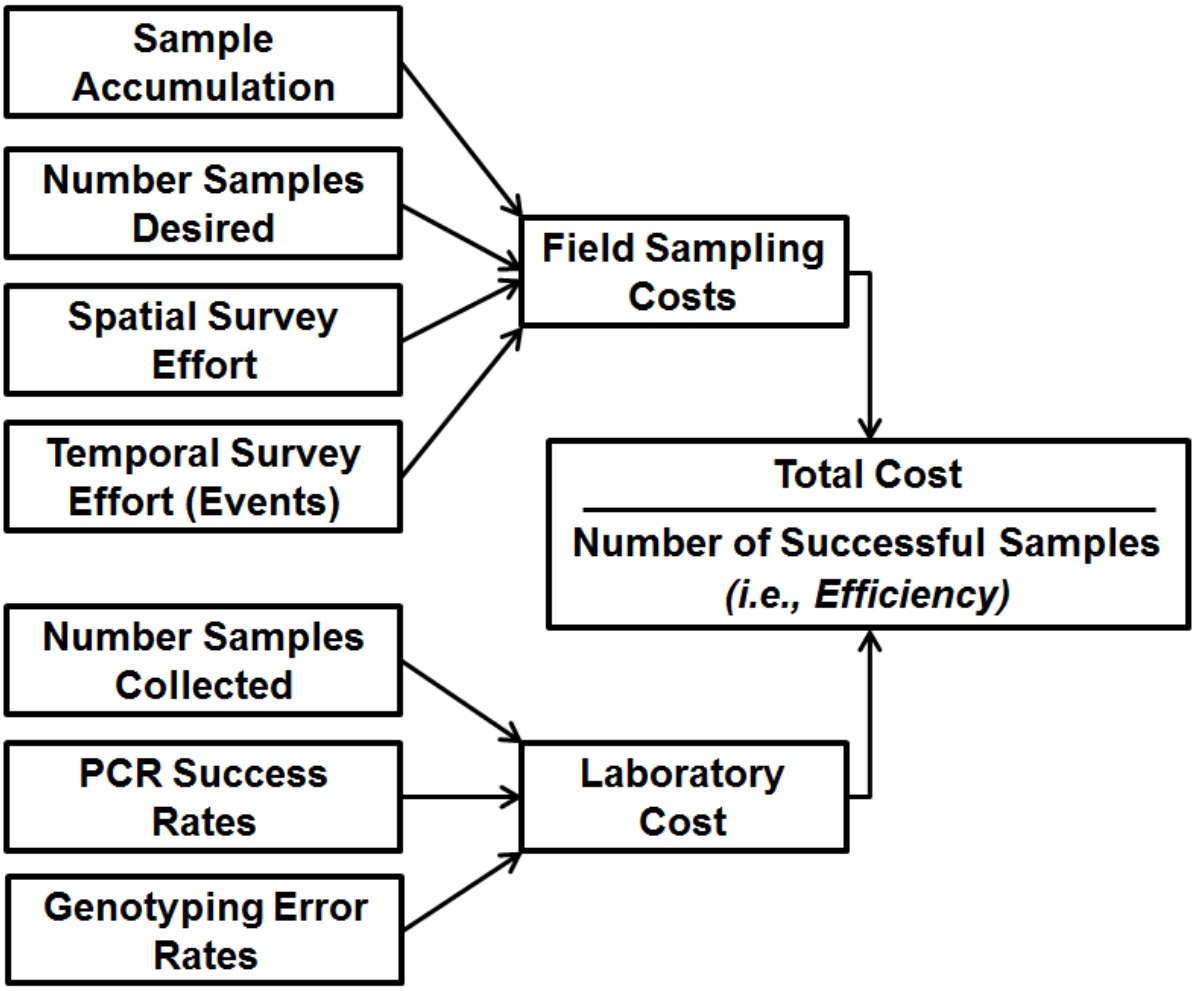

Figure 1.1. Conceptual diagram showing the major components required to balance field and laboratory efficiency for optimization of noninvasive genetic sampling for capture-recapture analysis.

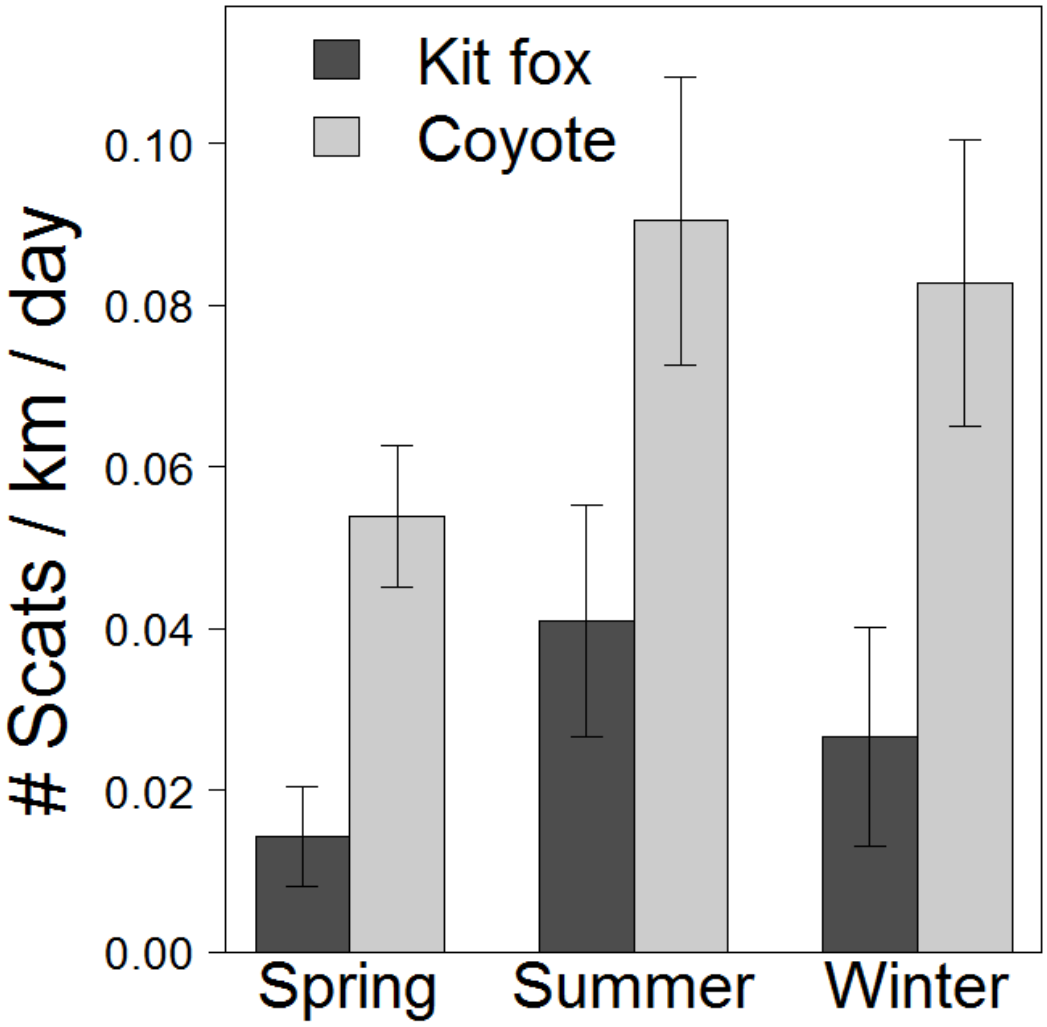

Figure 1.2. Mean scat accumulation rates ± *SE* for kit fox (*Vulpes macrotis*; dark gray) and coyote (*Canis latrans*; light gray) at Dugway Proving Ground, Utah, collected from September 2010 to July 2012. Coyote scat accumulation rates were significantly higher than kit fox ($P < 0.001$). Spring differed significantly from summer ($P < 0.001$) and winter ($P = 0.002$). Summer and winter differed marginally ($P = 0.059$).

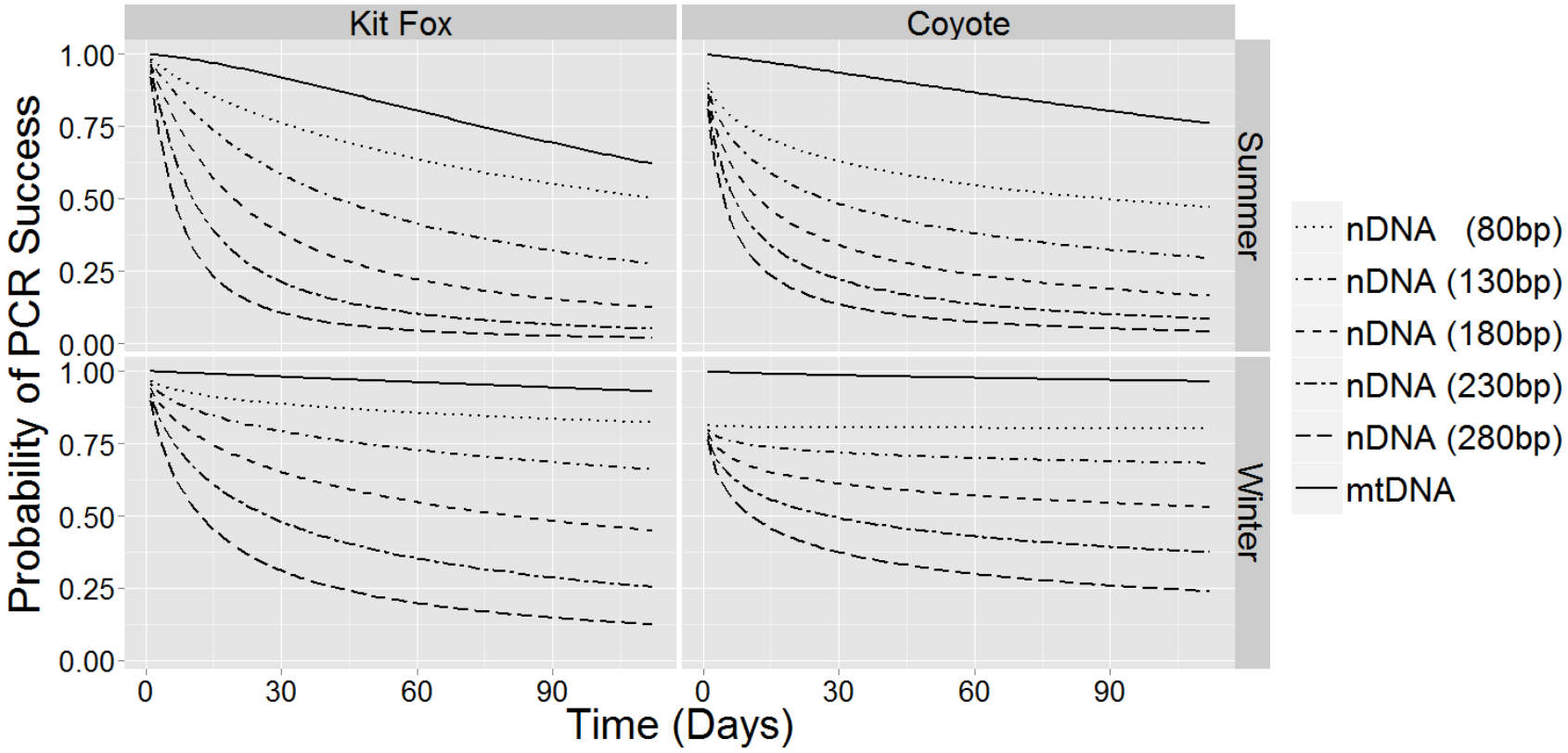

Figure 1.3. Mixed-effects logistic regression model results for PCR success for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) faecal DNA samples collected in 2012 during winter and summer at Dugway Proving Ground, Utah.

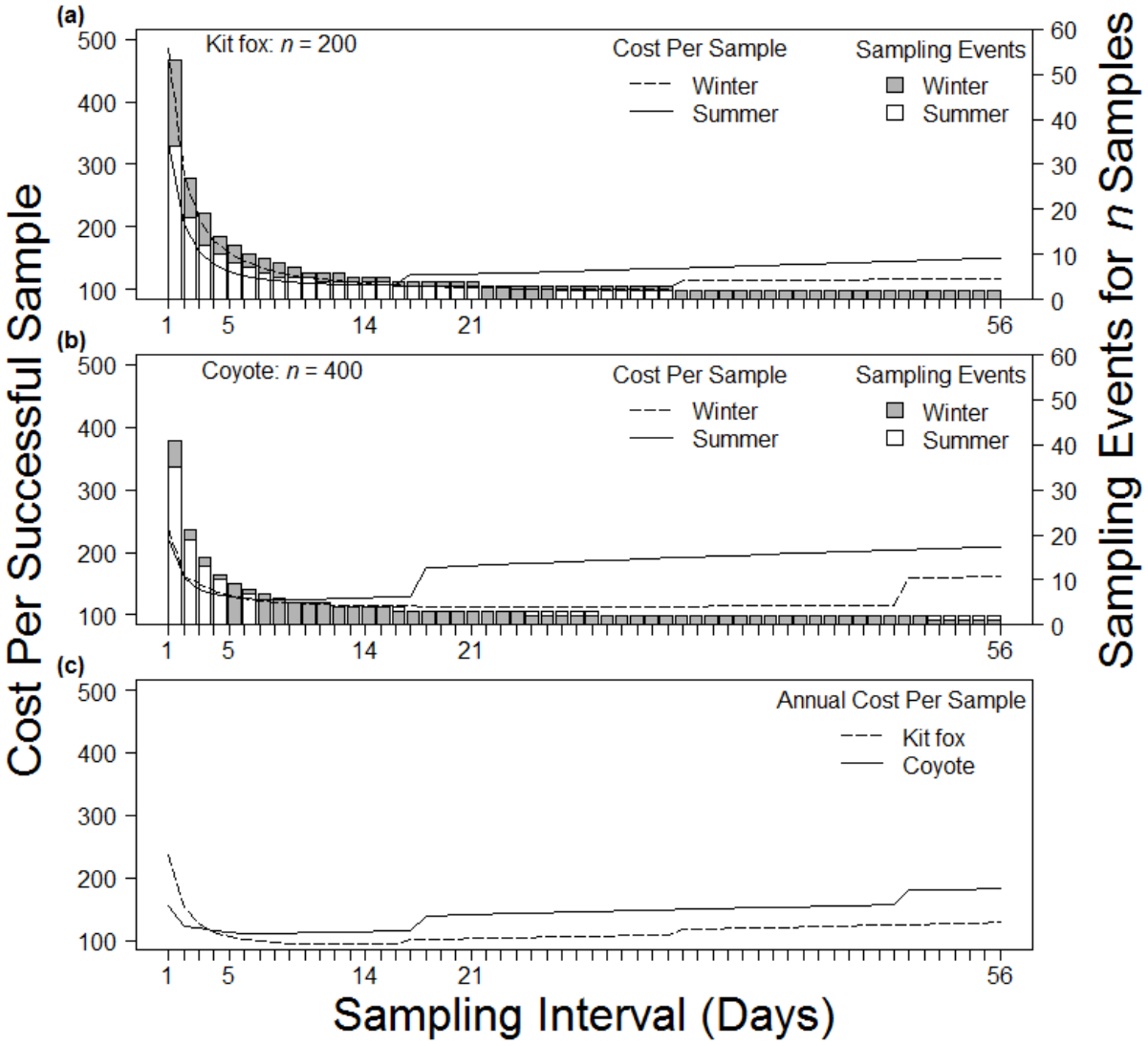

Figure 1.4. Evaluation of cost ($) per successful faecal DNA sample and number of sampling events required to obtain (a) *n* = 200 kit fox (*Vulpes macrotis*) and (b) *n* = 400 coyotes (*Canis latrans*) samples from surveying 150 km of transects at Dugway Proving Ground, Utah, for a range of sampling intervals in winter and summer. Sampling intervals represent the days between an initial clear and subsequent survey or between surveys. The average annual cost for surveying each species (c) is reduced when the two sympatric species are surveyed simultaneously.

Supporting Information

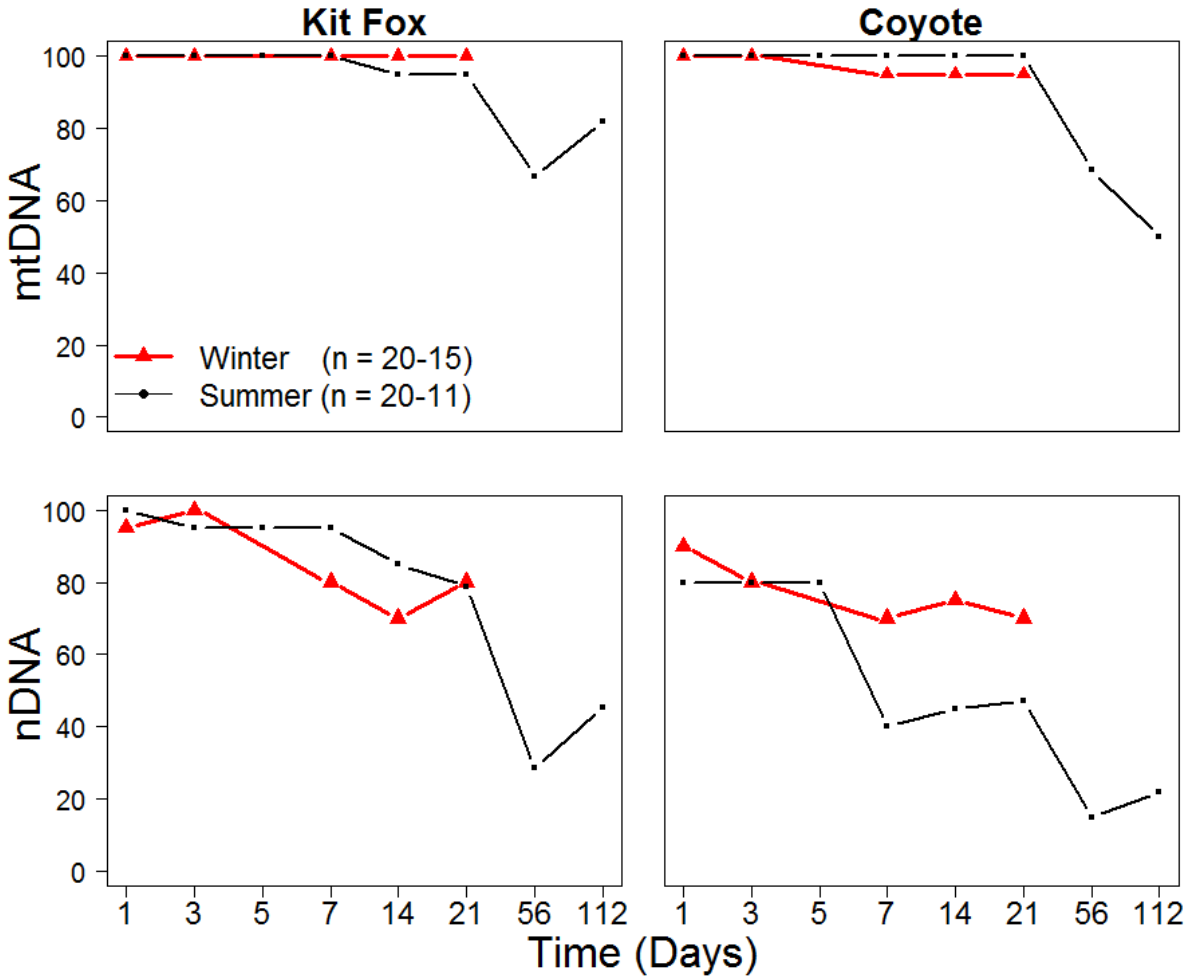

Figure 1.S1. Observed percent PCR success for mitochondrial (mtDNA) and nuclear (nDNA) DNA for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) faecal DNA samples collected in 2012 during winter and summer at Dugway Proving Ground, Utah. Percent PCR success for mtDNA is presented as the proportion of samples identified to species across each time point and season. Percent PCR success for nDNA is presented as the proportion of samples with successful amplification at ≥50% of the loci for each time point and species.

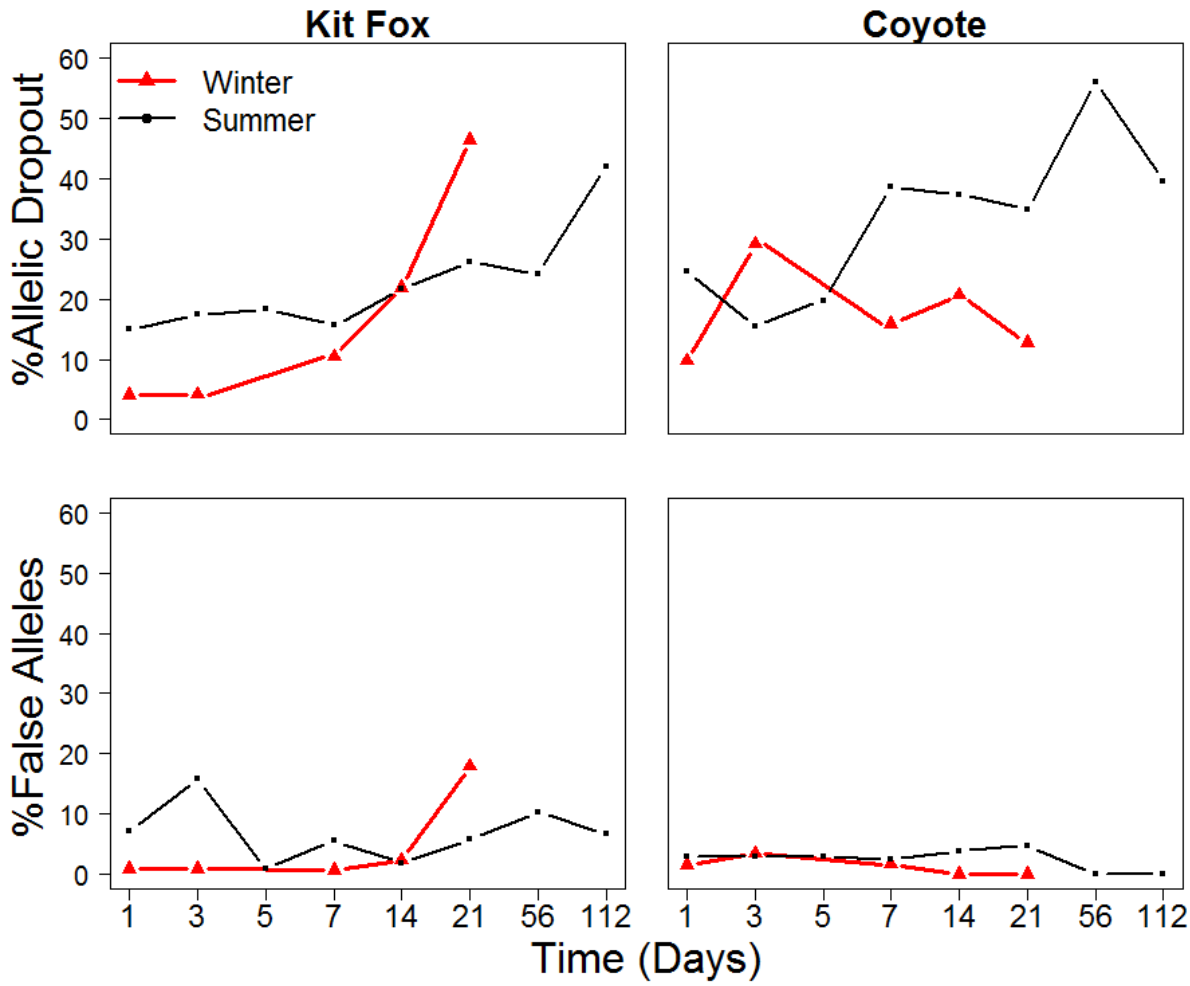

Figure 1.S2. Observed nuclear DNA genotyping error rates (i.e., allelic dropout and false alleles) for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) faecal DNA samples collected in 2012 during winter and summer at Dugway Proving Ground, Utah.

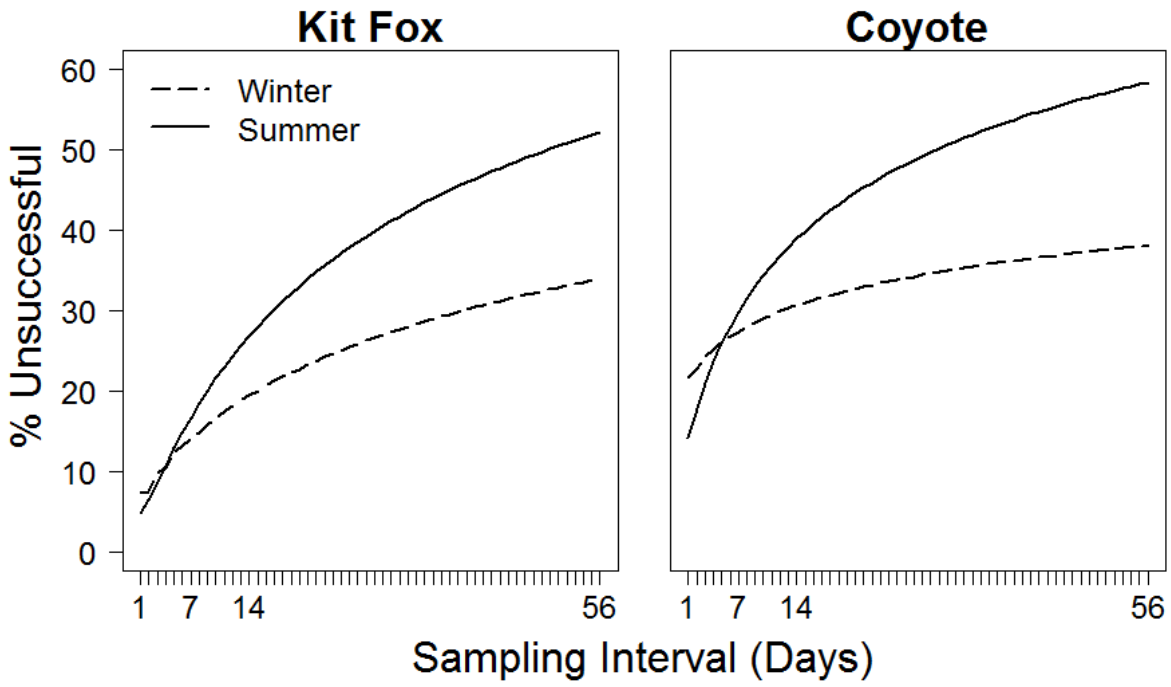

Figure 1.S3. Proportion of samples accumulated for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) in winter and summer at Dugway Proving Ground, Utah, that were predicted to fail for individual identification with nuclear DNA at sampling intervals from 1 to 56 days.

Chapter 2: Evaluating the Reliability of Field Identification and Morphometric Classifications for Carnivore Scats Confirmed with Genetic Analysis

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Abstract

Scat surveys are commonly used to monitor carnivore populations. Scats of sympatric carnivores can be difficult to differentiate and field-based identification can be misleading. We evaluated the success of field-based species identification for scats of 2 sympatric carnivores—coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*). We conducted scat surveys in the Great Basin desert of Utah, USA, during the winter and summer of 2013, and we detected 1,680 carnivore scats. We classified scats based on field identification, recorded morphometric measurements, and collected fecal DNA samples for molecular species identification. We subsequently evaluated the classification success of field identification and

the predictive power of 2 nonparametric classification techniques—*k*-nearest neighbors and classification trees—based on scat measurements. Overall, 12.2% of scats were misclassified by field identification, but misclassifications were not equitable between species. Only 7.1% of the scats identified as coyote with field identification were misclassified, compared with 22.9% of scats identified as kit fox. Results from both *k*-nearest neighbor and classification-tree analyses suggest that morphometric measurements provided an objective alternative to field identification that improved classification of rarer species. Overall misclassification rates for *k*-nearest neighbor and classification-tree analyses were 11.7% and 7.5%, respectively. Using classification trees, misclassification was reduced for kit foxes (8.5%) and remained similar for coyotes (7.2%), relative to field identification. Although molecular techniques provide unambiguous species identification, classification approaches may offer a cost-effective alternative. We recommend that monitoring programs employing scat surveys utilize molecular species identification to develop training data sets and evaluate the accuracy of field-based and statistical classification approaches.

Introduction

The development of sound and effective management and conservation strategies for wildlife populations requires reliable and accurate information on species distributions and population trends. For carnivores, invasive monitoring methods requiring capture and handling of animals can be challenging and costly, often limiting their utility for large spatial extents or long-term monitoring (Gese 2001, MacKenzie 2005, Gompper et al. 2006). Noninvasive surveys (Long et al. 2008, Kelly et al. 2012) are an appealing alternative for monitoring populations because they are simple, cost-efficient, and facilitate multispecies monitoring (Gompper et al. 2006). For many elusive or rare species, such as carnivores, scats

are often the most conspicuous indication of their presence and therefore noninvasive scat surveys are a widely used means of monitoring populations (e.g., Prugh and Ritland 2005, Gompper et al. 2006, Harrington et al. 2010, Long et al. 2011). Scat surveys are frequently employed to delineate distributions (Kozlowski et al. 2012), assess relative abundances (Schauster et al. 2002, Cunningham et al. 2006, Kamler et al. 2013), develop models of resource selection (Vynne et al. 2011, Dempsey 2013), and evaluate occupancy patterns (Long et al. 2011, Schooley et al. 2012). Scat surveys can provide additional information on diet (Kozlowski et al. 2008, Marucco et al. 2008), resource partitioning (Vanak and Gompper 2009, Kamler et al. 2012), and parasitology (Kohn and Wayne 1997). In addition, scat collections afford researchers the opportunity to obtain fecal DNA to assess measures of population genetics (Waits and Paetkau 2005), social and spatial ecology (Kitchen et al. 2005), and breeding strategies (Kitchen et al. 2006).

Correct inferences from scat surveys depend on accurate species identification, and misclassifications could bias results and potentially reduce the effectiveness of management strategies (Marucco et al. 2008, Harrington et al. 2010). Commonly, field-based species identification (hereafter, field identification) is determined through inspection of scat morphology including color, odor, overall size, and physical appearance (Vanak and Gompper 2009, Kamler et al. 2012); this is often coupled with auxiliary information, such as presence of tracks, dietary content, or distance from a den, to improve field identification confidence (Green and Flinders 1981, Prugh and Ritland 2005, Harrington et al. 2010, Kozlowski et al. 2012, Schooley et al. 2012). However, sympatric carnivores may produce scats with overlapping sizes (Green and Flinders 1981, Danner and Dodd 1982, Farrell et al. 2000, Reed et al. 2004, Gompper et al. 2006), and auxiliary information may be lacking,

misleading, or uninformative. For example, counter-marking is common among conspecifics (Ferkin and Pierce 2007) and may produce confounding sign; and dietary content may not contribute to improving field identification for species with high dietary overlap (Onorato et al. 2006, Foran et al. 1997). Consequently, carnivore scats can be difficult to discriminate and confidence in field identifications can be misleading or completely erroneous (Foran et al. 1997, Paxinos et al. 1997, Farrell et al. 2000, Davison et al. 2002, Harrington et al. 2010).

Molecular species identification (hereafter, molecular identification) provides a reliable alternative to field identification (Foran et al. 1997, Kohn and Wayne 1997, Farrell et al. 2000, Dalen et al. 2004, Prugh and Ritland 2005). Comparisons of field and molecular identifications have yielded contrasting results. Coyote (*Canis latrans*) scats could be distinguished from sympatric carnivores in Alaska, USA, with high accuracy using field identification (Prugh and Ritland 2005), whereas pine marten (*Martes martes*) and red fox (*Vulpes vulpes*) scats could not be confidently discriminated in Britain (Davison et al. 2002), and experienced researchers failed to successfully identify American mink (*Neovison vison*) scats in Scotland (Harrington et al. 2010). Despite the challenges and ambiguity associated with field identification, many wildlife managers and researchers still rely on field identification, likely because of the increased costs associated with molecular identification. Conservation and management programs often suffer from limited funding and the number of imperiled species continues to rise, increasing the need to improve and evaluate cost-effective monitoring strategies (Gese 2001).

We used molecular identification to evaluate the accuracy of field identification for scats of 2 sympatric carnivores, coyotes and kit foxes (*V. macrotis*), in the Great Basin desert of western Utah, USA. Coyote populations have increased notably over the past several

decades at this site, where they are now the most abundant carnivore (Arjo et al. 2007). The kit fox is a species of conservation concern; kit foxes are significantly smaller than coyotes and have been experiencing population declines that have been contributed, in part, to increased competition with and predation by coyotes (Arjo et al. 2007). Consequently, multiple studies have been conducted in western Utah to investigate kit fox and coyote populations, some of which have employed scat surveys (Kozlowski et al. 2008, 2012; Dempsey 2013; Dempsey et al. 2014). To evaluate alternative classifications to field and molecular identification, we explored 2 common nonparametric classification approaches—*k*-nearest neighbors and classification trees—based on morphometric measurements as objective, quantitative alternatives for discriminating scats. The *k*-nearest neighbor approach is among the simplest supervised classification algorithms and assigns an unknown observation to a class based on class majority of the *k* closest training observations within the parameter space (Cover and Hart 1967, Hastie et al. 2001). Classification-tree analysis, or recursive partitioning, searches all possible binary splits of the predictor variables to identify splits that optimize classification (i.e., prediction of the species) and produces a decision tree that provides clear classification rules and information on variable importance (Breiman et al. 1984). Both *k*-nearest neighbor and classification-tree analyses require sufficiently large samples sizes, though, to develop training data sets. Consequently, using these approaches may restrict analyses to species with sufficient representation (i.e., adequate sample sizes to characterize the population), whereas field identification and molecular identification do not have this requirement. Focusing on 2 target carnivore species, we hypothesized that field identification would be more reliable for the abundant species (coyotes) than for the rarer species (kit foxes) as observed in other systems (Davison et al. 2002, Prugh and Ritland

2005). We further hypothesized that scat diameters of the 2 species would overlap (e.g., Green and Flinders 1981, Danner and Dodd 1982), but that inclusion of additional morphometric measurements (i.e., length and no. of disjoint segments) into nonparametric classification methods would provide a more accurate and objective method of identifying scats than would field identification.

Study Area

The study was centered on the eastern portion of the U.S. Army's Dugway Proving Ground, Utah, and extended to surrounding federal lands managed by the U.S. Bureau of Land Management (Fig. 2.1). Elevations across this Great Basin Desert site ranged from 1,228 m to 2,154 m (Arjo et al. 2007). Winters were cold (Jan: $\bar{x}$ high = 4° C, $\bar{x}$ low = −10° C) and summers were moderate (Jul: $\bar{x}$ high = 36° C, $\bar{x}$ low = 15° C), with the majority of precipitation accumulating in the spring and autumn ($\bar{x}$ annual precipitation approx. 20 cm; Arjo et al. 2007). The site was characterized at low elevations by cold desert playa (dominated by *Allenrolfea occidentalis*), cold desert chenopod shrubland (dominated by *Atriplex confertifolia* and *Kochia americana*) and vegetated dunes, along with nonnative invasive grasslands (*Bromus tectorum*), which dominated in disturbed areas. Higher elevations supported arid shrubland (e.g., *Artemisia* spp., *Chrysothamnus viscidiflorus*) and open woodland (*Juniperus osteosperma*) complexes. *Sarcobatus vermiculatus* shrubland was distributed across the elevational gradient of the site but found more often at moderate to higher elevations.

Methods

Field Sampling and Identification of Carnivore Scats

We conducted surveys for carnivore scats in the winter and summer of 2013 along transects that followed 2-track or gravel roads. We surveyed 30 transects (5 km each; including 15 transects previously utilized to develop a resource selection function for kit foxes [Dempsey 2013], evaluate survey methods for kit foxes [Dempsey et al. 2014], and to evaluate scat-deposition rates for kit foxes and coyotes [Lonsinger et al. 2015]), and 15 additional random transects (Fig. 2.1). We conducted 3–4 surveys on each 5-km transect within each season. Additionally, we selected 240 shorter random transects (500 m each) that were surveyed once in each season (Fig. 2.1). Nine researchers participated in the surveys and were responsible for identifying and sampling scats. We surveyed each transect with 2 researchers, each searching half of the transect width for carnivore scats. When a carnivore scat was encountered, we determined field identification by inspecting the scat's morphology, including color, odor, overall size, and physical appearance (Kozlowski et al. 2012). We then collected a fecal DNA sample (approx. 0.7 mL) from the side of the scat (Stenglein et al. 2010), which was stored in 1.4 mL of DET buffer (20% DMSO, 0.25 M EDTA, 100 mM Tris, pH 7.5, and NaCl to saturation; Seutin et al. 1991). For a subset of scats sampled, we measured the diameter at widest point and total length with a sterilized digital caliper (resolution = 0.1 mm; Mitutoyo America Corporation, Aurora, IL) and recorded the number of disjoint segments, prior to fecal DNA sample collection. When scats consisted of multiple disjoint segments, the total length was determined by summing the lengths of the segments. Scats that lacked the typical physical structure (e.g., soft piles for

which accurate measurements could not be obtained) were not measured and were excluded from subsequent analyses.

Mitochondrial DNA Species Confirmation

We conducted fecal DNA extraction and mitochondrial DNA (mtDNA) polymerase-chain reaction (PCR) amplification in a laboratory dedicated to low-quality and low-quantity samples such as fecal samples. We randomized samples and extracted fecal DNA using QIAamp DNA Stool Mini Kits (Qiagen, Inc., Valencia, CA) with negative controls to monitor for contamination (Taberlet et al. 1999, Beja-Pereira et al. 2009). We performed mtDNA species identification tests by amplifying fragments of the control region using established protocols and including negative controls to monitor for contamination (De Barba et al. 2014). Qiagen Master Mix (1× concentration), Q solution (0.5× concentration), and 1 μL of DNA extract were combined with species identification primers into a 7-μL (total vol) multiplex. The PCR conditions for each primer were as follows: 0.29 μM SIDL, 0.20 μM H16145, 0.10 μM H3R, 0.13 μM FelidID F, 0.03 μM LRuf F, and 0.03 μM PCon R. The PCR thermal profile had an initial denaturation of 95° C for 15 minutes, 35 cycles of 94° C for 30 seconds (denaturation), 46° C for 90 seconds and 72° C for 60 seconds (elongation), and a final elongation stage of 60° C for 30 minutes. We conducted PCR on a BioRad Tetrad thermocycler (Bio-Rad, Hercules, CA) and included negative and positive controls. We visualized results using a 3130xl DNA Analyzer (Applied Biosystems, Foster City, CA) and scored allele sizes with Genemapper 3.7 (Applied Biosystems). Species-specific PCR product lengths were 335–337 base-pairs (bp) for kit foxes and 115–120 bp and 359–363 bp for coyotes. For samples that failed to amplify for mtDNA, we repeated the species identification test once to minimize sporadic effects (e.g., pipetting errors; Murphy et al.

2007). We classified samples that contained DNA from multiple species as mixed and removed these samples and any samples that failed from subsequent analyses. We calculated the proportion of samples that were misclassified (hereafter, misclassification rate) based on field identification, including an overall misclassification rate and species-specific misclassification rates.

Statistical Classification of Scats

Six species were identified with molecular identification (*see* Results) but only coyotes and kit foxes had sample sizes sufficient to evaluate species-specific classification techniques. Initially, we restricted classification of scats to samples that 1) were confirmed through molecular identification to have originated from coyotes or kit foxes, and 2) had morphometric measurements collected. For coyote and kit fox samples, we evaluated 3 predictor variables, including diameter, length, and number of segments, for normality with Shapiro–Wilk tests (Zar 1996, Razali and Wah 2011). We tested for predictor variable differences between coyote and kit fox scat using Mann–Whitney *U*-tests (Zar 1996).

To explore the ability of statistical classification algorithms to improve classification over field identification, we used 2 nonparametric classifiers, *k*-nearest neighbors and classification trees, to classify scats based on measurements. Differences in the distribution of all 3 predictors suggested that each may contribute to discriminating species, so we included all 3 predictors in classification models. The *k*-nearest neighbor classifier can be sensitive to the *k* selected and the structure of the training data set. Consequently, we evaluated classification success for values of *k* from 1 to 20. For each *k,* we randomly selected a training data set of 100 kit fox and 100 coyote scats and then used the remaining samples for model validation. To minimize the influence of the local structure, or

configuration in parameter space of a single random training data set, we repeated this procedure 500 times for each *k* and calculated the mean misclassification rate for each *k.* We then identified the *k* with the lowest mean misclassification rate for each species and overall. Classification trees may utilize predictor variables in >1 split. To account for over-fitting (i.e., branches resulting from noise or that provide limited contribution to classification), we used 10-fold cross-validation to generate an error rate for each split. We then pruned the tree back to the split corresponding to the lowest cross-validation error (Breiman et al. 1984, Therneau et al. 2014). Based on the pruned tree, we estimated variable importance, a measure of each variable's relative contribution (scaled to sum to 100) to the classification across splits (Therneau et al. 2014). We compared the performance of *k*-nearest neighbor and classification-tree models with one another and to field identification based on the misclassification rate. We used the 'class' (Venables and Ripley 2002) and 'rpart' (Therneau et al. 2014) packages in R (R Core Team 2014) to conduct *k*-nearest neighbor and classification-tree analyses, respectively.

We conducted additional classification-tree analyses to further assess the influence of each predictor (i.e., diameter, length, and no. of segments) and explore misclassification rates by season. Using the same procedures as above, we built classification-tree models for all possible combinations of the 3 predictor variables contained in the full model and evaluated the change in misclassification rates. Seasonal variation in misclassification rates may result from differences in juvenile body size or dietary changes. Using the model with the lowest misclassification rate overall (i.e., the full model), we evaluated differences in winter and summer misclassification rates. Finally, samples from nontarget, sympatric carnivores may occur relatively infrequently in our study system, and inclusion of these species in

classification approaches may increase misclassification rates of target species. To evaluate the potential influence of additional sympatric carnivores, we conducted a classification-tree analysis focusing on kit foxes. We conducted this analysis in the same fashion as reported above, but evaluated the classification success of kit fox scats versus all other scats. We limited these additional analyses to classification trees because this approach provided the lowest overall misclassification rate when comparing misclassifications of kit foxes and coyotes (*see* Results).

Results

Field Sampling and Identification of Carnivore Scats

We surveyed each 5-km transect (Fig. 2.1) 4 times from 8 January to 26 March 2013 (winter) and 3 times from 8 July to 28 August 2013 (summer). Sequential surveys at each site were approximately 14 days apart ($\bar{x}$ = 13.6 ± 1.11 SD, range = 9–18 days). We surveyed each 500-m transect (Fig. 2.1) once in each season. In total, 1,290 km of transects were surveyed across both seasons. We collected 1,680 (winter: n = 602; summer: n = 1,078) carnivore scats, and field identification and morphometric measurements were available for 1,498 scats.

Species Identification

We were able to confirm species with molecular identification for 1,203 scats. We removed those samples that failed to amplify (285) or were mixed (10) from subsequent analyses. Based on field identification, 70% (848) and 29% (345) of the scats were classified as coyote and kit fox, respectively. The remaining 1% (10) was classified as red fox (8) or bobcat (2; *Lynx rufus*). Using molecular identification, we confirmed 72% (865) and 24% (293) of the scats as coyote and kit fox, respectively, with <4% confirmed as bobcat (29), red

fox (9), domestic dog (6), or cougar (1; *Puma concolor*). The overall misclassification rate, or proportion of samples that were classified as a species different from that confirmed by molecular identification, was 12.2% (Table 2.1). The proportion of samples misclassified by field identification was lower for coyote than for kit fox samples. Of the scats classified as coyote with field identification, 7.1% (60) were misclassified and determined to be kit fox, bobcat, domestic dog, red fox, or cougar by molecular identification (Table 2.1). Among scats classified as kit fox with field identification, 22.9% (79) originated from coyotes, red foxes, or bobcats based on molecular identification (Table 2.1). All 8 of the scats classified as red fox based on field identification were coyote. Both scats classified as bobcat by field identification were correctly classified (Table 2.1).

Descriptive Statistics of Scats

Coyote scats were larger than kit fox scats in diameter (Mann–Whitney $U = 241{,}379$, $P < 0.001$) and length (Mann–Whitney $U = 228{,}186$, $P < 0.001$). Mean diameter and length of coyote scats were nearly 2 and 3 times larger than kit fox scats, respectively (Table 2.2). Coyote scats also had a greater number of disjoint segments (Mann–Whitney $U = 188{,}852$, $P < 0.001$) than kit fox scats (Table 2.2). For both coyote and kit fox scats, we found that scat diameter (coyote: $W = 0.99$, $P < 0.001$; kit fox: $W = 0.96$, $P < 0.001$) and length (coyote: $W = 0.96$, $P < 0.001$; kit fox: $W = 0.86$, $P < 0.001$) deviated from normality (Fig. 2.2). The number of disjoint segments also deviated from normality for both species (coyote: $W = 0.88$, $P < 0.001$; kit fox: $W = 0.64$, $P < 0.001$). We did not find many other sympatric carnivore species (Table 2.2). Of those species, mean scat diameter for bobcat and domestic dog fell within the range of diameter values for coyote, but scat length was shorter for these species

compared with coyote scat-length values (Table 2.2). Red fox scat sizes, with their high variability, overlapped the values found for kit fox scats (Table 2.2).

Statistical Classification of Scats

The *k*-nearest neighbor analysis resulted in overall mean misclassification rates from 11.7% to 16.6% across *k*-nearest neighbors (i.e., 1–20) with $k = 3$ achieving the lowest mean misclassification rate (Fig. 2.3). Mean misclassification rates for coyotes ranged from 12.4% to 18.4%, with the lowest mean misclassification at $k = 3$ (Fig. 2.3); whereas kit fox misclassifications were lower, ranging from 8.1% to 13.2%, with the lowest value at $k = 7$ (Fig. 2.3). At the optimal *k* values, the overall mean misclassification rate was reduced, coyote misclassifications increased, and kit fox misclassifications decreased substantially, relative to field identification (Table 2.3).

Classification-tree analyses for kit foxes and coyotes resulted in a decision tree with 4 splits and 5 terminal nodes (Fig. 2.4). Cross-validation indicated the resulting classification tree did not require pruning. Diameter had the highest importance (67/100) followed by length (30/100); segments had little importance (3/100). Decision rules classified scats with diameters ≥15.55 mm or lengths ≥91.70 mm as coyotes, as were scats with diameters <15.55 mm that were ≥63.75 mm in length (Fig. 2.4). Scats were classified as kit foxes when the diameter was <13.75 mm and the length was <91.7 mm, or when the diameter was <15.55 mm with a length <63.75 mm (Fig. 2.4). Misclassification rates produced by the classification-tree analysis were lower overall (7.5%) and lower for coyotes (7.2%), but were higher for kit foxes (8.5%), than those produced by the *k*-nearest neighbor analysis (Table 2.3). The classification tree produced a misclassification rate for coyotes similar to field

identification (7.1%); but overall misclassification and kit fox misclassification were substantially lower than those from field identification (Table 2.3).

Reduced classification-tree analyses provided support for the variable importance metric. Although the full model included all 3 predictors, the number of segments did not contribute to the final decision tree (Fig. 2.4). Consequently, a model including only diameter and length yielded an identical decision tree and misclassification rate to the full model. When the classification tree was built with only diameter and segments, only diameter contributed to the decision tree, which contained a single split and classified scats with a diameter ≥15.55 mm as coyote; models built with only diameter produced identical results. Misclassification rates for coyotes (7.6%), kit foxes (16%), and overall (9.8%) increased relative to the full classification-tree model, but were still similar (coyotes) or lower (kit foxes and overall) than misclassification rates based on field identification (Table 2.3). Classification trees built with length and number of segments (i.e., excluding diam) resulted in a decision tree with 5 splits and 6 terminal nodes relying on both predictors. Misclassification rates increased for coyotes (10.8%), kit foxes (23.9%), and overall (14.1%) to levels exceeding field identification misclassification rates. Removing segments (i.e., including only length) resulted in a decision tree with 10 terminal nodes and produced misclassification rates for coyotes (9.2%), kit foxes (28.0%), and overall (14.0%) that exceeded field identification misclassification rates.

Among the 1,158 scats identified as coyote or kit fox (via molecular identification) with measurement collected, 435 (coyote = 309; kit fox = 126) and 723 (coyote = 556; kit fox = 167) were collected in winter and summer, respectively. Compared with the full classification-tree model with samples combined across seasons, the winter classification-tree

model misclassification rates were lower for coyotes (4.5%) and overall (6.4%), but increased for kit foxes (11.1%). The summer classification-tree misclassification rates were higher for kit foxes (10.8%) and overall (8.0%), but were the same for coyotes (7.2%), relative to the full classification-tree model including all samples.

Less than 4% of samples were determined by molecular identification to be from carnivores other than coyotes or kit foxes. Classification-tree analysis for kit foxes versus nontarget species (i.e., all other carnivores including coyotes) resulted in a decision tree with 7 terminal nodes, which was pruned to 5 terminal nodes following cross-validation (Fig. 2.5). Relative to considering only kit foxes and coyotes, misclassifications of kit foxes increased to 9.6% when considering all observed carnivore species, but was still substantially lower than misclassifications from field identification. Decision rules were similar to those generated when considering only coyotes and kit foxes. Scats with diameters ≥15.55 mm or lengths ≥81.10 mm were classified as nontarget carnivores, as were scats with diameters <15.55 mm that were ≥63.75 mm in length. All other scats were classified as kit foxes (Fig. 2.5).

Discussion

Inferences drawn from scat surveys and the resulting management strategies rely on accurate species identification and therefore monitoring programs should aim to minimize misclassifications. Molecular identification of scats can provide reliable, unambiguous species identification (Davison et al. 2002, Reed et al. 2004, Prugh and Ritland 2005, Onorato et al. 2006, Harrington et al. 2010), but may be cost-prohibitive for long-term monitoring programs, particularly as the number of at-risk species increases and funding decreases. Conversely, field identification has no added cost, but may suffer from misidentification, particularly when sympatric carnivores produce scats of similar size and

characteristics (Davison et al. 2002, Reed et al. 2004, Gompper et al. 2006, McCarthy et al. 2008, Harrington et al. 2010). Our statistical approach provides a method for minimizing misclassification of scats, while reducing costs compared with continued use of molecular identification. The data needed for our models can all be easily and quickly obtained in the field and provide an objective, quantitative alternative to field identification. Despite coyotes and kit foxes having overlapping morphometric measurements, we were able to substantially reduce overall misclassification rates between the 2 species using *k*-nearest neighbor and classification-tree methods.

Misclassification of sympatric carnivore scats from field identification is expected to be influenced by similarity in body size and resource use (e.g., prey items, habitat), which result in scats with similar characteristics (Kohn and Wayne 1997). Disparity in scat encounter rates among sympatric carnivores (with otherwise similar scats) may further influence field identification success, with those species that are encountered less frequently being more often identified (incorrectly) as a more frequently detected species (Davison et al. 2002, Prugh and Ritland 2005). Disproportional encounter rates among sympatric carnivores may result from differences such as species abundance (e.g., relatively fewer scats of rarer species), inconspicuous size or placement (e.g., scats that are small and difficult to find, species that tend to bury scats), or removal (e.g., scat size, placement, or content may influence removal). Our use of molecular identification revealed that the number of scats that were misclassified in the field was inversely proportional to the total number of species-specific scats detected (i.e., rarer species were misclassified based on field identification more frequently). Prugh and Ritland (2005) also found that coyote scats could be discriminated in the field with high accuracy from sympatric carnivores, but suggested that

field identification may be more challenging in systems with higher species richness. Researchers conducting scat surveys for pine marten and red fox could not confidently discriminate scats of the 2 species, and misclassifications increased in areas where pine martens were less abundant (Davison et al. 2002). Thus, although misclassifications may result primarily from overlap in body size and corresponding scat characteristics, misclassifications from field identification may be higher for less frequently detected species. Consequently, scat surveys established to monitor endangered, threatened, imperiled, or otherwise rare species, may suffer from higher field-identification misclassification than those surveys being used to monitor abundant species. High levels of misclassifications may result in erroneous conclusions, such as inaccurate assessments of relative abundance or spatial distribution of species of concern (McCarthy et al. 2008).

Morphometric measurements, and primarily diameter of scats, have been used to provide quantitative thresholds for species identification (e.g., Gompper et al. 2006). Selecting a threshold based on a single measurement to discriminate common carnivore scats, such as coyotes, from sympatric carnivores may be appropriate for some objectives (Gompper et al. 2006), but ideal cut-off values likely vary by region (Weaver and Fritts 1979) and may bias results of studies investigating diets toward prey items that produce larger or smaller scats (Danner and Dodd 1982, Reed et al. 2004). In our study, we found overlap between coyote and kit fox scat sizes, but high levels of overlap in size among sympatric carnivore scats are not uncommon. Farrell et al. (2000) reported overlapping scat diameters for ocelots (*Leopardus pardalis*) and cougars, which are 2 sympatric felids with disparate body sizes. The diameters of coyote scats overlap with scats of the larger wolf (*Canis lupus;* Weaver and Fritts 1979, Reed et al. 2004) and with the smaller red fox (Green

and Flinders 1981), gray fox (*Urocyon cinereoargenteus*; Danner and Dodd 1982), and swift fox (*Vulpes velox;* Harrison et al. 2001).

Previous studies have explored an alternative statistical classification method for discriminating among the scats of sympatric carnivores: parametric discriminant function analysis. A discriminant function analysis based on diameter and mass misclassified 14% of coyote scats and 35% of Mexican gray wolf (*C. l. baileyi*) scats; and misclassification increased for both species when models of only diameter, diameter and length, or diameter, mass, and length were considered (Reed et al. 2004). Although diameter and mass provided relatively high accuracy for coyote scats, classification of Mexican wolf scats was inaccurate and, in general, measurements were deemed to be unreliable for classification (Reed et al. 2004). In another study, discriminant function analysis was evaluated as an approach to identify coyote scats from those of sympatric carnivores based on diameter, but proved unreliable and had an overall misclassification rate of 38.9% (Prugh and Ritland 2005).

Our approach differed in that we employed nonparametric classification methods, which do not require data to be normally distributed, and we incorporated information on scat diameter, length and number of segments. Unlike mass, which requires drying of scats prior to weighing, all 3 of the measures we employed can be collected quickly in the field. When comparing misclassifications for coyote and kit fox scats, we were able to improve overall classification success over field identification with both *k*-nearest neighbor and classification-tree methods but we think the best method was the classification tree because it produced the lowest overall misclassification rate.

Classification approaches remove the subjectivity commonly associated with field identification and are therefore an appealing quantitative technique that may improve

classification when molecular identification is unfeasible. Classification approaches may not work effectively for all species, however, and classification success will depend in part on the variation in scat among sympatric target species, how well training data reflect true variation in the population, the proportion of nontarget species in the sample evaluated, and the selection of the appropriate predictor variables. Our results suggest that classification trees may provide a reliable method of discriminating between coyote and kit fox scats in our study system when molecular identification is unfeasible (e.g., because of funding restrictions or insufficient DNA obtained). Classification trees provided intuitive decision rules that can be easily interpreted and implemented by wildlife practitioners for future classifications. Furthermore, inspection of misclassification rates at terminal nodes can guide practitioners to those samples that are most problematic (i.e., the nodes with the highest misclassifications, either overall or for target species) and for which molecular identification might be preferred to further reduce misclassifications. We also found that scat diameter and length were important for classifying scats. This is in contrast to studies using discriminant function analysis, which found that diameter was not a reliable metric for classifying scats (Reed et al. 2004, Prugh and Ritland 2005).

Often monitoring efforts are initiated primarily for species of conservation concern (i.e., endangered, threatened, or otherwise imperiled), such as kit foxes, and classification approaches may be restricted to species with adequate sample sizes. In our system, coyotes and kit foxes are the most abundant carnivore species. When nontarget species are detected relatively infrequently, this small proportion may not substantially change misclassification rates, as observed here. Alternatively, if samples from nontarget species are abundant and/or

encountered frequently, the associated increase in sample size should allow researchers to explicitly incorporate these species into the classification models.

Our results suggest that field identification of carnivore scats can suffer from high misclassification rates, even when sympatric species have disparate body sizes. Inaccurate species identification can bias inferences drawn from scat surveys and may lead to less effective management strategies. We encourage resource managers and researchers utilizing scat surveys to employ methods to minimize or eliminate misclassifications. Although unambiguous molecular identification provides reliable classification, managers conducting long-term monitoring, surveys over large spatial extents, and/or working with limited funding may not be able to utilize molecular identification for the duration of a monitoring program or study. Alternatively, nonparametric classification based on morphometric characteristics may decrease misclassification rates over field identification. Approaches that elucidate areas of greatest misclassification, such as classification trees where misclassification rate can be identified by node, can be used to direct molecular identification analyses to those samples most likely to be misidentified, reducing overall misclassification while keeping costs low. Additionally, for studies employing molecular identification, classification techniques may provide an avenue for reliably identifying scats that fail molecular identification, because of fecal DNA degradation; this may be particularly important in environments where fecal DNA degrades more rapidly. Future projects employing scat surveys should conduct pilot studies to quantify misclassification rates and evaluate the sensitivity of downstream analyses to misclassification. By incorporating molecular identification during pilot surveys, training data sets and reliable classification

schemes can be developed that may reduce future survey costs and minimize misclassifications.

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Tables

Table 2.1. Number of scat samples collected in western Utah, USA, during the winter and summer of 2013 that were classified to species based on field identification (determined by inspection of scat morphology including color, odor, overall size, and physical appearance) and molecular identification (determined by mitochondrial DNA). The gray diagonal represents the number of samples correctly classified based on field identification. The misclassification rate was the proportion of samples identified by field identification to a species that was in disagreement with molecular identification.

		Field identification					
		Coyote	Kit fox	Bobcat	Dog	Red fox	Cougar
	n =	848	345	2	0	8	0
Molecular identification	Coyote	788	69	0	0	8	0
	Kit fox	27	266	0	0	0	0
	Bobcat	23	4	2	0	0	0
	Dog	6	0	0	0	0	0
	Red fox	3	6	0	0	0	0
	Cougar	1	0	0	0	0	0
Number misclassified		60	79	0	0	8	0
Misclassification rate		7.1%	22.9%	0.0%		100.0%	

Table 2.2. Mean (±SE) diameter, length, and number of disjoint segments for carnivore scat samples collected in western Utah, USA, during the winter and summer of 2013. On account of sample sizes, only coyote and kit fox scats were subsequently classified based on morphometric measurements.

		Diameter		Length		Disjoint segments	
Scat type	*n*	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Coyote	865	20.3	0.16	127.4	2.26	2.6	0.05
Kit fox	293	11.5	0.16	45.1	1.25	1.5	0.05
Bobcat	29	18.3	0.82	73.6	9.90	1.8	0.26
Dog	6	21.2	2.77	88.6	7.69	2.3	0.33
Red fox	9	13.9	1.81	79.0	19.79	1.6	0.44
Cougar	1	15.9		65.0		1.0	

Table 2.3. Misclassification rates based on field identification (ID), *k*-nearest neighbor classification (KNN), and classification trees (CT) for carnivore scats collected in western Utah, USA, during the winter and summer of 2013. The misclassification rate was the proportion of samples classified to a species that was in disagreement with molecular identification as determined with mitochondrial DNA. Only scats for which measurements of diameter, length, and number of disjoint segments were available were evaluated. The lowest mean misclassification rates for k-nearest neighbor classification were achieved at $k = 3$ (overall and kit foxes) and $k = 7$ (coyotes).

	Misclassification rate			
Scat type	Field ID[a]	KNN[b]	CT[b]	CT[a]
Overall	12.2%	11.7%	7.5%	8.2%
Kit fox	22.9%	8.1%	8.5%	9.6%
Coyote	7.1%	12.4%	7.2%	
Nontarget carnivores[c]				7.8%
n =	1,203	1,158	1,158	1,203

[a] Misclassification rate incorporates all carnivore scats identified to species with molecular identification.
[b] Misclassification rate incorporates only scats identified as kit fox or coyote with molecular identification.
[c] Includes all carnivore species (including coyote) detected except for kit fox.

Figures

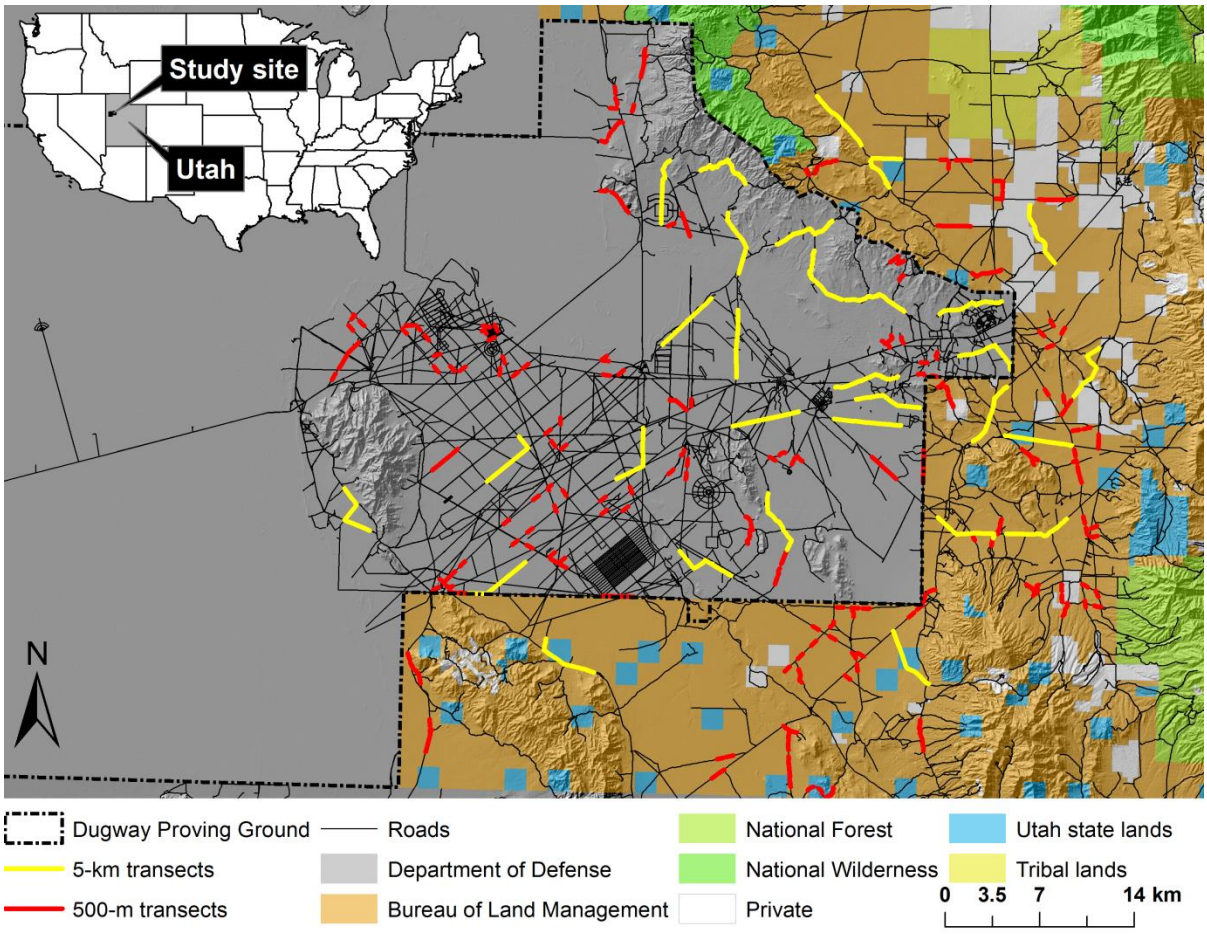

Figure 2.1. Location of 5-km (yellow) and 500-m (red) scat-deposition transects surveyed in Tooele County, Utah (USA) for coyote and kit fox scats in the winter and summer of 2013.

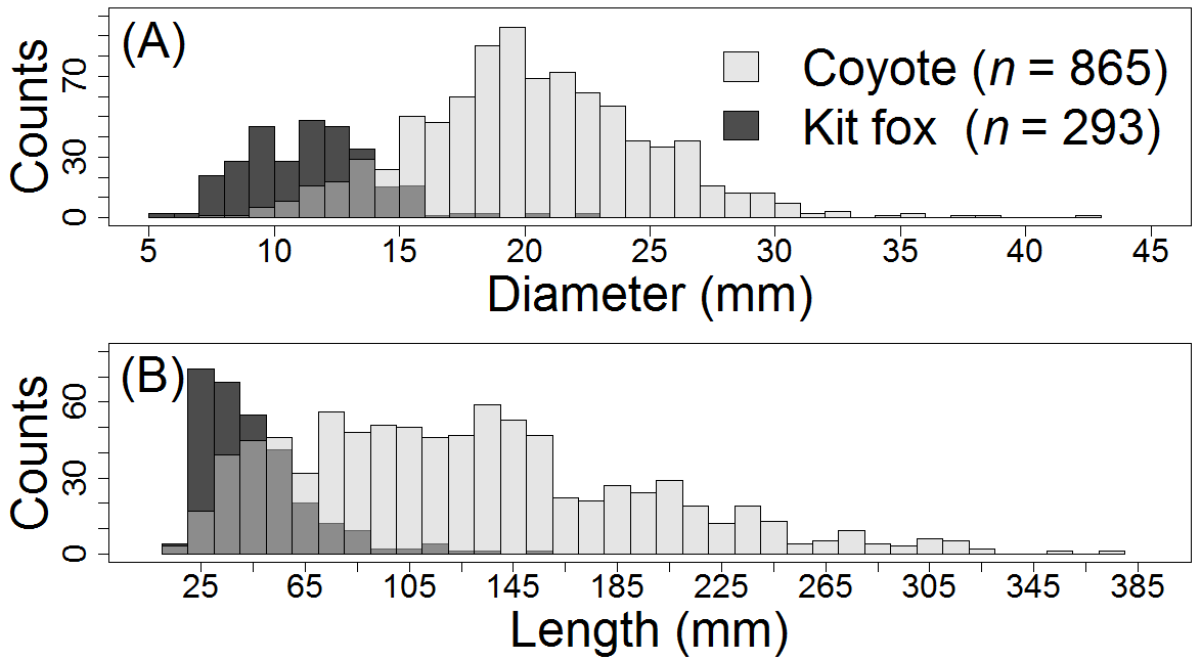

Figure 2.2. Distribution of (A) diameter at widest point, and (B) total length for coyote and kit fox scats collected in Tooele County, Utah (USA), in the winter and summer of 2013. The medium shade of gray indicates overlap in the distributions.

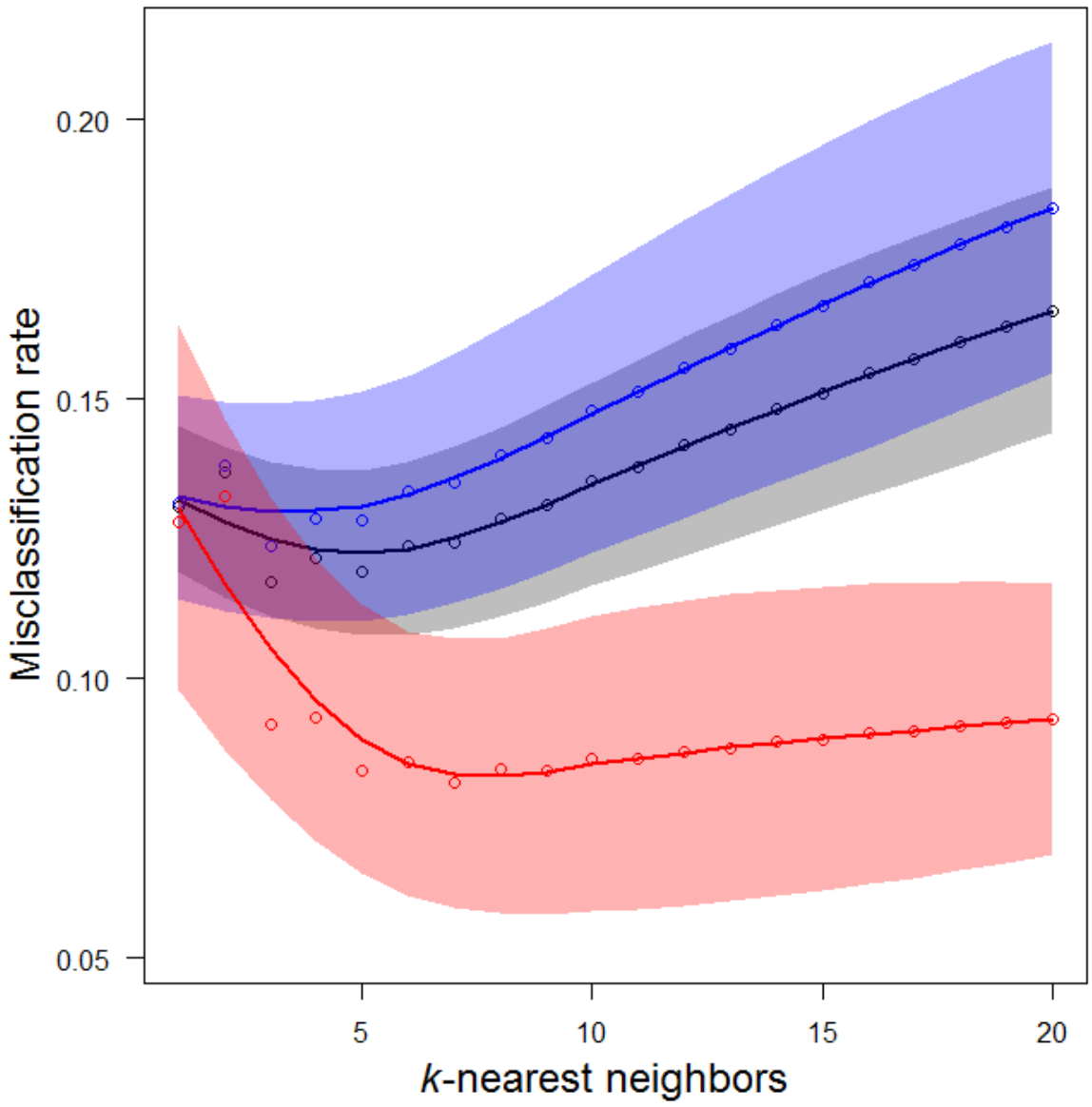

Figure 2.3. Mean misclassification rate (±1 SD; bands) for scats of coyotes (blue), kit foxes (red), and overall (black) evaluated at 1–20 *k*-nearest neighbors. The minimum mean misclassification rate was achieved for coyotes (12.4%) at $k = 3$, for kit foxes (8.1%) at $k = 7$, and overall (11.7%) at $k = 3$. Scat samples were collected in Tooele County, Utah (USA) in the winter and summer of 2013.

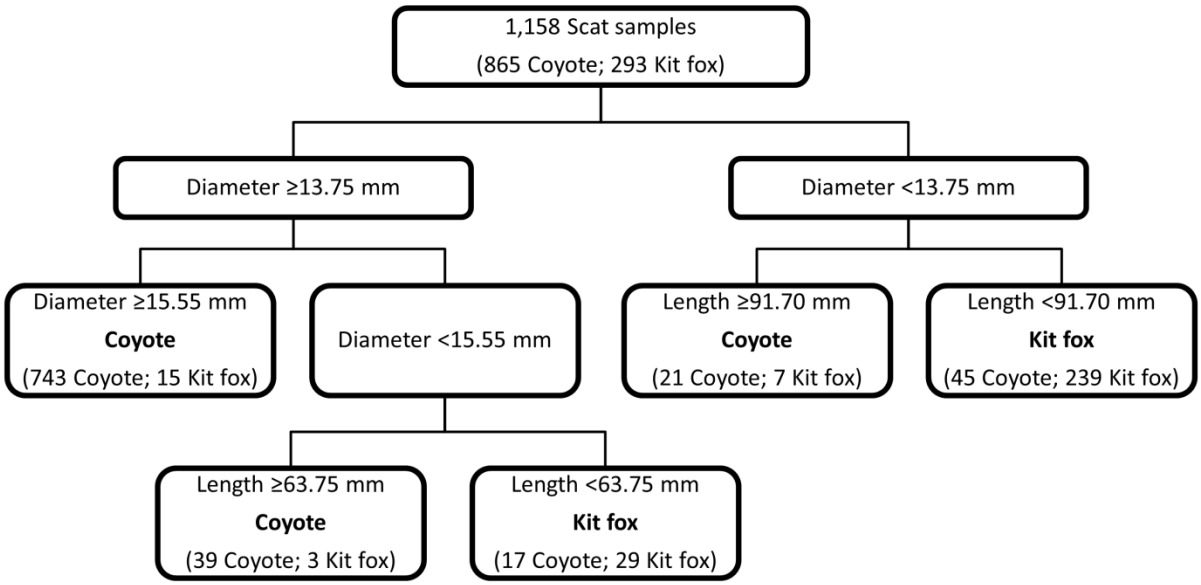

Figure 2.4. Classification tree for coyote and kit fox scats collected in Tooele County, Utah (USA) in the winter and summer of 2013. Terminal nodes indicate the predicted class (bold) based on the decision rules leading to the node and the number of each species that was classified to the node.

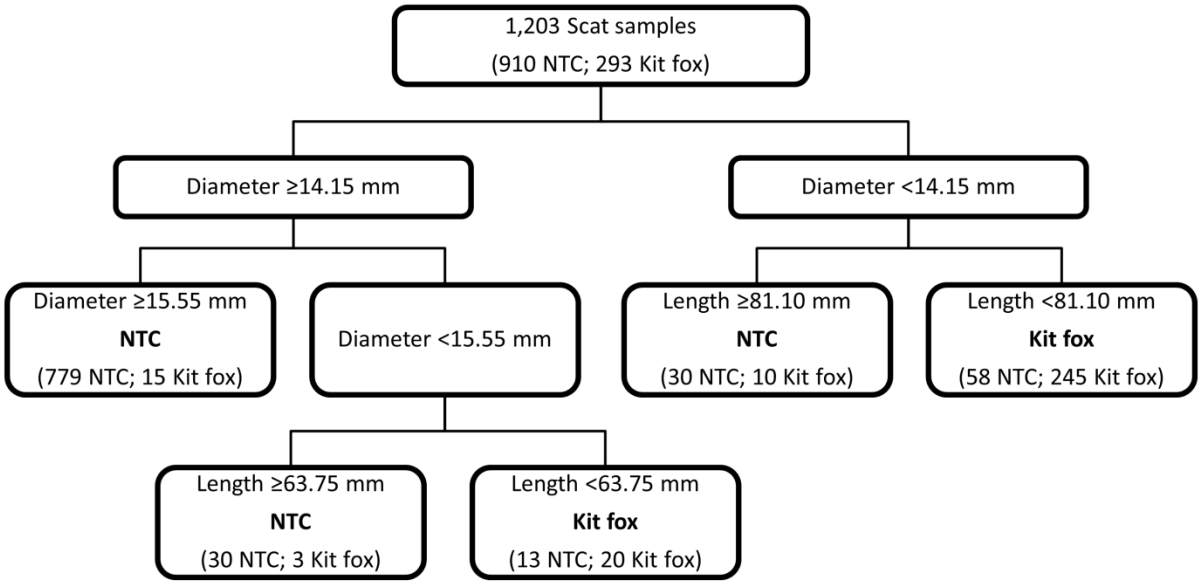

Figure 2.5. Classification tree for kit fox and nontarget carnivore (NTC; all other carnivore species) scats collected in Tooele County, Utah (USA) in the winter and summer of 2013. Terminal nodes indicate the predicted class (bold) based on the decision rules leading to the node and the number of each species that was classified to the node.

Chapter 3: Quantifying and Correcting for Scat Removal in Noninvasive Carnivore Scat Surveys

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Abstract

Scat surveys are commonly used to monitor wildlife populations. For carnivores, surveys are typically conducted along roads and trails. Scats available for detection may not reflect scats deposited and variation in disappearance may bias results. Previous research has investigated natural decay and deterioration, but scats deposited along roads or trails are likely influenced to a greater degree by anthropogenic disturbance in some systems. We used experimental plots to evaluate variation in scat removal for two model carnivores, coyote *Canis latrans* and kit fox *Vulpes macrotis*, along roads in the Great Basin Desert, USA. Using parametric survival regression, we predicted scat survival and developed persistence-rate correction factors, which were applied to results from relative abundance scat surveys conducted along 15 transects. Kit fox scats disappeared more rapidly than coyote scats, with 3.3% and 10.6%, respectively, persisting through 42 days. At 14 days, 90.8% – 41.7% of scats had been removed across road types. Survival models indicated species, road type, scat position and daily traffic were important predictors of scat persistence. Applying persistence-rate correction factors to scat survey results altered the inferred relative abundances. Across seasons, mean corrected:uncorrected relative abundance ratios ranged from 1.0 – 91.2 for coyotes and 1.3 – 139.3 for kit foxes, with higher mean ratios being influenced by high corrected relative abundances on roads with high traffic volumes. Understanding scat removal rates and patterns can improve inferences from surveys. Persistence-rate correction factors can be used to reduce bias in indices of abundance, but caution should be used when removal rates are high. Knowledge of spatial variation in persistence can elucidate concerns of false-positives and false-negatives in occupancy and capture-recapture studies. Considering the disparity in scat removal between species and among road types and

positions, we recommend practitioners quantify and consider variation in removal when interpreting scat survey results.

Introduction

Effective wildlife management relies on accurate estimates of population parameters (Sandercock 2006, Jones 2011). Despite their limitations, scat surveys remain a popular strategy commonly employed to monitor ungulates (Massei et al. 1998, Jenkins and Manley 2008), leporids (Prugh and Krebs 2004) and carnivores (Schauster et al. 2002, Dempsey et al. 2014), among other taxa. Scat surveys are inexpensive and noninvasive, while still providing information on relative abundance (Schauster et al. 2002, Kamler et al. 2013), habitat use and resource selection (Kozlowski et al. 2012), patterns of occupancy (Long et al. 2011) and diet (Kitchen et al. 1999). When combined with fecal DNA, scat surveys can produce estimates of demographic parameters (Lukacs and Burnham 2005) and genetic measures (Waits and Paetkau 2005). In practice, scats detected during a survey may not accurately reflect scats deposited, and it is essential to evaluate the reliability of such monitoring strategies (Jones 2011). The results of scat surveys may be biased if variation exists among survey sites in scat detection (Rhodes et al. 2011), decay and deterioration (Jenkins and Manly 2008) or scat removal (Livingston et al. 2005). Researchers utilizing pellet counts to monitor herbivores have invested considerable effort into understanding how weather, habitat and biotic factors influence scat detection, deterioration and removal (Massei et al. 1998, Prugh and Krebs 2004, Brodie 2006, Rhodes et al. 2011, Cristescu et al. 2012). Carnivore scat persistence has been studied less, but the influence of climate and biotic disturbances (insects and coprophagy) have been investigated (Sanchez et al. 2004, Livingston et al. 2005). These efforts focused primarily on natural disturbances and consequently, often evaluated scat

persistence over extended time periods (months to years). Over shorter periods (days to weeks), scat removal may be accelerated by anthropogenic disturbances, but these removal processes have received little attention (Kohn et al. 1999).

For carnivores, which are often elusive and occur at low densities, scats offer a noninvasive survey approach that can be efficiently employed over large spatial extents and for long-term monitoring (Gese 2001). Carnivore scat surveys typically involve surveying along roads (Schauster et al. 2002, Schwalm et al. 2012, Dempsey et al. 2014) or trails (Kohn et al. 1999, Gompper et al. 2006) at set sampling intervals. While decay, deterioration and biotic displacement may reduce the number of scats available for detection over extended time periods, anthropogenic sources of removal along roadways (vehicles) or trails (e.g., foot-traffic, off-road vehicles) may operate more rapidly. Although scat surveys provide a reliable method for detecting carnivores (Schauster et al. 2002, Dempsey et al. 2014), accelerated scat removal rates caused by anthropogenic disturbances may be problematic (Gese 2001, Schwalm et al. 2012).

Variation in scat removal, or inversely persistence, can influence results and conclusions from scat surveys. Estimates of relative abundance may be biased by inequitable removal rates among sites (Nchanji and Plumptre 2001, Livingston et al. 2005) and understanding removal can facilitate the development of correction factors (Brodie 2006), thereby improving estimates of abundance (Sanchez et al. 2004). When scats are used to model occupancy, high removal rates may lead to false-negatives (failure to detect a species when present), while low removal rates may result in false-positives (scats remain longer than the site is occupied), influencing parameter estimation (Rhodes et al. 2011). Thus,

understanding the influence of anthropogenic disturbances on scat persistence should be a priority for practitioners employing scat surveys along roads and trails.

We examined the factors influencing variation in carnivore scat removal under different anthropogenic disturbance levels to inform future scat surveys. We used scats of two sympatric species, coyotes *Canis latrans* and kit foxes *Vulpes macrotis*, as model carnivores and investigated factors influencing scat removal in summer and winter. Although decay, deterioration and removal have been used interchangeably, we distinguish removal, from decay and deterioration, as a more rapid process by which scats disappear, and we focused our investigation on removal. We hypothesized that removal rates would be (i) higher for kit fox scats than coyote scats due to their smaller size, (ii) higher at sites experiencing more frequent disturbance (higher traffic volumes), (iii) higher along roads with a higher intensity of disturbances (larger roads facilitate increased traffic speeds), (iv) highest for scats deposited in the tire tracks and lowest for those deposited on the shoulder and (v) higher in summer than winter due to additive influences of insects. Additionally, we evaluated the relative abundances of each species among 15 transects. Based on the results of the removal experiment, we developed persistence-rate correction factors and applied these to re-evaluate the relative abundance of each species. We hypothesized that due to uneven removal among transects, adjusting relative abundances by correction factors would alter conclusions.

Materials and Methods

Study Area

The study was conducted on the US Army Dugway Proving Ground, USA, and neighboring lands (Fig. 3.1). Vegetation was characterized by cold desert playa (*Allenrolfea*

occidentalis dominated), cold desert chenopod shrubland (*Atriplex confertifolia* and *Kochia Americana* dominated) and vegetated dunes at lower elevations, and by arid shrubland (e.g., *Artemisia* spp., *Chrysothamnus viscidiflorus*) and open woodland (*Juniperous osteosperma*) at higher elevations. *Sarcobatus vermiculatus* shrubland occurred across elevations. *Bromus tectorum* grasslands dominated in disturbed areas (Lonsinger et al. 2015b).

Scat Removal Experiments

We conducted carnivore scat removal experiments along gravel (maintained) and two-track dirt (unmaintained) roads during summer and winter, corresponding with periods preceding kit fox juvenile dispersal (July and August) and breeding (January and February), respectively. We identified three common road types across our study site including (i) two-lane gravel (large), (ii) one-lane gravel (medium) and (iii) two-track (small) roads, and then established three removal plots on roads representing each strata (Fig. 3.1). The locations of removal plots were selected to avoid overlap with transects being surveyed concurrently for native canids (Lonsinger et al. 2015b). This was important to avoid introducing scats from captive animals and minimize behavioral responses of native canids along sites being monitored with noninvasive genetic sampling, and to ensure a balanced design among strata. We used 360 fresh scats obtained from captive coyotes and kit foxes maintained at the USDA/NWRC/Predator Research Facility (Millville, UT, USA) and California Living Museum (Bakersfield, CA, USA), respectively. All scats were collected within 24 hours of deposition, frozen at time of collection for transport and thawed before placement into the field. In each season, we systematically placed 90 coyote and 90 kit fox scats across nine removal plots. We placed 10 scats of each species in each plot, with scats placed ~5 m apart and alternating between species, resulting in 30 scats per road type per species. Furthermore,

we systematically positioned scats either on the median, tire tracks or shoulder, so that among the 90 scats per species, each position was represented by 30 scats evenly distributed across road types and plots. Scats of captive canids were indistinguishable (i.e., based on physical size and/or shape) from those of native canids. We recorded the location and photographed each scat at the time of placement to distinguish scats should native canids defecate on the plot.

We initiated scat removal experiments and vehicle traffic monitoring on 29 July 2013 (summer) and 12 January 2014 (winter). We monitored removal of scats on each plot at 1, 3, 5, 7, 11, 14, 21, 28 and 42 days after setting and tracked the fate of each scat separately. We considered a scat removed when it could not be located or was damaged beyond recognition (could no longer be identified as a carnivore scat). We monitored vehicle traffic by placing traffic counters (Traffic Tally 2; Diamond Traffic Products, Oregon, USA) on eight plots. One plot (the most southeastern; Fig. 3.1) was set adjacent to a permanent traffic counter. We obtained the total number of vehicles crossing each plot each season and calculated mean daily vehicle rates. Although all scats were placed directly on transects, we estimated natural decay and disappearance rates by evaluating the proportion of scats that disappeared from plots during intervals when no traffic was recorded.

Relative Abundance Field Surveys

During summer and winter, we cleared 15 random 5 km transects (Fig. 3.1) of all carnivore scats, and subsequently conducted three (summer) to four (winter) scat deposition surveys (Schauster et al. 2002, Dempsey et al. 2014). Summer and winter surveys were conducted from 8 July to 23 August 2013 and 20 January to 20 March 2014, respectively. Transects followed roads with characteristics similar to those used for scat removal

experiments. Two researchers searched each transect for carnivore scats. When a carnivore scat was detected, we collected ~0.7 mL of fecal material into 1.4 mL of DETS buffer (20% DMSO, 0.25 M EDTA, 100 mM Tris, pH 7.5 and NaCl to saturation; Seutin et al. 1991). We measured each scat diameter, length and number of segments (Lonsinger et al. 2015b) and recorded the location and position (median, track or shoulder), before removing remaining portions. We identified scats to species using mitochondrial DNA (mtDNA; De Barba et al. 2014) following DNA storage, extraction, amplification, and scoring methods detailed in Lonsinger et al. (2015a). We classified scats failing mtDNA species identification or containing DNA from multiple species by applying a site-specific non-parametric classification tree with high accuracy based on measurements (Lonsinger et al. 2015b).

Survival Regression Analysis

We employed accelerated failure time parametric survival models to investigate the effects of species, season, position, road type and mean daily vehicle traffic on scat removal (Pyke and Thompson 1986, Hosmer et al. 2008). We specified models with interval-censoring of time until removal because scats were known to have been removed only *between* time points when observations were conducted; scats observed on day 42 were removed and recorded as right-censored. Species served as a surrogate for scat size (Lonsinger et al. 2015b), while season represented climatic differences between periods. Road type characterized road size and condition, which regulated vehicle speeds (intensity of disturbance). Traffic represented the mean daily vehicle passage rate (frequency of disturbance). We expected scat survival to fit an exponential distribution (Hosmer et al. 2008) because of its constant conditional hazard rate, but previous work investigating carcass survival indicated that in some cases, Weibull, log-logistic and log-normal distributions may

be more appropriate (Bispo et al. 2013). We used Akaike's Information Criterion with small sample size correction (AIC_c; Hurvich and Tsai 1989) to compare the relative fit for models containing all parameters (the full model) and fitted with each aforementioned distribution. We used the distribution producing the lowest AIC_c for subsequent analyses. We conducted survival regression analyses with the R 'survival' package (Therneau and Grambsch 2000, R Core Team 2015).

Our experimental design incorporated explanatory variables believed *a priori* to influence scat removal and to avoid overparameterization we included only these predictors in our model set. Two predictors, road type and traffic, may be correlated as gravel roads were likely maintained due to their higher use. Still, road type contains additional information not captured by traffic; more maintained roads facilitate faster travel, influencing disturbance intensity. We elected to retain both road type and traffic as simulations have suggested model selection procedures perform well even when correlated variables are included (Grueber et al. 2011). We evaluated 32 models, including all possible combinations of predictors and a null model. We calculated each model's AIC_c, relative likelihood, Akaike weight and log-likelihood (Burnham and Anderson 2002). We rescaled AIC_c to ΔAIC_{ci}, (the difference between AIC_c for model *i* and that for the best fit model; $\Delta_i = AIC_{ci} - AIC_{cmin}$; Burnham and Anderson 2002).

Although model averaging is commonly recommended (Burnham and Anderson 2002), only a single model was ≤ 2 ΔAIC_c from the best model; this model included one additional parameter and did not improve fit (*see Results*), suggesting little support for this model or the additional parameter (Arnold 2010). No other models had a $\Delta AIC_c < 10$ and

therefore we were able to clearly identify a top model among our model set (Burnham and Anderson 2002).

Persistence-Rate Correction Factor

The proportion of scats persisting through a discrete time period can be used to determine a persistence-rate correction factor (Brodie 2006). We used the top model to predict scat survival for each combination of species, road type and position over time based on the exponential survival function (Hosmer et al. 2008). We did not include seasonal variation, as model selection procedures indicated this predictor did not contribute to improving model fit (*see Results*). While we were able to obtain mean daily traffic volumes for each of our removal plots, in practice, estimates of traffic are rarely available for each scat transect. More realistically, traffic estimates may be available for a small number of roads, which are representative of road types surveyed. For each road type, we calculated an overall mean daily traffic volume by combining mean daily traffic estimates across replicates and seasons. We then used the overall mean daily traffic volume for each road type when predicting scat survival over time.

Given the data and model set, the exponential model had the best fit (*see Results*). To predict the proportion of scats surviving, we applied parameter estimates from the top model to the exponential survival function. The exponential survival function describing survival (S) over time (t) is $S(t) = \exp(-\lambda t)$, where $\lambda = \exp(-\beta_o - \beta_1 x_1 - \ldots - \beta_i x_i)$; β_o and β_i represent the regression parameters for the intercept and predictor variable i, respectively, while x_i represents the value of predictor variable i under consideration (Hosmer et al. 2008). Based on this survival function, we used the maximum likelihood parameter estimates from the top model to estimate the proportion of scats surviving for 1 – 42 days for all possible

combinations of species, road type and position, and applying the overall mean daily traffic for each road type. The resulting proportions constituted our persistence-rate correction factors (Brodie 2006). To further explore the role of traffic, we evaluated the decimating effect of traffic by predicting mean time until scat removal for each combination of predictor variables and considering mean daily traffic values from 1 – 84 (the highest observed traffic).

Relative Abundance Estimation

We calculated the relative abundance of coyotes and kit foxes for each of 15 transects in each season as the mean number of scats detected across temporal replicates. For each species-season combination, we then ranked and compared the relative abundance of transects. To correct for removal, we categorized each transect by road type and each scat by position. For each temporal survey of each transect, we used the survival function resulting from the top exponential regression model to develop a persistence-rate correction factor for each combination of species, road type and position. Time was set as the number of days since that transect was last surveyed. Although season was not supported as an important predictor, traffic was important and varied seasonally (*see Results*). Thus for each transect in each season, we identified the removal plot of the same road type that best reflected the amount of traffic on the transect, and used the corresponding mean daily traffic when developing the transect and survey specific persistence-rate correction factors.

For each species on each transect, we then calculated a corrected relative abundance. We divided the number of scats detected on each road type and in each position during a survey, by the persistence-rate correction factor (transect and survey specific); within a survey, these values were then summed to obtain the corrected survey-specific number of scats per species. In each season, we calculated the corrected relative abundance for coyotes

and kit foxes across each of the 15 transects as the mean corrected number of scats detected across temporal replicates. We then re-evaluated the rank and relative abundance of transects for each species-season combination based on corrected relative abundance, and compared this to the uncorrected relative abundance by calculating the ratio of corrected to uncorrected relative abundance.

We expected variation in corrected relative abundances would be driven by the same variables that influenced removal (*see Results*), and that variation in corrected relative abundance would be greater on transects with higher removal rates. To evaluate the variation in corrected relative abundances, we conducted randomization tests in which we generated 1000 random scat detection histories for each species in each season. We retained the structure of the observed dataset (i.e., the number of scats detected on each transect), but randomly assigned each scat a new position (i.e., shoulder, median, track), location along the transect (which could alter the road type for transects with >1 road type), and survey (i.e., temporal survey). All values were randomly selected with replacement and selection probabilities for each set of conditions were derived from the distributions of observed data. For each species-season combination, we calculated the mean (± SE), median, and range across 1000 randomizations.

Results

Scat Removal Experiments

Overall, 3.3% of kit fox scats and 10.6% of coyote scats persisted through 42 days. When comparing overall scat persistence by road type, 13.3%, 6.7% and <1.0% of scats on small, medium and large roads, respectively, persisted through 42 days. At 14 days (a common sampling interval for relative abundance estimation), the proportion of scats

removed was 90.8% for large roads, 64.2% for medium roads and 41.7% for small roads. By position, 10.0% and 10.8% of scats on the shoulder and median, respectively, persisted through 42 days, while no scats in tracks persisted to 42 days; 87.5% of scats in tracks were removed by day 14. We observed similar levels of overall persistence between seasons (proportion persisting to 42 days: summer = 7.2%; winter = 6.7%). Across road types, daily traffic rates were higher in summer (overall mean = 20.8 ± 10.6 SE) than winter (overall mean = 10.7 ± 5.5 SE). Across replicates, daily traffic rates were generally higher for large and medium roads than for small roads (Table 3.1). During periods with no traffic, persistence rates across seasons were high for kit fox (93.5%) and coyote (93.0%) scats. When considering the number of scats available (i.e., present for each species at the start of each interval without traffic) and duration of intervals without traffic, natural removal for kit fox and coyote scats occurred at a rate of 0.11 and 0.12 scats/day per 100 scats, respectively.

Scat Transect Surveys

Across transects and seasons, mean time between the initial clear and each sequential survey was 13.9 days (0.53 SD, range = 12 – 16 days). We collected 554 (summer: n = 363; winter: n = 191) carnivore scats and mtDNA species identification confirmed 462 scats as originating from coyotes (302), kit foxes (138), bobcats *Lynx rufus* (18) and red foxes *V. vulpes* (4). Eighty-four scats failed mtDNA species identification and eight contained DNA from both coyotes and kit foxes; of these, classification trees assigned 59 as coyote and 32 as kit fox based on diameter and length measurements. We excluded bobcat and red fox scats, as well as one scat which failed species identification and lacked measurements, from subsequent analyses.

Survival Regression Analysis

Given the data and model set, the exponential model had the best fit (AIC_c = 1388.8), but the Weibull model received similar support (AIC_c = 1389.8). Log-normal (AIC_c = 1400.5) and log-logistic (AIC_c = 1406.8) models received substantially less support. We used the exponential distribution for subsequent parametric analyses. Among the 32 parametric models evaluated with the exponential distribution, the top model included four predictor variables: species, road type, position and traffic (Table 3.2). The second model included these same predictors plus season and was 2 ΔAIC_c from the top model (Table 3.2), suggesting there was little support for this additional parameter or model (Arnold 2010). The next closest model was >10 ΔAIC_c from the top model, indicating relatively little or no support and the null model was among the models with the poorest fit (Table 3.2). The Akaike weight indicated that given the candidate model set and data, the top model received 73% of the support and the cumulative Akaike weight of the top two models was >99%, providing a high level of support that the four variables common to both models were important predictors (Table 3.2).

Estimates of the best model parameters provided a measure of the effect of each explanatory variable on scat survival. Coyote scats survived longer than kit fox scats (Table 3.3). Scats deposited in the median survived longer than those in the tracks; scats on the shoulder persisted the longest (Table 3.3). Scats on medium and small roads had 1.6 and 3.5 times longer survival, respectively, than scats on large roads (Table 3.3). Vehicle traffic was negatively associated with scat survival (Table 3.3).

Applying coefficient estimates from the best model and a single overall mean traffic volume for each road type (Table 3.1), we calculated the estimated proportion of scats

persisting over time for each combination of categorical predictors (Fig. 3.2). Survival decreased over time for coyote and kit fox scats, with survival declining more precipitously along larger roads and for scats positioned in the tracks and median (Fig. 3.2). When deposited on the shoulder, large proportions of coyote (>46%) and kit fox (>32%) scats may persist through 42 days on small roads (Fig. 3.2). Conversely scats were unlikely to persist through 42 days when deposited on the tracks, regardless of road type or species. As mean daily traffic increased, survival time decreased, with the rate of decline being greatest for scats on the shoulder and lowest for those on tracks (Fig. 3.3). Predicted time until removal was low for scats deposited on tracks, even with very low levels of traffic; this low initial time until removal in tracks leads to the decreased rate of decline relative to other positions. Coyote scats were predicted to persist longer than kit fox scats, with coyote scats deposited on the shoulder predicted to persist up to 55 days when traffic was low (Fig. 3.3).

Relative Abundance Estimation and Correction

Six transects (2, 10, 11, 12, 14 and 15) contained two road types (Appendix 3.1) and therefore six correction factors were applied to each species in each season. The remaining nine contained a single road type and three correction factors were applied to each species-season combination. We detected coyotes across 15 and 13 transects in summer and winter, respectively (Table 3.4, Appendix 3.1). Correcting relative abundance altered the rankings of transects for coyotes in both seasons (Table 3.4). In summer, corrected:uncorrected relative abundance ratios ranged from 1.8 – 91.2 (mean = 15.0 ± 6.4 SE) among transects (Table 3.4). In winter, corrected:uncorrected relative abundance ratios ranged from 1.0 – 36.9 (mean = 6.7 ± 2.7 SE) among transects. In both seasons, corrected:uncorrected relative abundance ratios were highest on those transects characterized as large roads with the highest traffic

volumes (transects 4, 5 and 15; Table 3.4). We failed to detect kit fox on one transect in summer and six transects in winter (Table 3.4, Appendix 3.1). In both seasons, we observed patterns similar to those for coyotes, in which transect rankings changed substantially when considering corrected relative abundance versus relative abundance (Table 3.4). Summer corrected:uncorrected relative abundance ratios ranged from 1.6 – 1111.3 (mean = 139.3 ± 89.7 SE) and winter ratios ranged from 1.3 – 56.3 (mean = 9.4 ± 5.9 SE). In summer, the corrected:uncorrected relative abundance ratios were extraordinarily high on two transects (transects 4 and 15; Table 3.4), which were both characterized as large roads and experienced the highest traffic volumes among transects surveyed; both transects either fully (transect 4) or partially (transect 15) included the same road as scat removal plot 9, which experienced daily traffic volumes >80 vehicles per day in the summer (Table 3.1).

Variation in corrected relative abundance was generally highest for transects characterized as large roads (Appendix 3.2). These roads often led to no carnivore scat detections, but when they did variance in corrected relative abundance was high, depending on the locational characteristics of scats detected; mean corrected relative abundance values were very high along large roads, suggesting that correcting for removal along these types of roads is unreliable (Appendix 3.2). As expected, the variance associated with corrected relative abundance values was low for both small and medium roads (Appendix 3.2), which received considerably less vehicle traffic than large roads.

Discussion

Scats are among the most commonly used sign for monitoring wildlife and yield higher detection rates for many species than alternative methods (Schauster et al. 2002, Gompper et al. 2006, Dempsey et al. 2014). Indirect sign surveys are often preferred for rare,

elusive or at-risk species (Long et al. 2011, Rhodes et al. 2011), but data quality produced by sign should be evaluated (Jones 2011). Variation in scat persistence can potentially bias scat survey results (Jenkins and Manly 2008); understanding spatial, temporal and interspecific variation in scat persistence can guide future sampling and improve inferences (Rhodes et al. 2011). Our study is the first to quantify the effects of anthropogenic disturbance on scat surveys. Our experimental approach demonstrated scat removal varied by species and spatially (Fig. 3.2) and that time until removal was influenced by survey conditions (road type) and frequency of disturbance (traffic; Fig. 3.3). Our results suggested that scat removal rates can be significant and may have important implications for interpreting the results of scat surveys. Inferences about relative abundance differed substantially when removal rates were quantified and persistence-rate correction factors applied (Table 3.4).

Factors Influencing Scat Removal

Species had a significant influence on scat survival, with kit fox scats being removed more rapidly (Fig. 3.2; Fig. 3.3). Few studies have compared persistence of scats from multiple species under the same conditions. Wild boar *Sus scrofa* pellets persisted longer than fallow deer *Dama dama* pellets under the same conditions and the larger size of boar pellets may have limited removal by invertebrates (Massei et al. 1998). Coyote scats are larger than kit fox scats and may be influenced to a lesser extent by invertebrates. Similarly, larger scats may be more resistant to vehicle disturbance, requiring higher speeds (intensity) and volumes (frequency) to be effectively removed. Coyote scats were removed more frequently than bobcat scats in two studies and these differences may reflect differences in dietary content and nutritional value to coprophagous species (Sanchez et al. 2004, Livingston et al. 2005). Sanchez et al. (2004) suggested nutritional value may influence

removal by conspecifics. Although some scats in our experiment may have been removed due to natural processes (e.g., coprophagy), disturbance from vehicles likely overpowered these effects. Our experimental design did not explicitly distinguish natural from anthropogenic sources of removal. Still, disappearance of scats from transects during periods with no traffic suggested that natural disappearance rates were low relative to removal rates in the presence of traffic.

Scats deposited on larger roads experienced higher removal rates and more precipitous declines in survival than those on smaller roads (Fig. 3.2). When traffic volumes were held constant across road types, models predicted that time until removal increased with decreasing road size (Fig. 3.3). Variation among road types in driving surface condition influenced maximum speed of travel and intensity of disturbance and this likely increased removal rates on larger roads. As expected, scats deposited in tracks disappeared the fastest and scats on the shoulder the slowest (Fig. 3.2). Across road types, scats positioned in tracks had more similar removal rates (Fig. 3.2) and persistence times (Fig. 3.3) relative to the other positions. Kohn et al. (1999) investigated effects of position on scat removal along trails and dirt roads experiencing anthropogenic use. Although they did not quantify physical differences or intensity of usage among transects, scats in tracks disappeared by 5 weeks, all but one scat on trails disappeared by 12 weeks and scats placed off transects lasted up to 31 weeks. To our knowledge, our study was the first to quantify vehicle traffic and evaluate its influence on scat persistence. As predicted, scats experiencing higher traffic volumes disappeared more rapidly (Fig. 3.2; Fig. 3.3). Few scats are predicted to persist to 14 days when vehicle traffic volumes are high, regardless of species, road type or position (Fig. 3.3). Indeed, traffic has been implicated for false-negatives, where scat surveys failed to detect

swift foxes *V. velox* in areas where they were confirmed with live-capture (Schwalm et al. 2012).

Season was not identified as an important predictor of scat removal, differing from findings of previous research. Among herbivore studies, seasonal climate was commonly identified as an important predictor of pellet removal with rainfall increasing removal rates (Massei et al. 1998, Nchanji and Plumptre 2001, Rhodes et al. 2011, Cristescu et al. 2012). Similarly, seasonal differences in climate and rainfall influenced carnivore scat removal (Sanchez et al. 2004, Livingston et al. 2005). We conducted our experiment during the two seasons with the lowest rainfall at our study site (Lonsinger et al. 2015a), and this may have limited the influence of season. Scats used in previous research were not typically exposed to anthropogenic disturbances. Thus, our failure to detect seasonal differences in removal may be the result of the overwhelming influence of anthropogenic disturbance on removal.

Application of Persistence-Rate Correction Factors

Our results indicated that the relative ranking of transects changed substantially for both species and that changes were greater in summer than winter (Table 3.4). Although season was not identified as an important predictor, vehicle traffic was important and was typically higher in summer than winter (Table 3.1). The application of a persistence-rate correction factor incorporating species, road type, position and traffic can reduce potential biases, but requires road type and position to be recorded during surveys and estimates of traffic to be ascertained. Although it may be impractical to evaluate traffic levels on every road surveyed, traffic may be monitored along fewer roads characterizing variation in traffic volumes experienced across the study site. Extremely high removal rates for species-position-road type combinations, as we experienced for kit fox scats (and to a lesser extent

for coyotes) on large roads with high traffic volumes, can result in exceptionally low persistence rates. In turn, corrected relative abundances and the resulting corrected:uncorrected relative abundance ratios can be extraordinarily high. For example, summer kit fox corrected relative abundance was 333.4 and the corrected:uncorrected ratio was 1111.3 for transect 4 (Table 3.4). The variance in corrected relative abundance for large roads experiencing high removal rates was also extremely high, suggesting that indices of abundances from these transects should be viewed cautiously. This issue reiterates the importance of understanding removal and provides an additional justification for avoiding surveys along highly disturbed roads.

Limitations

Brodie (2006) suggested scat loss should have minimal impacts on indices of relative abundance, so long as loss was equitable across survey sites and/or periods. This requires though, that a sufficient number of scats are deposited and that removal rates are sufficiently low, to allow some scats to remain available for detection, given the species was present. Results from our experimental removal plots indicated that carnivore scat removal rates varied substantially among survey conditions, and that when exposed to high levels of disturbance, carnivore scats had a low probability of persistence (Fig. 3.2, Fig. 3.3).

Although persistence-rate correction factors have been proposed to account for removal (Brodie 2006), our results suggested that such correction factors may introduce additional sources of error and may not be appropriate under all survey conditions or for all species. First, under high removal conditions, persistence-rate correction factors can result in extremely high corrected relative abundances, from of even a single scat detection (e.g., summer kit fox corrected relative abundances along transects 4 and 15; Table 3.4). Thus, the

difference between detecting no scats and a single scat can result in disparate estimates of corrected relative abundance. Additionally, randomization tests suggested that when removal rates were high, corrected relative abundance estimates could vary substantially based upon where each scat was detected. By evaluating scat removal rates experimentally, as we have done here, practitioners can elucidate those conditions expected to result in exceptionally high removal, and can use this information to identify appropriate survey routes and/or avoid transects with high removal rates.

Persistence-rate correction factors may be less appropriate for species with low deposition rates relative to removal rates, which when combined will increase the probability of false-negatives (Rhodes et al. 2011). At our study site, scat deposition rates were significantly lower for kit foxes than coyotes, and deposition rates were lower in winter than summer for both species (Lonsinger et al. 2015a). In winter 2014, we failed to detect kit fox scat along six transects which produced detections in summer 2013 (Table 3.4, Appendix 3.1). Although this may have reflected changes in space use or local extinctions, kit foxes are territorial and rely on dens year-round for relief from climatic extremes and predation (Dempsey et al. 2015). Alternatively, failure to detect kit foxes along these transects may have resulted from insufficient scat deposition rates under the observed removal rates. During winter 2014, we failed to detect coyotes on only two transects where they had previously been detected; these two transects were both characterized as large roads with very high traffic levels (Table 3.4, Appendix 3.1), suggesting that even for species with relatively high deposition rates, extremely high removal rates may limit detection.

Monitoring and Management Implications

Considering the regularity with which scat surveys are used to monitor carnivores, few studies have quantified carnivore scat removal processes and their impacts on data reliability. Previous research has focused primarily on natural decay and deterioration of carnivore scats and removal by conspecifics (Sanchez et al. 2004, Livingston et al. 2005). Yet carnivore scat surveys are typically conducted along roads and trails (e.g., Gompper et al. 2006, Dempsey et al. 2014, Lonsinger et al. 2015a), and anthropogenic disturbances are likely to have a more rapid influence on scat removal than natural processes. Monitoring programs employing scat surveys are often interested in evaluating relative abundance (Gese 2001), occupancy patterns (Long et al. 2011) or demographic parameters (Lukacs and Burnham 2005). Failure to account for spatial variation in scat removal may bias results of monitoring programs, leading to erroneous conclusions and/or ineffective management decisions. Disparity in scat removal among species stresses the importance of understanding interspecific variation in removal rates, particularly when employing multi-species monitoring. The effects of road type and position have important implications for study design and analyses. Larger roads may yield fewer scats and are more likely to produce low detection probabilities and false-negatives (Rhodes et al. 2011); it may be advantageous to survey smaller roads or trails in lieu of larger roads, whenever possible. When using scat surveys to conduct occupancy or capture-recapture modeling, incorporation of road type as a site level covariate may effectively account for some detection or capture heterogeneity and improve model fit (Lukacs and Burnham 2005). Understanding spatial variation in removal by position and road type allows researchers to conduct informed subsampling to reduce the probability of false-positives (Rhodes et al. 2011). For example, scats on the shoulder of

smaller road types may persist longer than the period for which the assumption of population closure can be met. This knowledge can be used to exclude scats with a high probability of introducing false-positives. If road type and position are documented during surveys, persistence-rate correction factors can adjust for variation in removal among road types and positions. We caution though, that when correcting relative abundance for removal, transects experiencing high removal rates, such as those observed on large roads in our system, are likely to introduce greater bias and produce very high corrected:uncorrected relative abundance ratios. Given the potential variation in bias introduced by disparity in removal rates, we encourage practitioners employing scat surveys along roads or trails to explicitly consider the potential implications of removal by anthropogenic impacts. Specifically, it would be prudent for practitioners to (i) conduct pilot studies to elucidate patterns and rates of scat deposition and removal, (ii) minimize variation in removal among surveys during the design phase of studies and (iii) and avoid surveys along transects with extremely high levels of disturbance and removal.

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Tables

Table 3.1. Daily traffic volume (mean number of vehicles per day over 42 days) for nine experimental removal plots used to investigate coyote and kit fox scat removal in western Utah, USA, during two seasons. Plots were distributed across large (two-lane gravel), medium (one-lane gravel), and small (two-track) roads. Overall mean ± SE for each road type is across seasons and replicates.

	Small			Medium			Large		
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9
Summer 2013	1.29	0.17	1.00	25.21	0.74	2.43	6.69	65.54	83.68
Winter 2014	0.48	0.19	0.12	11.33	0.98	1.69	4.07	33.57	43.57
Mean ± SE	0.54 ± 0.20			7.03 ± 3.98			39.52 ± 12.93		

Table 3.2. Ranking of parametric survival regression models for carnivore scat removal base on Akaike's Information Criterion with small sample size correction (AIC_c). Explanatory variables included species (coyote and kit fox), road type (two-lane gravel, one-lane gravel and two-track), scat position (shoulder, track and median), season (summer and winter) and mean daily traffic volume. Each model is ranked based on ΔAIC_c, where K = number of model parameters, w_i = Akaike weight and LL = log-likelihood. Only the top four models and null model are presented.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Position + Road + Species + Traffic	7	1386.74	0	0.730	-686.2
Position + Road + Species + Traffic + Season	8	1388.76	2.03	0.265	-686.2
Position + Road + Traffic	6	1397.44	10.70	0.003	-692.6
Position + Road + Traffic + Season	7	1399.51	12.78	0.001	-692.6
Null	1	1686.49	299.76	0.000	-842.2

Table 3.3. Regression coefficients, standard errors (SE), and *p*-values of the best fitting exponential survival model for carnivore scat persistence assessed by Akaike's Information Criterion with small sample size correction. Species included coyote and kit fox, road type included large (two-lane gravel), medium (one-lane gravel) and small (two-track) roads and position included the median, track, and shoulder. Traffic accounts for the mean daily number of vehicles passing sites.

Parameter	Coefficient	SE	*P*-value
Intercept	2.3652	0.192	<0.001
Shoulder (Position)	0.4187	0.142	0.003
Track (Position)	-1.2013	0.139	<0.001
Medium (Road type)	0.4733	0.176	0.007
Small (Road type)	1.2418	0.186	<0.001
Kit fox (Species)	-0.4046	0.113	<0.001
Traffic	-0.0192	0.003	<0.001

Table 3.4. Relative abundance (RA), corrected relative abundance (cRA), and ratio (R; cRA/RA) for coyotes and kit foxes along 15 transects (Tran) in western Utah, USA, over two seasons. Corrected relative abundance incorporates a persistence-rate correction factor estimated by scat removal experiments.

	Coyote						Kit Fox					
	Summer 2013			Winter 2014			Summer 2013			Winter 2014		
Tran	RA	cRA	R	RA	cRA	R	RA	cRA	R	RA	cRA	R
1	5.7	24.6	4.3	2.8	27.3	9.8	0.7	1.7	2.4	0.0	0.0	
2	4.3	19.7	4.6	1.0	1.9	1.9	2.0	4.7	2.4	0.0	0.0	
3	6.3	16.9	2.7	1.3	2.2	1.7	1.0	3.5	3.5	2.8	12.0	4.3
4	1.3	118.6	91.2	0.0	0.0		0.3	333.4	1111.3	0.0	0.0	
5	1.7	61.6	36.2	0.0	0.0		1.0	95.0	95.0	0.0	0.0	
6	7.0	17.1	2.4	0.3	0.3	1.0	0.3	2.3	7.7	0.3	1.7	5.7
7	10.7	27.4	2.6	5.3	12.2	2.3	1.3	3.7	2.8	1.3	5.7	4.4
8	7.0	12.5	1.8	4.3	9.6	2.2	3.0	9.8	3.3	0.0	0.0	
9	3.0	5.6	1.9	1.8	3.5	1.9	17.0	45.7	2.7	8.8	29.1	3.3
10	1.3	7.2	5.5	0.3	0.4	1.3	4.3	34.5	8.0	1.0	1.7	1.7
11	5.0	11.7	2.3	5.3	40.8	7.7	0.0	0.0		0.8	3.7	4.6
12	5.0	9.0	1.8	1.8	7.0	3.9	0.3	0.5	1.7	0.3	0.4	1.3
13	14.3	34.5	2.4	4.3	9.9	2.3	0.7	1.1	1.6	0.0	0.0	
14	6.3	159.1	25.3	0.8	29.5	36.9	2.0	12.0	6.0	1.5	5.0	3.3
15	2.7	106.6	39.5	0.3	4.2	14.0	0.3	210.4	701.3	0.3	16.9	56.3

Figures

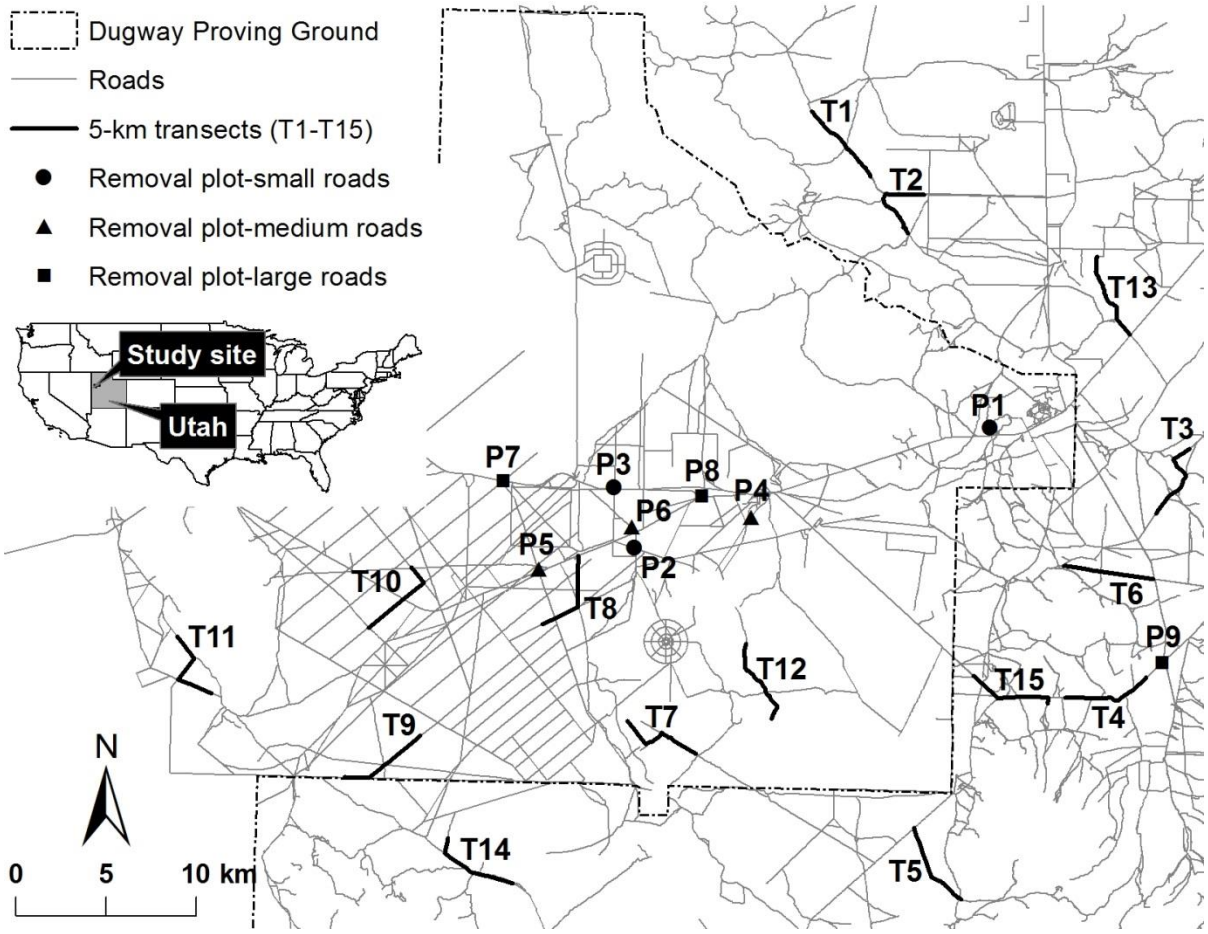

Figure 3.1. Locations of experimental plots on two-lane (large) and one-lane (medium) gravel roads and two-track roads (small) used to estimate scat removal, and 15 scat survey transects used to estimate relative abundance, for coyotes and kit foxes in western Utah, USA.

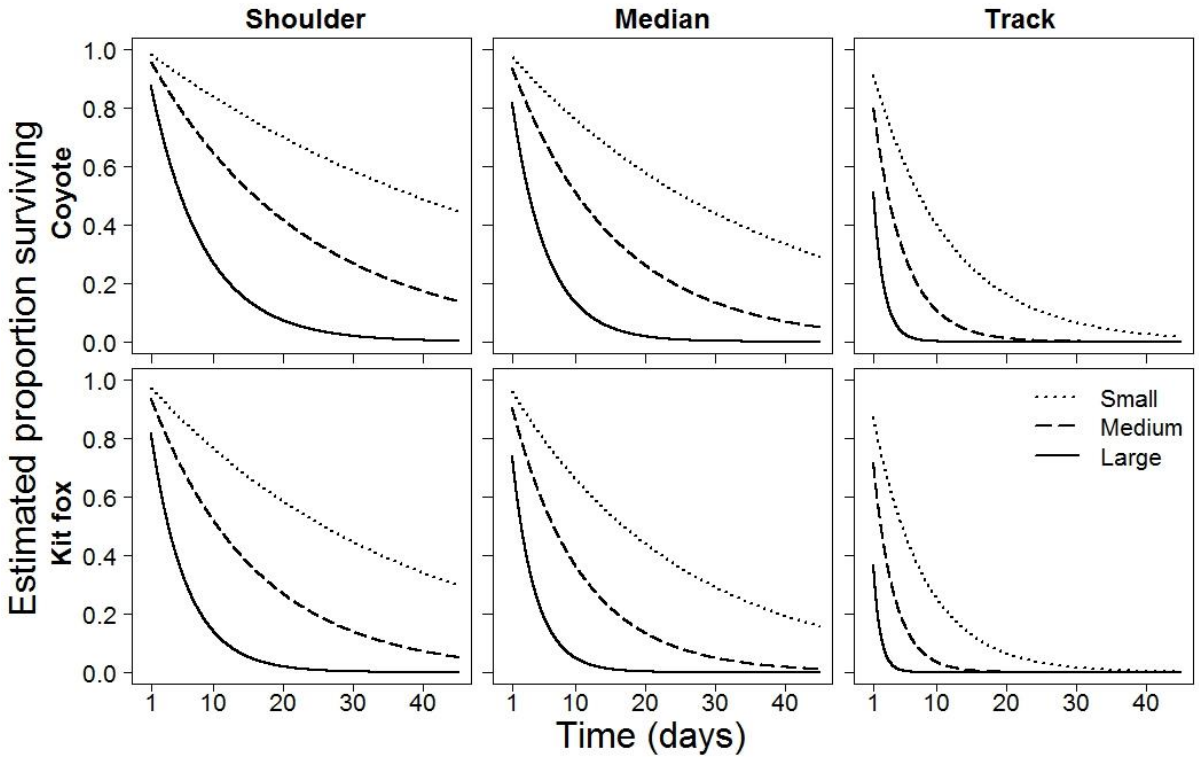

Figure 3.2. Estimated proportion of coyote and kit fox scats surviving over time on large (two-lane gravel), medium (one-lane gravel) and small (two-track) roadways when deposited in the median, track, or shoulder in western Utah, USA. Estimated survival was based on the exponential survival function assuming a mean daily traffic volume for each road type (large = 39.5; medium = 7.03; small = 0.54).

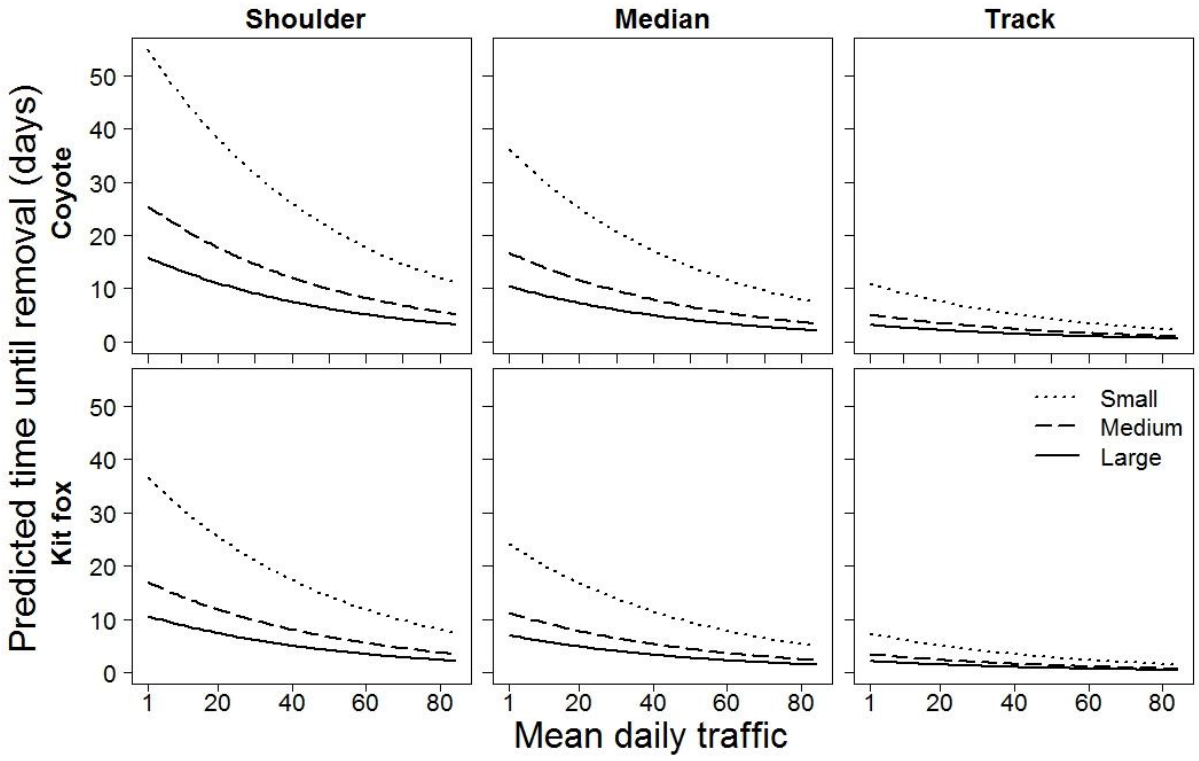

Figure 3.3. Predicted time until removal for coyote and kit fox scats as a function of mean daily vehicle traffic on large (two-lane gravel), medium (one-lane gravel) and small (two-track) roadways when deposited in the median, track or shoulder in western Utah, USA.

Chapter 4: ConGenR: Rapid Determination of Consensus Genotypes and Estimates of Genotyping Errors from Replicated Genetic Samples

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Abstract

ConGenR (available at http://www.uidaho.edu/cnr/research/facilities/leecg/publications-and-software) is an R based conservation genetics script that facilitates rapid determination of consensus genotypes from replicated samples, determines overall (successful amplifications / amplification attempted) and individual sample level (proportion of samples with successful amplifications at *n* loci) amplification success rates, and quantifies genotyping error rates. ConGenR is intended for use with codominant, multilocus microsatellite data generated primarily through noninvasive genetic sampling and processed with a multi-tubes approach. ConGenR handles input that can be easily exported from GENEMAPPER, a program commonly used to score allele sizes. Amplification success and genotyping error rates can be evaluated by sample class (i.e., any identifiable and meaningful subdivision of samples; e.g., sex, season, region, or sample condition), offering insights into processes driving amplification success and genotyping error rates. Additionally,

amplification success and genotyping error rates are calculated by locus, expediting the identification of problematic loci during pilot studies.

Main Body

Noninvasive genetic sampling is an appealing monitoring strategy when working with species that are difficult to observe or capture and provides the opportunity to identify individuals (Waits et al. 2001), estimate population demographic parameters (Marucco et al. 2011), and evaluate genetic health without observing or handling individuals (Waits and Paetkau 2005; Beja-Pereira et al. 2009). Noninvasive genetic samples are typically characterized by low quantity and quality DNA, leading to low polymerase chain reaction (PCR) success and the presence of genotyping errors, making it challenging to obtain reliable genotypes (Pompanon et al. 2005; Waits and Paetkau 2005; Broquet et al. 2006). A multi-tubes approach is frequently used to establish reliable consensus genotypes and minimize the influence of genotyping errors (Taberlet et al. 1996). Genotyping errors are typically classified as a false allele (FA), where an allele is observed within a replicate that is not present in the consensus or reference genotype, or allelic dropout (ADO), where an allele present in the consensus or reference genotype fails to amplify in a successful PCR replicate (Broquet and Petit 2004). Prior to initiating noninvasive genetic monitoring, pilot studies are recommended to quantify PCR and genotyping error rates (Bonin et al. 2004; Valière et al. 2006), determine sufficient sampling designs under observed rates (Rodgers and Janečka 2014; Lonsinger et al. 2015), and evaluate if errors are sufficiently low to avoid substantial biases (Waits and Leberg 2000; Luikart et al. 2010). Still, genotyping error is often neglected or not reported (Pompanon et al. 2005).

The program GENEMAPPER (Applied Biosystems, Foster City, CA, USA) is widely used for scoring alleles. Efficiently handling results files generated by GENEMAPPER can be cumbersome; particularly when working with noninvasive samples analyzed using a multi-tubes approach to achieve reliable consensus genotypes (Taberlet et al. 1996) and analyzed across a sufficient number of loci for individual identification (Waits et al. 2001). GENEMAPPER results files include a row for each PCR reaction-locus combination, leading to large files (e.g., 1,000 samples each analyzed in four replicates at 10 microsatellite loci would yield 40,000 rows of data; in practice, >4 replicates are usually required for reliable consensus genotypes and >10 loci may be necessary for individual identification). Decreasing costs are making noninvasive genetic sampling applicable to large scale surveys (Beja-Pereira et al. 2009) and consequently, noninvasive genetic monitoring projects collecting thousands of samples have become common (e.g., Kendall et al. 2008; Brinkman et al. 2010). Thus, GENEMAPPER results files can contain hundreds of thousands of lines, making data handling, comparing replicates and determining consensus genotypes, and calculating genotyping error rates time-consuming and error-prone if completed manually.

Our goal was to develop a method to quickly handle result files from GENEMAPPER and evaluate replicated genotype data. To this end, ConGenR facilitates the rapid determination of consensus genotypes from replicated samples, determines overall and individual sample level PCR success, and calculates observed genotyping error rates (i.e., ADO and FA rates). Additionally, ConGenR can be used to compare multilocus consensus genotypes across samples, identify samples that match at all or a specified number of loci, and evaluate the spatial relationship between matches and near matches. ConGenR is intended for use with codominant, multilocus microsatellite data generated primarily through

noninvasive genetic sampling and processed with a multi-tubes approach (Taberlet et al. 1996). ConGenR is written in the R programming language (R Core Team 2015) and is designed to handle input in a format that can be easily exported from GENEMAPPER or alternative databases such as Microsoft Access (Microsoft, Redmond, WA, USA). ConGenR allows users to efficiently compare overall and individual sample level PCR success rates, as well as genotyping error rates, by sample class (i.e., any identifiable and meaningful subdivision of samples such as sex, season, region, or sample condition). ConGenR also estimates PCR success and genotyping error rates by locus, expediting the identification of problematic loci during pilot studies. Researchers interested in calculating genotyping error rates by comparing low quality samples (e.g., noninvasive samples) to high quality reference samples (e.g., blood or tissue samples) can do so by directly calling the genotyping error function; this is particularly useful when conducting pilot studies to evaluate genotyping error rates using noninvasive samples collected from known individuals from which high quality samples have been obtained.

To determine consensus genotypes, ConGenR employs common protocols for replicated DNA samples (e.g., Frantz et al. 2003; Flagstad et al. 2004). Specifically, ConGenR requires that each allele of heterozygous genotypes be observed ≥2 times, while single alleles must be observed ≥3 times to confirm a homozygous genotype. ConGenR calculates an overall assessment of PCR success (the number of successful amplifications / the total number of amplifications attempted) and an individual sample level PCR success rate (the proportion of samples with successful amplifications at *n* loci; *n* will most appropriately be set to the number of loci required for individual identification [Waits et al. 2001]). ConGenR quantifies genotyping error rates by comparing each replicated genotype to

the consensus or reference genotype (Lampa et al. 2013) and generally follows procedures detailed by Broquet and Petit (2004), except ConGenR allows ADOs to be scored for genotypes confirmed as homozygous, when the presence of the FA indicates a successful PCR amplification but the confirmed allele fails to amplify. The ConGenR script, including source code, a supporting user manual, and example input files are available at http://www.uidaho.edu/cnr/research/facilities/leecg/publications-and-software.

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Chapter 5: Comparing Estimators of Abundance for Two Sympatric Carnivores Using Noninvasive Genetic Sampling

To be submitted to *Ecological Applications*

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Abstract

Advances in noninvasive genetic sampling (NGS) techniques and related abundance estimators have fueled an increase in the combined use of NGS and capture-recapture analyses among researchers. While resource managers often require estimates of animal abundance to evaluate management practices or determine the status of imperiled species,

NGS capture-recapture methods have not been adopted and implemented by many management agencies. When NGS methods are implemented, managers may be uncertain as to which estimator to employ or how their choice of estimator influences the resulting values. We employed NGS to monitor two sympatric carnivores, kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*), over two years in western Utah, USA. We compared likelihood-based estimates of abundance resulting from (i) robust design non-spatial capture-recapture models, (ii) multi-session spatially explicit capture-recapture (SECR) models, (iii) single-occasion capture with replacement (CAPWIRE) models, and (iv) multi-occasion CAPWIRE models. Estimates of abundance from SECR models were generally higher than those from robust design non-spatial models, but within each session and for each species, confidence intervals for each estimate had high levels of overlap. The magnitude of differences between SECR models and robust design non-spatial models were greater for coyotes than kit foxes. Developed specifically for NGS, CAPWIRE models allowed abundance estimates to be generated from a single sampling occasion, but estimates tended to be biased low yet had high precision. We suspected this resulted from of our dispersed sampling strategy, combined with temporal variation in space use by target species, limiting the number of individuals available for capture with a single sampling occasion. Employing a multi-occasion formulation of CAPWIRE resulted in abundance estimates more similar to multi-session estimators. Our estimated densities for kit foxes (0.02/km^2) and coyotes (0.07/km^2) were among the lowest reported in the literature, and kit fox densities were the lowest reported at our study site since 1997. These results demonstrated that when employing dispersed NGS and capture-recapture analyses, the choice of estimator and sampling design can influence

the resulting estimates of animal abundance and the differences among estimators can vary between species.

Introduction

Wildlife managers often require estimates of animal abundance ($\widehat{N}$) to evaluate management practices intended to maintain harvested populations or control nuisance species, or to determine the status of imperiled species and assess conservation efforts (Williams et al. 2002, Solberg et al. 2006, Brøseth et al. 2010). Capture-recapture techniques can provide reliable estimates of abundance (Williams et al. 2002, Royle et al. 2014), but conventional methods of capture and recapture (e.g., live-capture) are often expensive and challenging to implement, particularly when working with rare or elusive species (Gese 2001). While these constraints do not preclude the use of traditional capture-recapture techniques, they can limit their practicality over large spatial extents, for extended periods, or when monitoring multiple species concurrently. Noninvasive genetic sampling (NGS) can identify individuals (unique genotypes) through the collection of biological material (e.g., feces) left in the environment (Waits and Paetkau 2005, Schwartz et al. 2007), and provides an efficient alternative monitoring strategy that can be employed over extended spatial and temporal scales (Lonsinger et al. 2015a). Advancements in NGS techniques (Schwartz et al. 2007) and related statistical abundance estimators (Lukacs and Burnham 2005, Miller et al. 2005, Thompson et al. 2012) have fueled an increase in NGS use among researchers to estimate abundance (Solberg et al. 2006, Mondol et al. 2009, Brøseth et al. 2010), but NGS has not been implemented to a similar extent by management agencies (Waits and Paetkau 2005, Stenglein et al. 2010b).

Closed-population capture-recapture models commonly employed to evaluate $\widehat{N}$ assume geographic and demographic closure over a relatively short primary sampling period (e.g., days or weeks) and require ≥2 secondary sampling occasions, during which animals are captured, released, and remain available for recapture (Otis et al. 1978, Williams et al. 2002). Additional assumptions include tag permanency, accurate individual identification, and equal capture probability (p) among individuals; capture heterogeneity is common in natural populations, with p varying spatially, temporally, or due to individual heterogeneity and/or behavioral response (Otis et al. 1978, White et al. 1982). Abundance estimates from conventional models are often divided by the size of the study area to calculate density, but this assumes the effective sampling area can be accurately quantified and relies on buffering the trapping area to account for edge effects (Dice 1938, Otis et al. 1978, White et al. 1982, Wilson and Anderson 1985).

Spatially explicit capture-recapture (SECR) models are becoming increasingly popular and use spatially disparate captures of individuals to address capture heterogeneity among individuals associated with proximity to the trapping array, and to estimate density by directly delineating the effective sampling area (Borchers and Efford 2008). Data collected via NGS differs from conventional capture-recapture data in that individuals can be captured >1 time within a sampling occasion (Miller et al. 2005, Thompson et al. 2012). While SECR models can generate estimates based on a single sampling occasion (when individuals are captured >1 time across spatially disparate locations; Efford 2011), 'capture with replacement' (CAPWIRE) models have been developed specifically for NGS, exploiting repeat detections of individuals within a single sampling occasion to generate $\widehat{N}$ (Miller et al. 2005).

One species for which managers require estimates of abundance is the kit fox (*Vulpes macrotis*). Kit foxes are native to North American deserts and are believed to be declining across much of their range (Dempsey et al. 2014); one subspecies, the San Joaquin kit fox (*V. m. mutica*) is listed as an endangered species (USFWS 1998). Intraguild predation by coyotes (*Canis latrans*) is believed to be a major threat to kit fox persistence (Nelson et al. 2007, Kozlowski et al. 2012), and consequently, in the Great Basin Desert efforts to monitor kit foxes and coyotes have included scat deposition surveys, live-capture, den monitoring, and radio-telemetry (Arjo et al. 2007, Kozlowski et al. 2012, Kluever et al. 2013, Dempsey et al. 2014). Scat deposition surveys provide indices of relative abundance (Gese 2001), but may suffer from misidentification of sign (Lonsinger et al. 2015b). Live-captures and radio-telemetry are expensive and time consuming (Gese 2001), limiting the spatial and temporal extent of monitoring, and den monitoring often requires telemetered animals to locate dens (e.g., Arjo et al. 2003). Thus, managers still require cost-efficient and reliable methods to concurrently monitor trends in kit fox and coyote abundances and evaluate management strategies.

We employed NGS to monitor kit foxes and coyotes during four sessions over a two year period. For each species, we compared likelihood-based estimates of abundance from (i) robust design non-spatial models, (ii) multi-session SECR models, (iii) single-occasion CAPWIRE, and (iv) multi-occasion CAPWIRE models. Additionally, we aimed to use SECR models to explore the role of habitat characteristics on spatial variation in each species' density. We hypothesized that for each species within each session, $\widehat{N}$ would exceed the minimum number known alive (MNKA). Capture heterogeneity, if unaccounted for, can result in underestimation of abundance (Carothers 1973, Otis et al. 1978) and therefore we

expected $\widehat{N}$ from SECR to be higher than non-spatial model estimates, as SECR accounts for capture heterogeneity not addressed in non-spatial models. We hypothesized that robust design (non-spatial) and multi-session (spatial) approaches would have higher precision, as the estimators use capture information not only from within sessions, but also from across sessions to estimate *p* (Kendall et al. 1995). We hypothesized that coyote densities would be positively associated with shrub cover (Nelson et al. 2007, Kozlowski et al. 2012) and negatively associated with distance to water (Golightly and Ohmart 1984, Arjo et al. 2007). Finally, we hypothesized that kit fox densities would be negatively and positively related to shrub cover and distance to water, respectively, owing to avoidance of core coyote activity centers (Kozlowski et al. 2012).

Materials and Methods

Study Site

This study was conducted on the U.S. Army Dugway Proving Ground (Dugway) and surrounding federal lands, in western Utah, USA (Fig. 5.1; Lonsinger et al. 2015b), and encompassed ~3,015 km^2. Located within the Great Basin Desert, Dugway was characterized by low-lying basins demarcated by abrupt range formations with elevations ranging from ~1200 m to >2100 m (Arjo et al. 2007). Land cover at lower elevations included cold desert playa, cold desert chenopod shrubland, vegetated and unvegetated dunes, and non-native invasive grasslands, while higher elevations consisted of arid shrubland and open woodland; greasewood (*Sarcobatus vermiculatus*) shrubland was found across the study site (Lonsinger et al. 2015b).

Terminology

Literature associated with different abundance estimators has used different terminology to describe sampling. We define and use the same terminology across methods to avoid confusion. Using a robust design framework, sessions were relatively short sampling periods within which there were multiple sampling occasions and populations were assumed to be closed (Pollock et al. 1990; Fig. 5.2); populations were assumed to be open between sessions. For CAPWIRE, multi-occasion models refer to models including samples from >1 occasion per session, while single-occasion models incorporated only samples from the first occasion within each session. Season indicated sessions representing the same season across years (Fig. 5.2). Robust design and multi-session are both used to indicate that parameters were estimated across sessions within a single modeling framework, but are generally used for non-spatial and spatial models, respectively. Finally, we used 'capture' and 'recapture' to describe the identification of an individual (a unique genotype) through NGS, as opposed to traditional live-capture.

Sample Collection

We conducted carnivore scat surveys from January to March (winter) and July to August (summer) over two years (2013 and 2014). Fifteen 5 km transects were randomly distributed along dirt and gravel roads to monitor kit foxes and coyotes for another study (Dempsey et al. 2014), and we retained these transects. We selected 15 additional random transects by dividing the study area into 25 km^2 cells (a size similar to the average kit fox home range size at Dugway; Dempsey et al. 2015), randomly selecting 15 cells without replacement, and identifying a 5 km transect along dirt or gravel roads within each selected cell (Fig. 5.1; Lonsinger et al. 2015b). These 30 transects (hereafter, multi-occasion

transects) were surveyed 3–5 times per session (Fig. 5.2). We employed a sampling interval (the period between occasions within a session) of 14 days, which has been shown to be an efficient temporal NGS design for kit foxes and coyotes in our system (Lonsinger et al. 2015a). As part of a concurrent evaluation of canid occupancy, 60 sites (each 6.25 km^2) were randomly selected without replacement from a grid of 576 cells superimposed on the study area and excluding cells containing any portion of a multi-occasion transect. Within each site, we established 2 km of transects (comprised of four 500 m transects; hereafter, single-occasion transects) along roadways and surveyed each transect once per session. Two researchers surveyed each transect, each searching half of the transect for carnivore scats. We recorded the location of each scat detected and collected ~0.7 mL of fecal material from the side of the scat (Stenglein et al. 2010a). Samples were preserved in 1.4 mL of DET buffer (20% DMSO, 0.25 M EDTA, 100 µM Tris, pH 7.5, and NaCl to saturation; Seutin et al. 1991) and remaining portions of scats were removed.

Scat accumulation rates were greater in summer than winter for both species (Lonsinger et al. 2015a) and consequently, we surveyed multi-occasion transects four and three times during initial winter (2013) and summer (2013) sampling sessions, respectively. We expected these levels of effort to yield sample sizes for both species that were ≥3 times the expected population sizes (Solberg et al. 2006). We subsequently performed power analyses to evaluate the number of occasions required to achieve a coefficient of variation (CV) <10% for $\widehat{N}$ in each season when employing closed-capture analyses. For each analysis, 1,000 simulations were run in program MARK (White and Burnham 1999) using estimates of p generated from preliminary closed-capture models that considered temporal variation in p and the number of individuals captured in each session. Across simulations, we

assumed no behavioral response to sample collection and set recapture probabilities (*c*) equal to *p*. Power analyses indicated our sampling effort was insufficient to achieve desired levels of precision for kit fox estimates (*see Results*), and we therefore increased sampling in 2014 to five winter and four summer occasions (Fig. 5.2). To reduce costs, we collected only scats believed to be kit fox based on size (Lonsinger et al. 2015b) during the final sampling occasion (i.e., final occasion of summer 2014).

Genetic Analysis

We performed DNA extraction and polymerase-chain reaction (PCR) amplification in a laboratory dedicated to low quality samples to minimize contamination risk. We determined species identification for scats using mitochondrial DNA (mtDNA; De Barba et al. 2014) and followed DNA storage, extraction, amplification, and scoring methods detailed in Lonsinger et al. (2015a). For individual identification, we amplified kit fox and coyote samples with nine nuclear DNA (nDNA) and two sex identification primers (Appendix 5.1). PCR conditions, including primer concentrations and thermal profiles, are presented in Appendix 5.1.

To minimize genotyping errors, we employed multiple methods. We used a multi-tubes approach (Taberlet et al. 1996) and dropped low quality samples failing species identification (Kohn et al. 1999). For individual identification, we utilized the ConGenR script (Lonsinger and Waits 2015) to compare replicates and establish consensus genotypes. ConGenR requires that alleles of heterozygous and homozygous genotypes be observed ≥2 and ≥3 times, respectively. We initially amplified each sample in two PCR replicates and dropped samples failing at >50% of nDNA loci (Paetkau 2003). For those retained, we performed additional PCR replicates in duplicate, until consensus genotypes were achieved

across loci or we reached eight replicates for kit foxes or six replicates for coyotes. For each species, we used samples collected in winter 2013 that achieved consensus genotypes across loci and matched ≥1 other sample (kit fox = 24; coyote = 79) to calculate the probability that two siblings have identical multilocus genotypes ($P(ID)_{sibs}$; Waits et al. 2001) with GenAlEx 6.5 (Peakall and Smouse 2006). We then identified the number of loci required to reliably distinguish individuals at $P(ID)_{sibs} < 0.01$ for each species (Waits et al. 2001). We culled samples that failed to achieve consensus genotypes at a sufficient number of loci. We compared samples with identical or near identical multilocus genotypes (Creel et al. 2003) with ConGenR (Lonsinger and Waits 2015) and re-evaluated scoring of near matches to check for inconsistencies. For matches, we considered consistency in sex identification and compared inter-sample distances (Smith et al. 2006), scrutinizing and re-analyzing potential conflicts. We evaluated the reliability of multilocus genotypes observed only once with RELIOTYPE (Miller et al. 2002) and retained samples with a reliability ≥99%.

Model Covariates

Covariates used to model spatial variation in density for each species were obtained from available GIS layers, and we processed all layers with ArcGIS 10 (ESRI, Redlands, CA, USA). Soil was expected to influence kit foxes, which used burrows year-round (Arjo et al. 2003). We obtained a soil layer from Utah's Automated Geographic Reference Center (http://gis.utah.gov/) and reclassified soils into four categories (silt, fine sand, blocky loam, and gravel; sensu Dempsey et al. 2015). Vegetation data was obtained from the 2012 LANDFIRE program (http://landfire.cr.usgs.gov/) and reclassified into six major land-cover forms (woodland, shrubland, subshrubs, grasslands, sparsely vegetated, and developed). From this, the proportion of cover attributable to shrubland and woodland was calculated,

representing habitats expected to support greater densities of mammalian prey, an important prey source for both canids (Kozlowski et al. 2008, 2012). Water was expected to influence space use of carnivores in this arid environment (Arjo et al. 2007). Perennial water sources were identified by the Dugway Natural Resource Program GIS layers and were documented during field surveys. Google Earth imagery was used to identify additional water sources by following livestock and wild horse trails to convergence points; these points were ground-truthed to confirm the presence of water.

In non-spatial capture-recapture models, we included distance to water and individual heterozygosity as individual covariates on survival (*S*). For this purpose, distance to nearest water was calculated as the mean distance to nearest water across samples for each individual. Reduced heterozygosity can reflect inbreeding and thus a correlation between individual heterozygosity and fitness is often predicted (Reed and Frankham 2003). We calculated five measures of individual heterozygosity—proportion of heterozygous loci, standardized observed and expected heterozygosity, internal relatedness, and homozygosity by locus—with GENHET (Coulon 2010). All individual heterozygosity metrics were highly correlated (Spearman's rank correlations for all comparisons: $r > |0.91|$, $P < 0.001$) and we therefore used only the standardized observed heterozygosity. Additionally, an index of coyote activity was used as an individual covariate in kit fox models, where we estimated the mean number of coyote scats detected (standardized by the length of surveys) within 500 m of each kit fox's locations.

Capture-Recapture Analysis

Capture-recapture data were analysed using maximum likelihood methods applied in (i) non-spatial Huggins closed-capture models (Huggins 1989), (ii) SECR models (Borchers

and Efford 2008) and (iii) CAPWIRE models (Miller et al. 2005). Both the Huggins closed-capture models and SECR models were fit using the entire NGS data set (i.e., all samples resulting in individual identification). For non-spatial models, multiple captures of an individual within an occasion were collapsed into a binary response to construct individual encounter histories. For SECR models, we followed procedures of Thompson et al. (2012) and Russell et al. (2012), and gridded the study area into cells, using the center of each cell as a 'conceptual' trap. With a goal of monitoring kit foxes and coyotes concurrently, we selected a grid size of 6.25 km^2(2.5 x 2.5 km), by considering the home range size and movement capacity of both canids (Koopman et al. 2000, Nelson et al. 2007, Dempsey et al. 2015). The grid aligned with that used to identify single-occasion sites and each of these sites represented one trap. Additionally, the grid bisected longer, multi-occasion transects, demarcating multiple traps from each transect. Captures of an individual across multiple traps within a single occasion can be used by SECR to characterize the spatial point process (Borchers and Efford 2008). Consequently, capture histories included all captures and we assigned each detected scat to the location of a conceptual trap. As a result, scats of a single individual detected within a grid cell during a single occasion were assigned to the same location, effectively treating clusters of scats as single observations and reducing the influence of spatial autocorrelation on density estimates (Thompson et al. 2012).

Effort varied across transects and grid cells. To account for variation in effort between single-occasion and multi-occasion sites in Huggins capture-recapture models, we distinguished males and females captured on multi-occasion transects from those captured only on single-occasion transects (i.e., multi-occasion males, multi-occasion females, single-occasion males, single-occasion females), and for each sex applied the mean *p* estimated

from multi-occasion transects to single-occasion transects. For SECR models, effort related to each trap and we used the total length of transects surveyed within each grid cell to represent effort (where repeat surveys on multi-occasion transects were summed).

CAPWIRE assumes equal effort across sites (Miller et al. 2005). To compare the performance of CAPWIRE with multi-session models, we fit separate CAPWIRE models for each session, using a reduced data set that met the equal effort assumption and was intended to represent how managers would sample if using this estimator (single-occasion formulation). Specifically, we identified portions of the multi-occasion transects contained within one of the 576 grid cells used to select single-occasion transects, and that were ≥2 km in length, allowing four 500 m nested transects to be identified. For each session, we then considered captures from single-occasions transects and only the first occasion of multi-occasion transects, restricting captures to those on nested transects when estimating abundance. Initial CAPWIRE abundance estimates for both species were generally lower across sessions than those generated with multi-session models (*see Results*). To determine if CAPWIRE produced estimates more comparable to the multi-session models with a more complete dataset, we increased the number of captures included in the analysis by including captures from all occasions and dividing the number of captures by the number of occasions to standardize effort (multi-occasion formulation).

Non-spatial Huggins closed-capture models were fit using a robust design framework (Huggins 1989, Pollock et al. 1990) in program MARK (White and Burnham 1999). Although this modelling framework provides estimates of *S*, *p*, recapture (*c*), temporary immigration ($1 - \gamma''$) and temporary emigration (γ'), for purposes of comparing abundance estimators, we describe the model set, but focus on reporting parameter estimates related to *p*

and derived $\widehat{N}$. We tested for closure within each session with CLOSETEST (Stanley and Burnham 1999).

We modeled apparent survival considering models with constant, time-varying, or trend in survival (Otis et al. 1978, Williams et al.2002). We also considered models in which survival varied by season (winter-summer vs. summer-winter) or was influenced by an extreme winter (2013). We considered the effects of sex, individual heterozygosity, and distance to nearest water on survival. For kit fox survival, we also considered a covariate indexing coyote activity. We considered three movement models: random movement ($\gamma' = \gamma''$), constant but different γ parameters ($\gamma' \neq \gamma''$), and no movement ($\gamma' = \gamma'' = 0$). We did not expect a behavioural response to capture when using NGS and set $p = c$. We modeled p as constant or varying by time, trend, and sex within sessions, and considering additive models of sex with both time and trend. We combined each model for S, with each combination of models for movement and p. For each species, we used Akaike's Information Criterion with small sample size correction (AIC_c) and Akaike weights to compare the relative fit of models (Burnham and Anderson 2002). Parameter estimates accounting for model-selection uncertainty were achieved by model-averaging (Burnham and Anderson 2002). We calculated variances and confidence intervals for model-averaged estimates with the delta method (Williams et al. 2002).

We fit SECR models by maximizing the full likelihood with the R package 'secr' (Efford 2015; R Core Team 2015), and using a multi-session formulation, which allowed improved estimation of parameters shared across sessions (Efford et al. 2009). In addition to estimating density ($\widehat{D}$), SECR models estimate $g0$ and σ, which combined replace p and jointly describe the decline in detectability with increasing distance between the trapping

array and an animal's activity center (Efford et al. 2009). We utilized a half-normal detection function (or circular bivariate normal home range), in which *g0* and σ represent the intercept and scale parameter, respectively (Efford et al. 2009).

In order to estimate density (and derive $\widehat{N} = \widehat{D} *$ effective sampling area), the effective sampling area (i.e., the state space) must be appropriately defined. We evaluated the effect of buffer width around traps by considering changes in the log-likelihood, $\widehat{D}$, and the effective sampling area, while increasing widths from 1–15 km. We selected the width where the rate of change in both the log-likelihood and effective sampling area stabilized, and where $\widehat{D}$ stabilized at the fifth decimal place. We applied this buffer around traps, creating a habitat mask with grid points evenly distributed every 2.5 km; spatial covariates characterizing the area around each point (within a 1.25 km radius)—the majority soil type and habitat, the proportion of shrubland and woodland cover, and the mean distance to water—were extracted for modeling $\widehat{D}$. We first evaluated capture models in which *g0* and σ varied across sessions and was either constant or varied by time, trend, or sex within sessions. Additionally, we considered both interaction and additive effect models of sex with time and trend. We then used the best-fit capture model (i.e., the model with the lowest AIC_c), when fitting models for $\widehat{D}$. Models formulated for $\widehat{D}$ allowed variation among sessions. Additionally, we fit models of $\widehat{D}$ (overall and by sex) using the aforementioned spatial covariates believed to influence kit fox and/or coyote space-use, and combinations of these predictors. We used AIC_c and Akaike weights (Burnham and Anderson 2002) to compare the relative fit of models for each species. Single top models of capture and $\widehat{D}$ could be identified within each species' model set, with the next closest model having little to no support based on ΔAIC_c. We calculated $\widehat{N}$ and confidence bounds by multiplying session

specific $\widehat{D}$ and associated confidence limits by the effective sampling area (Russell et al. 2012).

For each species, CAPWIRE models were fit independently for each session with the R package 'capwire' (Pennell et al. 2013, R Core Team 2015). CAPWIRE models assume either that all individuals have equal *p* (equal capture model; ECM) or that two capture classes exist (two-innate rates model; TIRM) representing individuals with relatively low and high *p* (Miller et al. 2005). For each species, we fit both single-occasion and multi-occasion formulations of the ECM and TIRM for each session, and compared model fit using a likelihood-ratio test implemented in 'capwire' with 1,000 simulations; the ECM was rejected when $P < 0.1$. We subsequently generated 95% confidence intervals for the estimate of the best supported model using 1,000 parametric bootstraps (Miller et al. 2005, Pennell et al. 2013).

Results

Noninvasive Genetic Sampling and Species Identification

Within each session, 570–870 km of transects were surveyed (Table 5.1). The mean time between multi-occasion transect surveys (within a session) was ~14 days (mean = 13.7 ± 0.93 SD, range = 9–18), with departures from 14 days resulting from access constraints (e.g., heavy snow fall, military training activities). We collected 3,752 carnivore scats (Table 5.2). We observed high mtDNA amplification rates, with successful species identification for 93.3% of winter and 82.8% of summer samples. We identified 21.6% and 63.3% of samples as kit fox and coyote, respectively (Table 5.2). Only 2.5% of samples were non-target carnivores, 1.1% were mixed (i.e., contained DNA of >1 species), and 11.5% failed (Table 5.2).

For kit foxes, winter power analyses indicated four occasions failed to achieve a CV <10%. Observed *p* increased across occasions as snow melted (Table 5.3); nearly all snow had melted by the final occasion and we assumed that *p* of a fifth occasion would have been comparable to the fourth, so we set them equal to one another while conducting a power analysis for five occasions. Five winter occasions produced a CV = 6.5%. Observed kit fox *p* was relatively stable across summer occasions (Table 5.3). Three occasions were insufficient to achieve the desired level of precision. We again assumed that the *p* of a final occasion would be comparable to that observed during the subsequent occasion and set them equal to one another. Four occasions in summer produced a CV = 9.7%. Consequently, we increased sampling effort in 2014 to five winter and four summer occasions (Table 5.1; Fig. 5.2). For coyotes, power analyses indicated our initial sampling design was sufficient, with four occasions producing a CV = 7.7% in winter and three occasions producing a CV = 6.5% in summer. We elected to sample coyotes for the same number of occasions as kit foxes in winter 2014, but stopped sampling suspected coyote scats after three occasions in summer 2014 to reduce costs (Table 5.1).

Individual Identification

Six loci were required to achieve a $P(ID)_{sibs}$ <0.01 for kit foxes, excluding sex identification markers. Kit fox individual identification success rates (i.e., the proportion of samples identified to species for which a successful individual identification was achieved) ranged from 59.4% (summer 2013) to 91.4% (winter 2013). Across sessions, 109 kit foxes were identified (Table 5.2), among which 102 individuals had consensus genotypes at ≥8 loci. Sex was determined for all individuals. We captured 36–50 kit foxes each session (Table 5.2) and 37 individuals across >1 sessions. We captured more males (60%) than

females (Table 5.2). For samples in the final dataset, genotyping error rates were low (overall allelic dropout rate = 17.3%; overall false allele rate = 3.4%), suggesting the probability of a genotyping error with the mean number of replicates (5) was low (i.e., $[0.1733 + 0.0342]^5 = 3.85 \times 10^{-4}$).

Five loci were required to achieve a $P(ID)_{sibs} < 0.01$ for coyotes, excluding sex identification markers. Coyote individual identification success rates ranged from 63.1% (summer 2013) to 90.2% (winter 2013). Across sessions, 302 coyotes were identified (Table 5.2), among which we obtained consensus genotypes across ≥8 loci for 296 individuals and sex identification for all individuals. We captured 128–151 coyotes each session (Table 5.2), with 140 individuals being captured in multiple sessions. Overall, 53% of captured coyotes were male (Table 5.2). Genotyping error rates were low (overall allelic dropout rate = 14.7%; overall false allele rate = 4.2%) for samples in the final dataset, resulting in a low probability of a genotyping error (i.e., $[0.1472 + 0.0418]^5 = 2.41 \times 10^{-4}$) with the mean number of replicates (5).

Robust Design Non-Spatial Capture-Recapture Analysis

Program CLOSETEST supported the population closure assumption for kit foxes in 2013 (winter: $\chi^2 = 3.43$, df = 3, $P = 0.329$; summer: $\chi^2 = 1.19$, df = 2, $P = 0.550$), but not for 2014 (winter: $\chi^2 = 17.08$, df = 4, $P = 0.002$; summer: $\chi^2 = 8.38$, df = 3, $P = 0.006$). Component and subcomponent tests suggested closure violations may have resulted from population losses following the second occasion in both 2014 sessions. Similarly for coyotes, CLOSETEST supported the assumption of population closure in 2013 (winter: $\chi^2 = 1.16$, df = 4, $P = 0.884$; summer: $\chi^2 = 3.69$, df = 2, $P = 0.158$), but not for 2014 (winter: $\chi^2 = 35.97$, df = 6, $P < 0.001$; summer: $\chi^2 = 15.33$, df = 2, $P < 0.001$). Component and subcomponent tests

suggested closure violations may have resulted from additions and losses in winter, and additions in summer.

We compared the fit of 31 non-spatial models for kit fox and coyote *S* (Appendix 5.2); five additional models for kit fox *S* incorporating an index of coyote activity were also evaluated (Appendix 5.2). When fit with each combination of the six detection and three movement models (Appendix 5.2), each survival model was represented 18 times in initial model sets. We excluded models for which *S* or *p* were confounded, or where boundary effects resulted in estimates of *S* or *p* fixed at 1 (SE = 0). For both species, multiple models among the most supported shared similar structures for *S*, but differed in structure for *p* and movement (Appendix 5.3, Appendix 5.4). Model-averaged estimates of kit fox *p* were similar between sexes and ranged from 0.186–0.536 in winter and 0.276–0.432 in summer (Table 5.3). The best-fit models suggested a trend in *p* within sessions (Table 5.3, Appendix 5.3). We observed only slight differences in *p* between male and female coyotes, with *p* ranging from 0.221–0.543 in winter and 0.258–0.467 in summer (Table 5.3). Top coyote models supported time or trend variation in *p* (Table 5.3, Appendix 5.4).

Model-averaged $\widehat{N}$ from robust design non-spatial models suggested that there were 2.7–3.6 times more coyotes than kit foxes across the study site (Fig. 5.3). Kit fox $\widehat{N}$ ranged from 60.1–73.2, but 95% confidence intervals suggested population abundance was similar across sessions (Fig. 5.3). Coyote $\widehat{N}$ ranged from 198.1–230.7. Again, 95% confidence intervals suggested that populations were relatively stable over the four sessions (Fig. 5.3).

Multi-Session Spatially Explicit Capture-Recapture Analysis

Transects were distributed within 146 grid cells and mean spacing between these conceptual traps was 2.7 km. Effort remained constant across sessions at conceptual traps

characterized by single-occasion transects (2 km), but varied across sessions for traps associated with grid cells incorporating multi-occasion transects. Mean effort across sessions and species for multi-occasion sites was 4.9 km (SD = 4.0, range = <1–21 km). For both species, the change in effective sampling area, log-likelihood, and $\widehat{D}$ stabilized at a buffer width of 7.5 km, resulting in a state space of 3,663 km^2 (Fig. 5.1).

Among the 12 capture models for *g0* and σ, the top kit fox model included variation among sessions and a trend in capture parameters within sessions (Table 5.4). The next closest model was >23 ΔAIC_c from the top model, indicating relatively little or no support (Table 5.4). Similarly, the top coyote capture model included variation among sessions and time-varying capture parameters within sessions and the next closest model was >68 ΔAIC_c from the top model (Table 5.4). For both species, results aligned with capture probabilities estimated with non-spatial models (Table 5.3). We attempted to fit 24 models of density for each species. Models containing the covariate distance to nearest water failed to converge; we rescaled this parameter to mean = 0 and standard deviation = 1, but convergence still failed. We fit 14 models for each species (Appendix 5.5). For both species, the null model (i.e., *D* ~ session) received the greatest support, with the next closest kit fox and coyote models having a ΔAIC_c >136 and >728, respectively (Appendix 5.5). Due to the overwhelming support for each top model, we used $\widehat{D}$ from these top models. Kit fox $\widehat{D}$ was similar across sessions (0.018–0.022 animals/km^2; Table 5.5). Coyote $\widehat{D}$ (0.065–0.079 animals/km^2) was 3–4 times greater than that of kit foxes (Table 5.5).

Kit fox derived $\widehat{N}$ was slightly higher than estimates from robust design non-spatial models across three sessions, but confidence intervals suggested that SECR and non-spatial estimates were similar (Fig. 5.3). For coyotes, $\widehat{N}$ from SECR models were consistently

higher than those from robust design non-spatial models, and the magnitude of the differences between the two were greater than observed for kit foxes (Fig. 5.3). Although there was substantial overlap in $\widehat{N}$ confidence intervals for multi-session SECR and non-spatial models, confidence bounds failed to overlap the alternative point estimate in two sessions (Fig. 5.3).

Capture with Replacement Analysis

We identified 103 transects of equal effort for CAPWIRE analyses. For the single-occasion formulation, total sampling effort was equal across sessions (Table 5.6). Effort varied among sessions for the multi-occasion formulation, reflecting variation in occasions (Fig. 5.2, Table 5.6). Across sessions, we identified only 21–30 kit foxes and 72–103 coyotes, when considering only transects contributing to single-occasion CAPWIRE estimates (Table 5.6). With single-occasion CAPWIRE surveys, we detected a greater proportion of the MNKA for coyotes (56.3–71.6%) than for kit foxes (55.3–62.5%), within each session. When considering multi-occasion CAPWIRE surveys, we identified ≥86% of known kit foxes and ≥83% of known coyotes within each session (Table 5.6). We failed to detect a greater proportion of the MNKA due to the reduction in occasions (kit foxes = 27.8–36.8%; coyotes = 11.3–34.4%), than due to decreased transect length associated with identifying nested transects (kit foxes = 7.5–13.9%; coyotes = 10.2–17%). The number of captures per kit fox ranged from 1.6–2.3 for single-occasion and 1.9–2.4 for multi-occasion sampling. The number of captures per coyote ranged from 1.8–2.3 for single-occasion sampling and 1.8–3.1 for multi-occasion sampling.

For kit foxes, likelihood-ratio tests rejected the ECM for multi-occasion models (all $P < 0.02$) across sessions; for single-occasion models, the ECM was rejected for 2013 sessions

(both $P < 0.03$), but was not rejected for 2014 sessions (both $P > 0.1$). Because likelihood ratio tests may fail to reject the ECM when sample sizes are small and capture heterogeneity is present (Miller et al. 2005), we report results under the TIRM, but include ECM point estimates in Fig. 5.3. Likelihood-ratio tests for coyote models rejected the ECM across sessions for single-occasion and multi-occasion models (all $P < 0.001$).

Kit fox estimates from CAPWIRE were generally lower than those from robust design non-spatial models and SECR models (Fig. 5.3). From single-occasion CAPWIRE models, kit fox estimates were substantially lower (27.5–59.2%) than multi-session estimates, ranging from 30–53 (Fig. 5.3); $\widehat{N}$ was lower than the MNKA in three sessions. Generally, kit fox single-occasion CAPWIRE estimates had higher precision than alternative estimation approaches, and 95% confidence intervals failed to overlap multi-session point estimates in all but one session (Fig. 5.3). Kit fox multi-occasion CAPWIRE estimates were lower (5.3–27.0%) than multi-session estimates (with one exception, winter 2014), but confidence intervals overlapped considerably (Fig. 5.3). For coyotes, $\widehat{N}$ from single-occasion CAPWIRE models were lower (13.7–49.0%) than those from multi-session models (Fig. 5.3); winter 2014 single-occasion CAPWIRE $\widehat{N}$ was more similar to multi-session estimates. The relationship between multi-occasion CAPWIRE estimates and multi-session estimators was more variable for coyotes than kit foxes (Fig. 5.3).

Discussion

Abundance estimators are often evaluated using simulations (Petit and Valiere 2006, Borchers and Efford 2008, Lukacs et al. 2009, Efford and Fewster 2013), or by comparing estimates with known abundances (Carothers 1973, Puechmaille and Petit 2007). However in practice, wildlife managers are interested in generating $\widehat{N}$ for free-ranging populations and it

is often unclear how choice of estimator may influence resulting values. If $\widehat{N}$ varies substantially among estimators, reliance on a single estimator, without consideration of alternatives, may result in misinformed management strategies; recognizing differences in $\widehat{N}$ can be diagnostic of departures from model assumptions (Otis et al. 1978) and provide guidance on which estimators are likely to be robust.

Noninvasive Genetic Sampling Design and Capture Probabilities

Many carnivores utilize linear features for movements and consequently, noninvasive surveys along roads or trails are commonly employed to monitor carnivore populations (Kohn et al. 1999, Gompper et al. 2006, Dempsey et al. 2014). Sampling along linear features may bias parameters estimates due to the non-random nature of sampling (i.e., convenience sampling; Anderson 2001). We attempted to avoid the pitfalls of convenience sampling at a broad (landscape) scale by randomly selecting survey sites, and then delineating transects along roads within each site. Due to the high mobility of canids relative to the size of sites, it is unlikely that individuals occupying a site would fail to encounter a transect. Kit foxes in California did not avoid roads and scats were deposited equally along roads and away from roads (Cypher et al. 2009). Coyote fecal DNA sampling in California suggested that males and females defecated along linear features equally and that scat surveys were unbiased with respect to social status or age (Kohn et al. 1999). Nonetheless, individual heterogeneity in road use or the proximity to an individual's activity center to roads may influence *p* (Otis et al. 1978, Borchers and Efford 2008, Royle et al. 2014). We therefore considered individual covariates (e.g., sex) and spatial locations (via SECR models) to account for associated capture heterogeneity.

Efforts to maximize *p* and sample size can further minimize the influence of unaccounted for individual heterogeneity (Carother 1973, Otis et al. 1978, White et al. 1982, Kendall 1999, Lukacs and Burnham 2005). For canids, scat surveys along roads and trails can increase samples size and maximize *p*. Surveys along linear features often yield larger sample sizes than those away from linear features with equal intensity (Güthlin et al. 2014). At Dugway, scat deposition surveys produced higher detection rates for kit foxes than live-capture (Dempsey et al. 2014). Searcher efficiency (i.e., ability to detect scats) during scat surveys may vary by road and trail substrate (Kluever et al. 2015), but it is likely higher along these linear features than in vegetative cover or litter. Transects along linear features may also be easier to access and can be surveyed more quickly than alternative survey routes, allowing a greater number of surveys to be completed given available time and resources.

Individual Identification

Our mtDNA and nDNA amplification success rates and genotyping error rates were similar to those predicted by a pilot study (Lonsinger et al. 2015a). Capture-recapture techniques assume that individuals are correctly identified (Otis et al. 1978, White et al. 1982). Genotyping errors can therefore be a serious problem when employing NGS to estimate abundance (Mills et al. 2000, Lukacs et al. 2009). Petit and Valiere (2006) found that when employing a sufficient number of loci to discriminate among related individuals, genotyping error rates similar to ours had minimal effects on $\widehat{N}$ (i.e., bias $\leq$2.5%). For the majority of individuals, we achieved consensus genotypes at more loci than were required by $P(ID)_{sibs}$, and we believe this, combined with the efforts to minimize errors, effectively eliminated misidentification biases.

Comparing Multi-Session Estimators

Combining NGS and capture-recapture methods can yield reliable population estimates (e.g., Puechmaille and Petit 2007, Stenglein et al. 2010b). Advances in SECR models have expanded the modeling framework available to practitioners and allow for the estimation of both density and the effective sampling area under a unified framework (Borchers and Efford 2008, Royle et al. 2014); this alleviates the problem of interpreting the area to which abundance estimates pertain (Obbard et al. 2010). While the researcher must still determine a buffer width for use in SECR models to estimate density, diagnostics (e.g., change in density and effective sampling area) based on the data can be used to select an appropriate width. Comparisons between non-spatial capture-recapture and SECR models are often made by comparing density estimates (Obbard et al. 2010, Gray and Prum 2012). Converting $\widehat{N}$ from non-spatial models to $\widehat{D}$ requires the determination of the effective sampling area (Dice 1938, Otis et al. 1978, Wilson and Anderson 1985, Obbard et al. 2010, Royle et al. 2014). Without incorporating spatial data, metrics of animal movement from alternative data sources (e.g., telemetered animals) or study areas may need to be applied, and the choice of how to define the appropriate buffer width is not always clear. Abundance estimates are sufficient when working within a single site and at a fixed spatial scale (Blanc et al. 2013), and may be required when dealing with species that are listed or petitioned for listing (e.g., threatened or endangered; Neel et al. 2012).

True abundance is unknown for our target populations and we cannot explicitly infer bias for each estimator. Abundance estimates from robust design non-spatial and multi-session SECR models showed high levels of agreement for both species and across sessions (Fig. 5.3). In general, SECR estimates were slightly higher than robust design non-spatial

estimates (with one exception, kit fox winter 2013). Blanc et al. (2013) found SECR models tended to overestimate abundance for small populations (defined as $N = 10$), but produced estimates closer to the true abundance for larger populations (defined as $N = 50$). Our MNKA and abundance estimates suggested that our target species' populations were >50 individuals. Individual heterogeneity in capture, if unaccounted for, can bias $\widehat{N}$ downward (Otis et al. 1978, White et al. 1982). Spatial models address variation resulting from an individual's proximity to survey sites, a form of heterogeneity not accounted for by non-spatial models (Borchers and Efford 2008, Royle et al. 2014). Thus, lower $\widehat{N}$ from non-spatial models may be the result of this capture heterogeneity.

We observed greater differences between SECR and robust design non-spatial models for coyotes than kit foxes, and this may be related to the proportion of individuals that move out of, or partially out of, the survey area (Blanc et al. 2013). Our survey design was motivated primarily by kit fox monitoring needs and our study was centered on the low-lying basin (Fig. 5.1). Consequently, the study area was bounded by mountains in the east and south and by salt desert playa inhospitable to both species in the west. The study boundaries were more likely to bisect the activity centers of coyotes than kit foxes, and this may have resulted in the greater disparity between non-spatial and spatial model estimates for coyotes. While both Huggins closed-capture models and SECR models assume population closure (Otis et al. 1978, Royle et al. 2014), SECR models relax the assumption by taking into account an animal's activity center. Population losses or gains that violate closure assumptions can negatively or positively bias estimates, respectively (Kendall 1999). For kit foxes, closure tests suggested population losses in later sampling sessions, and this could have resulted from increased reproductive behavior (i.e., denning) in winter and initiation of

juvenile dispersal in summer. Closure test results should be viewed with caution though, as they assume no individual heterogeneity in *p* and closure is rejected at high rates in closed populations when heterogeneity exists (Stanley and Burnham 1999). We observed a similar magnitude in the differences between $\widehat{N}$ from robust design non-spatial models and SECR models in 2013 and 2014 for kit foxes. This, combined with knowledge that concurrent research involving telemetered kit foxes did not detect any movements to beyond our study extent (B. Kluever, personal communication), lead us to believe the kit fox population was effectively closed. For coyotes, failure to detect closure in winter 2014 may have reflected wider movements of individuals searching for mates along the study periphery, while failure in summer 2014 could result from increased pup availability. Although the temporal sampling frame increased from winter 2013 to winter 2014, winter 2014 closure violations were detected within the temporal time frame that aligned with winter 2013 sampling; summer temporal sampling was equivalent for coyotes across years. Consequently, we suspect individual heterogeneity in *p* likely influenced closure test results.

Non-spatial models do not account for 'holes' in the sampling frame (Williams et al. 2002, Efford and Fewster 2013), and this may also contribute to the lower $\widehat{N}$ resulting from non-spatial models. Our random sampling at the landscape scale resulted in several holes within our sampling frame (Fig. 5.1), from which animal's likely had low (or possibly zero) *p* due to their proximity to transects. By accounting for proximity to animal activity centers, SECR models effectively handle holes (Borchers and Efford 2008, Royle et al. 2014). The detection function we employed assumed a circular home range (Efford et al. 2009). Kit fox typically have circular home ranges (Koopman et al. 2000). Coyote home ranges may be approximately circular, but are often elongate (Bekoff 1977). Violating the circular home

range assumption is unlikely to influence $\widehat{N}$, but may influence variance estimates (Efford 2004; Obbard et al. 2010).

We observed similar levels of precision between non-spatial and spatial models. Spatial models are able to utilize more of the capture data (i.e., do not require collapsing of spatially disparate captures to a binary response) and often have higher precision than non-spatial models (Sollmann et al. 2011, Blanc et al. 2013). Trap spacing and sampling intervals may influence precision of SECR models though, as greater inter-trap spacing and shorter sampling intervals likely reduce opportunities for spatially disparate recaptures within an occasion. As the probability of spatially disparate recaptures decreases, capture histories for spatial and non-spatial models converge. Our average inter-trap distance (2.7 km) may have limited the opportunity for spatial recaptures within an occasion.

Comparing Multi-Session and Capture with Replacement Estimators

Multi-session models (i.e., robust design non-spatial models and SECR models) produced relatively consistent results, and we used these as a standard to evaluate the performance of single-occasion and multi-occasion CAPWIRE estimators. The MNKA nearly always underestimates abundance (Mills et al. 2000), and therefore we regard estimates at or below the MNKA as biased. In practice, limited resources often force managers to seek out cost-efficient sampling strategies. Consequently, there has been considerable interest in single-occasion sampling schemes, which have practical advantages (e.g., ease of implementation, lower cost; Miller et al. 2005, Petit and Valiere 2006, Williams et al. 2009). Reliable estimates have been reported for a range of taxa using CAPWIRE (Petit and Valiere 2006, Puechmaille and Petit 2007, Robinson et al. 2009, Stenglein et al. 2010b), but in some cases, CAPWIRE estimates do not align with alternative estimates (Ruell et al.

2009, Williams et al. 2009, Stansbury et al. 2014). Simulations have suggested that single-occasion sampling can produce abundance estimates as reliable as multi-occasion sampling when the number captures per individual is >1.7 (Miller et al. 2005, Petit and Valiere 2006, Stenglein et al. 2010b). Our captures per individual exceeded 1.7 for both species across sessions, with one exception (kit fox winter 2014 = 1.6). Still, single-occasion CAPWIRE estimates were substantially lower than multi-session estimates for both species across sessions. For kit foxes, single-occasion estimates fell below the MNKA for three of four sessions; all estimates fell below the MNKA when employing the ECM where it was supported (Fig. 5.3). A similar pattern was observed for coyotes, though only one estimate was less than the MNKA. When employing the multi-occasion framework, CAPWIRE estimates for kit foxes were similar to those of multi-session estimators and 95% confidence intervals overlapped considerably (Fig. 5.3). Coyote multi-occasion CAPWIRE estimates were less consistent and there was substantial variation in their relationship to multi-session estimates (e.g., some estimates were higher while others were lower; some had lower precision while others had higher precision).

The CAPWIRE model assumes independence among captures and equal sampling effort (Miller et al. 2005). Independence among captures may be violated when individuals are captured multiple times within a site and restricting recaptures to spatially disparate sites can reduce this concern (Stenglein et al. 2010b). Placing restrictions on how recaptures are defined, however, can reduce already limited datasets available for rare carnivores and will likely result in fewer captures per individual (Stansbury et al. 2014). Consequently, many researchers opt to include all captures (Miller et al. 2005, Williams et al. 2009, Stansbury et al. 2014) as we have, and this may bias results and artificially inflate precision. CAPWIRE

models are based on a simple urn model (Miller et al. 2005) and may best apply to sampling situations that mimic this, such as sampling where animals congregate (e.g., rendezvous sites, breeding grounds, roosting colonies). Our sampling was relatively dispersed and we did not target animal concentration areas. Temporal variation in space-use may limit the number of individuals available for capture during a single occasion, biasing CAPWIRE estimates (Kendall 1999). Ensuring that >1 single-occasion transect is within each potential home range may alleviate this concern, but may be impractical or restrict the spatial extent that can be surveyed. Alternatively, combining the results from multiple occasions, while accounting for variable effort to meet model assumptions, may increase the probability of capturing individuals with temporal variation in space-use. Our data suggests that this may be the case with kit foxes and coyotes, as we substantially increased the number of individuals captured ≥1x by increasing the number of occasions and resulting estimates were generally more similar to those from multi-session estimators.

Individuals captured many times more than the mean number of captures can bias results and artificially increase precision. The CAPWIRE model estimates a ratio α, between the probabilities of capture for 'seldom' and 'often' captured individuals and outlier individuals can severely bias this estimate (Miller et al. 2005, Stansbury et al. 2014), effectively inflating the *p* of the 'often' captured class. For example, the coyote summer 2014 multi-occasion CAPWIRE estimate was significantly lower than those of multi-session estimators and had high precision (Fig. 5.3). The capture history contained two outlier individuals captured 19 and 25 times. Removal of these individuals increased the respective population estimate, decreased precision slightly, and resulted in overlap of the upper

confidence bound with the confidence intervals of multi-session estimators (results not shown).

Across estimators and species, we expected to observe an increase (or pulse) in $\widehat{N}$ in summer, relative to winter, resulting from annual reproduction. We failed to detect these reproductive pulses and this likely reflects the precision of estimates. Alternatively, capture probability of juveniles may be lower along linear features. If nightly foraging events by juveniles are shorter in distance than adults, juveniles may have lower probability of encountering survey transects. If foraging events are shorter in duration or less frequent, juveniles may be less likely to deposit scats along a transect, even if one is encountered. One limitation of scat sampling is the inability to determine the age of individuals, and we therefore were unable to assess the potential for such differences.

Modeling Variation in Density

We suspected kit fox and coyote densities would be influenced by habitat characteristics. Previous research suggested that coyotes selected shrubland habitats to maximize cover and prey, while kit foxes selected habitats that reduced predation risk (Nelson et al. 2007, Kozlowski et al. 2012). It has been hypothesized that increased coyote abundance at Dugway was facilitated by increased water availability and that this, in turn, has influenced kit fox populations negatively (Arjo et al. 2007). Indeed, coyotes have higher water demands than kit foxes (Golightly and Ohmart 1984) and at our study site coyotes were documented at water sources 231x more than kit foxes (Hall et al. 2013). Despite this, full-likelihood SECR models incorporating spatial covariates received little to no support and SECR models including distance to nearest water failed to converge. Both canids are territorial and therefore density may be relatively consistent across the study site.

Alternatively, the resolution of our covariates, scale of study, or sample sizes may have been inadequate to model inhomogeneous density surfaces. Nevertheless, abundance can be estimated reliably with a homogenous density model, even when true density is heterogeneous (Efford and Fewster 2013).

Our average kit fox density (0.02 kit foxes/km^2) matched the lowest density reported for kit foxes at Dugway (in 1997; Arjo et al. 2007) and was significantly lower than historical estimates, which were believed to exceed 0.3 kit foxes/km^2 (Egoscue 1962). Arjo et al. (2007) provide a detailed discussion of the potential drivers of declining kit fox densities, including habitat loss and degradation, increased water availability and associated coyote abundance and intraguild predation, and changing prey communities. Despite the interest in coyote–kit fox interactions at Dugway (and elsewhere), coyote density estimates at have not been reported for the site. Knowlton et al. (1999) reported coyote densities ranging from 0.2–2.3 coyotes/km^2 across their range, but lower densities (0.14 coyotes/km^2) have been reported where coyotes compete with kit foxes (Ralls and White 1995). Our density estimates are lower still (<0.1 coyotes/km^2), and may reflect limited resources at the site.

Management Implications

Population abundance estimates are often required to inform management strategies, but managers may be uncertain as to which estimator to employ or how choice of estimator influences results. Carnivores are notoriously difficult to monitor (Gese 2001, Dempsey et al. 2014) and this is a primary challenge for managers investigating carnivore population trends. Employing NGS can alleviate some of these challenges (Kohn et al. 1999, Petit and Valiere 2006, Mondol et al. 2009, Kéry et al. 2010) and may facilitate concurrent monitoring of multiple species at broader scales (Long et al. 2007, Williams et al. 2009, Jones 2011).

Capture with replacement models developed to compliment NGS may further reduce costs by allowing managers to monitor populations with a single sampling event (Miller et al. 2005). Using fecal DNA sampling to compare multiple population abundance estimators for two sympatric carnivore populations, we demonstrated that choice of estimator and sampling design significantly influenced resulting estimates, and that the relationship between estimators varied between species. Notably, when a single-occasion sampling strategy was employed, CAPWIRE models performed poorly and estimates were biased low with artificially high precision. Previous applications of the CAPWIRE model have focused on monitoring populations by sampling animal concentration points and have indicated that CAPWIRE provided reliable results; our sampling was dispersed in nature, and this different sampling strategy likely failed to capture a sufficient portion of the population with only a single sampling event. We obtained relatively consistent abundance estimates from both spatial and non-spatial multi-session models for kit foxes. Kit foxes are a species of conservation concern and our density estimates (corresponding with the highest mean abundance estimate among estimators) suggested that kit fox populations may be at their lowest documented level at our study site. Our results suggest that fecal DNA sampling can be used to effectively monitor both kit fox and coyote populations, but that care should be taken when selecting the appropriate estimator and sampling design. We were unable to detect an increase in population size following reproduction for either species. This, combined with the fact that scat deposition and DNA degradation are both lower in winter (Lonsinger et al. 2015a), suggest that if monitoring occurs only once annually, that winter would be the ideal season (i.e., fewer samples collected and higher laboratory success = reduced costs).

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Tables

Table 5.1. Survey effort for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) fecal DNA sampling used to estimate population abundance of each species in western Utah, USA, over two winter (W) and two summer (S) sessions. Multi-occasion transects were 5 km in length. Single-occasion transects each totaled 2 km in length (four 500 m transects).

	Multi-occasion transects (30)		Single-occasion transects (60)		All transects
Session	Occasions	Total (km)[a]	Occasion	Total (km)	Total (km)
W 2013	4	600	1	120	720
S 2013	3	450	1	120	570
W 2014	5	750	1	120	870
S 2014	4	600	1	120	720

[a]Summer 2014 totals reflect effort for kit fox; coyote samples were not collected on the final sampling occasion of multi-occasion transects (coyote multi-session effort = 450 km).

Table 5.2. Number of scats detected during fecal DNA surveys identified as kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), or non-target carnivore species based on mitochondrial DNA species identification. Minimum number known alive (MNKA) and proportion male (M) for each target species indicates the number of unique genotypes detected. Total MKNA is the number of unique individuals identified throughout the study. Non-target carnivores (NTC) included domestic dog, red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*). Mixed samples contained mitochondrial DNA from >1 species. Samples were collected in over two winter (W) and two summer (S) sessions in western Utah, USA, 2013–2014.

	Kit fox		Coyote		Other			
Session	Scats	MNKA (M)	Scats	MNKA (M)	NTC	Mixed	Failed	Total
W 2013	151	40 (0.68)	378	128 (0.54)	9	3	61	602
S 2013	175	36 (0.56)	626	128 (0.47)	37	10	230	1,078
W 2014	301	50 (0.58)	645	141 (0.51)	23	16	28	1,013
S 2014	183	38 (0.47)	725	151 (0.52)	23	15	113	1,059
Total	810	109 (0.60)	2,374	302 (0.53)	92	44	432	3,752

Table 5.3. Model-averaged estimates of capture probability (*p*) and unconditional standard error (SE) produced by program MARK by sex for kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) surveyed with noninvasive genetic fecal sampling over two winter (W) and two summer (S) sessions in western Utah, USA, 2013–2014. Behavioral response was not expected with noninvasive sampling and thus recapture probability (*c)* was modeled as $p = c$.

		Kit fox				Coyote			
		Male		Female		Male		Female	
Session[a]	Occasion[b]	*p*	SE	*p*	SE	*p*	SE	*p*	SE
W 2013									
	1	0.207	0.068	0.207	0.069	0.321	0.055	0.332	0.054
	2	0.236	0.064	0.236	0.065	0.271	0.046	0.281	0.049
	3	0.414	0.074	0.414	0.075	0.277	0.045	0.288	0.049
	4	0.536	0.093	0.536	0.094	0.330	0.055	0.340	0.054
S 2013									
	1	0.432	0.094	0.431	0.095	0.426	0.056	0.411	0.055
	2	0.369	0.072	0.368	0.074	0.400	0.058	0.386	0.068
	3	0.322	0.081	0.321	0.083	0.269	0.044	0.258	0.049
W 2014									
	1	0.489	0.074	0.489	0.074	0.541	0.045	0.543	0.045
	2	0.413	0.057	0.413	0.057	0.455	0.040	0.457	0.040
	3	0.373	0.084	0.373	0.084	0.378	0.041	0.380	0.040
	4	0.259	0.048	0.259	0.048	0.265	0.038	0.267	0.038
	5	0.186	0.053	0.186	0.053	0.221	0.034	0.223	0.034
S 2014									
	1	0.276	0.088	0.272	0.087	0.405	0.045	0.406	0.045
	2	0.368	0.099	0.363	0.097	0.432	0.040	0.433	0.040
	3	0.415	0.088	0.409	0.087	0.466	0.047	0.467	0.047
	4	0.408	0.096	0.403	0.095				

[a]Sessions represent primary sampling periods within a robust design.
[b]Occasions represent secondary sampling periods within a robust design.

Table 5.4. Ranking of multi-session spatially explicit capture models with parameters *g0* and σ (which jointly describe capture probability) fit for kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) in western Utah, USA, based on Akaike's Information Criterion with small sample size correction (AIC_c). Each model is ranked based on ΔAIC_c ($\Delta_i = AIC_{ci} - AIC_{cmin}$), where K = number of parameters, w_i = Akaike weight, and LL = log-likelihood. Across models, T = trend, t = time-varying, and session = primary sampling periods. Only models ranking among the top four for each species and the null model are presented.

		Kit fox					Coyote				
Model[a,b]		K	AIC_c	ΔAIC_c	w_i	LL	K	AIC_c	ΔAIC_c	w_i	LL
g0 ~ T*session	σ ~ T*session	20	3146.569	0	1	-1550.348	20	9468.274	68.924	0	-4713.339
g0 ~ t*session	σ ~ t*session	44	3169.765	23.196	0	-1524.244	44	9399.350	0	1	-4651.731
g0 ~ t+session	σ ~ t+session	20	3178.621	32.052	0	-1566.373	20	9502.588	103.238	0	-4730.496
g0 ~ T+session	σ ~ T+session	14	3215.218	68.649	0	-1592.200	14	9537.492	138.142	0	-4754.351
g0 ~ session	σ ~ session	12	3220.637	74.068	0	-1597.285	12	9592.022	192.672	0	-4783.719

[a]Density (*D*) was modeled as varying only by session.
[b]All models employed half-normal detection function.

Table 5.5. Estimates of density ($\widehat{D}$) and standard error (SE) for kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) over two winter (W) and two summer (S) sessions in western Utah, USA, 2013–2014. Estimates are based on spatially explicit capture-recapture models implemented with the R package 'secr'.

	Kit fox[a,c]		Coyote[b,c]	
Session	$\widehat{D}$	SE	$\widehat{D}$	SE
W 2013	0.018	0.003	0.072	0.007
S 2013	0.019	0.003	0.068	0.006
W 2014	0.022	0.003	0.065	0.006
S 2014	0.020	0.003	0.079	0.007

[a]Density ~ session, *g0* ~ T*session, σ ~ T*session (T = trend).
[b]Density ~ session, *g0* ~ t*session, σ ~ t*session (t = time-varying).
[c]Based on half-normal detection function where *g0* and σ jointly describe capture probability.

Table 5.6. Total survey effort, number of unique kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) captured, and proportion male (M) that were considered when employing capture with replacement models to estimate population abundances over two winter (W) and two summer (S) sessions in western Utah, USA, based on single-occasion (Single) and multi-occasion (Multi) sampling schemes.

			Number of individual detected (M)			
	Total Effort (km)[a]		Kit fox		Coyote	
Session	Single	Multi	Single	Multi	Single	Multi
W 2013	206	464	25 (0.68)	37 (0.68)	72 (0.50)	116 (0.55)
S 2013	206	378	21 (0.57)	31 (0.52)	87 (0.47)	115 (0.47)
W 2014	206	550	30 (0.53)	45 (0.64)	101 (0.53)	117 (0.53)
S 2014	206	464	21 (0.52)	35 (0.49)	103 (0.57)	131 (0.54)

[a]Summer 2014 multi-occasion effort reflects effort for kit fox; coyote samples were not collected on the final sampling occasion of multi-occasion transects (coyote effort = 378 km).

Figures

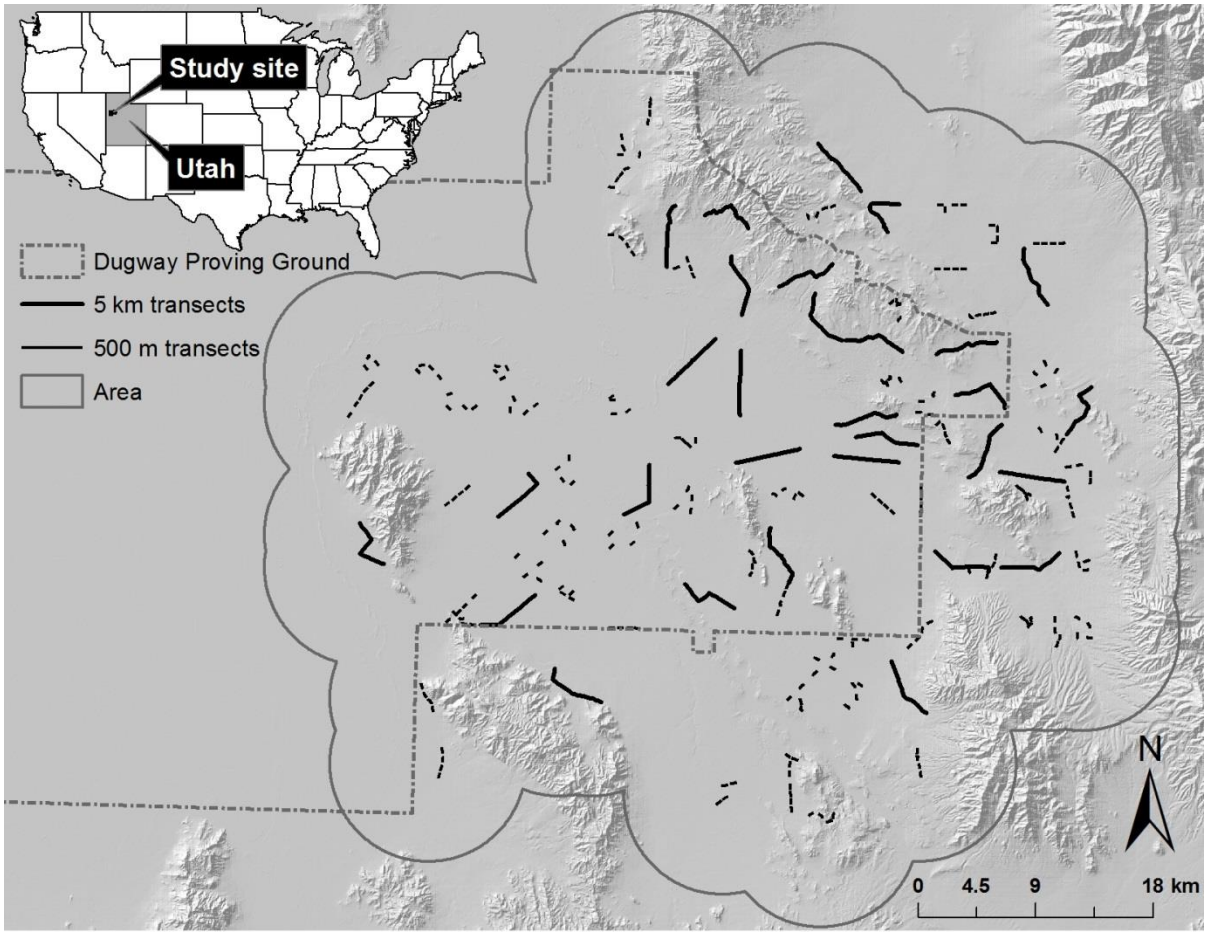

Figure 5.1. Location of 5 km multi-occasion and 500 m single-occasion transects surveyed for kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) scats in the Great Basin desert, Utah, 2013–2014. Area boundary represents the effective sampling area used in spatially explicit capture-recapture models.

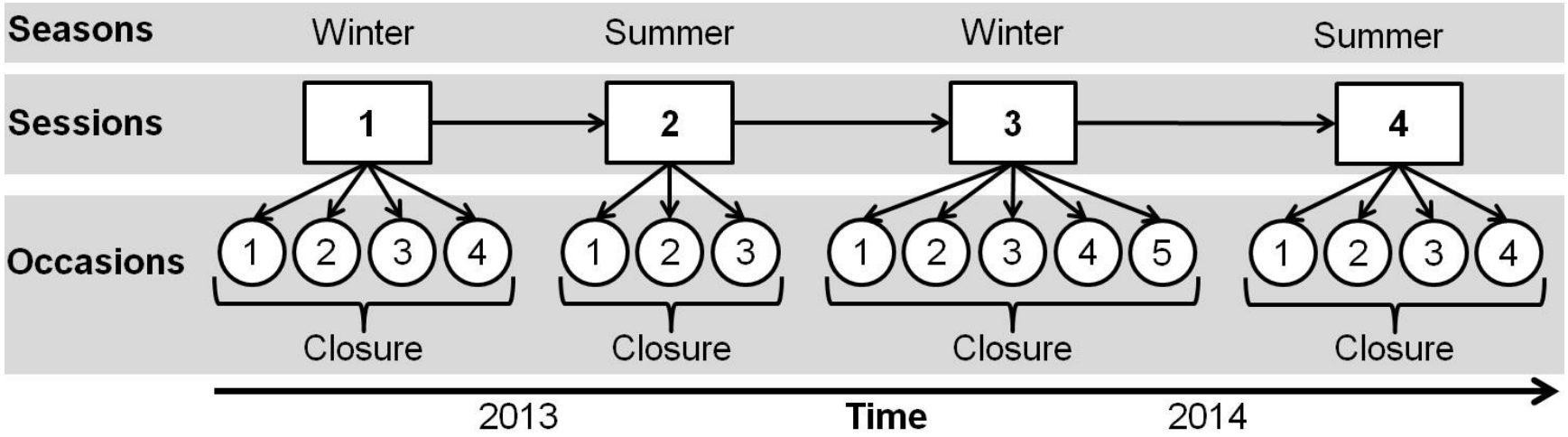

Figure 5.2. Graphical representation of the temporal sampling scheme (robust design) employed along multi-occasion transects for kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) in the Great Basin desert, Utah, 2013–2014. Populations were assumed to be geographically and demographically closed within sessions, and open between sessions.

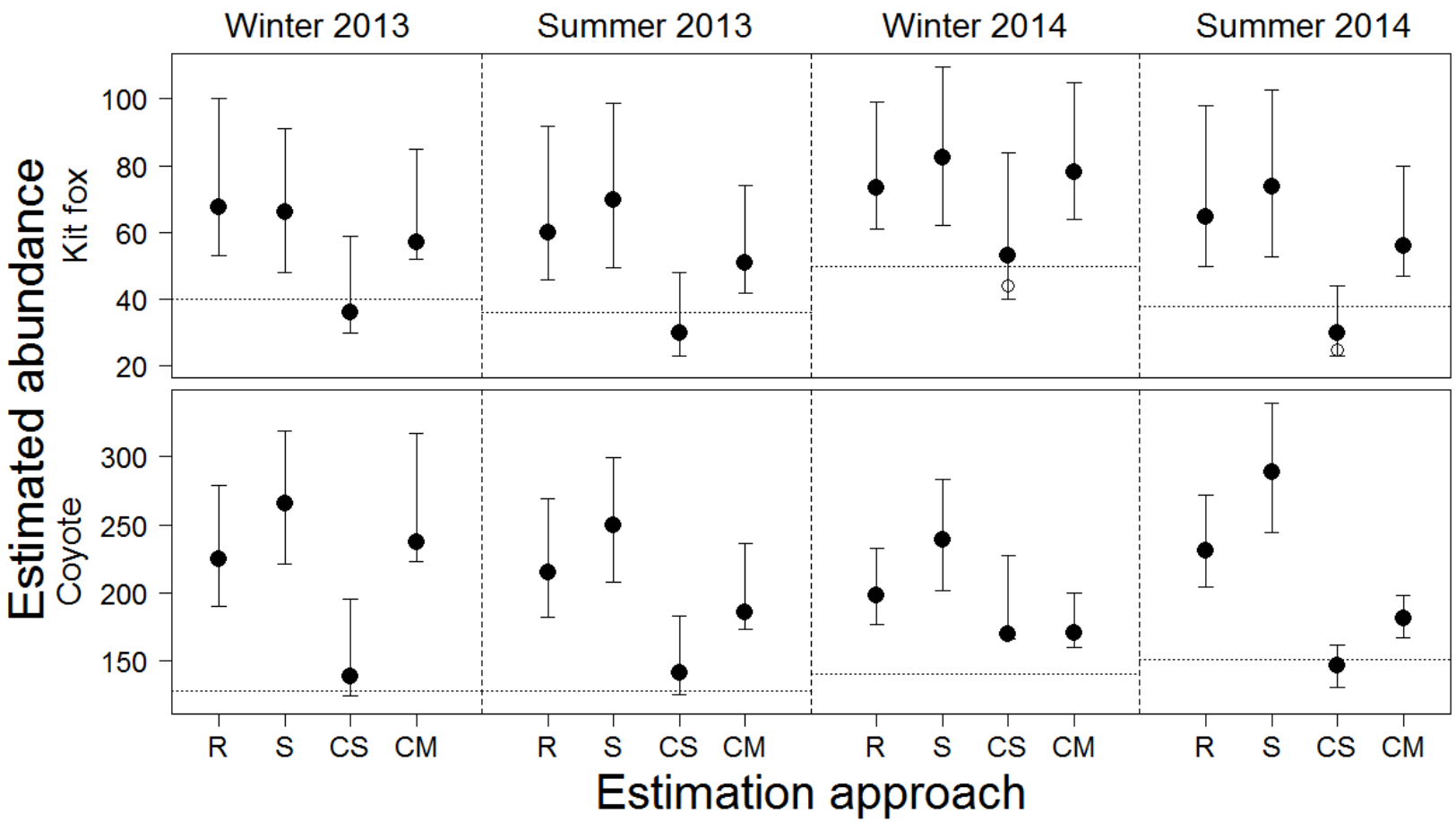

Figure 5.3. Estimated abundances and 95% confidence intervals for kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) in western Utah over four sessions, 2013–2014. Multiple estimators were used including robust design non-spatial Huggins closed-capture models (R), multi-session spatially explicit capture-recapture models (S), and two formulations of two-innate rates capture with replacement models based on single-occasion (CS) and multi-occasion (CM) sampling. Open circles represent capture with replacement point estimates under an equal capture model, where likelihood ratio tests failed to reject equal capture. The dashed horizontal line indicates the number of unique individuals identified within each session based on nuclear DNA.

Chapter 6: The Role of Interspecific Competition and Predation on the Spatial Dynamics of Sympatric Carnivores

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Abstract

Intraguild predation (IGP) by a dominant predator can drive the spatial dynamics of a subordinate predator and may explain space use that deviates from predictions of the resource availability hypothesis. Mesopredators experiencing IGP are often suppressed, but spatial resource partitioning frequently facilitates coexistence, with the subordinate carnivore

relegated to suboptimal habitats. In desert ecosystems, free-standing water was historically a scarce resource, limiting the distribution of large-bodied predators and offering large areas of refugia for smaller, arid adapted species, such as the kit fox (*Vulpes macrotis*). In the Great Basin desert, increased anthropogenic water sources have allowed larger carnivores (e.g., coyotes [*Canis latrans*]) to increase in distribution and abundance, perhaps to the detriment of kit foxes. We coupled noninvasive genetic sampling and dynamic occupancy models to evaluate the spatial dynamics of kit foxes and their intraguild predators, coyotes, in western Utah, USA. We employed a multi-stage approach to evaluate the influence of habitat characteristics on coyote occupancy patterns, and then investigated the role of habitat and coyotes on kit fox space use at multiple scales. Coyote occupancy was unrelated to water availability, but was positively related to the proportion of shrubland and woodland habitat. Kit fox occupancy displayed an inverse relationship, being negatively related to shrubland and woodland habitat. Kit fox probability of local extinction was positively related to unit-level coyote activity, and within an occupied unit, the probability of kit fox detection was positively related to survey-level coyote activity (i.e., kit fox detection was higher on spatially replicated surveys with more coyote sign). Our results support IGP theory predictions that at broad scales kit foxes distributed themselves to minimize overlap with coyotes, but suggested that at finer scales kit foxes may still adhere to expectations of the resource availability hypothesis. These results elucidated the importance of considering scale when investigating interspecific interactions.

Introduction

The resource availability hypothesis predicts that species will utilize areas that maximize availability of limiting resources (Ernest et al. 2000, Blaum et al. 2007).

Interspecific interactions can influence space use and may explain distributions that deviate from expectations (Heithaus 2001, Thompson and Gese 2007, Vanak et al. 2013). Intraguild predation (IGP) characterizes interactions between a dominant (IG predator) and subordinate (IG prey) predator, in which both species compete for shared resources, but the IG predator also preys upon the IG prey (Polis et al. 1989, Holt and Polis 1997, Verdy and Amarasekare 2010). In many cases, IGP may be an extreme form of interference competition: interspecific competitive killing (Palomares and Caro 1999, Lourenço et al. 2013). Motivations for IGP are not always clear and likely depend on environmental conditions (Ralls and White 1995), but common drivers among mammalian carnivores include energy acquisition (active or opportunistic), reducing competition, and territorial aggression (Lourenço et al. 2013).

The related mesopredator release hypothesis posits that removal of an IG predator frees IG prey from pressures imposed by the IG predator, allowing the IG prey to increase in abundance and/or distribution (Soulé et al. 1988, Prugh et al. 2009). Many recent conservation efforts have focused on restoring large predators, and their cascading effects have received considerable attention (Estes et al. 2011, Ritchie et al. 2012); mesopredator suppression is often a motivation or welcomed ecological response to apex predator restoration (Ritchie and Johnson 2009). Conversely, large predators may be unwelcomed additions to communities historically void of such predators (Courchamp et al. 2003), or where mesocarnivores naturally filled apex predator roles (Roemer et al. 2002). The introduction or expansion of dominant predators into such systems can force mesopredators into the role of IG prey, potentially threatening population persistence (e.g., Roemer et al. 2002).

Arid environments may naturally exclude large mammalian predators with high water demands. Deserts experience low precipitation, high temperatures, and potentially high evapotranspiration rates, limiting productivity (Ayal 2007) and natural surface water (Krausman et al. 2006). To increase habitat quality for wildlife, and extend grazing opportunities for livestock, artificial water sources have been commonly developed in desert systems (Krausman et al. 2006, Atwood et al. 2011). The addition of water sources to arid environments may benefit some species, but may also alter the structure of carnivore communities and increase the frequency or magnitude of negative interspecific interactions (Arjo et al. 2007, Atwood et al. 2011, Brawata and Neeman 2011, Hall et al. 2013).

In the Great Basin desert of western Utah, USA, free-standing water was historically scarce (Kamler et al. 2003, Arjo et al. 2007), offering a refuge for arid adapted carnivores. The kit fox (*Vulpes macrotis*) is among the smallest canids in North America and was historically the numerically dominant mammalian predator in the desert of western Utah (Egoscue 1956, Arjo et al. 2007). Physiological and behavioral adaptions (e.g., low use of evaporative cooling, small body size, year-round den use, and nocturnal activities) allowed kit foxes to exploit arid environments in the absence of perennial surface water (Egoscue 1962, Golightly and Ohmart 1983, 1984). Over the past 50–100 years, anthropogenic water sources associated with infrastructure, agriculture, and wildlife management have been developed in western Utah, and carnivores previously excluded from these arid environments have responded by expanding in distribution and abundance (Kamler et al. 2003, Arjo et al. 2007, Hall et al. 2013). Although historically absent or rare in western Utah, coyotes (*Canis latrans*) have increased in distribution and abundance (Arjo et al. 2007). Coyotes lack many of the adaptations that facilitated persistence in desert systems; they are large bodied, do not

use subterranean dens year-round, and rely on evaporative cooling (Golightly and Ohmart 1983, 1984). Consequently, it has been hypothesized that increasing coyote populations are, in part, due to increased water availability (Arjo et al. 2007, Kozlwowski et al. 2008, 2012).

Kit foxes populations have declined range-wide (Dempsey et al. 2015) and in western Utah, recent density estimates are the lowest reported in the region (Arjo et al. 2007, Chapter 5). The arrival of coyotes (an IG predator) relegated kit foxes to the role of IG prey and may limit kit fox abundance and distribution (Palomares and Caro 1999, Arjo et al. 2007, Kozlowski et al. 2008, 2012). We coupled noninvasive genetic sampling (Waits and Paetkau 2005) and dynamic occupancy modeling (MacKenzie et al. 2006) to evaluate the spatial dynamics of kit foxes and coyotes, in western Utah. Mammalian IGP is typically unidirectional (Verdy and Amarasekare 2010, Lourenço et al. 2013), so we first identified environmental covariates influencing coyote distribution and dynamics. Then, we used environmental covariates and spatial heterogeneity in coyote activity to evaluate the spatial dynamics of kit foxes.

We tested hypotheses related to the probability of occurrence (occupancy; ψ) and dynamic parameters (local extinction [ε] and colonization [γ]) for coyotes and kit foxes. We hypothesized that coyote occupancy and colonization would be positively related to water and proportion of shrubland and woodland cover (%SW), owing to their high water requirements (Golightly and Ohmart 1984, Hall et al. 2013) and the association of %SW to greater mammalian prey resources (Arjo et al. 2007, Kozlowski et al. 2008, 2012) and thermal refugia (Braum et al. 2007), respectively. We hypothesized the inverse relationship between these predictors and coyote local extinction. For kit foxes we tested hypotheses related to the influence of coyotes on kit foxes. Previous research investigating fox–coyote

interactions suggested foxes selected habitats to maximize safety (Thompson and Gese 2007, Kozlowski et al. 2012). We hypothesized that landscape features expected to be favored by coyotes (i.e., higher %SW and water availability) would negatively influence kit fox occupancy and colonization, as would higher unit-level coyote activity; we hypothesized these same predictors would be positively related to kit fox local extinction. Given the fossorial nature of kit foxes (Arjo et al. 2003), we hypothesized that soil type would be an important predictor of kit fox occupancy parameters. For both species, we suspected that road density may influence occupancy and/or dynamic parameters, but it was unclear *a priori* whether or not the relationships would be positive or negative. Finally, given a unit was occupied by both coyotes and kit foxes, we hypothesized that kit foxes would respond behaviorally by using areas with lower coyote activity (i.e., safety-matching; Heithaus 2001, Thompson and Gese 2007) and that this would be demonstrated by decreased probability of detection (*p*) for kit foxes along surveys with higher indices of coyote activity.

Methods

Study Area

The study area encompassed ~3,015 km^2 of Great Basin desert in western Utah and included the U.S. Army Dugway Proving Ground (Dugway) and surrounding federal lands (Fig. 6.1). Land cover was characterized by cold desert playa (primarily pickleweed [*Allenrolfea occidentalis*]), cold desert chenopod shrubland (*Atriplex confertifolia* and *Kochia americana* dominated), and vegetated and unvegetated dunes at low elevations. Sagebrush (*Artemisia* spp.) shrubland and open woodland (dominated by juniper [*Juniperus osteosperma*]) were found at higher elevations, while greasewood (*Sarcobatus vermiculatus*) shrubland was distributed across elevations. Invasive grasslands (primarily cheatgrass

[*Bromus tectorum*]) were common in areas disturbed by wildfires or military activities, but were most common at lower elevations. During our study, winters were cold (January–February mean high = 2.6 °C) and summers hot (July–August mean high = 34.9 °C); mean annual precipitation was 17.4 cm. Elevation ranged from ~1200 m in the basin to >2100 m in the mountains. Historically, perennial water sources were restricted to natural springs located primarily in the mountains (Arjo et al. 2007). Anthropogenic water developments increased since 1970 and water is now widespread (Fig. 6.1; Arjo et al. 2007, Hall et al. 2013).

Field Surveys and Species Identification

We referred to each sampling season, over which occupancy was assumed to be constant, as a 'session', each randomly selected patch as a 'unit', and each spatial replicate (i.e., transect) within a unit as a 'survey'. We identified a desired unit size of 6.25 km^2 (2.5 x 2.5 km), an area similar to the average home ranges reported for both kit foxes (2.5–11.6 km^2; Cypher and List 2003) and coyotes (5.5–6.9 km^2; Gese et al. 1988, Nelson et al. 2007). We conducted four surveys across 103 units per session (Appendix 6.1). To maximize spatial coverage and minimize field costs, we used spatial replication by establishing four 500 m transects (spatial replicates) within each randomly selected unit. Although sampling spatial replicates without replacement can bias parameter estimates (Kendall and White 2009), sampling with replacement may be impractical for noninvasive genetic sampling when all surveys are conducted within a single visit and searcher efficiency is high (i.e., all or most of the scats present are detected). Alternatively, sampling spatial replicates without replacement does not bias results if occupancy is constant for each transect (Guillera-Arroita 2011) or the target species is highly mobile (Kendall and White 2009, Harris et al. 2014). Using ArcGIS 10 (ESRI, Redlands, CA, USA), we divided the study site into 576 units (each 6.25km^2).

Thirty 5 km transects had already been randomly selected across the study site to monitor kit fox and coyote abundances as part of a concurrent study (Chapter 5) and therefore 43 units already contained ≥2 km of transects, from which we identified four 500 m segments in each unit to constitute spatial replicates. We then randomly selected 60 additional units and identified four 500 m transects within each. All transects followed dirt or gravel roads.

We conducted carnivore scat surveys during two winter (14 January to 6 March 2013; 13 January to 19 March 2014) and two summer (12 July to 16 August 2013; 10 July to 21 August 2014) sessions. Each unit was visited once per session during which each transect was surveyed by two researchers for carnivore scats. We collected ~0.7 mL of fecal material from detected scats (Stenglein et al. 2010) and samples were preserved in 1.4 mL of DETS buffer (Seutin et al. 1991).

We performed DNA extraction and polymerase-chain reaction amplification in a laboratory dedicated to low-quality samples to minimize contamination risk. We determined species identification using mitochondrial DNA fragment analysis (mtDNA; De Barba et al. 2014) following methods detailed in Lonsinger et al. (2015a). Samples that failed to amplify, were mixed (i.e., amplified DNA for >1 species), or were identified as a non-target species were excluded from subsequent analyses.

Model Covariates

Covariates used to model variation in occupancy parameters were obtained from available GIS layers. We processed all GIS layers with ArcGIS 10. We expected soil to influence only kit foxes, as they utilize burrows year-round (Arjo et al. 2003, Kozlowski et al. 2008); soil layers were obtained from the Utah Automated Geographic Reference Center (http://gis.utah.gov/), and we reclassified soil types into four categories (silt, fine sand,

blocky loam, and gravel; sensu Dempsey et al. 2015). Data on prey densities and diversity were not available across units, but land cover influences prey abundance and diversity. Shrubland and woodland habitats (i.e., shrub-steppe, greasewood, vegetated dunes, and open juniper woodland) at Dugway supported higher prey diversity and abundance than grasslands, and chenopod, pickleweed, and urban habitats supported the lowest prey resources (Arjo et al. 2007, Kozlowski et al. 2008, 2012). We utilized 2012 LANDFIRE (http://landfire.cr.usgs.gov/) vegetation layers to calculate the %SW in each unit, presumably representing relatively prey-rich habitats (Kozlowski et al. 2012) and greater thermal cover (Blaum et al. 2007). Water availability was predicted to influence canid space use (Arjo et al. 2007, Hall et al. 2013). Perennial water sources were identified by the Dugway Natural Resource Program GIS layers. We utilized Google Earth imagery to locate additional (unmapped) water sources by following livestock and horse trails to convergence points and ground-truthing points to confirm the presence of water. For each unit, we characterized water in three ways: (i) distance to nearest water, and the number of water sources within (ii) 2.5 km and (iii) 5 km from the unit center. Road density may influence the canid detection or occupancy. We obtained road layers from the Utah Automated Geographic Reference Center and calculated road density for each unit.

We collected additional covariates during field surveys. Road characteristics can influence scat persistence (Lonsinger et al. In press) and detection (Kluever et al. 2015). During each survey, we characterized the transect's road type as (i) an unmaintained two-track road, or a maintained (ii) single-lane or (iii) two-lane gravel road (sensu Lonsinger et al. In press). Detection of scats may be influenced by snow cover, survey date, and/or survey time (Harris et al. 2014); we recorded these covariates during each survey. Snow can reduce

detection by covering scats. Date may further influence detection, if canid activity changes throughout winter (e.g., during reproduction) or summer (e.g., increased juvenile activity). The time of surveys was used to characterize the angle of the sun, which may influence visibility and shadowing effects, and was standardized across seasons as time from solar noon. Finally, to evaluate the influence of coyotes on kit fox occupancy and dynamics, we characterized coyote activity at the unit and survey levels. At the unit level, we characterized coyote activity as (i) the total number of coyote scats detected, and (ii) the total number of transects on which coyotes were detected. At the survey (i.e., transect) level, we characterized coyote activity as (i) the number scats detected, and (ii) the detection or non-detection of coyotes.

Occupancy Modeling

We assumed kit fox occurrence did not influence coyote space use. We employed a multi-stage approach using program MARK (White and Burnham 1999). For each stage, we used Akaike's Information Criterion with small sample size correction (AIC_c) to compare the relative fit of models and cumulative Akaike weights to evaluate predictor importance (Burnham and Anderson 2002). First, we used dynamic single-species occupancy models (MacKenzie et al. 2003) to estimate coyote occupancy and identify environmental covariates that influenced detection, occupancy, local extinction, and colonization. We initially considered using dynamic co-occurrence models to evaluate the influence of coyotes on kit fox occupancy (Richmond et al. 2010). However, coyote occupancy was very high (*see Results*), effectively eliminating our ability to evaluate patterns of co-occurrence at the unit level (Richmond et al. 2010). Instead, we used dynamic single-species occupancy models for kit foxes that included both environmental covariates and indices of coyote activity,

exploiting the variation in coyote activity at the unit and survey (i.e., transect) levels to explore the influence of coyotes on kit fox spatial dynamics at multiple scales. Under this framework, we interpreted variation in kit fox *p* among spatial replicates of an occupied unit as reflecting differences in fine-scale space use (i.e., a behavioral response).

We evaluated correlations among covariates with a Kendall's rank correlation test. Only the three characterizations of water were correlated with one another ($r > |.48|$, $P < 0.001$) and we never included >1 water variable in a given model. Within each species, we used a structured modeling approach, first identifying the best global model and then sequentially fitting models for *p*, ψ, and the dynamic parameters (ε and γ, together). For coyotes, we considered global models for ψ, ε, and γ that contained %SW, road density, and water availability (and time variation for ε and γ), and global models for *p* containing road type, road density, presence of snow, date, sun (i.e., difference between survey time and solar noon), and variation among sessions. Road type (ordinal vs. categorical) and water availability (distance to nearest vs. sources within 2.5 or 5 km) both had >1 characterization. To identify the best global model, we first compared the fit of models containing all possible combinations of each of the water and road type characterizations. The most supported characterizations of each predictor were used in subsequent coyote analyses. In addition to predictors found in the coyote global models, for kit foxes we also included soil and unit-level coyote activity into the global model for ψ, soil and unit-level coyote activity in the preceding session for global models of ε and γ, and survey-level coyote activity in the global model for *p*. In addition to road type and water availability, coyote activity at both the unit (number of scats vs. number of transects) and survey (number of scats vs. detection/non-detection) levels had >1 characterization. To identify the best global model, we fit models

with all possible combinations for each characterization of road type, water, and unit- and survey-level indices of coyote activity. The most supported characterizations of each predictor were retained for subsequent kit fox analyses.

After identifying the best-fit global model for each species, we then fit all possible combinations of predictors for *p*, while maintaining the global models for ψ, ε, and γ, to identify the best detection model. Next, using the best-fit model for *p*, and the global models for ε and γ, we fit all possible combinations of predictors for ψ and identified the model with the lowest AIC_c. Finally, we used the best-fit models for *p* and ψ and simultaneously evaluated models for the dynamic parameters, considering all possible combinations of predictors for ε and γ both within and across parameters. Coyote extinction and colonization were positively related to water, and to a lesser extent %SW (*see Results*). Mean water availability and %SW were higher for units off of Dugway than on (*see Results*), and we suspected these patterns may have reflected greater pressure on coyotes on public lands where access and harvest were unrestricted. To explore this further, we conducted a post-hoc comparison between the best-fit model for coyote occupancy and dynamics to models containing a binary predictor for ψ, ε, and γ, indicating if units were on or off Dugway.

Results

Field Sampling and Species Identification

Sampling effort was constant across sessions, with 103 units each being surveyed via four 500 m transects per session, resulting in 824 km of surveys (206 km/session). We collected 1,702 fecal samples, of which 64% were coyote and 18% were kit fox. We also detected domestic dog (<1%), red fox (*V. vulpes*; 1%), bobcat (*Lynx rufus*; 2%), and cougar (*Puma concolor*; <1%), and 15% of samples failed or were mixed (Table 6.1). Across

sessions, naïve estimates of coyote occupancy were >0.7 in all but the first session and kit fox occupancy was ≤0.3 (Fig. 6.1, Table 6.1).

Unit and Survey Characteristics

Among 103 units, 63 were on Dugway and 40 were located on neighboring lands (Fig. 6.1). Soil for the majority of units was predominantly silt (46) or fine sand (36), with fewer units being primarily blocky loam (12) or gravel (9). Mean %SW for units was 21.8% (± 2.25 SE), though the distribution was right skewed (median = 13.0%, range = 0–97%), and the mean was lower on Dugway (15.6% ± 1.91 SE) than off (31.6% ± 4.60 SE). Distance to nearest water ranged from 0.2–12.4 km (mean = 3.96 km ± 0.28 SE). The mean number of water sources within 2.5 and 5 km was 0.54 (± 0.08 SE) and 1.95 (± 0.02 SE), respectively; 64 units had no water within 2.5 km (median = 0, range = 0–5) and 28 had no water within 5 km (median = 2, range = 0–7). Water was more scarce on Dugway (means: distance to water = 4.72 ± 0.39 SE, water within 2.5 km = 0.49 ± 0.11 SE, water within 5 km = 1.68 ± 0.22 SE) than off Dugway (means: distance to water = 2.76 ± 0.28 SE, water within 2.5 km = 0.63 ± 0.12 SE, water within 5 km = 2.38 ± 0.25 SE). Mean road density across units was 1.17 km/km^2 (± 0.05 SE). Over half (55%) of 500 m transects were along unmaintained two-track roads, and 31% and 14% were along single-lane and two-lane gravel roads, respectively. Snow was present during surveys at 92% (95) and 49% (50) of the units in winter 2013 and 2014, respectively.

Coyote Dynamic Occupancy Modeling

The best-fit global coyote model included water characterized as the number of sources within 2.5 km and an ordinal relationship between road types (Appendix 6.2), and these formulations for each covariate carried the highest cumulative weights (Table 6.2). The

best-fit detection model suggested *p* was negatively influenced by road type (β = –0.49 ± 0.09 SE), road density (β = –0.31 ± 0.12 SE), snow (β = –0.54 ± 0.14 SE), and the angle of the sun (β = –0.06 ± 0.03 SE; Appendix 6.2). Road type and road density had the greatest cumulative model weights (Table 6.2). Mean coyote *p* was lower in winters (2013 = 0.30 ± 0.02 SE, 2014 = 0.34 ± 0.02 SE) than summers (2013 = 0.41 ± 0.02 SE, 2014 = 0.41 ± 0.02 SE) at mean covariate values.

For coyote occupancy, the best-fit model indicated that initial ψ was high (Fig. 6.2). Water availability did not influence ψ, %SW had a strong influence on ψ (β = 25.13 ± 10.03 SE; Fig. 6.3), and road density influenced ψ to a lesser extent (β = 2.39 ± 0.96 SE; Table 6.2, Appendix 6.2); models including road density and/or water without %SW, received less support than the null model (Appendix 6.2). Among models jointly evaluating coyote ε and γ, the best-fit model included water and %SW covariates for both parameters, and time variation for γ (Appendix 6.2). Water availability was positively related to both ε (β = 1.78 ± 0.50 SE) and γ (β = 12.64 ± 10.42 SE). Similarly, %SW was positively related to ε (β = 3.31 ± 1.35 SE) and γ (β = 58.32 ± 42.43 SE). For γ, 95% confidence intervals (CIs) for the β estimates of both predictors overlapped zero. Among predictors, water and %SW had the greatest cumulative weights for ε and γ, respectively (Table 6.2). Based on the best-fit models, derived estimates of coyote ψ for sessions 2–4 remained high (Fig. 6.2). In contrast to predictions, ψ was more stable for units with lower water availability (Fig. 6.4A). Model fit was improved slightly when land management was included as a covariate on ε (AIC = 1931.00), yet the relationship was relatively flat (β = –1.77 ± 1.02 SE) and 95% CIs overlapped zero.

Kit Fox Dynamic Occupancy Modeling

The best-fit global kit fox model included water characterized as the distance to nearest water and an ordinal relationship between road types (Appendix 6.3); these formulations for each covariate carried the highest cumulative weights (Table 6.2). The influence of coyotes on kit foxes was best characterized as the total number of coyote scats detected (coyote activity) at both the unit and survey levels (Table 6.2, Appendix 6.3). The best-fit detection model suggested that kit fox *p* was positively related to survey-level coyote activity ($\beta = 0.20 \pm 0.06$ SE). Road type ($\beta = 0.23 \pm 0.15$ SE) was present in the best-fit kit fox *p* model, but had a negligible relationship with the β estimate's 95% CI overlapping zero. Mean kit fox *p* was similar across sessions (winter: 2013 = 0.24 ± 0.02 SE, 2014 = 0.25 ± 0.02 SE; summer: 2013 = 0.26 ± 0.02 SE, 2014 = 0.26 ± 0.02 SE).

Initial ψ was substantially lower for kit foxes than for coyotes (Fig. 6.2). The best-fit model indicated %SW had a strong negative ($\beta = -13.46 \pm 3.98$ SE) influence on kit fox ψ (Fig. 6.3). The cumulative weight for %SW was high and no other predictors carried substantial weight (Table 6.2; Appendix 6.3). Among models for kit fox dynamic parameters (Appendix 6.3), the best-fit model suggested that unit-level coyote activity positively influenced both ε ($\beta = 0.97 \pm 0.45$ SE) and γ ($\beta = 0.23 \pm 0.15$ SE), though the effect on γ was weak, with 95% CIs for β overlapping zero. Additionally, ε varied temporally and soil type influenced γ (Appendix 6.3). Coyote activity carried substantial model weight for ε (Table 6.2). For γ, soil had the greatest influence based on cumulative model weights, followed by coyote activity (Table 6.2). Derived estimates of kit fox ψ from the best-fit model were similar across sessions (Fig. 6.2). As predicted, ψ was more stable for units with less coyote activity (Fig. 6.4B).

Discussion

Predators are typically elusive, wide-ranging, and occur at low densities (Palomares and Caro 1999, Gompper et al. 2006). Mammalian IGP systems are notoriously challenging to investigate, as these attributes often apply to both the IG predator and IG prey. Indirect species sign (e.g., scat) is often conspicuous and noninvasive monitoring alleviates many of challenges of detecting carnivores and facilitates multispecies monitoring (Gompper et al. 2006). Imperfect detection of indirect sign can bias inferences regarding species occurrence (MacKenzie et al. 2002). Occupancy modeling explicitly addresses this concern and dynamic models improve our understanding of occupancy states by providing insights into the processes of local extinction and colonization driving observed patterns (MacKenzie et al. 2003, 2006).

Coupling noninvasive sampling with co-occurrence occupancy modeling offers an efficient framework to investigate IGP systems (e.g., Robinson et al. 2015). To our knowledge, our study is the first to employ noninvasive genetic sampling and dynamic occupancy models to explore an IGP system. In our system, coyote occupancy was high, and thus we were unable to employ a co-occurrence framework (i.e., if either the IG predator or IG prey are widely distributed [occupancy is ~1], insufficient heterogeneity will exist in occupancy to effectively evaluate competitive exclusion). Instead, we demonstrated how variation in coyote sign among and within units can be exploited to investigate the influence of IGP on spatial dynamics of kit foxes (IG prey) using a single-species dynamic modeling framework. Canid systems consisting of foxes and a larger IG predator (e.g., coyotes, jackals [*C. mesomelas*], dingos [*C. lupus dingo*]) have become model systems for exploring

mammalian IGP (Nelson et al. 2007, Thompson and Gese 2007, Brawata and Neeman 2011, Kozlowski et al. 2012, Robinson et al. 2015).

Patterns of Coyote and Kit Fox Detection

For canids, scat surveys tend to yield higher detection probabilities than alternative monitoring strategies (i.e., scent stations, spotlighting, and live-trapping; Dempsey et al. 2014). When using scats, misidentification of species, and particularly false-positives, can significantly bias occupancy parameter estimation (Royle and Link 2006, Rhodes et al. 2011). Kit fox scats are generally smaller than coyote scats, but field identification can be misleading and scats of non-target species (e.g., red fox) may be mistakenly identified as kit fox or coyote (Lonsinger et al. 2015b). To eliminate misidentification, we relied on genetic species identification.

An ordinal relationship between road types was supported during global model evaluations; this relationship aligns with results from experimental scat removal plots at our study site (Lonsinger et al. In press). As predicted, coyote detection was higher on smaller roads. Scats persisted longer on smaller roads (Lonsinger et al. In press), which typically were narrower and had finer substrates than larger roads, improving detection (Kluever et al. 2015). As predicted, coyote detections decreased when snow was present, when the sun approached the horizon, and as road density increased. Kit fox detection was associated with survey-level coyote activity, with detection being higher along transects where more coyote scats were detected.

Patterns of Coyote and Kit Fox Occurrence

Canids commonly employ spatial partitioning to facilitate coexistence, with IG predators conforming to predictions of the resource availability hypothesis (Ernest et al.

2000, Blaum et al. 2007), while IG prey occupy habitats that minimize risk of IGP, aligning with expectations of IGP theory and mesopredator suppression (Soulé et al. 1988, Heithaus 2001). Swift foxes (*V. velox*) selected habitat that minimized risk of IGP by coyotes, which occupied resource-rich habitats (Thompson and Gese 2007). Coyotes displaced endangered San Joaquin kit foxes (*V. m. mutica*) from prey-rich shrubland habitats to grasslands (Nelson et al. 2007). Robinson et al. (2015) suggested coyotes avoided areas where resources were too scarce, resulting in large-scale spatial partitioning with kit foxes. At Dugway, both coyote avoidance of resource-poor habitats and kit fox selection of habitats minimizing IGP risk may facilitate coexistence (Kozlowski et al. 2012). Our results met our expectations and aligned with these other works. Coyote occupancy declined precipitously when shrubland and woodland cover dropped below 20%, while kit fox occupancy displayed an inverse relationship (Fig. 6.3). Shrubland and woodland habitats at our study site tend to support greater mammalian prey abundance and diversity than alternative habitats (Arjo et al.2007, Kozloswki et al. 2012), and the vegetative structure provides greater thermal cover for large-bodied predators (Blaum et al. 2007). Low vegetation enhances kit fox visibility (Egoscue 1956) and may improve predator detection (Arjo et al. 2003, Dempsey et al. 2015).

In arid environments, increased water availability can reduce physiological stress, increase survival, and facilitate persistence of large-bodied predators (Brawata and Neeman 2011), increasing the potential for negative interactions with IG prey near water sources (Atwood et al. 2011). It has been suggested that increased water availability has facilitated the arrival and persistence of coyotes at Dugway (Arjo et al. 2007, Kozlowski et al. 2012). While investigating carnivore water use at Dugway, Hall et al. (2013) applied a buffer width of 2.6 km, based on expected daily movements of coyotes. Our coyote global models

supported a buffer of 2.5 km. Still, in contrast to our predictions, we were unable to detect a relationship between coyote occupancy and water, supporting conclusions of Hall et al. (2013) that despite frequent water use by coyotes, occupancy was not a function of water at the scale of inquiry. Coyotes have high movement capacities and at the scale of study, water may be sufficiently distributed to accommodate their needs. Kit foxes are capable of meeting their water demands through their prey (Golightly and Ohmart 1983). We expected then, that the primary influence of water on kit fox occupancy would be through an indirect effect of influencing coyote space use. We did not detect a relationship between kit fox occupancy and either water or unit-level coyote activity.

Patterns of Local Extinction and Colonization

Investigations of model canid IGP systems have focused primarily on static occupancy, but elucidating drivers of local extinction and colonization can improve our understanding of how covariates and species interactions drive space use (MacKenzie et al. 2003). Our results suggested that water did not influence coyote occupancy, but did influence local extinction and colonization (Fig. 6.4); to a lesser extent, local extinction and colonization were also related to %SW. These results conformed to our predictions for colonization, but were contradictory for predictions for extinction. Mean water availability and %SW were higher off Dugway, where public access and coyote harvest were unrestricted, and this may have affected the observed patterns. Post-hoc analyses considering land management did not yield convincing results, with the relationship between extinction and land management not differing substantially from zero. Dynamic parameters for coyotes should be viewed with prudence though, as dynamic patterns were inferred from relatively few units experiencing changes in occupancy.

Observed occupancy states result from preceding patterns of local extinction and colonization. As predicted, kit fox probability of local extinction was elevated across units that experienced higher coyote activity. Intraguild predation theory predicts local extinctions of IG prey may be regulated by an IG predator, and that IGP effects will be more acute when the two have high dietary overlap (Polis et al. 1989, Holt and Polis 1997). Dietary overlap of coyotes and kit foxes was high at Dugway (Kozlowski et al. 2008) and when sympatric, coyote predation accounts for a significant proportion of kit fox mortalities (56–78%; Ralls and White 1995, Nelson et al. 2007, Kozlowski et al. 2008). Consequently, local extinction may result from a decreased ability to avoid IGP pressures at units with higher coyote activity.

Kit foxes utilize burrows year-round to provide relief from environmental conditions and predators (Arjo et al. 2003). Thus, it was not surprising that silty soil, which facilitates burrow excavation (Egoscue 1956), promoted kit fox colonization. At Dugway, Egoscue (1962) indicated kit foxes utilized primarily silt and/or clay soils, and Dempsey et al. (2015) found a negative relationship between kit fox presence and blocky loam soil.

Patterns of Fine-Scale Kit Fox Space Use

Coexistence among intraguild predators often requires subordinate species to adjust their activity patterns or fine-scale space use; few empirical examples of such behavioral responses exist for mammalian IGP systems. Vanak et al. (2013) found that predators were aware of competitors at various spatial scales and subordinate species adjusted movement patterns in the presence of IG predators. Similarly, cape fox (*V. chama*) habitat selection did not differ in the presence of jackals at broad scales, but they had atypically large home ranges

in the presence of jackals, presumably to facilitate jackal avoidance during foraging (Kamler et al. 2013).

Recent research at our study site found that among survey methods, scat surveys produced results that most closely aligned with minimum known canid abundance (Dempsey et al. 2014). Thus, we assumed that the number of coyote scats detected along each spatial replicate was reflective of coyote activity. The diets and nightly activity patterns of kit foxes and coyotes overlap significantly at Dugway, and it has been suggested that broad scale habitat partitioning and safety matching facilitates coexistence (Arjo et al. 2007, Kozlowski et al. 2008, 2012). Hall et al. (2013) supported the lack of temporal separation between species, but failed to detect spatial partitioning. The scale of inference is essential to understanding patterns of co-occurrence and space use. At broad scales, our results align with those of Kozlowski et al. (2012): coyote occupancy increased with increasing shrubland and woodland cover, presumably reflecting resource matching, while kit foxes occupancy was inversely related to shrubland and woodland cover, reflecting patterns consistent with safety matching. At finer scales, our results are consistent with those of Hall et al. (2013) indicating a lack of spatial separation: kit foxes space use was highest where coyote activity was highest, suggesting that within their home ranges, kit foxes may use riskier habitats to secure sufficient resources (i.e., resource matching). Similar patterns were recently observed in New Mexico, where kit foxes exhibited broad scale spatial partitioning with coyotes, but were more likely to occupy sites with, than without, coyotes (Robinson et al. 2015). The nature of our sampling design (i.e., noninvasive with no temporal replication within sessions) precludes any inference on fine-scale temporal partitioning. Though nightly activity periods were similar for kit foxes and coyotes (Kozlowski et al. 2008), temporal partitioning may be

occurring at an intermediate temporal scale, with kit fox avoiding coyotes by using similar areas but doing so over different periods (e.g., over different nights).

Conclusions

Occupancy modeling approaches can be extended to test for evidence of competitive exclusion but recent advancements in co-occurrence modeling (Richmond et al. 2010) are limited to systems in which both the dominant and subordinate species have restricted patterns of occurrence (occupancy < 1). Here, we have demonstrated that when co-occurrence modeling was not practical, spatial replication can be used to explore fine-scale patterns of space use. Our study builds upon and benefits from a wealth of previous and concurrent investigations of the model fox–coyote IGP system at Dugway, and elsewhere. When our results are considered in light of these other studies, it suggests that coexistence was facilitated by kit foxes employing broad-scale safety matching and fine-scale resource matching. Intraguild predation theory predicts exclusion of the IG prey when shared resources are abundant and of the IG predator when resources are scarce (Holt and Polis 1997, Verdy and Amarasekare 2010). Stable co-existence may occur at intermediate resource levels, such as those observed at Dugway, with both the IG predator and IG prey occurring at densities lower than either would occur individually (Holt and Polis 1997, Verdy and Amarasekare 2010).

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Tables

Table 6.1. Number of carnivore scats identified as coyote (*Canis latrans*), kit fox (*Vulpes macrotis*), or non-target carnivore (NTC) species based on mitochondrial DNA (mtDNA) species identification, mtDNA amplification success rates, and naïve occupancy (ψ) for kit foxes and coyotes. Scat surveys were conducted within 103 units (each 6.25 km^2) over four sessions (winter 2013, summer 2013, winter 2014, and summer 2014) in Utah, USA. Non-target carnivores included domestic dog, red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*). Mixed samples contained DNA from >1 species.

	Number of carnivore scats						mtDNA success rate	Naïve ψ	
Session	Total	Coyote	Kit fox	NTC	Mixed	Failed		Coyote	Kit fox
1	218	136	60	3	2	17	92.2%	0.52	0.21
2	628	340	97	27	5	159	74.7%	0.72	0.28
3	363	247	87	7	5	17	95.3%	0.74	0.30
4	493	362	65	11	6	49	90.1%	0.73	0.23
Total	1,702	1,085	309	48	18	242	85.8%		

Table 6.2. Cumulative Akaike model weights (Σw_i) for predictors of coyote (*Canis latrans*) and kit fox (*Vulpes macrotis*) detection, occupancy, and probability of local extinction and colonization across 103 units in western Utah, USA, 2013–2014, from the complete model sets used to evaluate each parameter (see Appendix B–C for full model sets by parameter).

	Global		Detection		Occupancy		Extinction		Colonization	
Species	Pred	Σw_i	Pred	Σw_i	Pred	Σw_i	Pred	Σw_i	Pred	Σw_i
Coyote	W2	**0.97**	RTO	**0.99**	SW	**0.99**	W2	**0.99**	t	**0.63**
	DistW	0.02	RD	**0.90**	RD	**0.85**	SW	**0.60**	SW	**0.57**
	W5	0.01	Snow	**0.78**	W2	0.32	t	0.50	W2	**0.50**
	RTO	**0.75**	Sun	**0.66**			RD	0.47	RD	0.38
	RTC	0.25	Date	0.44						
			t	0.32						
Kit fox	DistW	**0.70**	CA	**0.97**	SW	**0.99**	CS	**0.95**	Soil	**0.80**
	W5	0.18	RTO	**0.77**	CS	0.37	t	**0.94**	CS	**0.56**
	W2	0.11	Date	0.32	RD	0.25	SW	0.32	DistW	0.40
	RTO	**0.83**	Snow	0.28	DistW	0.24	DistW	0.28	SW	0.40
	RTC	0.17	RD	0.26	Soil	0.16	RD	0.26	RD	0.30
	CS	**0.77**	Sun	0.25			Soil	0.16	t	0.26
	CT	0.23	t	0.18						
	CA	**0.78**								
	CP	0.22								

Bold indicates predictors present in the best-fit model. Global represents the evaluation of different formulations for water, road type, and unit and transect level coyote activity to identify a single global model for each species. Predictors: DistW = distance to nearest water source (km), W2 = number of water sources within 2.5 km of unit center, W5 = number of water sources within 5 km of unit center, RTO = ordinal road type coding, RTC = categorical road type coding, RD = road density (km/km2), Snow = presence or absence, Sun = difference between survey time and solar noon, Date = days since surveys were initiated within sampling session, SW = proportion of land cover attributable to shrubland and woodland habitats, Soil = categorical classification of the majority soil type for a unit (four types: silt, fine sand, blocky loam, or gravelly), CS = total number of coyote scats detected at the unit level, CT = total number of transects on which coyotes were detected at the unit level, CA = number of coyote scats detected at the transect level, CP = binary detection (1) or non-detection (0) of coyotes at the transect level, t = time-varying.

Figures

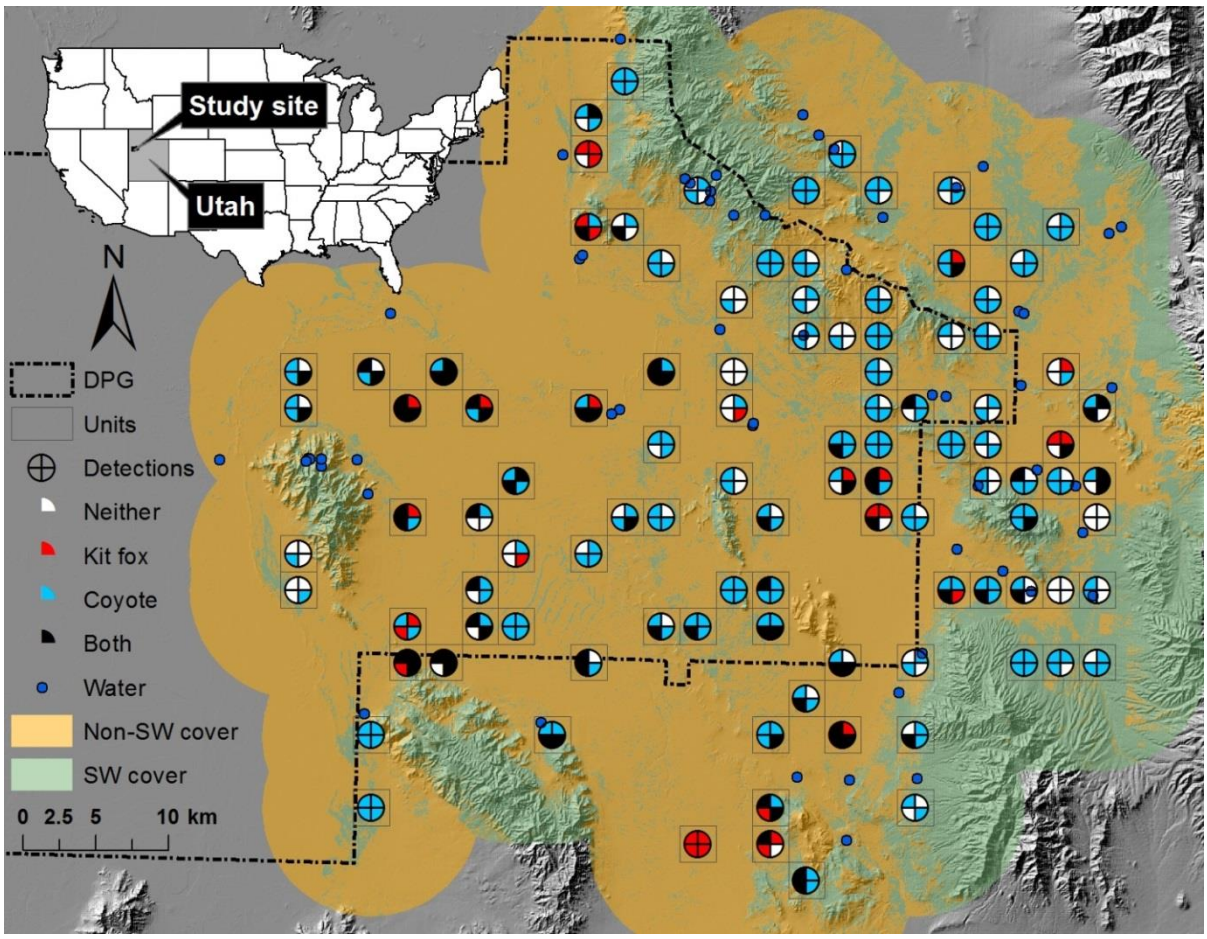

Figure 6.1. Location of 103 units (each 6.25 km^2) surveyed for coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) over four sessions in Utah, USA, 2013–2014. The pie charts indicate whether kit fox, coyote, both, or neither was detected during winter 2013 (upper right), summer 2013 (lower right), winter 2014 (lower left), and summer 2014 (upper left). Habitat classifications display the distribution of shrubland and woodland cover (SW) versus areas with lower (e.g., grasslands) or more sparse (e.g., playa) vegetative cover, within 7.5 km of units.

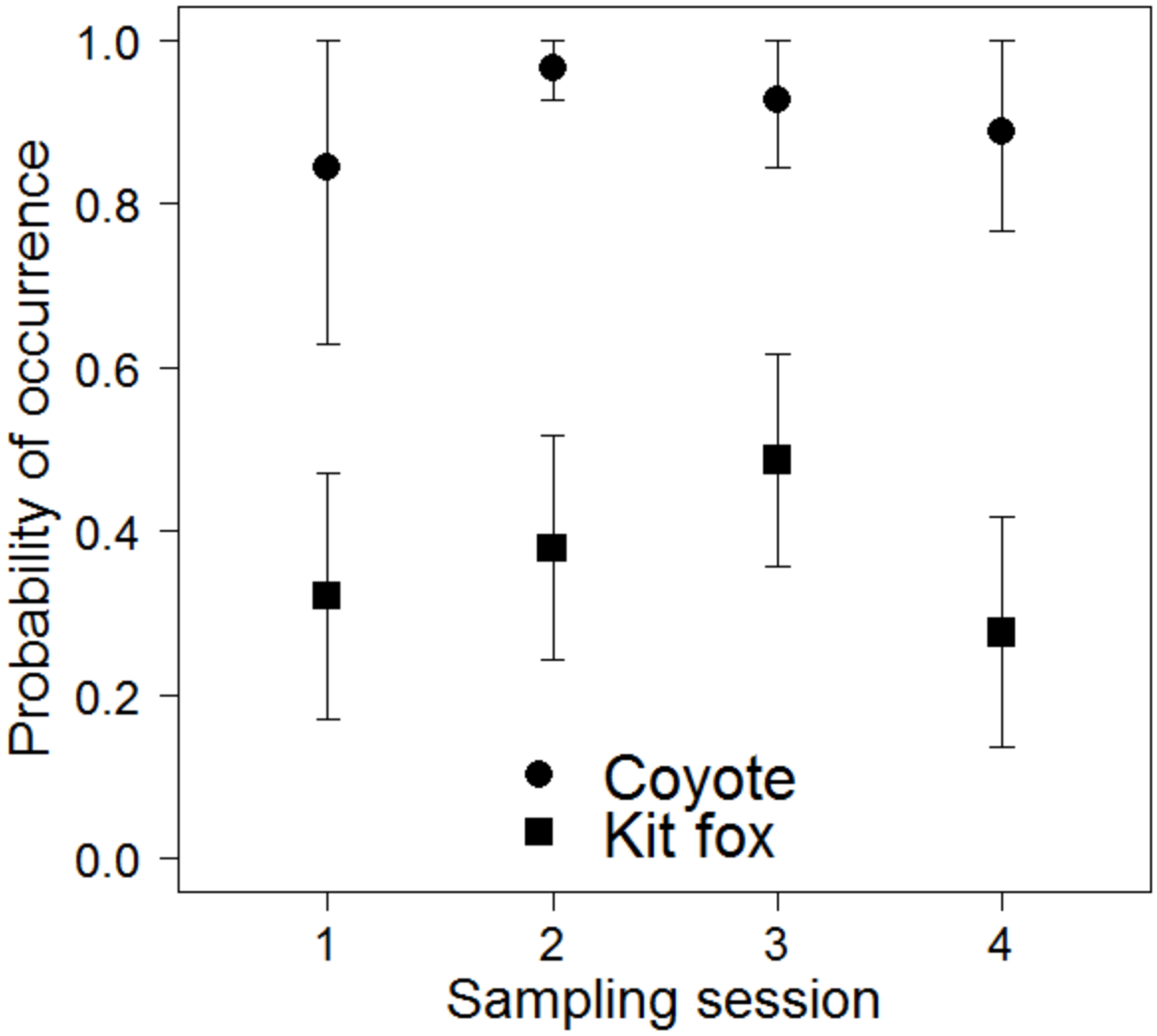

Figure 6.2. Initial (session 1) and derived (sessions 2–4) probabilities of occurrence with 95% confidence intervals for coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) over four sessions in Utah, USA, 2013–2014. Probability of occurrence is plotted based on the best-fit models for each species and the median proportion of shrubland and woodland cover (13.0%).

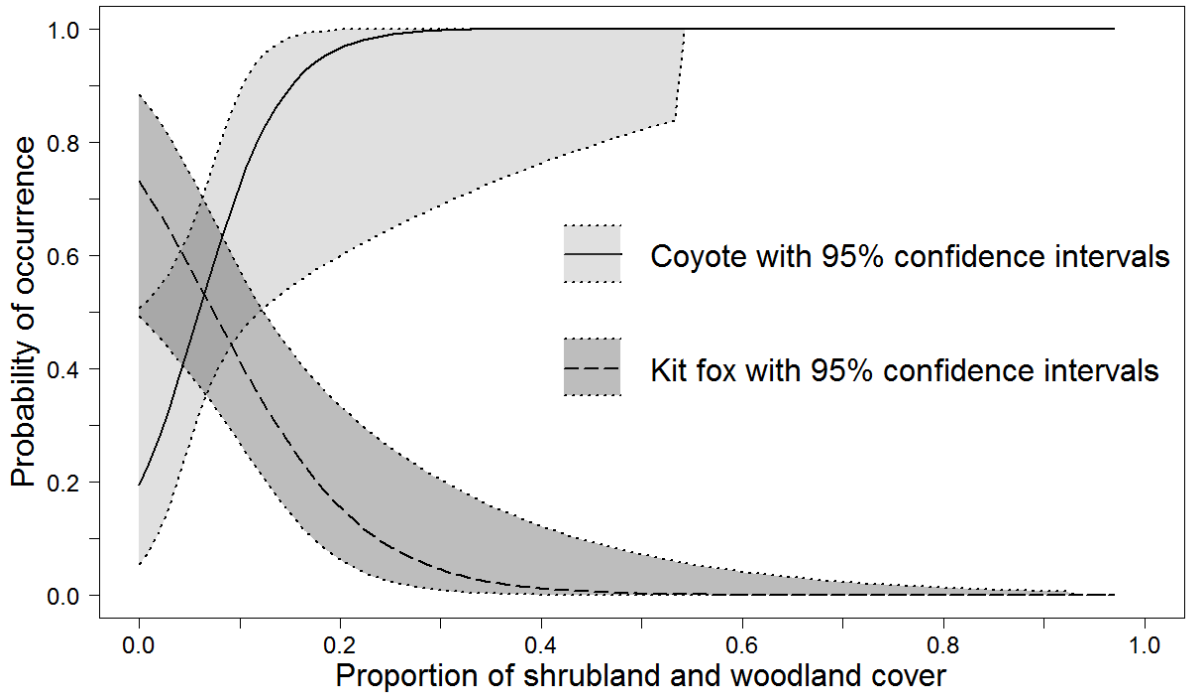

Figure 6.3. Initial probability of occurrence with 95% confidence intervals for coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) as a function of shrubland and woodland cover in Utah, USA, 2013–2014. Probability of occurrence is plotted based on the best-fit model for each species and mean covariate values.

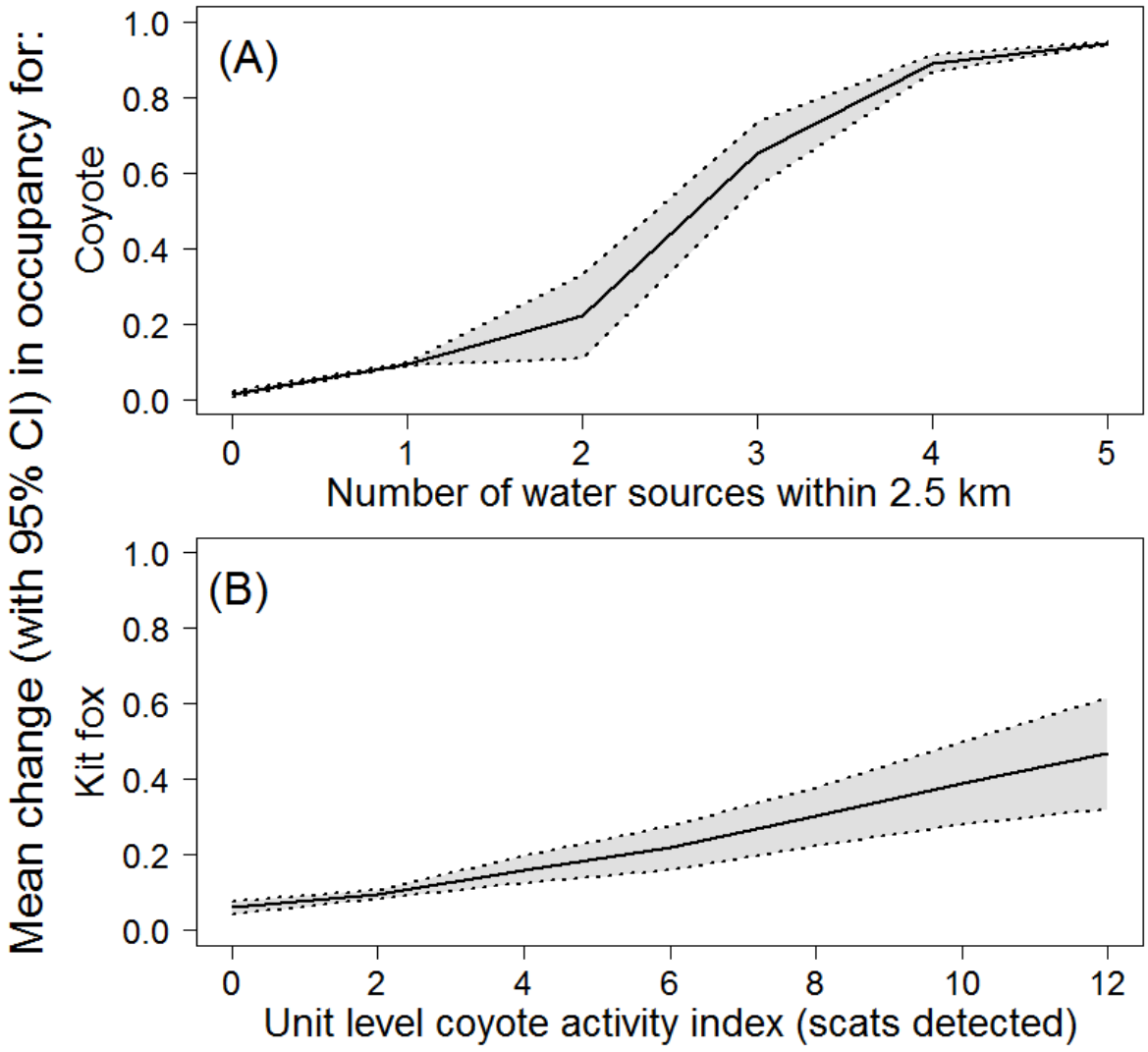

Figure 6.4. Mean change in probability of occurrence with 95% confidence intervals (CI) across sessions for (A) coyotes (*Canis latrans*) and (B) kit foxes (*Vulpes macrotis*) as a function of water availability and coyote activity, respectively, in Utah, USA, 2013–2014. Mean change in occupancy for each species is based on the best-fit models and mean covariate values.

Appendix 1.1

PCR Conditions, Including Primer Concentrations and Thermal Profiles, for Mitochondrial and Nuclear DNA Amplification.

We performed mitochondrial DNA (mtDNA) species identification tests by amplifying fragments of the control region (Onorato *et al.* 2006; De Barba *et al.* 2014). Qiagen Master Mix (1x concentration), Q solution (0.5x concentration) and 1 µl of DNA extract were combined with species identification primers into a 7µl (total volume) multiplex with the following PCR conditions for each primer: 0.29 µM SIDL, 0.20 µM H16145, 0.10 µM H3R, 0.13 µM FelidID F, 0.03 µM LRuf F and 0.03 µM PCon R. The PCR thermal profile had an initial denaturation of 95°C for 15 minutes, 35 cycles of 94°C for 30 seconds (denaturation), 46°C for 90 seconds and 72°C for 60 seconds (elongation), and a final elongation stage of 60°C for 30 minutes.

For individual identification, we amplified kit fox samples with a multiplex of seven nuclear DNA (nDNA) microsatellite loci (Ostrander *et al.* 1993; Fredholm and Wintero 1995; Fransicso *et al.* 1996). The PCR conditions for the 7 µl (total volume) multiplex for each primer pair were 0.14 µM CPH3, 0.27 µM CXX403, 0.14 µM CXX250, 0.08 µM FH2054, 0.17 µM CXX20, 0.07 µM CXX173 and 0.06 µM CXX377, combined with 1x concentrated Qiagen Master Mix, 0.5x concentrated Q solution and 1 µl of DNA extract. The PCR thermal profile had an initial denaturation of 95°C for 15 minutes, 20 touchdown cycles at 94°C for 30 seconds (denaturation), 55°C for 90 seconds (annealing; decreasing by 0.3°C per cycle) and 72°C for 60 seconds (elongation), 20 cycles at 94°C for 30 seconds (denaturation), 51°C for 90 seconds (annealing) and 72°C for 60 seconds (elongation), and a final elongation at 60°C for 30 minutes. Size ranges in base pairs (bp) for kit fox loci were as

follows: CPH3 (150–160 bp), CXX403 (269–281 bp), CXX250 (131–153 bp), FH2054 (167–191 bp), CXX20 (119–146 bp), CXX173 (123–129 bp), and CXX377 (173–193 bp). For coyote individual identification, we employed a multiplex with nine nDNA microsatellite loci (Ostrander *et al.* 1993; Holmes *et al.* 1994; Fransicso *et al.* 1996; Neff *et al.* 1999; Breen *et al.* 2001; Guyon *et al.* 2003). The PCR conditions for the 7µl (total volume) multiplex for each primer pair were 0.23 µM CXX119, 0.04 µM CXX173, 0.09 µM FH2001, 0.06 µM FH2054, 0.06 µM FH2088, 0.06 µM FH2137, 0.10 µM FH2611, 0.14 µM FH2670, and 0.09 µM FH3725, combined with 1x concentrated Qiagen Master Mix, 0.5x concentrated Q solution and 2 µl of DNA extract. The PCR thermal profile has an initial denaturation of 94°C for 15 minutes, 13 touchdown cycles at 94°C for 30 seconds (denaturation), 62°C for 90 seconds (annealing; decreasing by 0.4°C per cycle) and 72°C for 60 seconds (elongation), 33 cycles at 94°C for 30 seconds (denaturation), 57°C for 90 seconds (annealing) and 72°C for 60 seconds (elongation), and a final elongation at 60°C for 30 minutes. Size ranges for coyote loci were as follows: CXX119 (79–101 bp), CXX173 (96–114 bp), FH2001 (125–153 bp), FH2054 (142–171 bp), FH2088 (93–137 bp), FH2137 (161–205 bp), FH2611 (186–216 bp), FH2670 (150–226 bp), and FH3725 (116–184 bp). We conducted all PCR procedures on a BioRad Tetrad thermocycler (Bio-Rad, Hercules, CA, USA) with negative and positive controls included with each reaction.

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Appendix 3.1

Results of Carnivore Scat Surveys Along 15 Transects to Evaluate Relative Abundances for Kit Foxes (*Vulpes macrotis*) and Coyotes (*Canis latrans*) in Western Utah, USA, 2013–2014.

Table 3.A1. Results of carnivore scat surveys for kit fox and coyote scats in western Utah in summer 2013, including transect road types (RT; two-lane gravel [large; L], one-lane gravel [medium; M] and two-track [small; S]) and the number of scats detected for each species in the median, tire tracks or shoulder. Traffic indicates the mean daily traffic volume from the removal plot of the same road type that best reflected the traffic on a given transect (Tran).

			Kit Fox Scats by Position			Coyote Scats by Position		
Tran	RT	Traffic	Median	Track	Shoulder	Median	Track	Shoulder
1	M	6.69	0	0	2	1	2	14
2	S, M	1.00, 6.69	1	0	5	0	9	4
3	S	1.29	2	1	0	1	11	7
4	L	83.68	0	0	1	0	0	4
5	L	65.54	0	0	3	1	0	4
6	S	1.00	0	1	0	6	11	4
7	S	0.17	3	1	0	5	19	8
8	S	0.17	3	3	3	12	4	5
9	S	1.00	9	11	31	2	2	5
10	S, M	0.17, 0.74	2	5	6	1	1	2
11	S, M	1.29, 2.43	0	0	0	1	6	8
12	S, M	0.17, 2.43	0	0	1	6	3	6
13	S	0.00	1	0	1	10	19	14
14	S, M	0.17, 6.69	1	2	3	4	5	10
15	M, L	2.43, 83.68	0	0	1	3	1	4

Table 3.A2. Results of carnivore scat surveys for kit fox and coyote scats in western Utah in winter 2013, including transect road types (RT; two-lane gravel [large; L], one-lane gravel [medium; M] and two-track [small; S]) and the number of scats detected for each species in the median, tire tracks or shoulder. Traffic indicates the mean daily traffic volume from the removal plot of the same road type that best reflected the traffic on a given transect (Tran).

			Kit Fox Scats by Position			Coyote Scats by Position		
Tran	RT	Traffic	Median	Track	Shoulder	Median	Track	Shoulder
1	M	4.07	0	0	0	6	5	0
2	S, M	0.12, 4.17	0	0	0	2	0	2
3	S	0.48	1	6	4	1	1	3
4	L	43.57	0	0	0	0	0	0
5	L	33.57	0	0	0	0	0	0
6	S	0.12	0	1	0	0	0	1
7	S	0.19	0	3	2	4	10	7
8	S	0.19	0	0	0	6	7	4
9	S	0.12	9	12	14	2	2	3
10	S, M	0.19, 0.98	1	0	3	0	0	1
11	S, M	0.48, 1.69	0	2	1	1	19	1
12	S, M	0.19, 1.69	1	0	0	2	2	3
13	S	0.00	0	0	0	9	7	1
14	S, M	0.19, 4.07	0	1	5	0	1	2
15	M, L	1.69, 43.57	0	1	0	0	1	0

Appendix 3.2

Results of Randomization Tests for Corrected Relative Abundances of Kit Foxes (*Vulpes macrotis*) and Coyotes (*Canis latrans*) Along 15 Transects in Western Utah, USA, 2013–2014.

Table 3.A3. Kit fox mean (± SE), median, and range for corrected relative abundance (cRA) values based on 1000 randomizations and generated across 15 transects under the conditions observed in western Utah in summer 2013. Corrected relative abundance incorporated a persistence-rate correction factor estimated by scat removal experiments. Observed cRA (Obs cRA) indicates the cRA calculated under observed scat deposition patterns for kit foxes in summer 2013. Road types (RT) included unmaintained two-track roads (small; S), one-lane gravel roads (medium; M), and two-lane gravel roads (large; L).

		cRA from 1000 Randomized Datasets					
Transect	RT	Mean	SE	Median	Min	Max	Obs cRA
1	M	13.0	0.733	1.9	1.7	133.8	1.7
2	S, M	21.6	0.884	7.0	3.1	141.9	4.7
3	S	3.1	0.045	3.3	1.5	7.0	3.5
4	L	1073.8	81.168	210.4	132.7	12111.4	333.4
5	L	200.1	5.393	95.0	95.0	1014.4	95.0
6	S	1.0	0.024	0.5	0.5	2.3	2.3
7	S	3.8	0.045	3.7	1.9	8.9	3.7
8	S	8.5	0.068	8.0	4.3	15.8	9.8
9	S	50.5	0.170	50.0	34.7	71.0	45.7
10	S, M	36.8	0.686	31.4	8.6	130.5	34.5
11	S,M	-	-	-	-	-	-
12	S,M	2.3	0.170	0.8	0.5	24.0	0.5
13	S	2.0	0.036	1.1	1.0	5.1	1.1
14	S, L	9.0	0.049	8.7	5.0	14.5	11.9
15	M, L	463.7	45.258	24.0	0.8	6014.1	210.4

Table 3.A4. Kit fox mean (± SE), median, and range for corrected relative abundance (cRA) values based on 1000 randomizations and generated across 15 transects under the conditions observed in western Utah in winter 2014. Corrected relative abundance incorporated a persistence-rate correction factor estimated by scat removal experiments. Observed cRA (Obs cRA) indicates the cRA calculated under observed scat deposition patterns for kit foxes in winter 2014. Road types (RT) included unmaintained two-track roads (small; S), one-lane gravel roads (medium; M), and two-lane gravel roads (large; L).

		cRA from 1000 Randomized Datasets					
Transect	RT	Mean	SE	Median	Min	Max	Obs cRA
1	M	-	-	-	-	-	-
2	S, M	-	-	-	-	-	-
3	S	10.3	0.069	10.6	4.1	16.3	12.0
4	L	-	-	-	-	-	-
5	L	-	-	-	-	-	-
6	S	0.9	0.020	0.4	0.4	1.7	1.7
7	S	4.5	0.043	4.5	1.8	8.4	5.7
8	S	-	-	-	-	-	-
9	S	31.8	0.120	31.6	19.8	44.4	29.1
10	S, M	27.4	0.474	32.8	1.7	64.0	1.7
11	S,M	10.0	0.327	3.7	1.1	50.8	3.7
12	S,M	5.3	0.230	0.6	0.4	16.9	0.4
13	S	-	-	-	-	-	-
14	S, L	6.0	0.022	6.1	3.5	8.1	5.0
15	M, L	7.2	0.197	5.0	0.6	16.9	16.9

Table 3.A5. Coyote mean (± SE), median, and range for corrected relative abundance (cRA) values based on 1000 randomizations and generated across 15 transects under the conditions observed in western Utah in summer 2013. Corrected relative abundance incorporated a persistence-rate correction factor estimated by scat removal experiments. Observed cRA (Obs cRA) indicates the cRA calculated under observed scat deposition patterns for coyotes in summer 2013. Road types (RT) included unmaintained two-track roads (small; S), one-lane gravel roads (medium; M), and two-lane gravel roads (large; L).

		cRA from 1000 Randomized Datasets					
Transect	RT	Mean	SE	Median	Min	Max	Obs cRA
1	M	151.4	2.543	149.3	15.4	481.5	24.6
2	S, M	66.9	1.587	53.1	8.4	380.9	19.7
3	S	25.6	0.123	26.1	11.6	36.7	16.9
4	L	7.4×10^{13}	2.5×10^{12}	6690.7	608.6	1.0×10^{15}	118.5
5	L	1.9×10^{9}	7.7×10^{7}	771.2	158.3	1.3×10^{10}	61.6
6	S	26.5	0.121	26.3	14.9	37.7	17.1
7	S	39.6	0.142	39.8	27.4	55.9	27.4
8	S	26.1	0.116	26.3	16.3	37.7	12.5
9	S	12.1	0.084	11.8	4.6	18.9	5.5
10	S, M	14.9	0.441	4.9	2.0	65.0	7.2
11	S,M	36.2	0.617	37.9	10.9	137.0	11.7
12	S,M	47.1	0.756	41.6	9.4	138.2	9.0
13	S	59.2	0.192	59.0	40.7	76.7	34.5
14	S, L	984.7	22.564	1166.4	23.8	4021.2	159.2
15	M, L	1.9×10^{13}	9.1×10^{11}	6660.4	6.6	1.4×10^{14}	106.6

Table 3.A6. Coyote mean (± SE), median, and range for corrected relative abundance (cRA) values based on 1000 randomizations and generated across 15 transects under the conditions observed in western Utah in winter 2014. Corrected relative abundance incorporated a persistence-rate correction factor estimated by scat removal experiments. Observed cRA (Obs cRA) indicates the cRA calculated under observed scat deposition patterns for coyotes in winter 2014. Road types (RT) included unmaintained two-track roads (small; S), one-lane gravel roads (medium; M), and two-lane gravel roads (large; L).

		cRA from 1000 Randomized Datasets					
Transect	RT	Mean	SE	Median	Min	Max	Obs cRA
1	M	113.6	0.981	116.2	8.6	226.7	27.3
2	S, M	21.6	0.516	22.5	1.4	82.4	1.9
3	S	5.2	0.046	4.9	1.9	9.2	2.2
4	L	-	-	-	-	-	-
5	L	-	-	-	-	-	-
6	S	1.0	0.019	0.4	0.4	1.7	0.3
7	S	20.4	0.087	20.6	12.1	30.7	12.2
8	S	16.4	0.081	16.5	7.7	25.1	9.6
9	S	7.0	0.053	6.7	2.8	11.7	3.5
10	S, M	6.7	0.233	0.9	0.4	16.0	0.4
11	S,M	72.2	0.840	68.9	14.8	181.8	40.8
12	S,M	41.6	0.590	38.7	3.1	102.5	7.0
13	S	16.8	0.086	16.8	8.9	25.3	9.9
14	S, L	232.7	7.032	299.2	1.7	893.4	29.5
15	M, L	151137.2	10679.030	5.0	0.6	904976.2	4.2

Appendix 3.3

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Appendix 5.1

Individual Identification PCR Conditions for Fecal DNA Samples Collected from Kit Foxes (*Vulpes macrotis*) and Coyotes (*Canis latrans*) Sampled in Utah, USA, 2013–2014.

For individual identification of kit fox samples, we combined nine nuclear DNA (nDNA) microsatellite loci (Cxx103 [Holmes et al. 1995]; Cxx250 [Ostrander et al. 1993]; Cxx377 [Ostrander et al. 1995]; FH2001, FH2010, FH2054, FH2088 [Francisco et al. 1996]; CPH3 [Fredholm and Wintero 1995]; VVE-M19 [Cullingham et al. 2006]), and two sex identification primers (CF-hprt, VV-sry [Berry et al. 2007]) into a single multiplex. The PCR conditions for the 7 µl (total volume) multiplex for each primer pair were 0.29 µM Cxx103, 0.09 µM VVE-M19, 0.06 µM FH2054, 0.04 µM Cxx250, FH2001, FH2010, and CPH3, 0.03 µM FH2088 and CF-hprt, and 0.01 µM Cxx377 and VV-sry, combined with 1x concentrated Qiagen Master Mix, 0.5x concentrated Q solution and 1 µl of DNA extract. The PCR thermal profile had an initial denaturation of 94°C for 15 minutes, 15 touchdown cycles at 94°C for 30 seconds (denaturation), 63°C for 90 seconds (annealing; decreasing by 0.5°C per cycle) and 72°C for 60 seconds (elongation), 20 cycles at 94°C for 30 seconds (denaturation), 55°C for 90 seconds (annealing) and 72°C for 60 seconds (elongation), and a final elongation at 60°C for 30 minutes. For coyote individual identification, we combined nine nDNA microsatellite loci (Cxx119 [Holmes et al. 1995]; Cxx173 [Ostrander et al. 1993]; FH2001, FH2054, FH2088, FH2137 [Fancisco et al. 1996]; FH2611 [Eichmann et al. 2004]; FH2670, FH3725, [Guyon et al. 2003]), and two sex identification primers (DBX6, DBY7; Seddon 2005) into a single multiplex. The PCR conditions for the 7µl (total volume) multiplex for each primer pair were 0.11 µM Cxx119, 0.07 µM FH2670, 0.05 µM FH2611 and DBX6, 0.04 µM FH2001, FH3725, and DBY7, 0.03 µM FH2054, FH2088, and FH2137, and 0.02

µM Cxx173, combined with 1x concentrated Qiagen Master Mix, 0.5x concentrated Q solution and 2 µl of DNA extract. The PCR thermal profile has an initial denaturation of 94°C for 15 minutes, 13 touchdown cycles at 94°C for 30 seconds (denaturation), 62°C for 90 seconds (annealing; decreasing by 0.4°C per cycle) and 72°C for 60 seconds (elongation), 28 cycles at 94°C for 30 seconds (denaturation), 57°C for 90 seconds (annealing) and 72°C for 60 seconds (elongation), and a final elongation at 60°C for 30 minutes. We conducted all PCR procedures on a BioRad Tetrad thermocycler (Bio-Rad, Hercules, CA, USA) with negative and positive controls included with each reaction.

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Appendix 5.2

List of Robust Design Models Evaluating Kit Fox (*Vulpes macrotis*) and Coyote (*Canis latrans*) Survival (*S*), Capture (*p*) and Recapture (*c*) Probabilities, and Movement (Temporary Immigration = 1 – γ"; Temporary Emigration = γ').

Parameters	Models considered		
Survival	*S*(.)	*S* (sex+ExWinter)	*S* (sex*DistW)
	S (t)	*S* (sex+DistW)	*S* (sex*IndHet)
	S (T)	*S* (sex+IndHet)	*S* (DistW*t)
	S (sex)	*S* (DistW+t)	*S* (DistW+Season)
	S (Season)	*S* (DistW+Season)	*S* (DistW*ExWinter)
	S (ExWinter)	*S* (DistW+ExWinter)	*S* (DistW+IndHet)
	S (DistW)	*S* (DistW+IndHet)	*S* (DistW*t+sex)
	S (DistW2)	*S* (DistW*t+IndHet)	*S*(C.idx)[d]
	S (IndHet)	*S* (sex*t)	*S*(C.idx*t)[d]
	S (sex+t)	*S* (sex*T)	*S*(C.idx*sex)[d]
	S (sex+T)	*S* (sex*Season)	*S*(C.idx*DistW)[d]
	S (sex+Season)	*S* (sex*ExWinter)	*S*(C.idx*DistW2)[d]
Capture probability[a,b]	*p*(.)	*p*(t)	*p*(T)
	p(sex)	*p*(t+sex)	*p*(T+sex)
Movement[c]	γ '(.),γ"(.)	γ '(t)=γ"(t)	γ '=γ"=0

Abbreviations are as follows: "." = constant, "t" = time-varying, "T" = trend, "Season" = variation between seasons, "ExWinter" = difference following an extreme winter season, "DistW" = Euclidean distance to nearest water, "DistW2" = Quadratic distance to nearest water, "IndHet" = individual heterozygosity, "C.idx" = index of coyote activity.

[a]In all capture models, $p = c$ and the mean p across occasions (secondary sampling periods) was applied to individuals captured only at single-occasion sites.

[b]All capture models considered variation in p among sessions (primary sampling periods).

[c]For movement models, $\gamma'(t) = \gamma''(t)$ represents random movement and $\gamma' = \gamma'' = 0$ represents no movement.

[d]Model was only considered for kit foxes.

Appendix 5.3

Ranking of Robust Design Models Fit for Kit Fox (*Vulpes macro*tis) Survival (*S*), Capture (*p*) and Recapture (*c*) Probabilities, and Movement (Temporary Immigration = 1 – γ"; Temporary Emigration = γ'), 2013–2014, with the Program MARK Based on Akaike's Information Criterion with Small Sample Size Correction (AIC_c). Each Model is Ranked Based on ΔAIC_c, where K = Number of Parameters and w_i = Akaike Weight. Only Models with $w_i > 0.001$ are presented.

Survival	Capture[a,b]	Movement[c]	K	AIC_c	ΔAIC_c	w_i	Deviance
S(sex+T)	*p*=*c*(T)	γ'=γ"=0	11	905.447	0.000	0.0497	882.424
S(DistW2)	*p*=*c*(T)	γ'(.), γ"(.)	12	905.789	0.342	0.0419	880.575
S(C.idx*t)	*p*=*c*(T)	γ'=γ"=0	14	905.854	0.407	0.0405	876.207
S(DistW)	*p*=*c*(T)	γ'(.), γ"(.)	12	906.150	0.702	0.0350	880.936
S(DistW+ExWinter)	*p*=*c*(T)	γ'(.), γ"(.)	13	906.314	0.867	0.0322	878.892
S(sex+t)	*p*=*c*(T)	γ'=γ"=0	12	906.321	0.874	0.0321	881.107
S(sex+T)	*p*=*c*(T)	γ'(.), γ"(.)	13	906.932	1.484	0.0237	879.509
S(sex+T)	*p*=*c*(T)	γ'(t)=γ"(t)	13	907.084	1.636	0.0219	879.662
S(sex+T)	*p*=*c*(t)	γ'=γ"=0	19	907.283	1.835	0.0199	866.243
S(C.idx*DistW)	*p*=*c*(T)	γ'(.), γ"(.)	14	907.341	1.894	0.0193	877.694
S(C.idx*t)	*p*=*c*(T)	γ'(.), γ"(.)	16	907.386	1.938	0.0189	873.236
S(DistW+t)	*p*=*c*(T)	γ'(.), γ"(.)	14	907.436	1.989	0.0184	877.789
S(T)	*p*=*c*(T)	γ'=γ"=0	10	907.507	2.059	0.0178	886.657
S(sex*T)	*p*=*c*(T)	γ'=γ"=0	12	907.638	2.190	0.0166	882.424
S(C.idx*t)	*p*=*c*(T)	γ'(t)=γ"(t)	16	907.679	2.232	0.0163	873.529
S(t)	*p*=*c*(T)	γ'(.), γ"(.)	12	907.690	2.243	0.0162	882.476
S(DistW2)	*p*=*c*(t)	γ'(.), γ"(.)	20	908.086	2.638	0.0133	864.712
S(C.idx*t)	*p*=*c*(t)	γ'=γ"=0	22	908.088	2.641	0.0133	859.991
S(t)	*p*=*c*(T)	γ'=γ"=0	11	908.149	2.702	0.0129	885.126

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S(DistW2)	*p*=*c*(T)	γ'(t)=γ''(t)	12	908.175	2.727	0.0127	882.961
S(sex+t)	*p*=*c*(t)	γ'=γ''=0	20	908.266	2.819	0.0121	864.893
S(DistW*t)	*p*=*c*(T)	γ'(.), γ''(.)	16	908.323	2.876	0.0118	874.173
S(DistW+IndHet)	*p*=*c*(T)	γ'(.), γ''(.)	13	908.331	2.883	0.0118	880.909
S(C.idx*DistW)	*p*=*c*(T)	γ'(t)=γ''(t)	14	908.337	2.890	0.0117	878.690
S(DistW+Season)	*p*=*c*(T)	γ'(.), γ''(.)	13	908.34	2.892	0.0117	880.918
S(DistW+sex)	*p*=*c*(T)	γ'(.), γ''(.)	13	908.356	2.908	0.0116	880.934
S(sex+t)	*p*=*c*(T)	γ'(.), γ''(.)	14	908.358	2.911	0.0116	878.711
S(DistW)	*p*=*c*(t)	γ'(.), γ''(.)	20	908.438	2.991	0.0111	865.065
S(DistW)	*p*=*c*(T)	γ'(t)=γ''(t)	12	908.458	3.011	0.011	883.244
S(DistW+t)	*p*=*c*(T)	γ'=γ''=0	12	908.475	3.028	0.0109	883.261
S(sex+t)	*p*=*c*(T)	γ'(t)=γ''(t)	14	908.62	3.173	0.0102	878.973
S(DistW+ExWinter)	*p*=*c*(t)	γ'(.), γ''(.)	21	908.675	3.228	0.0099	862.949
S(sex+T)	*p*=*c*(t)	γ'(.), γ''(.)	21	908.925	3.478	0.0087	863.199
S(DistW*t+sex)	*p*=*c*(T)	γ'(.), γ''(.)	17	909.000	3.553	0.0084	872.572
S(T)	*p*=*c*(T)	γ'(t)=γ''(t)	12	909.054	3.607	0.0082	883.840
S(sex+T)	*p*=*c*(t)	γ'(t)=γ''(t)	21	909.107	3.659	0.008	863.381
S(DistW*t+sex)	*p*=*c*(T)	γ'(t)=γ''(t)	17	909.158	3.711	0.0078	872.729
S(T)	*p*=*c*(t)	γ'=γ''=0	18	909.206	3.759	0.0076	870.481
S(sex*T)	*p*=*c*(T)	γ'(t)=γ''(t)	14	909.308	3.861	0.0072	879.661
S(C.idx)	*p*=*c*(T)	γ'(t)=γ''(t)	12	909.429	3.982	0.0068	884.215
S(DistW*t)	*p*=*c*(T)	γ'(t)=γ''(t)	16	909.456	4.009	0.0067	875.306
S(C.idx)	*p*=*c*(T)	γ'=γ''=0	10	909.538	4.091	0.0064	888.689
S(C.idx)	*p*=*c*(T)	γ'(.), γ''(.)	12	909.592	4.144	0.0063	884.378
S(sex*T)	*p*=*c*(t)	γ'=γ''=0	20	909.616	4.169	0.0062	866.243
S(C.idx*DistW2)	*p*=*c*(t)	γ'(.), γ''(.)	22	909.798	4.351	0.0056	861.701
S(DistW*t+IndHet)	*p*=*c*(T)	γ'(.), γ''(.)	17	909.837	4.39	0.0055	873.409
S(DistW*t+IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	17	909.842	4.395	0.0055	873.414

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S(DistW+t)	*p*=*c*(t)	γ'(.), γ''(.)	22	909.870	4.422	0.0055	861.773
S(DistW+ExWinter)	*p*=*c*(T)	γ'(t)=γ''(t)	13	909.893	4.446	0.0054	882.471
S(C.idx*DistW)	*p*=*c*(t)	γ'(.), γ''(.)	22	909.945	4.497	0.0053	861.847
S(t)	*p*=*c*(t)	γ'=γ''=0	19	909.956	4.509	0.0052	868.916
S(DistW*t)	*p*=*c*(T)	γ'=γ''=0	14	909.998	4.551	0.0051	880.351
S(DistW*Season)	*p*=*c*(T)	γ'(t)=γ''(t)	14	910.071	4.623	0.0049	880.423
S(C.idx*t)	*p*=*c*(t)	γ'(t)=γ''(t)	24	910.130	4.682	0.0048	857.232
S(DistW*Season)	*p*=*c*(T)	γ'(.), γ''(.)	14	910.192	4.744	0.0046	880.545
S(C.idx*DistW2)	*p*=*c*(T)	γ'(.), γ''(.)	14	910.220	4.773	0.0046	880.573
S(DistW*t+IndHet)	*p*=*c*(T)	γ'=γ''=0	15	910.230	4.782	0.0046	878.339
S(t)	*p*=*c*(T)	γ'(t)=γ''(t)	13	910.314	4.867	0.0044	882.892
S(DistW2)	*p*=*c*(t)	γ'(t)=γ''(t)	20	910.350	4.902	0.0043	866.976
S(DistW+t)	*p*=*c*(T)	γ'(t)=γ''(t)	14	910.442	4.994	0.0041	880.795
S(DistW+t)	*p*=*c*(t)	γ'=γ''=0	20	910.453	5.006	0.0041	867.079
S(sex+t)	*p*=*c*(t)	γ'(.), γ''(.)	22	910.489	5.042	0.004	862.392
S(DistW+Season)	*p*=*c*(T)	γ'(t)=γ''(t)	13	910.508	5.061	0.004	883.086
S(DistW+IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	13	910.523	5.075	0.0039	883.101
S(C.idx*sex)	*p*=*c*(T)	γ'=γ''=0	12	910.537	5.089	0.0039	885.323
S(DistW*IndHet)	*p*=*c*(T)	γ'(.), γ''(.)	14	910.543	5.096	0.0039	880.896
S(C.idx*sex)	*p*=*c*(T)	γ'(t)=γ''(t)	14	910.568	5.120	0.0038	880.921
S(DistW)	*p*=*c*(t)	γ'(t)=γ''(t)	20	910.629	5.182	0.0037	867.255
S(DistW*t+sex)	*p*=*c*(T)	γ'=γ''=0	15	910.630	5.183	0.0037	878.740
S(sex*t)	*p*=*c*(T)	γ'=γ''=0	14	910.633	5.186	0.0037	880.986
S(C.idx*sex)	*p*=*c*(T)	γ'(.), γ''(.)	14	910.704	5.256	0.0036	881.057
S(DistW*t)	*p*=*c*(t)	γ'(.), γ''(.)	24	910.749	5.301	0.0035	857.851
S(sex+t)	*p*=*c*(t)	γ'(t)=γ''(t)	22	910.763	5.316	0.0035	862.667
S(DistW+IndHet)	*p*=*c*(t)	γ'(.), γ''(.)	21	910.763	5.316	0.0035	865.038
S(DistW+Season)	*p*=*c*(t)	γ'(.), γ''(.)	21	910.767	5.319	0.0035	865.041

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S(DistW+sex)	*p*=*c*(t)	γ'(.), γ''(.)	21	910.789	5.341	0.0034	865.063
S(sex+T)	*p*=*c*(T+g)	γ'=γ''=0	15	910.812	5.364	0.0034	878.922
S(C.idx*DistW)	*p*=*c*(t)	γ'(t)=γ''(t)	22	910.826	5.379	0.0034	862.729
S(DistW+sex)	*p*=*c*(T)	γ'(t)=γ''(t)	13	910.890	5.443	0.0033	883.469
S(T)	*p*=*c*(t)	γ'(t)=γ''(t)	20	910.935	5.488	0.0032	867.562
S(sex+ExWinter)	*p*=*c*(T)	γ'=γ''=0	11	910.950	5.502	0.0032	887.927
S(ExWinter*DistW)	*p*=*c*(T)	γ'(t)=γ''(t)	14	910.962	5.514	0.0032	881.315
S(C.idx*DistW2)	*p*=*c*(T)	γ'(t)=γ''(t)	14	911.028	5.581	0.0031	881.381
S(sex)	*p*=*c*(T)	γ'(t)=γ''(t)	12	911.170	5.722	0.0028	885.956
S(sex+ExWinter)	*p*=*c*(T)	γ'(t)=γ''(t)	13	911.446	5.999	0.0025	884.024
S(sex*T)	*p*=*c*(t)	γ'(t)=γ''(t)	22	911.478	6.030	0.0024	863.380
S(sex)	*p*=*c*(T)	γ'(.), γ''(.)	12	911.519	6.071	0.0024	886.305
S(sex+Season)	*p*=*c*(T)	γ'(t)=γ''(t)	13	911.536	6.088	0.0024	884.114
S(sex+ExWinter)	*p*=*c*(T)	γ'(.), γ''(.)	13	911.555	6.107	0.0023	884.133
S(DistW*t+sex)	*p*=*c*(t)	γ'(.), γ''(.)	25	911.562	6.115	0.0023	856.234
S(C.idx)	*p*=*c*(t)	γ'(t)=γ''(t)	20	911.574	6.127	0.0023	868.201
S(DistW*t+sex)	*p*=*c*(t)	γ'(t)=γ''(t)	25	911.746	6.299	0.0021	856.418
S(C.idx)	*p*=*c*(t)	γ'=γ''=0	18	911.761	6.313	0.0021	873.036
S(C.idx)	*p*=*c*(t)	γ'(.), γ''(.)	20	911.776	6.329	0.0021	868.402
S(sex+t)	*p*=*c*(T+g)	γ'=γ''=0	16	911.893	6.445	0.0020	877.743
S(DistW*t)	*p*=*c*(t)	γ'(t)=γ''(t)	24	911.897	6.450	0.0020	858.999
S(sex)	*p*=*c*(T)	γ'=γ''=0	10	912.170	6.723	0.0017	891.321
S(IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	12	912.174	6.727	0.0017	886.959
S(DistW+ExWinter)	*p*=*c*(t)	γ'(t)=γ''(t)	21	912.196	6.749	0.0017	866.471
S(Season)	*p*=*c*(T)	γ'(t)=γ''(t)	12	912.200	6.753	0.0017	886.986
S(sex+Season)	*p*=*c*(T)	γ'(.), γ''(.)	13	912.290	6.842	0.0016	884.868
S(t)	*p*=*c*(t)	γ'(t)=γ''(t)	21	912.310	6.862	0.0016	866.584
S(sex+Season)	*p*=*c*(T)	γ'=γ''=0	11	912.314	6.866	0.0016	889.290

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S(.)	*p*=*c*(T)	γ'(t)=γ''(t)	11	912.356	6.909	0.0016	889.333
S(DistW*t)	*p*=*c*(t)	γ'=γ''=0	22	912.386	6.938	0.0016	864.289
S(sex+IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	13	912.410	6.962	0.0015	884.988
S(DistW*t+IndHet)	*p*=*c*(t)	γ'(.), γ''(.)	25	912.410	6.963	0.0015	857.082
S(C.idx*DistW2)	*p*=*c*(T)	γ'=γ''=0	12	912.424	6.977	0.0015	887.210
S(DistW*t+IndHet)	*p*=*c*(t)	γ'(t)=γ''(t)	25	912.427	6.980	0.0015	857.099
S(DistW*Season)	*p*=*c*(t)	γ'(t)=γ''(t)	22	912.428	6.981	0.0015	864.331
S(IndHet)	*p*=*c*(T)	γ'(.), γ''(.)	12	912.603	7.155	0.0014	887.389
S(DistW*IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	14	912.612	7.164	0.0014	882.965
S(DistW+t)	*p*=*c*(t)	γ'(t)=γ''(t)	22	912.620	7.173	0.0014	864.523
S(sex+T)	*p*=*c*(T+g)	γ'(.), γ''(.)	17	912.671	7.224	0.0013	876.242
S(sex+T)	*p*=*c*(t+g)	γ'=γ''=0	23	912.677	7.230	0.0013	862.189
S(.)	*p*=*c*(T)	γ'(.), γ''(.)	11	912.703	7.256	0.0013	889.680
S(DistW*Season)	*p*=*c*(t)	γ'(.), γ''(.)	22	912.754	7.306	0.0013	864.656
S(DistW*t+IndHet)	*p*=*c*(t)	γ'=γ''=0	23	912.758	7.311	0.0013	862.270
S(DistW+Season)	*p*=*c*(t)	γ'(t)=γ''(t)	21	912.805	7.358	0.0013	867.079
S(sex+IndHet)	*p*=*c*(T)	γ'(.), γ''(.)	13	912.806	7.359	0.0013	885.384
S(ExWinter)	*p*=*c*(T)	γ'=γ''=0	10	912.821	7.374	0.0012	891.972
S(DistW+IndHet)	*p*=*c*(t)	γ'(t)=γ''(t)	21	912.838	7.390	0.0012	867.112
S(sex*t)	*p*=*c*(t)	γ'=γ''=0	22	912.872	7.425	0.0012	864.775
S(C.idx*DistW)	*p*=*c*(T)	γ'=γ''=0	12	912.896	7.449	0.0012	887.682
S(sex+T)	*p*=*c*(T+g)	γ'(t)=γ''(t)	17	912.928	7.481	0.0012	876.499
S(sex*t)	*p*=*c*(T)	γ'(t)=γ''(t)	16	912.950	7.503	0.0012	878.800
S(Season)	*p*=*c*(T)	γ'(.), γ''(.)	12	913.006	7.559	0.0011	887.792
S(C.idx*sex)	*p*=*c*(t)	γ'(t)=γ''(t)	22	913.015	7.568	0.0011	864.918
S(sex*T)	*p*=*c*(T+g)	γ'=γ''=0	16	913.038	7.591	0.0011	878.888
S(DistW*t+sex)	*p*=*c*(t)	γ'=γ''=0	23	913.039	7.591	0.0011	862.551
S(sex*ExWinter)	*p*=*c*(T)	γ'=γ''=0	12	913.084	7.637	0.0011	887.870

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S(sex+ExWinter)	*p*=*c*(t)	γ'=γ''=0	19	913.089	7.642	0.0011	872.049
S(C.idx*t)	*p*=*c*(T+g)	γ'=γ''=0	18	913.090	7.643	0.0011	874.365
S(C.idx*sex)	*p*=*c*(t)	γ'=γ''=0	20	913.095	7.647	0.0011	869.721
S(DistW*IndHet)	*p*=*c*(t)	γ'(.), γ''(.)	22	913.123	7.676	0.0011	865.026
S(DistW+sex)	*p*=*c*(T)	γ'=γ''=0	11	913.182	7.735	0.0010	890.159
S(C.idx*sex)	*p*=*c*(t)	γ'(.), γ''(.)	22	913.189	7.742	0.0010	865.092
S(DistW+sex)	*p*=*c*(t)	γ'(t)=γ''(t)	21	913.226	7.778	0.0010	867.499
S(DistW+ExWinter)	*p*=*c*(T)	γ'=γ''=0	11	913.241	7.794	0.0010	890.218
S(ExWinter)	*p*=*c*(T)	γ'(t)=γ''(t)	12	913.267	7.820	0.0010	888.053

Abbreviations are as follows: "." = constant, "t" = time-varying, "T" = trend, "Season" = variation between Seasons, "ExWinter" = difference following an extreme winter Season, "DistW" = Euclidean distance to nearest water, "DistW2" = Quadratic distance to nearest water, "IndHet" = individual heterozygosity, "C.idx" = index of coyote activity.

[a]In all capture models, $p = c$ and the mean p across sessions was applied to individuals captured only at single-session sites.

[b]All capture models considered variation in p among sessions (primary sampling periods).

[c]For movement models, $\gamma'(t) = \gamma''(t)$ represents random movement and $\gamma' = \gamma'' = 0$ represents no movement.

Appendix 5.4

Ranking of Robust Design Models Fit for Coyote (*Canis latrans*) Survival (*S*), Capture (*p*) and Recapture (*c*) Probabilities, and Movement (Temporary Immigration = 1 – γ"; Temporary Emigration = γ'), 2013–2014, with the Program MARK Based on Akaike's Information Criterion with Small Sample Size Correction (AIC_c). Each Model is Ranked Based on ΔAIC_c, where K = Number of Parameters and w_i = Akaike Weight. Only Models with $w_i > 0.001$ are Presented.

Survival	Capture[a,b]	Movement[c]	K	AIC_c	ΔAIC_c	w_i	Deviance
S(DistW*t+IndHet)	*p*=*c*(t)	γ'(t)=γ"(t)	24	2854.661	0	0.0747	2805.258
S(DistW+IndHet)	*p*=*c*(T)	γ'(.),γ"(.)	13	2855.037	0.375	0.0619	2828.616
S(DistW+IndHet)	*p*=*c*(t)	γ'(.),γ"(.)	20	2855.376	0.715	0.0523	2814.398
S(DistW*t+IndHet)	*p*=*c*(T)	γ'=γ"=0	15	2855.402	0.741	0.0516	2824.847
S(DistW*IndHet)	*p*=*c*(T)	γ'(.),γ"(.)	14	2855.569	0.908	0.0475	2827.083
S(DistW*Season)	*p*=*c*(T)	γ'(.),γ"(.)	14	2855.647	0.986	0.0457	2827.162
S(DistW*t+IndHet)	*p*=*c*(t)	γ'=γ"=0	22	2855.921	1.260	0.0398	2810.740
S(DistW*IndHet)	*p*=*c*(t)	γ'(.),γ"(.)	21	2855.940	1.278	0.0394	2812.863
S(DistW*Season)	*p*=*c*(t)	γ'(.),γ"(.)	21	2856.007	1.346	0.0381	2812.931
S(DistW*t)	*p*=*c*(T)	γ'(.),γ"(.)	16	2856.593	1.932	0.0284	2823.963
S(DistW*Season)	*p*=*c*(T)	γ'=γ"=0	12	2856.921	2.260	0.0241	2832.561
S(DistW*t)	*p*=*c*(t)	γ'(.),γ"(.)	23	2856.966	2.305	0.0236	2809.677
S(DistW*Season)	*p*=*c*(t)	γ'=γ"=0	19	2857.377	2.716	0.0192	2818.493
S(DistW*Season)	*p*=*c*(T)	γ'(t)=γ"(t)	14	2857.381	2.720	0.0192	2828.896
S(DistW*t)	*p*=*c*(T)	γ'(t)=γ"(t)	16	2857.493	2.832	0.0181	2824.863
S(DistW*Season)	*p*=*c*(t)	γ'(t)=γ"(t)	21	2857.828	3.166	0.0153	2814.751
S(DistW+IndHet)	*p*=*c*(T+sex)	γ'(.),γ"(.)	17	2858.008	3.347	0.0140	2823.298
S(DistW*t)	*p*=*c*(t)	γ'(t)=γ"(t)	23	2858.010	3.349	0.0140	2810.721
S(DistW*t+sex)	*p*=*c*(T)	γ'(.),γ"(.)	17	2858.029	3.368	0.0139	2823.319

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S(DistW)	*p*=*c*(T)	γ'(.),γ''(.)	12	2858.030	3.369	0.0139	2833.670
S(DistW+ExWinter)	*p*=*c*(T)	γ'(.),γ''(.)	13	2858.174	3.513	0.0129	2831.754
S(DistW*t+IndHet)	*p*=*c*(T+sex)	γ'=γ''=0	19	2858.179	3.518	0.0129	2819.295
S(DistW)	*p*=*c*(t)	γ'(.),γ''(.)	19	2858.340	3.679	0.0119	2819.456
S(DistW*ExWinter)	*p*=*c*(T)	γ'(.),γ''(.)	14	2858.421	3.760	0.0114	2829.936
S(DistW*t+sex)	*p*=*c*(t)	γ'(.),γ''(.)	24	2858.435	3.774	0.0113	2809.031
S(DistW+ExWinter)	*p*=*c*(t)	γ'(.),γ''(.)	20	2858.447	3.786	0.0113	2817.469
S(sex+DistW)	*p*=*c*(T)	γ'(.),γ''(.)	13	2858.555	3.894	0.0107	2832.135
S(DistW*IndHet)	*p*=*c*(T+sex)	γ'(.),γ''(.)	18	2858.556	3.895	0.0107	2821.762
S(DistW*ExWinter)	*p*=*c*(t)	γ'(.),γ''(.)	21	2858.725	4.064	0.0098	2815.648
S(DistW*Season)	*p*=*c*(T+sex)	γ'(.),γ''(.)	18	2858.775	4.114	0.0096	2821.981
S(sex+DistW)	*p*=*c*(t)	γ'(.),γ''(.)	20	2858.899	4.238	0.0090	2817.922
S(DistW*t)	*p*=*c*(T)	γ'=γ''=0	14	2858.933	4.271	0.0088	2830.447
S(DistW*t+sex)	*p*=*c*(T)	γ'(t)=γ''(t)	17	2859.179	4.518	0.0078	2824.469
S(DistW*Season)	*p*=*c*(T+sex)	γ'=γ''=0	16	2859.222	4.561	0.0076	2826.592
S(DistW+IndHet)	*p*=*c*(T)	γ'=γ''=0	11	2859.406	4.745	0.0070	2837.102
S(DistW+IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	13	2859.418	4.757	0.0069	2832.998
S(DistW*t)	*p*=*c*(t)	γ'=γ''=0	21	2859.421	4.760	0.0069	2816.344
S(DistW*t+sex)	*p*=*c*(t)	γ'(t)=γ''(t)	24	2859.730	5.069	0.0059	2810.326
S(DistW*Season)	*p*=*c*(T+sex)	γ'(t)=γ''(t)	18	2859.771	5.110	0.0058	2822.977
S(DistW+IndHet)	*p*=*c*(t)	γ'(t)=γ''(t)	20	2859.830	5.168	0.0056	2818.852
S(DistW+IndHet)	*p*=*c*(t)	γ'=γ''=0	18	2859.836	5.174	0.0056	2823.041
S(DistW*IndHet)	*p*=*c*(T)	γ'=γ''=0	12	2859.836	5.175	0.0056	2835.476
S(DistW*t+IndHet)	*p*=*c*(t+sex)	γ'(t)=γ''(t)	28	2859.843	5.181	0.0056	2801.934
S(sex*DistW)	*p*=*c*(T)	γ'(.),γ''(.)	14	2860.002	5.340	0.0052	2831.516
S(DistW*IndHet)	*p*=*c*(T)	γ'(t)=γ''(t)	14	2860.106	5.445	0.0049	2831.621
S(DistW*t)	*p*=*c*(T+sex)	γ'(.),γ''(.)	20	2860.136	5.475	0.0048	2819.158
S(DistW*IndHet)	*p*=*c*(t)	γ'=γ''=0	19	2860.299	5.638	0.0045	2821.415

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S(sex*DistW)	*p*=*c*(t)	γ'(.),γ''(.)	21	2860.378	5.717	0.0043	2817.301
S(DistW+IndHet)	*p*=*c*(t+sex)	γ'(.),γ''(.)	24	2860.396	5.735	0.0043	2810.992
S(DistW*t+sex)	*p*=*c*(T)	γ'=γ''=0	15	2860.474	5.812	0.0041	2829.918
S(DistW*IndHet)	*p*=*c*(t)	γ'(t)=γ''(t)	21	2860.554	5.892	0.0039	2817.477
S(T)	*p*=*c*(T)	γ'(.),γ''(.)	12	2860.701	6.040	0.0037	2836.341
S(T)	*p*=*c*(t)	γ'(.),γ''(.)	19	2860.923	6.261	0.0033	2822.039
S(DistW*IndHet)	*p*=*c*(t+sex)	γ'(.),γ''(.)	25	2860.976	6.315	0.0032	2809.454
S(DistW*t+sex)	*p*=*c*(t)	γ'=γ''=0	22	2860.997	6.335	0.0032	2815.816
S(DistW)	*p*=*c*(T+sex)	γ'(.),γ''(.)	16	2861.047	6.385	0.0031	2828.416
S(DistW*t+IndHet)	*p*=*c*(t+sex)	γ'=γ''=0	26	2861.078	6.417	0.0030	2807.432
S(DistW*Season)	*p*=*c*(t+sex)	γ'(.),γ''(.)	25	2861.092	6.431	0.0030	2809.569
S(DistW*t+sex)	*p*=*c*(T+sex)	γ'(.),γ''(.)	21	2861.451	6.790	0.0025	2818.374
S(sex+DistW)	*p*=*c*(T+sex)	γ'(.),γ''(.)	17	2861.463	6.802	0.0025	2826.753
S(DistW*t)	*p*=*c*(T+sex)	γ'=γ''=0	18	2861.659	6.998	0.0023	2824.865
S(DistW+ExWinter)	*p*=*c*(T+sex)	γ'(.),γ''(.)	17	2861.665	7.003	0.0023	2826.955
S(DistW+IndHet)	*p*=*c*(T+sex)	γ'=γ''=0	15	2861.718	7.057	0.0022	2831.162
S(DistW+IndHet)	*p*=*c*(T+sex)	γ'(t)=γ''(t)	17	2861.810	7.149	0.0021	2827.100
S(DistW*t)	*p*=*c*(t+sex)	γ'(.),γ''(.)	27	2861.995	7.333	0.0019	2806.219
S(DistW*ExWinter)	*p*=*c*(T+sex)	γ'(.),γ''(.)	18	2862.043	7.382	0.0019	2825.249
S(DistW*IndHet)	*p*=*c*(T+sex)	γ'=γ''=0	16	2862.195	7.533	0.0017	2829.564
S(T)	*p*=*c*(t)	γ'(t)=γ''(t)	19	2862.336	7.674	0.0016	2823.452
S(DistW*Season)	*p*=*c*(t+sex)	γ'=γ''=0	23	2862.490	7.828	0.0015	2815.199
S(DistW+ExWinter)	*p*=*c*(T)	γ'=γ''=0	11	2862.506	7.844	0.0015	2840.202
S(DistW*IndHet)	*p*=*c*(T+sex)	γ'(t)=γ''(t)	18	2862.549	7.888	0.0015	2825.755
S(sex+T)	*p*=*c*(T)	γ'(.),γ''(.)	13	2862.726	8.065	0.0013	2836.306
S(sex+ExWinter)	*p*=*c*(T)	γ'(.),γ''(.)	13	2862.730	8.069	0.0013	2836.309
S(IndHet)	*p*=*c*(T)	γ'(.),γ''(.)	12	2862.745	8.084	0.0013	2838.385
S(T)	*p*=*c*(T+sex)	γ'(t)=γ''(t)	15	2862.788	8.127	0.0013	2832.233

Appendix 5.4, cont'd

S(DistW*ExWinter)	*p*=*c*(t)	γ'(t)=γ''(t)	21	2862.850	8.189	0.0013	2819.773
S(DistW+ExWinter)	*p*=*c*(t)	γ'=γ''=0	18	2862.890	8.228	0.0012	2826.096
S(DistW*Season)	*p*=*c*(t+sex)	γ'(t)=γ''(t)	25	2862.900	8.238	0.0012	2811.377
S(sex*IndHet)	*p*=*c*(T)	γ'(.),γ''(.)	14	2862.917	8.255	0.0012	2834.431
S(sex*DistW)	*p*=*c*(T+sex)	γ'(.),γ''(.)	18	2862.971	8.309	0.0012	2826.176
S(sex+T)	*p*=*c*(t)	γ'(.),γ''(.)	20	2862.9812	8.320	0.0012	2822.003
S(DistW)	*p*=*c*(T)	γ'=γ''=0	10	2862.985	8.323	0.0012	2842.732
S(sex+ExWinter)	*p*=*c*(t)	γ'(.),γ''(.)	20	2862.987	8.326	0.0012	2822.009
S(IndHet)	*p*=*c*(t)	γ'(.),γ''(.)	19	2863.062	8.401	0.0011	2824.179
S(DistW)	*p*=*c*(T)	γ'(t)=γ''(t)	12	2863.114	8.453	0.0011	2838.754
S(DistW*t+sex)	*p*=*c*(T+sex)	γ'=γ''=0	19	2863.161	8.500	0.0011	2824.277
S(DistW*t)	*p*=*c*(t+sex)	γ'(t)=γ''(t)	27	2863.172	8.510	0.0011	2807.397
S(sex*IndHet)	*p*=*c*(t)	γ'(.),γ''(.)	21	2863.297	8.635	0.0010	2820.219

Abbreviations are as follows: "." = constant, "t" = time-varying, "T" = trend, "Season" = variation between seasons, "ExWinter" = difference following an extreme winter season, "DistW" = Euclidean distance to nearest water, "DistW2" = distance to nearest water squared, "IndHet" = individual heterozygosity.

[a]In all capture models, $p = c$ and the mean p across sessions was applied to individuals captured only at single-session sites.

[b]All capture models considered variation in p among sessions (primary sampling periods).

[c]For movement models, $\gamma'(t) = \gamma''(t)$ represents random movement and $\gamma' = \gamma'' = 0$ represents no movement.

Appendix 5.5

Ranking of Multi-Session Spatially Explicit Capture-Recapture Models Fit with the R Package 'secr' for Kit Fox (*Vulpes macrotis*) and Coyote (*Canis latrans*) Densities, 2013–2014. Model Support was Evaluated Based on Akaike's Information Criterion with Small Sample Size Correction (AIC_c). Each Model is Ranked Based on ΔAIC_c, where K = Number of Parameters, w_i = Akaike Weight, and LL = Log-Likelihood.

	Model[a,b]	K	AIC_c	ΔAIC_c	w_i	LL
Kit fox[c]						
	D(session)	20	3146.57	0	1	-1550.348
	D(session+SW)	21	3283.12	136.56	0	-1617.308
	D(session+SW+sex)	22	3283.77	137.20	0	-1616.296
	D(session+soil)	24	3285.05	138.48	0	-1614.206
	D(session*SW)	24	3291.10	144.53	0	-1617.233
	D(session*SW*sex)	32	3310.40	163.83	0	-1615.138
	D(session*soil)	36	3322.66	176.10	0	-1614.844
	D(session+habitat)	24	3340.95	194.38	0	-1642.157
	D(session+x+y)	22	3358.19	211.62	0	-1653.508
	D(session*x+y)	25	3362.83	216.26	0	-1651.704
	D(Session)	18	3364.84	218.27	0	-1662.060
	D(session+sex)	21	3368.19	221.62	0	-1659.841
	D(session*habitat)	36	3369.94	223.37	0	-1638.482
	D(session*sex)	24	3373.22	226.65	0	-1658.293
Coyote[d]						
	D(session)	44	9399.35	0	1	-4651.731
	D(session+x+y)	46	10128.05	728.70	0	-5013.702
	D(session+habitat)	48	10128.65	729.30	0	-5011.603
	D(session*SW)	48	10130.35	731.00	0	-5012.450
	D(Session)	42	10131.31	731.96	0	-5020.073

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D(session*x+y)	49	10134.78	735.43	0	-5013.461
D(session+SW)	45	10136.34	736.99	0	-5019.038
D(session+sex)	45	10136.71	737.36	0	-5019.222
D(session*habitat)	60	10136.71	737.36	0	-5000.824
D(session+SW+sex)	46	10139.02	739.67	0	-5019.184
D(session+soil)	48	10139.04	739.69	0	-5016.797
D(session*sex)	48	10142.46	743.11	0	-5018.508
D(session*SW*sex)	56	10146.45	747.10	0	-5010.712
D(session*soil)	60	10157.53	758.18	0	-5011.234

[a]Models for *g0* and σ (which jointly describe capture probability) are described in footnotes c and d.
[b]All models employed half-normal detection function.
[c]Capture probability modeled as *g0* ~ T*session and σ ~ T*session (T = trend)
[d]Capture probability modeled as *g0* ~ t*session and σ ~ t*session (t = time-varying)
Abbreviations are as follows: "session" = varying among sessions, "Session" = trend among sessions, "x+y" = linear trend surface, "habitat" = categorical habitat classifications, "SW" = proportion of site characterized as shrubland or woodland, "soil" = categorical soil classifications, "sex" = sex groupings. All models incorporating distance to water failed to converge for both species and are not included.

Appendix 6.1

Optimal Allocation of Sampling Effort for Coyotes (*Canis latrans*) and Kit Foxes (*Vulpes macrotis*) in Western Utah, USA, 2013–2014.

Although we aimed to investigate occupancy dynamics of kit foxes and coyotes, resource managers of the study area were particularly interested in the status of kit fox populations. Based on previous research in the region, we anticipated kit foxes had a more limited distribution and lower probability of detection than coyotes (Kozlowski et al. 2008, Dempsey et al. 2014), and we therefore aimed to establish a sampling design that would ensure kit foxes were adequately sampled. Probabilities of detection (p) and occurrence (ψ) for kit foxes were unknown, but we expected these to be lower than for coyotes. In order to approximate the sampling intensity required to achieve a standard error ≤ 0.05 (for ψ) and optimize allocation of effort, we employed methods presented in MacKenzie et al. (2006). We predicted $p = 0.5$ and $\psi = 0.3$ for kit foxes and evaluated the required effort (i.e., number of units) for values of p from 0.4–0.6 and values of ψ from 0.2–0.4, considering 2–4 surveys (K) per unit (Table 6.A1); we did not consider $K > 4$ due to the size of the desired sampling cells (6.25 km^2) and the requirement that K transects would need to be placed within each.

Across parameter values considered, ≥100 units would be required if conducting only $K = 2$ surveys (Table 6.A1). Increasing the number of surveys to $K = 3$, still produced optimal sampling requirements exceeding 100 units for the majority of parameter values considered, including the predicted values (Table 6.A1). When considering $K = 4$, 67–136 (mean = 96) units were required among parameter values considered, and >100 units was required for less than half of the parameters combinations (Table 6.A1). We suspected that it would be logistically impractical to survey more than ~100 units given the available

resources, and we therefore elected to employ $K = 4$ surveys and we aimed to survey ~100 units, exceeding the number of units required based on predicted estimates of p and ψ.

Table 6.A1. Number of sampling units required to achieve a standard error ≤0.05 under a range of estimates for the probability of detection (p) and probability of occurrence (ψ), under varying number of replicates (K), or surveys per unit for occupancy modeling. Bold values represent the estimated values for kit fox (*Vulpes macrotis*) in Utah, USA, 2013–2014.

		Sampling units required		
Detection (p)	Occupancy (ψ)	$K = 4$	$K = 3$	$K = 2$
0.6	0.2	67	72	100
0.5	0.2	71	84	144
0.4	0.2	84	113	244
0.6	0.3	88	96	137
0.5	**0.3**	**95**	**114**	**204**
0.4	0.3	114	158	354
0.6	0.4	101	112	167
0.5	0.4	111	136	256
0.4	0.4	136	194	456

References

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MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Inc, New York.

Appendix 6.2

Model Selection Results from Dynamic Single-Species Occupancy Models for Coyotes (*Canis latrans*) in Western Utah, USA, 2013–2014, Used to Identify the Most Supported Global Model Parameterization and to Subsequently Evaluate the Importance of Covariates on the Probabilities of Detection (*p*), Occurrence (ψ), and Local Extinction (ε) and Colonization (γ), with the Program MARK.

For Tables 6.A2–6.A5, abbreviations are as follows: DistW = distance to nearest water source (km) from a unit center, W2 = number of water sources within 2.5 km of a unit center, W5 = number of water sources within 5 km of a unit center, RTO = ordinal coding of road types, RTC = categorical coding of road types, RD = road density (km/km^2), Snow = binary presence or absence of snow during a survey of a unit, Sun = time between solar noon and survey start time (representing the relative angle of the sun), Date = days since surveys were initiated within a sampling session, SW = proportion of land cover attributable to shrubland and woodland habitats, t = time-varying. All model sets were evaluated with the program MARK based on Akaike's Information Criterion with small sample size correction (AIC_c). Each model was ranked based on ΔAIC_c, where K = number of parameters, w_i = Akaike weight, and LL = –2log(Likelihood).

Table 6.A2. Ranking of global dynamic single-species occupancy models for coyotes (*Canis latrans*). The model set included all possible combinations of water characterizations (where only a single characterization was used within a model) and road type characterizations. Water and road type characterizations were varied within the following global model: ψ (water + RD + SW), ε(t + water + RD + SW), γ (t + water + RD + SW), and p(t + Sun + Date + road type + Snow + RD).

Covariate characterization						
Water	Road type	K	AIC_c	ΔAIC_c	w_i	LL
W2	RTO	26	1942.96	0.00	0.725	1887.32
W2	RTC	27	1945.13	2.17	0.245	1887.19
DistW	RTO	26	1951.47	8.50	0.010	1895.82
W5	RTO	26	1951.6	8.64	0.009	1895.96
DistW	RTC	27	1952.62	9.66	0.006	1894.67
W5	RTC	27	1953.52	10.56	0.004	1895.58

Table 6.A3. Ranking of coyote (*Canis latrans*) detection (*p*) models for dynamic single-species models. The model set included all possible combinations of detection covariates and time variation. Across detection models, models for occupancy (ψ), extinction (ε), and colonization (γ) were held constant at their best supported global models: ψ (W2 + RD + SW), ε(t + W2 + RD + SW), and γ (t + W2 + RD + SW).

Detection (*p*) model	K	AIC_c	ΔAIC_c	w_i	LL
p(Sun+RTO+Snow+RD)	21	1937.34	0.00	0.202	1892.97
p(Sun+Date+RTO+Snow+RD)	23	1937.47	0.13	0.189	1888.63
p(Date+RTO+Snow+RD)	22	1938.14	0.80	0.135	1891.54
p(t+Sun+RTO+RD)	23	1938.80	1.46	0.098	1889.95
p(RTO+Snow+RD)	20	1939.41	2.07	0.072	1897.26
p(t+Sun+RTO+Snow+RD)	24	1939.62	2.28	0.065	1888.52
p(t+RTO+RD)	22	1940.59	3.25	0.040	1893.98
p(t+RTO+Snow+RD)	23	1941.14	3.80	0.030	1892.30
p(Sun+RTO+Snow)	20	1941.80	4.46	0.022	1899.66
p(t+Sun+RTO)	22	1942.34	5.00	0.017	1895.74
p(t+Sun+Date+RTO+RD)	25	1942.37	5.03	0.016	1889.00
p(Sun+Date+RTO+Snow)	22	1942.39	5.05	0.016	1895.79
p(Sun+Date+RTO+RD)	22	1942.88	5.54	0.013	1896.28
p(t+Sun+Date+RTO+Snow+RD)	26	1942.96	5.62	0.012	1887.32
p(t+Date+RTO+RD)	24	1943.05	5.71	0.012	1891.95
p(Date+RTO+Snow)	21	1943.30	5.96	0.010	1898.93
p(Date+RTO+RD)	21	1943.50	6.16	0.009	1899.13
p(t+Date+RTO+Snow+RD)	25	1943.52	6.18	0.009	1890.15
p(RTO+Snow)	19	1944.25	6.91	0.006	1904.31
p(t+RTO)	21	1944.61	7.27	0.005	1900.24
p(t+Sun+RTO+Snow)	23	1944.99	7.65	0.004	1896.14
p(t+Sun+Date+RTO)	24	1945.00	7.66	0.004	1893.90
p(t+Date+RTO)	23	1945.89	8.55	0.003	1897.04
p(t+Sun+Date+RTO+Snow)	25	1945.89	8.55	0.003	1892.52

Table 6.A3, cont'd					
p(t+Date+RTO+Snow)	24	1946.63	9.29	0.002	1895.53
p(Sun+Date+RTO)	21	1946.75	9.41	0.002	1902.38
p(t+RTO+Snow)	22	1947.06	9.72	0.002	1900.46
p(Date+RTO)	20	1947.36	10.02	0.001	1905.21
p(Sun+RTO+RD)	20	1951.78	14.44	0.000	1909.63
p(RTO+RD)	19	1955.30	17.96	0.000	1915.36
p(Sun+RTO)	19	1957.96	20.62	0.000	1918.02
p(t+Sun+RD)	22	1958.63	21.29	0.000	1912.03
p(RTO)	18	1959.61	22.27	0.000	1921.87
p(t+RD)	21	1960.35	23.01	0.000	1915.98
p(t+Sun+Snow+RD)	23	1960.81	23.47	0.000	1911.97
p(t+Sun+Date+RD)	24	1961.73	24.39	0.000	1910.63
p(Sun+Date+Snow+RD)	22	1961.90	24.56	0.000	1915.30
p(Date+RD+Snow)	21	1962.08	24.74	0.000	1917.71
p(t+Date+RD)	23	1962.30	24.96	0.000	1913.45
p(t+Snow+RD)	22	1962.45	25.11	0.000	1915.84
p(t+Sun+Date+Snow+RD)	25	1963.94	26.60	0.000	1910.57
p(t+Date+Snow+RD)	24	1964.44	27.10	0.000	1913.34
p(t+Sun)	21	1965.75	28.41	0.000	1921.38
p(t)	20	1965.81	28.47	0.000	1923.66
p(Sun+Date+RD)	21	1965.82	28.48	0.000	1921.45
p(Date+RD)	20	1965.91	28.57	0.000	1923.76
p(t+Sun+Date)	23	1966.29	28.95	0.000	1917.45
p(t+Date+Snow)	23	1966.30	28.96	0.000	1917.45
p(t+Date)	22	1966.52	29.18	0.000	1919.92
p(Date+Snow)	20	1966.58	29.24	0.000	1924.43
p(Snow+RD)	19	1966.80	29.46	0.000	1926.86
p(t+Snow)	21	1967.54	30.21	0.000	1923.18

Table 6.A3, cont'd					
p(t+Sun+Snow)	22	1967.57	30.23	0.000	1920.96
p(Sun+Snow+RD)	20	1968.14	30.80	0.000	1925.99
p(Sun+Date+Snow)	21	1968.51	31.17	0.000	1924.14
p(t+Sun+Date+Snow)	24	1970.65	33.31	0.000	1919.55
p(Sun+Snow)	19	1970.69	33.35	0.000	1930.75
p(Date)	19	1970.77	33.43	0.000	1930.83
p(Snow)	18	1972.53	35.19	0.000	1934.79
p(Sun+Date)	20	1974.55	37.21	0.000	1932.40
p(Sun+RD)	19	1980.17	42.83	0.000	1940.23
p(RD)	18	1981.70	44.36	0.000	1943.96
p(.)	17	1988.05	50.71	0.000	1952.50
p(Sun)	18	1990.24	52.90	0.000	1952.50

Table 6.A4. Ranking of coyote (*Canis latrans*) occupancy (ψ) models for dynamic single-species models. The model set included all possible combinations of occupancy covariates. Across occupancy models, the best fit detection (*p*) model and global extinction (ε) and colonization (γ) models were held constant at *p*(Sun + RTO + Snow + RD), ε(t + W2 + RD + SW), and γ (t + W2 + RD + SW), respectively.

Occupancy (ψ) model	K	AIC_c	ΔAIC_c	w_i	LL
ψ(RD+SW)	20	1935.93	0.00	0.570	1893.78
ψ(W2+RD+SW)	21	1937.34	1.41	0.282	1892.97
ψ(SW)	19	1939.24	3.31	0.109	1899.30
ψ(W2+SW)	20	1941.30	5.37	0.039	1899.15
ψ(.)	18	1954.59	18.66	0.000	1916.85
ψ(W2)	19	1954.63	18.70	0.000	1914.69
ψ(RD)	19	1956.55	20.62	0.000	1916.61
ψ(W2+RD)	20	1959.65	23.73	0.000	1917.51

Table 6.A5. Concurrent ranking of coyote (*Canis latrans*) local extinction (ε) and colonization (γ) models for dynamic single-species models. The model set included all possible combinations of extinction and colonization covariates both within and between each parameter. Across models fit, the best fit detection (*p*) and occupancy (ψ) models were held constant at *p*(Sun + RTO + Snow + RD) and ψ(RD + SW), respectively.

Extinction (ε) model	Colonization (γ) model	K	AIC_c	ΔAIC_c	w_i	LL
ε(W2+SW)	γ(t+W2+SW)	16	1933.47	0.00	0.058	1900.09
ε(t+W2+SW)	γ(t+W2+RD+SW)	19	1933.72	0.25	0.051	1898.02
ε(t+W2+RD+SW)	γ(t+W2+SW)	19	1934.07	0.60	0.043	1894.13
ε(W2+RD+SW)	γ(t+W2+SW)	17	1934.75	1.28	0.031	1899.20
ε(t+W2+RD+SW)	γ(t+SW)	18	1934.92	1.45	0.028	1897.18
ε(t+W2+RD+SW)	γ(.)	15	1935.35	1.88	0.023	1904.14
ε(W2)	γ(t+W2+SW)	15	1935.36	1.89	0.023	1904.15
ε(W2)	γ(.)	11	1935.45	1.98	0.022	1912.79
ε(t+W2+RD)	γ(t+W2+SW)	18	1935.50	2.03	0.021	1897.76
ε(W2+RD)	γ(t+W2+RD+SW)	17	1935.66	2.19	0.019	1900.11
ε(W2+SW)	γ(.)	12	1935.79	2.32	0.018	1911.01
ε(W2+SW)	γ(t+SW)	15	1935.86	2.39	0.018	1904.65
ε(t+W2+RD+SW)	γ(t)	17	1935.91	2.44	0.017	1900.35
ε(t+W2+RD+SW)	γ(t+W2+RD+SW)	20	1935.93	2.46	0.017	1893.78
ε(W2+SW)	γ(t+RD)	15	1936.07	2.59	0.016	1904.85
ε(t+W2+RD)	γ(t+SW)	17	1936.09	2.62	0.016	1900.54
ε(W2)	γ(RD)	12	1936.13	2.66	0.015	1911.35
ε(t+W2+SW)	γ(t+W2+SW)	18	1936.14	2.67	0.015	1898.40
ε(W2+SW)	γ(RD)	13	1936.29	2.82	0.014	1909.38
ε(W2+RD)	γ(t+W2+SW)	16	1936.43	2.95	0.013	1903.05
ε(t+W2+SW)	γ(t+SW)	17	1936.44	2.97	0.013	1900.89
ε(W2)	γ(t+RD)	14	1936.45	2.98	0.013	1907.39
ε(t+W2+RD+SW)	γ(RD)	16	1936.79	3.32	0.011	1903.41
ε(t+W2)	γ(t+SW)	16	1936.92	3.45	0.010	1903.54

Table 6.A5, cont'd

ε(W2)	γ(W2+SW)	13	1936.98	3.51	0.010	1910.07
ε(t+W2+RD+SW)	γ(t+RD+SW)	19	1937.04	3.57	0.010	1897.10
ε(W2+RD)	γ(.)	12	1937.10	3.63	0.010	1912.31
ε(t+W2)	γ(.)	13	1937.18	3.71	0.009	1910.27
ε(W2)	γ(W2)	12	1937.21	3.74	0.009	1912.43
ε(t+W2+RD)	γ(t)	16	1937.21	3.74	0.009	1903.83
ε(W2+RD+SW)	γ(.)	13	1937.23	3.76	0.009	1910.31
ε(W2)	γ(t+SW)	14	1937.29	3.82	0.009	1908.23
ε(t+W2+RD+SW)	γ(SW)	16	1937.32	3.85	0.009	1903.94
ε(t+W2+RD)	γ(t+W2+RD+SW)	19	1937.39	3.92	0.008	1897.46
ε(W2+RD+SW)	γ(t+RD)	16	1937.45	3.98	0.008	1904.07
ε(t+W2+RD+SW)	γ(W2)	16	1937.47	4.00	0.008	1904.09
ε(W2)	γ(SW)	12	1937.49	4.02	0.008	1912.71
ε(W2+SW)	γ(W2)	13	1937.52	4.05	0.008	1910.61
ε(W2)	γ(W2+RD)	13	1937.60	4.13	0.007	1910.69
ε(W2+SW)	γ(W2+RD)	14	1937.61	4.14	0.007	1908.55
ε(t+W2+RD+SW)	γ(W2+RD)	17	1937.62	4.15	0.007	1902.06
ε(t+W2+RD)	γ(.)	14	1937.63	4.16	0.007	1908.57
ε(W2+SW)	γ(SW)	13	1937.67	4.20	0.007	1910.76
ε(t+W2)	γ(t)	15	1937.68	4.21	0.007	1906.47
ε(t+W2+SW)	γ(.)	14	1937.70	4.23	0.007	1908.64
ε(t+W2+RD+SW)	γ(t+W2)	18	1937.74	4.26	0.007	1900.00
ε(t+W2+RD+SW)	γ(t+RD)	18	1937.75	4.28	0.007	1900.01
ε(t+W2)	γ(t+W2+SW)	17	1937.76	4.28	0.007	1902.20
ε(W2+RD+SW)	γ(RD)	14	1937.77	4.30	0.007	1908.72
ε(W2+SW)	γ(t+W2)	15	1937.87	4.40	0.006	1906.66
ε(t+W2)	γ(RD)	14	1937.87	4.40	0.006	1908.82
ε(W2+SW)	γ(RD+SW)	14	1937.91	4.44	0.006	1908.85

Table 6.A5, cont'd

ε(W2+RD)	γ(RD)	13	1937.94	4.47	0.006	1911.03
ε(W2)	γ(RD+SW)	13	1937.95	4.48	0.006	1911.04
ε(t+W2+RD+SW)	γ(RD+SW)	17	1938.05	4.58	0.006	1902.49
ε(W2+SW)	γ(t+W2+RD)	16	1938.05	4.58	0.006	1904.67
ε(t+W2+SW)	γ(t)	16	1938.07	4.60	0.006	1904.69
ε(W2+SW)	γ(t+RD+SW)	16	1938.09	4.62	0.006	1904.71
ε(W2)	γ(t)	13	1938.11	4.64	0.006	1911.19
ε(W2)	γ(t+W2)	14	1938.15	4.68	0.006	1909.10
ε(W2+RD)	γ(t+RD)	15	1938.21	4.74	0.005	1907.00
ε(t+W2+SW)	γ(RD)	15	1938.25	4.78	0.005	1907.04
ε(t+W2+RD)	γ(t+RD+SW)	18	1938.27	4.80	0.005	1900.53
ε(t+W2)	γ(W2+SW)	15	1938.32	4.85	0.005	1907.11
ε(t+W2+SW)	γ(t+RD+SW)	18	1938.33	4.86	0.005	1900.59
ε(W2)	γ(t+W2+RD)	15	1938.36	4.89	0.005	1907.15
ε(t+W2+RD)	γ(t+W2)	17	1938.38	4.91	0.005	1902.83
ε(W2+SW)	γ(t)	14	1938.40	4.93	0.005	1909.34
ε(W2)	γ(t+RD+SW)	15	1938.43	4.96	0.005	1907.22
ε(W2+RD+SW)	γ(t+SW)	16	1938.53	5.06	0.005	1905.15
ε(t+W2)	γ(t+W2)	16	1938.53	5.06	0.005	1905.15
ε(W2+RD)	γ(W2+SW)	14	1938.57	5.10	0.005	1909.51
ε(W2+RD)	γ(t+RD+SW)	16	1938.70	5.22	0.004	1905.32
ε(t+W2)	γ(W2)	14	1938.77	5.30	0.004	1909.72
ε(t+W2+RD)	γ(RD)	15	1938.78	5.31	0.004	1907.57
ε(t+W2)	γ(t+RD+SW)	17	1938.78	5.31	0.004	1903.23
ε(W2+RD)	γ(W2)	13	1938.91	5.44	0.004	1912.00
ε(W2+RD+SW)	γ(W2+RD)	15	1938.94	5.47	0.004	1907.73
ε(W2+RD+SW)	γ(W2)	14	1939.05	5.58	0.004	1909.99
ε(W2+RD+SW)	γ(SW)	14	1939.12	5.65	0.003	1910.06

Table 6.A5, cont'd

ε(t+W2)	γ(W2+RD)	15	1939.16	5.69	0.003	1907.95
ε(W2+RD)	γ(SW)	13	1939.16	5.69	0.003	1912.25
ε(t+W2+SW)	γ(t+RD)	17	1939.18	5.71	0.003	1903.63
ε(W2+RD+SW)	γ(RD+SW)	15	1939.21	5.74	0.003	1908.00
ε(t+W2+SW)	γ(t+W2)	17	1939.24	5.77	0.003	1903.69
ε(W2+RD+SW)	γ(t+RD+SW)	17	1939.25	5.78	0.003	1903.69
ε(t+W2)	γ(SW)	14	1939.26	5.79	0.003	1910.20
ε(t+W2+RD)	γ(t+RD)	17	1939.34	5.87	0.003	1903.79
ε(t+W2+SW)	γ(W2)	15	1939.36	5.89	0.003	1908.15
ε(W2+RD)	γ(W2+RD)	14	1939.39	5.92	0.003	1910.33
ε(W2+RD+SW)	γ(t+W2+RD)	17	1939.40	5.93	0.003	1903.84
ε(t+W2+SW)	γ(W2+RD)	16	1939.40	5.93	0.003	1906.02
ε(t+W2+RD+SW)	γ(W2+SW)	17	1939.48	6.01	0.003	1903.92
ε(t+W2+RD+SW)	γ(W2+RD+SW)	18	1939.53	6.06	0.003	1901.79
ε(t+W2)	γ(RD+SW)	15	1939.54	6.07	0.003	1908.33
ε(t+W2+RD)	γ(W2+RD)	16	1939.60	6.13	0.003	1906.22
ε(t+W2+RD)	γ(W2)	15	1939.60	6.13	0.003	1908.39
ε(t+W2)	γ(t+W2+RD+SW)	18	1939.60	6.13	0.003	1901.86
ε(W2+RD+SW)	γ(t+W2)	16	1939.61	6.14	0.003	1906.23
ε(W2+RD)	γ(t)	14	1939.63	6.16	0.003	1910.58
ε(t+W2)	γ(t+RD)	16	1939.64	6.16	0.003	1906.26
ε(W2+SW)	γ(W2+SW)	14	1939.66	6.19	0.003	1910.60
ε(t+W2+SW)	γ(SW)	15	1939.67	6.20	0.003	1908.46
ε(W2+SW)	γ(W2+RD+SW)	15	1939.68	6.21	0.003	1908.47
ε(W2+RD)	γ(RD+SW)	14	1939.72	6.25	0.003	1910.66
ε(W2+RD+SW)	γ(t)	15	1939.73	6.26	0.003	1908.52
ε(t+W2+RD)	γ(SW)	15	1939.74	6.27	0.003	1908.52
ε(W2)	γ(W2+RD+SW)	14	1939.74	6.27	0.003	1910.68

Table 6.A5, cont'd

ε(t+W2+SW)	γ(RD+SW)	16	1939.76	6.29	0.003	1906.38
ε(t+W2+RD+SW)	γ(t+W2+RD)	19	1939.76	6.29	0.003	1899.82
ε(t+W2)	γ(t+W2+RD)	17	1939.91	6.44	0.002	1904.35
ε(W2+RD)	γ(t+W2)	15	1939.92	6.45	0.002	1908.70
ε(t+W2+RD)	γ(W2+SW)	16	1939.96	6.49	0.002	1906.59
ε(W2+SW)	γ(t+W2+RD+SW)	17	1940.06	6.59	0.002	1904.50
ε(t+W2+RD)	γ(RD+SW)	16	1940.12	6.65	0.002	1906.75
ε(W2+RD)	γ(t+W2+RD)	16	1940.13	6.66	0.002	1906.76
ε(W2)	γ(t+W2+RD+SW)	16	1940.24	6.77	0.002	1906.86
ε(t+W2+RD)	γ(t+W2+RD)	18	1940.52	7.04	0.002	1902.78
ε(t+W2+SW)	γ(t+W2+RD)	18	1940.62	7.15	0.002	1902.88
ε(W2+RD)	γ(t+SW)	15	1940.79	7.32	0.002	1909.57
ε(W2+RD+SW)	γ(W2+RD+SW)	16	1940.95	7.48	0.001	1907.57
ε(W2+RD+SW)	γ(W2+SW)	15	1941.19	7.72	0.001	1909.97
ε(W2+RD+SW)	γ(t+W2+RD+SW)	18	1941.24	7.77	0.001	1903.50
ε(t+W2)	γ(W2+RD+SW)	16	1941.25	7.78	0.001	1907.87
ε(t+W2+SW)	γ(W2+RD+SW)	17	1941.43	7.96	0.001	1905.87
ε(t+W2+SW)	γ(W2+SW)	16	1941.51	8.04	0.001	1908.13
ε(W2+RD)	γ(W2+RD+SW)	15	1941.52	8.05	0.001	1910.31
ε(t+W2+RD)	γ(W2+RD+SW)	17	1941.58	8.10	0.001	1906.02
ε(.)	γ(.)	10	1948.12	14.65	0.000	1927.57
ε(t)	γ(t+SW)	15	1949.41	15.93	0.000	1918.19
ε(t+SW)	γ(t+SW)	16	1949.41	15.94	0.000	1916.03
ε(RD)	γ(t+RD+SW)	15	1949.69	16.22	0.000	1918.48
ε(.)	γ(RD)	11	1949.70	16.23	0.000	1927.04
ε(SW)	γ(.)	11	1949.71	16.24	0.000	1927.05
ε(t)	γ(t)	14	1949.73	16.26	0.000	1920.67
ε(.)	γ(t+SW)	13	1949.98	16.50	0.000	1923.06

Table 6.A5, cont'd

ε(.)	γ(W2)	11	1950.18	16.71	0.000	1927.52
ε(.)	γ(t)	12	1950.19	16.72	0.000	1925.40
ε(RD)	γ(.)	11	1950.21	16.74	0.000	1927.55
ε(.)	γ(SW)	11	1950.22	16.75	0.000	1927.56
ε(t)	γ(.)	12	1950.36	16.89	0.000	1925.58
ε(t+SW)	γ(t)	15	1950.47	17.00	0.000	1919.26
ε(t+SW)	γ(t+W2+SW)	17	1950.49	17.02	0.000	1914.94
ε(RD)	γ(t+W2+RD+SW)	16	1950.65	17.18	0.000	1917.28
ε(SW)	γ(t+SW)	14	1951.01	17.54	0.000	1921.95
ε(t+SW)	γ(t+RD+SW)	17	1951.03	17.56	0.000	1915.48
ε(t)	γ(t+RD+SW)	16	1951.11	17.64	0.000	1917.74
ε(.)	γ(t+W2+SW)	14	1951.23	17.76	0.000	1922.18
ε(SW)	γ(RD)	12	1951.29	17.82	0.000	1926.51
ε(t+RD+SW)	γ(t+SW)	17	1951.53	18.06	0.000	1915.98
ε(t+RD)	γ(t+SW)	16	1951.57	18.10	0.000	1918.19
ε(t)	γ(t+W2+SW)	16	1951.57	18.10	0.000	1918.19
ε(t+SW)	γ(.)	13	1951.58	18.11	0.000	1924.67
ε(t)	γ(t+RD)	15	1951.72	18.25	0.000	1920.50
ε(RD)	γ(RD)	12	1951.73	18.26	0.000	1926.94
ε(t)	γ(t+W2)	15	1951.74	18.27	0.000	1920.53
ε(SW)	γ(t)	13	1951.76	18.29	0.000	1924.84
ε(SW)	γ(SW)	12	1951.78	18.31	0.000	1927.00
ε(.)	γ(W2+RD)	12	1951.79	18.32	0.000	1927.01
ε(SW)	γ(W2)	12	1951.80	18.33	0.000	1927.02
ε(RD+SW)	γ(.)	12	1951.81	18.34	0.000	1927.03
ε(.)	γ(RD+SW)	12	1951.82	18.34	0.000	1927.03
ε(t+RD)	γ(t)	15	1951.87	18.40	0.000	1920.66
ε(SW)	γ(t+W2+SW)	15	1951.99	18.52	0.000	1920.78

Table 6.A5, cont'd

ε(t)	γ(RD)	13	1952.08	18.61	0.000	1925.16
ε(RD)	γ(t+SW)	14	1952.11	18.64	0.000	1923.05
ε(.)	γ(t+RD)	13	1952.21	18.74	0.000	1925.30
ε(.)	γ(W2+SW)	12	1952.25	18.78	0.000	1927.47
ε(RD)	γ(W2)	12	1952.28	18.81	0.000	1927.50
ε(RD)	γ(t)	13	1952.30	18.83	0.000	1925.39
ε(.)	γ(t+W2)	13	1952.31	18.84	0.000	1925.39
ε(RD)	γ(SW)	12	1952.33	18.86	0.000	1927.54
ε(.)	γ(t+RD+SW)	14	1952.35	18.88	0.000	1923.29
ε(SW)	γ(t+RD+SW)	15	1952.36	18.89	0.000	1921.15
ε(t+RD+SW)	γ(t+W2+SW)	18	1952.40	18.92	0.000	1914.65
ε(t)	γ(W2)	13	1952.42	18.95	0.000	1925.51
ε(t+SW)	γ(t+RD)	16	1952.44	18.97	0.000	1919.06
ε(t)	γ(SW)	13	1952.46	18.99	0.000	1925.55
ε(t+RD)	γ(.)	13	1952.47	19.00	0.000	1925.55
ε(t+SW)	γ(t+W2)	16	1952.47	19.00	0.000	1919.10
ε(t+RD+SW)	γ(t)	16	1952.63	19.16	0.000	1919.26
ε(RD+SW)	γ(t+SW)	15	1953.17	19.69	0.000	1921.95
ε(t+RD+SW)	γ(t+RD+SW)	18	1953.22	19.75	0.000	1915.48
ε(t+SW)	γ(t+W2+RD+SW)	18	1953.22	19.75	0.000	1915.48
ε(t+RD)	γ(t+RD+SW)	17	1953.24	19.77	0.000	1917.69
ε(t)	γ(t+W2+RD+SW)	17	1953.27	19.80	0.000	1917.71
ε(t+SW)	γ(RD)	14	1953.31	19.84	0.000	1924.25
ε(.)	γ(t+W2+RD+SW)	15	1953.33	19.86	0.000	1922.12
ε(RD+SW)	γ(RD)	13	1953.34	19.87	0.000	1926.43
ε(SW)	γ(W2+RD)	13	1953.37	19.90	0.000	1926.45
ε(SW)	γ(RD+SW)	13	1953.38	19.91	0.000	1926.46
ε(RD)	γ(t+W2+SW)	15	1953.38	19.91	0.000	1922.17

Table 6.A5, cont'd

ε(SW)	γ(t+W2+RD+SW)	16	1953.61	20.14	0.000	1920.24
ε(t+SW)	γ(SW)	14	1953.63	20.15	0.000	1924.57
ε(t+SW)	γ(W2)	14	1953.67	20.20	0.000	1924.61
ε(SW)	γ(t+RD)	14	1953.71	20.24	0.000	1924.65
ε(t+RD+SW)	γ(.)	14	1953.72	20.25	0.000	1924.66
ε(t)	γ(t+W2+RD)	16	1953.74	20.27	0.000	1920.36
ε(t+RD)	γ(t+W2+SW)	17	1953.74	20.27	0.000	1918.19
ε(SW)	γ(W2+SW)	13	1953.81	20.34	0.000	1926.89
ε(RD)	γ(W2+RD)	13	1953.82	20.35	0.000	1926.90
ε(t+RD)	γ(t+RD)	16	1953.82	20.35	0.000	1920.44
ε(RD)	γ(RD+SW)	13	1953.85	20.38	0.000	1926.94
ε(SW)	γ(t+W2)	14	1953.88	20.41	0.000	1924.82
ε(RD+SW)	γ(SW)	13	1953.89	20.42	0.000	1926.98
ε(RD+SW)	γ(t)	14	1953.89	20.42	0.000	1924.84
ε(t+RD)	γ(t+W2)	16	1953.90	20.43	0.000	1920.52
ε(RD+SW)	γ(W2)	13	1953.92	20.45	0.000	1927.00
ε(.)	γ(W2+RD+SW)	13	1953.92	20.45	0.000	1927.01
ε(t)	γ(W2+RD)	14	1954.05	20.57	0.000	1924.99
ε(t)	γ(RD+SW)	14	1954.09	20.62	0.000	1925.03
ε(RD+SW)	γ(t+W2+SW)	16	1954.14	20.67	0.000	1920.76
ε(t+RD)	γ(RD)	14	1954.15	20.67	0.000	1925.09
ε(RD)	γ(t+RD)	14	1954.24	20.76	0.000	1925.18
ε(.)	γ(t+W2+RD)	14	1954.36	20.88	0.000	1925.30
ε(RD)	γ(W2+SW)	13	1954.36	20.89	0.000	1927.45
ε(RD)	γ(t+W2)	14	1954.43	20.96	0.000	1925.37
ε(t)	γ(W2+SW)	14	1954.43	20.96	0.000	1925.37
ε(t+SW)	γ(t+W2+RD)	17	1954.46	20.99	0.000	1918.91
ε(RD+SW)	γ(t+RD+SW)	16	1954.51	21.04	0.000	1921.14

Table 6.A5, cont'd

ε(t+RD)	γ(W2)	14	1954.55	21.07	0.000	1925.49
ε(t+RD)	γ(SW)	14	1954.58	21.11	0.000	1925.53
ε(t+RD+SW)	γ(t+RD)	17	1954.60	21.13	0.000	1919.05
ε(t+RD+SW)	γ(t+W2)	17	1954.65	21.18	0.000	1919.10
ε(t+SW)	γ(W2+RD)	15	1955.22	21.75	0.000	1924.01
ε(t+SW)	γ(RD+SW)	15	1955.24	21.76	0.000	1924.02
ε(t+RD)	γ(t+W2+RD+SW)	18	1955.40	21.93	0.000	1917.66
ε(t+RD+SW)	γ(t+W2+RD+SW)	19	1955.42	21.94	0.000	1915.48
ε(RD+SW)	γ(W2+RD)	14	1955.42	21.95	0.000	1926.36
ε(t+RD+SW)	γ(RD)	15	1955.44	21.96	0.000	1924.22
ε(RD+SW)	γ(RD+SW)	14	1955.45	21.98	0.000	1926.39
ε(SW)	γ(W2+RD+SW)	14	1955.50	22.03	0.000	1926.45
ε(t+SW)	γ(W2+SW)	15	1955.58	22.11	0.000	1924.37
ε(RD+SW)	γ(t+RD)	15	1955.76	22.29	0.000	1924.55
ε(t+RD+SW)	γ(SW)	15	1955.78	22.31	0.000	1924.56
ε(RD+SW)	γ(t+W2+RD+SW)	17	1955.78	22.31	0.000	1920.23
ε(t+RD+SW)	γ(W2)	15	1955.82	22.35	0.000	1924.61
ε(SW)	γ(t+W2+RD)	15	1955.86	22.39	0.000	1924.64
ε(t+RD)	γ(t+W2+RD)	17	1955.86	22.39	0.000	1920.31
ε(RD+SW)	γ(W2+SW)	14	1955.93	22.46	0.000	1926.88
ε(RD)	γ(W2+RD+SW)	14	1955.96	22.49	0.000	1926.90
ε(RD+SW)	γ(t+W2)	15	1956.02	22.55	0.000	1924.81
ε(t+RD)	γ(W2+RD)	15	1956.13	22.66	0.000	1924.92
ε(t+RD)	γ(RD+SW)	15	1956.19	22.72	0.000	1924.97
ε(RD)	γ(t+W2+RD)	15	1956.39	22.92	0.000	1925.18
ε(t)	γ(W2+RD+SW)	15	1956.40	22.93	0.000	1925.19
ε(t+RD)	γ(W2+SW)	15	1956.57	23.09	0.000	1925.35
ε(t+RD+SW)	γ(t+W2+RD)	18	1956.64	23.17	0.000	1918.90

Table 6.A5, cont'd

ε(t+SW)	γ(W2+RD+SW)	16	1957.29	23.82	0.000	1923.91
ε(t+RD+SW)	γ(W2+RD)	16	1957.37	23.90	0.000	1923.99
ε(t+RD+SW)	γ(RD+SW)	16	1957.39	23.92	0.000	1924.01
ε(RD+SW)	γ(W2+RD+SW)	15	1957.57	24.10	0.000	1926.36
ε(t+RD+SW)	γ(W2+SW)	16	1957.74	24.27	0.000	1924.37
ε(RD+SW)	γ(t+W2+RD)	16	1957.92	24.45	0.000	1924.54
ε(t+RD)	γ(W2+RD+SW)	16	1958.27	24.79	0.000	1924.89
ε(t+RD+SW)	γ(W2+RD+SW)	17	1959.45	25.98	0.000	1923.90

Appendix 6.3

Model Selection Results from Dynamic Single-Species Occupancy Models for Kit Foxes (*Vulpes macrotis*) in Western Utah, USA, 2013–2014, Used to Identify the Most Supported Global Model Parameterization and to Subsequently Evaluate the Importance of Covariates (Including Indices of Coyote [*Canis latrans*] Activity) on the Probabilities of Detection (*p*), Occurrence (ψ), and Local Extinction (ε) and Colonization (γ), with the Program MARK.

Tables 6.A6–6.A9, abbreviations are as follows: DistW = distance to nearest water source (km) from a unit center, W2 = number of water sources within 2.5 km of a unit center, W5 = number of water sources within 5 km of a unit center, RTO = ordinal coding of road types, RTC = categorical coding of road types, RD = road density (km/km^2), Snow = binary presence or absence of snow during a survey of a unit, Sun = time between solar noon and survey start time (representing the relative angle of the sun), Date = days since surveys were initiated within a sampling session, SW = proportion of land cover attributable to shrubland and woodland habitats, Soil = categorical classification of the majority soil type for a unit (four types: silt, fine sand, blocky loam, or gravelly), CS = total number of coyote scats detected at the unit level by session, CT = total number of transects on which coyotes were detected at the unit level by session, CA = number of coyote scats detected at the transect level by session, CP = binary detection (1) or non-detection (0) of coyotes at the transect level by session, t = time-varying. Unit level characterizations of coyote activity (CS and CT) applied only to ψ, ε, and γ, with models for ε and γ using the CS or CT value of the preceding sampling session. Survey level characterizations of coyote activity (CA and CP) applied only to *p*.

Table 6.A6. Ranking of global dynamic single-species occupancy models for kit foxes (*Vulpes macrotis*). The model set included all possible combinations of water characterizations (where only a single characterization was used within a model), road type characterizations, and coyote activity characterizations at the unit (for ψ, ε, and γ) and survey (for *p*) levels. Characterizations of water, road type, and coyote indices varied within the following global model: ψ (Soil + RD + SW + unit level coyote index + water), ε(t + Soil + RD + SW + unit level coyote index + water), γ (t + Soil + RD + SW + unit level coyote index + water), and p(s + Day + Sun + Snow + RD + road type + survey level coyote index).

Covariate characterization								
Water	Road type	Coyote index (unit)	Coyote index (survey)	K	AIC_c	ΔAIC_c	w_i	LL
DistW	RTO	CS	CA	39	944.12	0.00	0.678	857.73
W5	RTO	CT	CP	39	948.63	4.51	0.071	862.24
W5	RTC	CT	CA	40	948.82	4.70	0.065	859.98
W5	RTC	CT	CP	40	949.57	5.45	0.044	860.73
W2	RTO	CS	CP	39	949.86	5.74	0.039	863.47
W2	RTC	CS	CP	40	950.16	6.04	0.033	861.32
W2	RTO	CT	CA	39	951.49	7.37	0.017	865.11
DistW	RTO	CS	CP	39	952.73	8.61	0.009	866.34
W2	RTC	CT	CA	40	952.76	8.64	0.009	863.92
W2	RTO	CT	CP	39	952.87	8.75	0.009	866.49
W2	RTC	CT	CP	40	953.73	9.61	0.006	864.89
DistW	RTO	CT	CA	39	953.86	9.74	0.005	867.48
DistW	RTC	CS	CP	40	954.60	10.48	0.004	865.76
DistW	RTC	CT	CA	40	954.87	10.75	0.003	866.03
DistW	RTC	CT	CP	40	955.35	11.23	0.002	866.51
DistW	RTO	CT	CP	39	955.99	11.87	0.002	869.61
W5	RTO	CS	CA	39	956.20	12.07	0.002	869.81
W5	RTO	CS	CP	39	956.95	12.83	0.001	870.57
W5	RTC	CS	CA	40	957.72	13.59	0.001	868.87
W5	RTC	CS	CP	40	958.06	13.94	0.001	869.22

Table 6.A7. Ranking of kit fox (*Vulpes macrotis*) detection (*p*) models for dynamic single-species models. The model set included all possible combinations of detection covariates and time variation. Across detection models, models for occupancy (ψ), extinction (ε), and colonization (γ) were held constant at their best supported global models: ψ (Soil + RD + SW + CS + DistW), ε(t + Soil + RD + SW + CS + DistW), and γ (t + Soil + RD + SW + CS + DistW).

Detection (*p*) model	K	AIC_c	ΔAIC_c	w_i	LL
p(RTO+CA)	31	941.47	0.00	0.206	874.24
p(Sun+RTO+CA)	32	943.58	2.12	0.071	874.01
p(Snow+RTO+CA)	32	943.73	2.26	0.066	874.16
p(RD+RTO+CA)	32	943.81	2.34	0.064	874.24
p(Date+RTO+CA)	33	944.04	2.58	0.057	872.11
p(RD+CA)	31	944.48	3.02	0.046	877.26
p(Snow+CA)	31	944.48	3.02	0.046	877.26
p(Date+Sun+RTO+CA)	34	944.66	3.20	0.042	870.35
p(Date+CA)	32	945.25	3.79	0.031	875.68
p(Sun+Snow+RTO+CA)	33	945.41	3.95	0.029	873.48
p(t+Date+RTO+CA)	36	945.70	4.24	0.025	866.60
p(Sun+RD+RTO+CA)	33	945.94	4.48	0.022	874.01
p(Snow+RD+RTO+CA)	33	946.09	4.63	0.020	874.15
p(Date+RD+RTO+CA)	34	946.30	4.83	0.018	871.98
p(Date+Snow+RTO+CA)	34	946.42	4.96	0.017	872.11
p(t+Date+CA)	35	946.47	5.00	0.017	869.77
p(t+CA)	33	946.58	5.12	0.016	874.65
p(Date+Sun+RD+RTO+CA)	35	946.90	5.43	0.014	870.19
p(t+RTO+CA)	34	946.93	5.46	0.013	872.62
p(Date+Sun+Snow+RTO+CA)	35	947.01	5.55	0.013	870.31
p(t+Date+Snow+RTO+CA)	37	947.22	5.76	0.012	865.70
p(t+Date+Snow+CA)	36	947.26	5.80	0.011	868.16
p(Sun+Snow+RD+RTO+CA)	34	947.78	6.32	0.009	873.47

Table 6.A7, cont'd					
p(t+RD+RTO+CA)	35	948.03	6.57	0.008	871.33
p(t+Date+RD+RTO+CA)	37	948.12	6.65	0.007	866.60
p(t+Snow+RTO+CA)	35	948.21	6.75	0.007	871.51
p(Date+Snow+RD+RTO+CA)	35	948.68	7.22	0.006	871.98
p(Sun+CA)	31	948.75	7.28	0.005	881.53
p(RTO)	30	948.76	7.30	0.005	883.88
p(t+Snow+CA)	34	948.80	7.34	0.005	874.49
p(t+Date+RD+CA)	36	948.81	7.34	0.005	869.70
p(t+Sun+CA)	34	948.85	7.39	0.005	874.54
p(t+Date+Sun+CA)	36	948.87	7.40	0.005	869.76
p(t+RD+CA)	34	948.89	7.43	0.005	874.58
p(t+Sun+RTO+CA)	35	949.26	7.79	0.004	872.55
p(Date+Sun+Snow+RD+RTO+CA)	36	949.27	7.81	0.004	870.17
p(t+Date+Snow+RD+CA)	37	949.63	8.16	0.003	868.11
p(t+Date+Snow+RD+RTO+CA)	38	949.64	8.18	0.003	865.69
p(t+Date+Sun+Snow+CA)	37	949.67	8.21	0.003	868.15
p(Date+Snow+RD+CA)	34	949.71	8.24	0.003	875.40
p(t+Snow+RD+RTO+CA)	36	950.38	8.92	0.002	871.28
p(t+Sun+RD+RTO+CA)	36	950.42	8.95	0.002	871.31
p(Sun+RTO)	31	950.56	9.10	0.002	883.34
p(Date+RTO)	32	950.58	9.11	0.002	881.01
p(Date)	31	950.59	9.12	0.002	883.37
p(t+Sun+Snow+RTO+CA)	36	950.61	9.14	0.002	871.50
p(t+Snow+RD+CA)	35	950.66	9.19	0.002	873.96
p(t+Sun+Snow+CA)	35	950.70	9.24	0.002	874.00
p(Snow+RTO)	31	951.00	9.53	0.002	883.78
p(Sun+Snow+CA)	32	951.01	9.54	0.002	881.43
p(RD+RTO)	31	951.10	9.63	0.002	883.88

Table 6.A7, cont'd					
p(t+Date+Sun+RD+CA)	37	951.19	9.72	0.002	869.67
p(t+Sun+RD+CA)	35	951.19	9.72	0.002	874.49
p(Snow+RD+CA)	32	951.38	9.92	0.001	881.81
p(Date+Sun+RTO)	33	951.39	9.92	0.001	879.45
p(Sun+RD+CA)	32	951.64	10.18	0.001	882.07
p(Date+Sun)	32	951.74	10.28	0.001	882.17
p(t+Date+Sun+Snow+RD+CA)	38	952.04	10.58	0.001	868.10
p(t)	32	952.55	11.08	0.001	882.97
p(Date+RD)	32	952.60	11.13	0.001	883.03
p(t+Date)	34	952.63	11.16	0.001	878.31
p(Date+Snow)	32	952.66	11.20	0.001	883.09
p(Date+RD+RTO)	33	952.74	11.27	0.001	880.80
p(Date+Snow+RTO)	33	952.74	11.28	0.001	880.80
p(t+Sun+Snow+RD+RTO+CA)	37	952.78	11.32	0.001	871.26
p(t+Date+RTO)	35	952.87	11.40	0.001	876.17
p(Sun+RD+RTO)	32	952.91	11.45	0.001	883.34
p(Date+Sun+CA)	33	952.92	11.46	0.001	880.98
p(t+Date+Snow)	35	953.16	11.70	0.001	876.46
p(t+RTO)	33	953.28	11.81	0.001	881.34
p(Snow+RD+RTO)	32	953.35	11.88	0.001	883.77
p(Date+Sun+Snow+RTO)	34	953.37	11.91	0.001	879.06
p(t+Sun+Snow+RD+CA)	36	953.48	12.02	0.001	874.38
p(Sun+Snow+RD+CA)	33	953.48	12.02	0.001	881.55
p(Date+Sun+RD+RTO)	34	953.49	12.03	0.001	879.18
p(Date+Sun+Snow)	33	953.67	12.20	0.000	881.73
p(Date+Sun+RD)	33	953.68	12.22	0.000	881.75
p(t+Date+Snow+RTO)	36	954.04	12.58	0.000	874.94
p(Date+Sun+RD+CA)	34	954.10	12.63	0.000	879.79

Table 6.A7, cont'd					
p(t+RD)	33	954.77	13.30	0.000	882.83
p(t+Date+RD)	35	954.78	13.32	0.000	878.08
p(t+Sun)	33	954.88	13.41	0.000	882.94
p(Date+Snow+RD+RTO)	34	954.95	13.48	0.000	880.64
p(Sun+RD)	31	955.00	13.54	0.000	887.78
p(t+Date+Sun)	35	955.01	13.54	0.000	878.31
p(t+Snow)	33	955.09	13.62	0.000	883.15
p(Sun+Snow+RD+RTO)	33	955.14	13.67	0.000	883.20
p(t+Date+Sun+RTO)	36	955.18	13.72	0.000	876.08
p(t+Date+RD+RTO)	36	955.23	13.76	0.000	876.13
p(Date+Sun+Snow+CA)	34	955.33	13.86	0.000	881.02
p(t+RD+RTO)	34	955.34	13.88	0.000	881.03
p(t+Date+Snow+RD)	36	955.47	14.00	0.000	876.36
p(Date+Sun+Snow+RD+RTO)	35	955.55	14.09	0.000	878.85
p(t+Date+Sun+Snow)	36	955.56	14.10	0.000	876.46
p(t+Sun+RTO)	34	955.65	14.18	0.000	881.33
p(Date+Sun+Snow+RD)	34	955.70	14.24	0.000	881.39
p(Date+Sun+Snow+RD+CA)	35	956.32	14.85	0.000	879.61
p(t+Date+Sun+Snow+RTO)	37	956.38	14.92	0.000	874.86
p(t+Date+Snow+RD+RTO)	37	956.45	14.98	0.000	874.93
p(t+Snow+RD)	34	956.95	15.48	0.000	882.64
p(t+Sun+RD)	34	957.12	15.66	0.000	882.81
p(t+Sun+Snow)	34	957.14	15.67	0.000	882.82
p(t+Date+Sun+RD)	36	957.19	15.72	0.000	878.08
p(t+Snow+RTO)	34	957.28	15.81	0.000	882.96
p(t+Date+Sun+RD+RTO)	37	957.55	16.09	0.000	876.03
p(t+Snow+RD+RTO)	35	957.64	16.17	0.000	880.93
p(t+Sun+RD+RTO)	35	957.73	16.26	0.000	881.02

Table 6.A7, cont'd					
p(t+Date+Sun+Snow+RD)	37	957.88	16.42	0.000	876.36
p(t+Sun+Snow+RTO)	35	958.01	16.54	0.000	881.30
p(t+Date+Sun+Snow+RD+RTO)	38	958.81	17.34	0.000	874.86
p(t+Sun+Snow+RD)	35	959.32	17.85	0.000	882.61
p(t+Sun+Snow+RD+RTO)	36	960.03	18.57	0.000	880.93
p(Sun+Snow+RD)	32	970.27	28.80	0.000	900.70
p(Date+Snow+RD)	33	970.78	29.32	0.000	898.85

Table 6.A8. Ranking of kit fox (*Vulpes macrotis*) occupancy (ψ) models for dynamic single-species models. The model set included all possible combinations of occupancy covariates. Across occupancy models, the best fit detection (*p*) model and global extinction (ε) and colonization (γ) models were held constant at *p*(RTO + CA), ε(t + Soil + RD + SW + CS + DistW), and γ (t + Soil + RD + SW + CS + DistW), respectively.

Occupancy (ψ) model	K	AIC_c	ΔAIC_c	w_i	LL
ψ(SW)	25	933.93	0.00	0.326	880.56
ψ(SW+CS)	26	935.39	1.46	0.157	879.75
ψ(SW+DistW)	26	936.20	2.27	0.105	880.55
ψ(RD+SW)	26	936.21	2.28	0.104	880.56
ψ(RD+SW+CS)	27	937.66	3.73	0.051	879.72
ψ(SW+CS+DistW)	27	937.68	3.75	0.050	879.74
ψ(Soil+SW+CS)	29	937.71	3.78	0.049	875.16
ψ(Soil+SW)	28	938.40	4.47	0.035	878.16
ψ(RD+SW+DistW)	27	938.49	4.56	0.033	880.55
ψ(Soil+RD+SW+CS)	30	939.20	5.27	0.023	874.32
ψ(RD+SW+CS+DistW)	28	939.96	6.03	0.016	879.72
ψ(Soil+SW+CS+DistW)	30	940.00	6.08	0.016	875.12
ψ(Soil+SW+DistW)	29	940.64	6.72	0.011	878.09
ψ(Soil+RD+SW)	29	940.71	6.79	0.011	878.16
ψ(Soil+RD+SW+CS+DistW)	31	941.47	7.54	0.008	874.24
ψ(Soil+RD+SW+DistW)	30	942.91	8.98	0.004	878.03
ψ(CS)	25	948.11	14.18	0.000	894.74
ψ(CS+DistW)	26	948.93	15.00	0.000	893.28
ψ(RD+CS)	26	950.16	16.23	0.000	894.51
ψ(Soil+CS)	28	950.57	16.64	0.000	890.33
ψ(RD+CS+DistW)	27	951.06	17.13	0.000	893.12
ψ(Soil+CS+DistW)	29	952.81	18.88	0.000	890.25
ψ(Soil+RD+CS)	29	952.82	18.89	0.000	890.26
ψ(Soil)	27	954.06	20.13	0.000	896.12

Table 6.A8, cont'd

ψ(Soil+RD+CS+DistW)	30	955.06	21.13	0.000	890.18
ψ(Soil+RD)	28	956.31	22.38	0.000	896.07
ψ(Soil+DistW)	28	956.41	22.48	0.000	896.17
ψ(Soil+RD+DistW)	29	957.34	23.42	0.000	894.79
ψ(.)	24	958.80	24.87	0.000	907.70
ψ(DistW)	25	960.85	26.92	0.000	907.48
ψ(RD)	25	961.04	27.12	0.000	907.68

Table 6.A9. Concurrent ranking of kit fox (*Vulpes macrotis*) local extinction (ε) and colonization (γ) models for dynamic single-species models. The model set included all possible combinations of extinction and colonization covariates both within and between each parameter. Across models fit, the best fit detection (*p*) and occupancy (ψ) models were held constant at *p*(RTO + CA) and ψ(SW), respectively. Only models with Akaike weight ≥ 0.001 are presented.

Extinction (ε) model	Colonization (γ) model	K	AIC_c	ΔAIC_c	w_i	LL
ε(CS+t)	γ(Soil+CS)	14	919.15	0.00	0.030	890.09
ε(CS+t)	γ(Soil)	13	920.04	0.89	0.019	893.13
ε(CS+t)	γ(Soil+SW)	14	920.21	1.06	0.018	891.15
ε(CS+t)	γ(Soil+SW+CS)	15	920.21	1.06	0.018	889.00
ε(CS+t)	γ(Soil+CS+DistW)	15	920.57	1.43	0.015	889.36
ε(CS+t)	γ(t+Soil+CS)	16	920.84	1.69	0.013	887.46
ε(CS+t)	γ(Soil+RD+CS)	15	920.84	1.69	0.013	889.63
ε(SW+CS+t)	γ(Soil+CS)	15	921.07	1.92	0.012	889.85
ε(RD+CS+t)	γ(Soil+CS)	15	921.09	1.94	0.012	889.88
ε(CS+DistW+t)	γ(Soil+CS)	15	921.28	2.13	0.010	890.07
ε(CS+t)	γ(Soil+RD)	14	921.32	2.17	0.010	892.26
ε(CS+t)	γ(Soil+DistW)	14	921.38	2.23	0.010	892.32
ε(CS+t)	γ(Soil+SW+DistW)	15	921.66	2.51	0.009	890.45
ε(CS+t)	γ(Soil+RD+SW)	15	921.72	2.57	0.008	890.51
ε(CS+t)	γ(t+Soil+SW+CS)	17	921.75	2.60	0.008	886.20

Table 6.A9, cont'd

ε(SW+CS+DistW+t)	γ(Soil+CS)	16	921.88	2.73	0.008	888.50
ε(CS+t)	γ(Soil+SW+CS+DistW)	16	921.88	2.73	0.008	888.50
ε(CS+t)	γ(DistW)	11	921.88	2.73	0.008	899.22
ε(SW+CS+t)	γ(Soil)	14	921.98	2.83	0.007	892.92
ε(CS+t)	γ(Soil+RD+SW+CS)	16	921.99	2.84	0.007	888.62
ε(CS+DistW+t)	γ(Soil)	14	922.06	2.91	0.007	893.00
ε(RD+CS+t)	γ(Soil)	14	922.06	2.91	0.007	893.01
ε(CS+DistW+t)	γ(Soil+SW)	15	922.18	3.03	0.007	890.97
ε(SW+CS+t)	γ(Soil+SW+CS)	16	922.21	3.06	0.007	888.83
ε(SW+CS+t)	γ(Soil+SW)	15	922.21	3.06	0.007	891.00
ε(CS+t)	γ(t+Soil+CS+DistW)	17	922.22	3.07	0.007	886.67
ε(RD+CS+t)	γ(Soil+SW+CS)	16	922.24	3.09	0.006	888.86
ε(RD+CS+t)	γ(Soil+SW)	15	922.26	3.12	0.006	891.05
ε(CS+DistW+t)	γ(Soil+SW+CS)	16	922.34	3.19	0.006	888.96
ε(CS+t)	γ(CS+DistW)	12	922.35	3.20	0.006	897.57
ε(SW+CS+t)	γ(Soil+CS+DistW)	16	922.49	3.34	0.006	889.11
ε(CS+t)	γ(Soil+RD+CS+DistW)	16	922.52	3.37	0.006	889.14
ε(RD+CS+t)	γ(Soil+CS+DistW)	16	922.52	3.37	0.006	889.14
ε(Soil+CS+t)	γ(Soil+CS)	17	922.54	3.39	0.006	886.99

Table 6.A9, cont'd

ε(SW+DistW+t)	γ(SW+DistW)	13	922.54	3.39	0.006	908.41
ε(SW+DistW+t)	γ(DistW)	12	922.65	3.50	0.005	909.56
ε(CS+DistW+t)	γ(Soil+CS+DistW)	16	922.68	3.53	0.005	889.30
ε(CS+t)	γ(t+Soil+RD+CS)	17	922.70	3.55	0.005	887.15
ε(RD+CS+t)	γ(Soil+RD+CS)	16	922.70	3.55	0.005	889.32
ε(SW+CS+t)	γ(t+Soil+CS)	17	922.72	3.57	0.005	887.16
ε(RD+CS+t)	γ(t+Soil+CS)	17	922.74	3.59	0.005	887.18
ε(SW+CS+t)	γ(Soil+RD+CS)	16	922.77	3.62	0.005	889.39
ε(CS+t)	γ(Soil+RD+DistW)	15	922.98	3.83	0.004	891.77
ε(CS+DistW+t)	γ(Soil+RD+CS)	16	922.98	3.84	0.004	889.61
ε(SW+CS+DistW+t)	γ(Soil+CS+DistW)	17	922.99	3.84	0.004	887.44
ε(CS+DistW+t)	γ(t+Soil+CS)	17	923.02	3.87	0.004	887.46
ε(RD+SW+CS+t)	γ(Soil+CS)	16	923.16	4.01	0.004	889.78
ε(CS+t)	γ(t+Soil+SW+CS+DistW)	18	923.18	4.03	0.004	885.44
ε(RD+CS+DistW+t)	γ(Soil+CS)	16	923.18	4.04	0.004	889.81
ε(RD+CS+t)	γ(Soil+RD)	15	923.27	4.12	0.004	892.06
ε(SW+CS+t)	γ(Soil+RD)	15	923.27	4.12	0.004	892.06
ε(SW+CS+t)	γ(Soil+DistW)	15	923.33	4.18	0.004	892.12
ε(CS+DistW+t)	γ(Soil+RD)	15	923.35	4.20	0.004	892.13

Table 6.A9, cont'd

ε(CS+t)	γ(SW+DistW)	12	923.41	4.26	0.004	898.63
ε(RD+CS+t)	γ(Soil+DistW)	15	923.41	4.26	0.004	892.20
ε(CS+t)	γ(Soil+RD+SW+DistW)	16	923.42	4.27	0.004	890.04
ε(CS+DistW+t)	γ(Soil+DistW)	15	923.49	4.34	0.003	892.27
ε(SW+CS+DistW+t)	γ(Soil+RD+CS)	17	923.49	4.34	0.003	887.94
ε(CS+t)	γ(t+Soil+SW)	16	923.49	4.34	0.003	890.12
ε(SW+CS+t)	γ(RD+SW+CS)	14	923.53	4.38	0.003	899.92
ε(CS+t)	γ(t+Soil)	15	923.54	4.39	0.003	892.32
ε(RD+SW+CS+DistW+t)	γ(t+Soil+RD+SW+CS+DistW)	22	923.55	4.40	0.003	876.95
ε(Soil+SW+CS+t)	γ(Soil+CS)	18	923.63	4.48	0.003	885.89
ε(SW+CS+t)	γ(Soil+SW+DistW)	16	923.66	4.51	0.003	890.28
ε(RD+CS+t)	γ(t+Soil+SW+CS)	18	923.68	4.53	0.003	885.94
ε(CS+DistW+t)	γ(Soil+RD+SW)	16	923.68	4.54	0.003	890.31
ε(SW+CS+DistW+t)	γ(CS+DistW)	14	923.69	4.54	0.003	894.63
ε(CS+t)	γ(t+Soil+RD+SW+CS)	18	923.70	4.55	0.003	885.96
ε(SW+CS+t)	γ(t+Soil+SW+CS)	18	923.70	4.55	0.003	885.96
ε(RD+CS+t)	γ(Soil+RD+SW)	16	923.71	4.56	0.003	890.33
ε(SW+CS+t)	γ(DistW)	12	923.72	4.57	0.003	898.93
ε(RD+CS+t)	γ(Soil+SW+DistW)	16	923.72	4.57	0.003	890.34

Table 6.A9, cont'd

ε(SW+CS+t)	γ(Soil+RD+SW)	16	923.72	4.57	0.003	890.34
ε(SW+CS+DistW+t)	γ(t+Soil+CS)	18	923.74	4.59	0.003	886.00
ε(CS+DistW+t)	γ(Soil+SW+DistW)	16	923.74	4.59	0.003	890.36
ε(CS+t)	γ(SW+CS+DistW)	13	923.74	4.59	0.003	896.82
ε(Soil+CS+t)	γ(Soil)	16	923.74	4.59	0.003	890.37
ε(Soil+CS+t)	γ(Soil+SW+CS)	18	923.79	4.64	0.003	886.05
ε(SW+CS+t)	γ(Soil+SW+CS+DistW)	17	923.85	4.70	0.003	888.30
ε(RD+CS+t)	γ(Soil+SW+CS+DistW)	17	923.86	4.71	0.003	888.31
ε(Soil+CS+t)	γ(Soil+CS+DistW)	18	923.88	4.73	0.003	886.14
ε(CS+t)	γ(Soil+RD+SW+CS+DistW)	17	923.88	4.73	0.003	888.33
ε(CS+DistW+t)	γ(t+Soil+SW+CS)	18	923.93	4.78	0.003	886.19
ε(CS+DistW+t)	γ(CS+DistW)	13	923.96	4.81	0.003	897.04
ε(Soil+CS+t)	γ(Soil+SW)	17	923.96	4.81	0.003	888.41
ε(RD+CS+t)	γ(Soil+RD+SW+CS)	17	923.97	4.82	0.003	888.42
ε(RD+CS+t)	γ(DistW)	12	923.98	4.83	0.003	899.20
ε(SW+CS+t)	γ(Soil+RD+SW+CS)	17	923.99	4.84	0.003	888.44
ε(CS+DistW+t)	γ(DistW)	12	924.00	4.85	0.003	899.22
ε(CS+t)	γ(.)	10	924.01	4.86	0.003	903.46
ε(CS+DistW+t)	γ(Soil+SW+CS+DistW)	17	924.02	4.87	0.003	888.47

Table 6.A9, cont'd

ε(CS+t)	γ(RD+CS+DistW)	13	924.08	4.93	0.003	897.16
ε(SW+CS+t)	γ(t+Soil+CS+DistW)	18	924.09	4.94	0.003	886.35
ε(SW+CS+DistW+t)	γ(Soil)	15	924.10	4.95	0.003	892.89
ε(RD+SW+CS+t)	γ(Soil)	15	924.11	4.96	0.003	892.90
ε(CS+DistW+t)	γ(Soil+RD+SW+CS)	17	924.12	4.97	0.003	888.57
ε(RD+CS+DistW+t)	γ(Soil)	15	924.13	4.98	0.003	892.92
ε(RD+CS+t)	γ(t+Soil+CS+DistW)	18	924.14	5.00	0.003	886.40
ε(SW+CS+t)	γ(CS+DistW)	13	924.16	5.01	0.002	897.25
ε(Soil+CS+t)	γ(t+Soil+CS)	19	924.24	5.09	0.002	884.30
ε(RD+CS+DistW+t)	γ(Soil+SW)	16	924.28	5.13	0.002	890.90
ε(CS+t)	γ(t+Soil+RD+CS+DistW)	18	924.28	5.13	0.002	886.54
ε(SW+CS+DistW+t)	γ(DistW)	13	924.28	5.13	0.002	897.37
ε(CS+t)	γ(t+CS+DistW)	14	924.29	5.14	0.002	895.23
ε(SW+CS+DistW+t)	γ(Soil+SW)	16	924.29	5.14	0.002	890.91
ε(Soil+CS+t)	γ(Soil+RD+CS)	18	924.31	5.16	0.002	886.57
ε(RD+SW+CS+t)	γ(Soil+SW+CS)	17	924.33	5.19	0.002	888.78
ε(RD+SW+CS+t)	γ(Soil+SW)	16	924.34	5.20	0.002	890.97
ε(SW+CS+DistW+t)	γ(Soil+SW+CS)	17	924.38	5.23	0.002	888.83
ε(CS+DistW+t)	γ(t+Soil+CS+DistW)	18	924.40	5.25	0.002	886.66

Table 6.A9, cont'd

ε(RD+CS+DistW+t)	γ(Soil+SW+CS)	17	924.40	5.25	0.002	888.85
ε(RD+CS+t)	γ(CS+DistW)	13	924.40	5.25	0.002	897.49
ε(RD+CS+t)	γ(Soil+RD+CS+DistW)	17	924.41	5.26	0.002	888.86
ε(Soil+RD+CS+t)	γ(Soil+CS)	18	924.44	5.29	0.002	886.70
ε(SW+CS+t)	γ(Soil+RD+CS+DistW)	17	924.45	5.30	0.002	888.89
ε(CS+t)	γ(SW)	11	924.50	5.35	0.002	901.84
ε(RD+CS+t)	γ(t+Soil+RD+CS)	18	924.52	5.37	0.002	886.78
ε(SW+CS+t)	γ(t+Soil+RD+CS)	18	924.59	5.44	0.002	886.85
ε(RD+SW+CS+t)	γ(Soil+CS+DistW)	17	924.60	5.45	0.002	889.04
ε(CS+DistW+t)	γ(Soil+RD+CS+DistW)	17	924.64	5.49	0.002	889.09
ε(SW+CS+DistW+t)	γ(Soil+SW+CS+DistW)	18	924.64	5.49	0.002	886.90
ε(Soil+CS+DistW+t)	γ(Soil+CS)	18	924.69	5.54	0.002	886.95
ε(Soil+CS+t)	γ(CS+DistW)	15	924.76	5.61	0.002	893.55
ε(CS+t)	γ(t+Soil+DistW)	16	924.78	5.63	0.002	891.41
ε(CS+t)	γ(CS)	11	924.80	5.65	0.002	902.14
ε(RD+SW+CS+t)	γ(t+Soil+CS)	18	924.81	5.66	0.002	887.07
ε(RD+SW+CS+t)	γ(Soil+RD+CS)	17	924.81	5.66	0.002	889.26
ε(CS+t)	γ(t+Soil+SW+DistW)	17	924.83	5.68	0.002	889.27
ε(Soil+SW+CS+t)	γ(Soil)	17	924.84	5.70	0.002	889.29

Table 6.A9, cont'd

ε(SW+CS+DistW+t)	γ(t+Soil+CS+DistW)	19	924.85	5.70	0.002	884.91
ε(CS+DistW+t)	γ(t+Soil+RD+CS)	18	924.89	5.74	0.002	887.15
ε(RD+CS+DistW+t)	γ(t+Soil+CS)	18	924.89	5.74	0.002	887.15
ε(Soil+CS+t)	γ(DistW)	14	924.93	5.78	0.002	895.87
ε(Soil+SW+CS+t)	γ(Soil+CS+DistW)	19	924.94	5.79	0.002	885.00
ε(SW+CS+t)	γ(Soil+RD+DistW)	16	924.94	5.79	0.002	891.56
ε(RD+CS+t)	γ(Soil+RD+DistW)	16	924.95	5.80	0.002	891.57
ε(SW+CS+DistW+t)	γ(Soil+RD+CS+DistW)	18	924.95	5.81	0.002	887.21
ε(CS+t)	γ(t+Soil+RD)	16	924.96	5.81	0.002	891.59
ε(Soil+CS+t)	γ(Soil+DistW)	17	925.01	5.86	0.002	889.45
ε(CS+t)	γ(RD)	11	925.08	5.93	0.002	902.42
ε(CS+DistW+t)	γ(Soil+RD+DistW)	16	925.08	5.93	0.002	891.70
ε(Soil+SW+CS+t)	γ(Soil+SW+CS)	19	925.10	5.95	0.002	885.16
ε(CS+t)	γ(t+Soil+RD+SW)	17	925.10	5.95	0.002	889.55
ε(Soil+CS+t)	γ(Soil+RD)	17	925.11	5.96	0.002	889.55
ε(SW+CS+t)	γ(t+Soil+SW+CS+DistW)	19	925.13	5.98	0.002	885.19
ε(RD+CS+t)	γ(t+Soil+SW+CS+DistW)	19	925.13	5.98	0.002	885.20
ε(Soil+CS+t)	γ(t+Soil+SW+CS)	20	925.16	6.01	0.002	883.01
ε(CS+t)	γ(RD+SW+DistW)	13	925.20	6.05	0.001	898.28

Table 6.A9, cont'd

ε(Soil+CS+t)	γ(Soil+SW+CS+DistW)	19	925.22	6.07	0.001	885.28
ε(CS+DistW+t)	γ(t+Soil+SW)	17	925.25	6.10	0.001	889.69
ε(CS+t)	γ(t+Soil+RD+SW+CS+DistW)	19	925.28	6.13	0.001	885.34
ε(RD+CS+t)	γ(SW+DistW)	13	925.32	6.17	0.001	898.40
ε(Soil+SW+CS+t)	γ(t+Soil+CS)	20	925.33	6.18	0.001	883.18
ε(RD+CS+DistW+t)	γ(Soil+RD)	16	925.34	6.19	0.001	891.96
ε(Soil+CS+t)	γ(Soil+SW+DistW)	18	925.34	6.19	0.001	887.60
ε(RD+SW+CS+t)	γ(Soil+RD)	16	925.36	6.21	0.001	891.98
ε(SW+CS+DistW+t)	γ(SW+CS+DistW)	15	925.36	6.21	0.001	894.15
ε(SW+CS+t)	γ(SW+DistW)	13	925.36	6.21	0.001	898.45
ε(CS+DistW+t)	γ(t+Soil+SW+CS+DistW)	19	925.37	6.23	0.001	885.44
ε(SW+CS+t)	γ(RD+DistW)	13	925.39	6.24	0.001	898.47
ε(Soil+SW+CS+t)	γ(Soil+SW)	18	925.40	6.25	0.001	887.66
ε(CS+t)	γ(t+SW+CS+DistW)	15	925.40	6.25	0.001	894.19
ε(SW+CS+DistW+t)	γ(Soil+RD)	16	925.41	6.26	0.001	892.03
ε(Soil+SW+CS+t)	γ(Soil+RD+CS)	19	925.42	6.27	0.001	885.48
ε(CS+DistW+t)	γ(SW+CS+DistW)	14	925.42	6.27	0.001	896.36
ε(CS+DistW+t)	γ(t+Soil)	16	925.42	6.27	0.001	892.05
ε(SW+CS+t)	γ(Soil+RD+SW+DistW)	17	925.43	6.28	0.001	889.88

Table 6.A9, cont'd

ε(RD+CS+t)	γ(Soil+RD+SW+DistW)	17	925.43	6.28	0.001	889.88
ε(RD+SW+CS+t)	γ(Soil+DistW)	16	925.47	6.32	0.001	892.09
ε(SW+CS+t)	γ(t+Soil)	16	925.48	6.33	0.001	892.10
ε(CS+DistW+t)	γ(Soil+RD+SW+DistW)	17	925.49	6.34	0.001	889.93
ε(SW+CS+DistW+t)	γ(Soil+DistW)	16	925.50	6.35	0.001	892.12
ε(SW+CS+t)	γ(t+Soil+SW)	17	925.50	6.35	0.001	889.94
ε(Soil+CS+t)	γ(Soil+RD+SW)	18	925.52	6.37	0.001	887.78
ε(RD+CS+t)	γ(t+Soil+SW)	17	925.53	6.38	0.001	889.98
ε(RD+CS+t)	γ(t+Soil)	16	925.54	6.39	0.001	892.16
ε(SW+CS+DistW+t)	γ(t+Soil+RD+CS)	19	925.54	6.39	0.001	885.60
ε(CS+DistW+t)	γ(SW+DistW)	13	925.54	6.39	0.001	898.63
ε(Soil+CS+t)	γ(t+Soil+CS+DistW)	20	925.55	6.40	0.001	883.40
ε(RD+CS+DistW+t)	γ(Soil+DistW)	16	925.56	6.41	0.001	892.18
ε(RD+CS+t)	γ(t+Soil+RD+SW+CS)	19	925.57	6.42	0.001	885.63
ε(CS+t)	γ(SW+CS)	12	925.59	6.44	0.001	900.81
ε(RD+SW+CS+t)	γ(DistW)	13	925.64	6.49	0.001	898.73
ε(SW+CS+t)	γ(SW+CS+DistW)	14	925.64	6.49	0.001	896.59
ε(Soil+SW+CS+DistW+t)	γ(Soil+CS)	19	925.66	6.51	0.001	885.72
ε(SW+CS+t)	γ(t+Soil+RD+SW+CS)	19	925.66	6.51	0.001	885.72

Table 6.A9, cont'd

ε(RD+CS+t)	γ(RD+DistW)	13	925.66	6.51	0.001	898.75
ε(Soil+CS+t)	γ(Soil+RD+SW+CS)	19	925.67	6.52	0.001	885.73
ε(CS+t)	γ(RD+DistW)	13	925.67	6.52	0.001	898.76
ε(CS+DistW+t)	γ(RD+DistW)	13	925.67	6.52	0.001	898.76
ε(RD+SW+CS+DistW)	γ(t+Soil+RD+CS)	18	925.68	6.53	0.001	887.94
ε(RD+CS+DistW+t)	γ(Soil+RD+SW)	17	925.69	6.54	0.001	890.14
ε(CS+t)	γ(RD+SW+CS+DistW)	14	925.71	6.56	0.001	896.65
ε(Soil+RD+SW+CS+t)	γ(Soil+CS)	19	925.75	6.60	0.001	885.81
ε(SW+CS+DistW+t)	γ(SW+DistW)	14	925.77	6.62	0.001	896.72
ε(Soil+SW+CS+t)	γ(CS+DistW)	16	925.78	6.63	0.001	892.40
ε(CS+t)	γ(t+DistW)	13	925.79	6.64	0.001	898.88
ε(RD+SW+CS+t)	γ(t+Soil+SW+CS)	19	925.79	6.64	0.001	885.86
ε(SW+CS+t)	γ(.)	11	925.80	6.65	0.001	903.14
ε(Soil+RD+CS+t)	γ(Soil+CS+DistW)	19	925.80	6.66	0.001	885.87
ε(RD+SW+CS+t)	γ(Soil+SW+DistW)	17	925.81	6.66	0.001	890.25
ε(SW+CS+DistW+t)	γ(Soil+RD+SW)	17	925.81	6.66	0.001	890.25
ε(Soil+RD+CS+t)	γ(Soil+SW+CS)	19	925.82	6.67	0.001	885.88
ε(SW+CS+DistW+t)	γ(Soil+SW+DistW)	17	925.82	6.67	0.001	890.27
ε(RD+SW+CS+t)	γ(Soil+RD+SW)	17	925.82	6.67	0.001	890.27

Table 6.A9, cont'd

ε(RD+CS+t)	γ(Soil+RD+SW+CS+DistW)	18	925.83	6.68	0.001	888.09
ε(RD+CS+DistW+t)	γ(Soil+SW+DistW)	17	925.84	6.69	0.001	890.29
ε(SW+CS+t)	γ(Soil+RD+SW+CS+DistW)	18	925.86	6.71	0.001	888.12
ε(SW+CS+DistW+t)	γ(t+CS+DistW)	16	925.87	6.72	0.001	892.49
ε(Soil+RD+CS+t)	γ(Soil)	17	925.88	6.73	0.001	890.32
ε(SW+CS+t)	γ(RD+CS+DistW)	14	925.88	6.73	0.001	896.82
ε(CS+DistW+t)	γ(.)	11	925.88	6.73	0.001	903.22
ε(SW+CS+DistW+t)	γ(t+Soil+SW+CS)	19	925.88	6.73	0.001	885.94
ε(CS+t)	γ(RD+SW)	12	925.89	6.74	0.001	901.11
ε(RD+CS+t)	γ(SW+CS+DistW)	14	925.89	6.74	0.001	896.83
ε(Soil+CS+t)	γ(Soil+RD+CS+DistW)	19	925.89	6.74	0.001	885.95
ε(CS+DistW+t)	γ(t+Soil+RD+SW+CS)	19	925.89	6.74	0.001	885.95
ε(Soil+CS+DistW+t)	γ(Soil+CS+DistW)	19	925.92	6.77	0.001	885.98
ε(RD+CS+DistW+t)	γ(Soil+SW+CS+DistW)	18	925.95	6.81	0.001	888.21
ε(Soil+CS+DistW+t)	γ(Soil+SW+CS)	19	925.96	6.81	0.001	886.02
ε(RD+SW+CS+t)	γ(Soil+SW+CS+DistW)	18	925.96	6.82	0.001	888.22
ε(Soil+CS+DistW+t)	γ(Soil)	17	925.97	6.82	0.001	890.41
ε(Soil+CS+t)	γ(SW+DistW)	15	925.97	6.83	0.001	894.76
ε(SW+CS+t)	γ(t+CS+DistW)	15	925.98	6.83	0.001	894.77

Table 6.A9, cont'd

ε(RD+SW+CS+t)	γ(CS+DistW)	14	926.00	6.86	0.001	896.95
ε(Soil+CS+t)	γ(SW+CS+DistW)	16	926.01	6.87	0.001	892.64
ε(CS+t)	γ(RD+CS)	12	926.04	6.89	0.001	901.25
ε(CS+DistW+t)	γ(RD+CS+DistW)	14	926.06	6.91	0.001	897.00
ε(Soil+SW+CS+t)	γ(DistW)	15	926.06	6.91	0.001	894.85
ε(Soil+RD+CS+t)	γ(Soil+SW)	18	926.09	6.94	0.001	888.35
ε(RD+SW+CS+t)	γ(Soil+RD+SW+CS)	18	926.09	6.94	0.001	888.35
ε(Soil+RD+CS+t)	γ(Soil+RD+CS)	19	926.09	6.94	0.001	886.15
ε(Soil+SW+CS+t)	γ(Soil+DistW)	18	926.11	6.96	0.001	888.37
ε(RD+CS+t)	γ(.)	11	926.11	6.96	0.001	903.45
ε(Soil+RD+CS+t)	γ(t+Soil+CS)	20	926.11	6.96	0.001	883.96
ε(RD+CS+DistW+t)	γ(DistW)	13	926.11	6.97	0.001	899.20
ε(CS+DistW+t)	γ(Soil+RD+SW+CS+DistW)	18	926.12	6.97	0.001	888.38
ε(CS+t)	γ(t+RD+CS+DistW)	15	926.13	6.98	0.001	894.92
ε(CS)	γ(t+Soil+CS+DistW)	14	926.14	6.99	0.001	897.09
ε(Soil+CS+DistW+t)	γ(Soil+SW)	18	926.15	7.00	0.001	888.40
ε(RD+CS+DistW+t)	γ(Soil+RD+SW+CS)	18	926.15	7.00	0.001	888.41
ε(Soil+CS+t)	γ(t+Soil+RD+CS)	20	926.16	7.01	0.001	884.01
ε(RD+CS+t)	γ(t+Soil+RD+CS+DistW)	19	926.16	7.01	0.001	886.22

Table 6.A9, cont'd

ε(SW+CS+t)	γ(t+Soil+RD+CS+DistW)	19	926.17	7.02	0.001	886.23
ε(SW+CS+DistW+t)	γ(Soil+RD+SW+CS)	18	926.18	7.03	0.001	888.44
ε(Soil+SW+CS+t)	γ(Soil+RD)	18	926.20	7.05	0.001	888.46
ε(RD+SW+CS+t)	γ(t+Soil+CS+DistW)	19	926.21	7.06	0.001	886.27
ε(RD+CS+t)	γ(RD+CS+DistW)	14	926.22	7.07	0.001	897.16
ε(RD+SW+CS+DistW+t)	γ(Soil)	16	926.24	7.09	0.001	892.86
ε(RD+CS+t)	γ(t+CS+DistW)	15	926.27	7.12	0.001	895.06
ε(Soil+RD+CS+DistW+t)	γ(Soil+CS)	19	926.32	7.17	0.001	886.38
ε(CS+DistW+t)	γ(t+CS+DistW)	15	926.39	7.24	0.001	895.18
ε(Soil+CS+DistW+t)	γ(t+Soil+CS)	20	926.41	7.26	0.001	884.26
ε(SW+CS+t)	γ(SW)	12	926.41	7.26	0.001	901.63
ε(RD+SW+CS+DistW+t)	γ(Soil+SW)	17	926.44	7.29	0.001	890.88
ε(Soil+CS+DistW+t)	γ(Soil+RD+CS)	19	926.47	7.33	0.001	886.54
ε(CS+DistW+t)	γ(t+Soil+RD+CS+DistW)	19	926.48	7.33	0.001	886.54
ε(Soil+SW+CS+t)	γ(Soil+SW+CS+DistW)	20	926.49	7.34	0.001	884.34
ε(Soil+CS+DistW+t)	γ(CS+DistW)	16	926.50	7.35	0.001	893.12
ε(CS+t)	γ(t+Soil+RD+DistW)	17	926.52	7.37	0.001	890.96
ε(CS+DistW+t)	γ(SW)	12	926.52	7.37	0.001	901.74
ε(CS+t)	γ(t+CS)	13	926.52	7.37	0.001	899.60

Table 6.A9, cont'd

ε(RD+SW+CS+DistW+t)	γ(Soil+SW+CS)	18	926.52	7.37	0.001	888.78
ε(RD+SW+CS+t)	γ(Soil+RD+CS+DistW)	18	926.52	7.37	0.001	888.78
ε(Soil+SW+CS+t)	γ(t+Soil+SW+CS)	21	926.53	7.38	0.001	882.16
ε(Soil+CS+t)	γ(t+Soil+SW+CS+DistW)	21	926.53	7.38	0.001	882.16
ε(Soil+RD+CS+t)	γ(CS+DistW)	16	926.56	7.41	0.001	893.18
ε(SW+CS+t)	γ(CS)	12	926.57	7.42	0.001	901.79
ε(Soil+CS+t)	γ(t+CS+DistW)	17	926.58	7.43	0.001	891.02
ε(SW+CS+DistW+t)	γ(RD+CS+DistW)	15	926.60	7.45	0.001	895.39
ε(Soil+SW+CS+t)	γ(t+Soil+CS+DistW)	21	926.60	7.45	0.001	882.23
ε(RD+CS+t)	γ(SW)	12	926.61	7.46	0.001	901.82
ε(SW+CS+DistW+t)	γ(RD+DistW)	14	926.61	7.46	0.001	897.55
ε(RD+SW+CS+t)	γ(t+Soil+RD+CS)	19	926.64	7.49	0.001	886.70
ε(SW+CS+DistW+t)	γ(Soil+RD+SW+CS+DistW)	19	926.65	7.51	0.001	886.72
ε(Soil+CS+t)	γ(RD+DistW)	15	926.67	7.52	0.001	895.46
ε(Soil+CS+t)	γ(RD+CS+DistW)	16	926.69	7.54	0.001	893.31
ε(CS+t)	γ(t+Soil+RD+SW+DistW)	18	926.69	7.54	0.001	888.95
ε(CS)	γ(Soil+SW)	12	926.71	7.56	0.001	901.92
ε(CS+t)	γ(t+SW+DistW)	14	926.72	7.57	0.001	897.66
ε(SW+CS+t)	γ(t+Soil+DistW)	17	926.73	7.58	0.001	891.18

Table 6.A9, cont'd

ε(Soil+CS+t)	γ(Soil+RD+DistW)	18	926.75	7.60	0.001	889.01
ε(Soil+SW+CS+t)	γ(Soil+SW+DistW)	19	926.76	7.61	0.001	886.82
ε(Soil+SW+CS+DistW+t)	γ(Soil+CS+DistW)	20	926.78	7.63	0.001	884.63
ε(CS+DistW+t)	γ(t+Soil+SW+DistW)	18	926.78	7.63	0.001	889.04
ε(RD+CS+t)	γ(t+Soil+DistW)	17	926.79	7.64	0.001	891.24
ε(CS+DistW+t)	γ(t+Soil+RD+SW)	18	926.81	7.67	0.001	889.07
ε(Soil+CS+DistW+t)	γ(DistW)	15	926.83	7.68	0.001	895.62
ε(CS+DistW+t)	γ(t+Soil+RD)	17	926.83	7.69	0.001	891.28
ε(SW+CS+t)	γ(t+Soil+SW+DistW)	18	926.84	7.69	0.001	889.09
ε(CS+DistW+t)	γ(t+Soil+DistW)	17	926.85	7.70	0.001	891.29
ε(Soil+RD+CS+t)	γ(DistW)	15	926.85	7.70	0.001	895.64
ε(CS+DistW+t)	γ(CS)	12	926.86	7.71	0.001	902.07
ε(RD+CS+t)	γ(t+Soil+SW+DistW)	18	926.87	7.72	0.001	889.13
ε(SW+CS+t)	γ(RD)	12	926.88	7.73	0.001	902.09
ε(RD+CS+t)	γ(t+Soil+RD)	17	926.88	7.73	0.001	891.33
ε(SW+CS+t)	γ(RD+SW+DistW)	14	926.90	7.75	0.001	897.84
ε(RD+CS+t)	γ(CS)	12	926.92	7.77	0.001	902.13
ε(SW+CS+t)	γ(t+Soil+RD)	17	926.92	7.77	0.001	891.36
ε(SW+CS+DistW+t)	γ(t+Soil+RD+CS+DistW)	20	926.93	7.78	0.001	884.78

Table 6.A9, cont'd

ε(RD+CS+DistW+t)	γ(t+Soil+SW+CS)	19	926.93	7.78	0.001	886.99
ε(Soil+SW+CS+t)	γ(Soil+RD+SW)	19	926.93	7.79	0.001	887.00
ε(CS+DistW+t)	γ(RD)	12	926.96	7.81	0.001	902.17
ε(Soil+SW+CS+t)	γ(Soil+RD+CS+DistW)	20	926.97	7.82	0.001	884.82
ε(CS+t)	γ(t+SW+CS)	14	926.97	7.82	0.001	897.91
ε(Soil+SW+CS+t)	γ(Soil+RD+SW+CS)	20	926.97	7.82	0.001	884.83
ε(Soil+RD+SW+CS+t)	γ(Soil)	18	927.02	7.87	0.001	889.28
BRK)	γ(Soil+SW)	11	927.03	7.88	0.001	904.37
ε(RD+SW+CS+t)	γ(Soil+RD+DistW)	17	927.04	7.89	0.001	891.49
ε(RD+CS+t)	γ(t+Soil+RD+SW)	18	927.07	7.92	0.001	889.33
ε(Soil+RD+SW+CS+t)	γ(Soil+CS+DistW)	20	927.08	7.93	0.001	884.93
ε(RD+SW+CS+t)	γ(SW+DistW)	14	927.08	7.93	0.001	898.02
ε(CS+t)	γ(RD+SW+CS)	13	927.08	7.94	0.001	900.17
ε(SW+CS)	γ(t+Soil+CS)	15	927.09	7.94	0.001	895.88
ε(t)	γ(Soil+SW)	13	927.11	7.96	0.001	900.19
ε(RD+CS+DistW+t)	γ(Soil+RD+DistW)	17	927.11	7.96	0.001	891.56
ε(RD+CS+t)	γ(RD+SW+DistW)	14	927.11	7.96	0.001	898.05
ε(SW+CS+DistW+t)	γ(Soil+RD+DistW)	17	927.11	7.96	0.001	891.56
ε(SW+CS+t)	γ(t+Soil+RD+SW)	18	927.11	7.96	0.001	889.37

Table 6.A9, cont'd

ε(Soil+RD+CS+t)	γ(Soil+DistW)	18	927.13	7.98	0.001	889.39
ε(Soil+RD+CS+t)	γ(t+Soil+SW+CS)	21	927.14	8.00	0.001	882.78
ε(Soil+RD+CS+t)	γ(Soil+RD)	18	927.15	8.00	0.001	889.41
ε(Soil+CS+t)	γ(t+Soil+RD+SW+CS)	21	927.16	8.01	0.001	882.79
ε(Soil+CS+t)	γ(Soil+RD+SW+DistW)	19	927.16	8.01	0.001	887.22
ε(Soil+SW+CS+DistW+t)	γ(Soil+SW+CS)	20	927.17	8.02	0.001	885.02
ε(RD+CS+DistW+t)	γ(t+Soil+SW)	18	927.18	8.03	0.001	889.44
ε(RD+CS+t)	γ(RD)	12	927.20	8.05	0.001	902.42
ε(RD+CS+t)	γ(t+Soil+RD+SW+CS+DistW)	20	927.20	8.05	0.001	885.05
ε(Soil+SW+CS+t)	γ(SW+CS+DistW)	17	927.20	8.06	0.001	891.65
ε(Soil+CS+DistW+t)	γ(Soil+DistW)	18	927.23	8.09	0.001	889.49
ε(Soil+SW+CS+t)	γ(SW+DistW)	16	927.24	8.09	0.001	893.86
ε(SW+CS+t)	γ(t+Soil+RD+SW+CS+DistW)	20	927.24	8.09	0.001	885.09
ε(Soil+RD+CS+t)	γ(Soil+SW+CS+DistW)	20	927.25	8.10	0.001	885.10
ε(RD+SW+CS+t)	γ(t+Soil+SW+CS+DistW)	20	927.25	8.10	0.001	885.10
ε(Soil+CS+t)	γ(.)	13	927.26	8.11	0.001	900.34
ε(t)	γ(Soil)	12	927.26	8.11	0.001	902.48
ε(Soil+RD+SW+CS+t)	γ(Soil+SW+CS)	20	927.26	8.11	0.001	885.11
ε(SW+CS+t)	γ(t+SW+CS+DistW)	16	927.27	8.12	0.001	893.89

Table 6.A9, cont'd

ε(SW+CS+DistW+t)	γ(t+Soil+SW+CS+DistW)	20	927.27	8.13	0.001	885.13
ε(Soil+SW+CS+t)	γ(t+Soil+RD+CS)	21	927.28	8.13	0.001	882.91
ε(Soil+CS+t)	γ(Soil+RD+SW+CS+DistW)	20	927.28	8.13	0.001	885.13
ε(Soil+CS+DistW+t)	γ(Soil+SW+CS+DistW)	20	927.29	8.14	0.001	885.14
ε(RD+CS+DistW+t)	γ(t+Soil+SW+CS+DistW)	20	927.30	8.15	0.001	885.15
ε(Soil+CS+t)	γ(t+Soil+SW)	19	927.31	8.16	0.001	887.37
ε(RD+SW+CS+DistW)	γ(t+Soil+RD+SW+CS)	19	927.32	8.18	0.001	887.39
ε(SW+CS+DistW+t)	γ(RD+SW+CS+DistW)	16	927.33	8.18	0.001	893.95
ε(RD+CS+DistW+t)	γ(t+Soil)	17	927.33	8.18	0.001	891.78
ε(CS+DistW+t)	γ(RD+SW+DistW)	14	927.34	8.19	0.001	898.28
ε(Soil+SW+CS+DistW+t)	γ(t+Soil+CS)	21	927.34	8.19	0.001	882.97
ε(RD+CS+t)	γ(t+SW+CS+DistW)	16	927.34	8.19	0.001	893.97
ε(Soil+CS+DistW+t)	γ(t+Soil+SW+CS)	21	927.35	8.20	0.001	882.98
ε(CS)	γ(t+Soil+CS)	14	927.35	8.20	0.001	898.29
ε(Soil+CS+DistW+t)	γ(Soil+RD)	18	927.35	8.20	0.001	889.61
ε(SW+CS+DistW+t)	γ(t+SW+CS+DistW)	17	927.36	8.21	0.001	891.81
ε(RD+SW+CS+t)	γ(RD+DistW)	14	927.36	8.21	0.001	898.30
ε(CS+DistW+t)	γ(RD+SW+CS+DistW)	15	927.37	8.22	0.001	896.15