CSIRO PUBLISHING
Wildlife Research, 2015, **42**, 75–82
http://dx.doi.org/10.1071/WR14244

The influence of road characteristics and species on detection probabilities of carnivore faeces

Bryan M. Kluever[A,C], *Eric M. Gese*[A,B] *and Steven J. Dempsey*[A]

[A]Department of Wildland Resources, Utah State University, Logan, UT 84322, USA.
[B]United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Department of Wildland Resources, Utah State University, Logan, UT 84322, USA.
[C]Corresponding author. Email: klueverb@gmail.com

Abstract

Context. Determining reliable estimates of carnivore population size and distributions are paramount for developing informed conservation and management plans. Traditionally, invasive sampling has been employed to monitor carnivores, but non-invasive sampling has the advantage of not needing to capture the animal and is generally less expensive. Faeces sampling is a common non-invasive sampling technique and future use is forecasted to increase due to the low costs and logistical ease of sampling, and more advanced techniques in landscape and conservation genetics. For many species, faeces sampling often occurs on or alongside roads. Despite the commonality of road-based faeces sampling, detectability issues are often not addressed.

Aim. We sought to test whether faeces detection probabilities varied by species – coyote (*Canis latrans*) versus kit fox (*Vulpes macrotis*) – and to test whether road characteristics influenced faeces detection probabilities.

Methods. We placed coyote and kit fox faeces along roads, quantified road characteristics, and then subsequently conducted 'blind' road-based faeces detection surveys in Utah during 2012 and 2013. Technicians that surveyed the faeces deposition transects had no knowledge of the locations of the placed faeces.

Key results. Faeces detection probabilities for kit foxes and coyotes were 45% and 74%, respectively; larger faeces originated from coyotes and were more readily detected. Misidentification of placed faeces was rare and did not differ by species. The width of survey roads and the composition of a road's surface influenced detection probabilities.

Conclusion. We identified factors that can influence faeces detection probabilities. Not accounting for variable detection probabilities of different species or not accounting for or reducing road-based variables influencing faeces detection probabilities could hamper reliable counts of mammalian faeces, and could potentially reduce precision of population estimates derived from road-based faeces deposition surveys.

Implications. We recommend that wildlife researchers acknowledge and account for imperfect faeces detection probabilities during faecal sampling. Steps can be taken during study design to improve detection probabilities, and during the analysis phase to account for variable detection probabilities.

Additional keywords: *Canis latrans*, coyote, kit fox, population estimate, scat deposition, survey, *Vulpes macrotis*.

Received 12 June 2014, accepted 19 April 2015, published online 22 May 2015

Introduction

Many carnivore populations are declining worldwide (Gittleman *et al*. 2001; Purvis *et al*. 2001), or they are intensively managed due to human–wildlife conflicts (Treves and Bruskotter 2014). Determining reliable estimates of population state variables (i.e. abundance, occupancy) for carnivores through space and time is paramount for developing informed conservation and management plans (Schaller 1996). Difficulties inherent in monitoring carnivores include their tendency to be elusive, wary, far-ranging, occupy remote areas or densely vegetated habitats, or exist at low density (Gese 2001; Long *et al*. 2008). Invasive sampling is often employed to monitor carnivores using capture–mark–recapture, radio-collaring, or catch-per-unit-effort techniques (Gese 2001). These methods are often costly, stressful and risky to the animal, time consuming, and difficult (Proulx *et al*. 2012). The use of non-invasive sampling (Long *et al*. 2008; Kelly *et al*. 2012) has the advantage of not needing to capture the animal and has been shown to be less expensive (Dempsey *et al*. 2014).

A host of non-invasive sampling methodologies have been employed to monitor populations of carnivores. Commonly, abundance indices are used to derive relative, rather than absolute, abundance estimates from non-invasive sampling data. Such abundance indices are often based on animal sign, such as faeces counts, track counts, vocalisations, dens, photographs, and harvest records or road traffic casualties

(Güthlin *et al.* 2014). Faeces counts, in particular, have been extensively used to derive relative abundance estimates for a host of mammalian carnivores (Clark 1972; Stoddart 1984; Harrison *et al.* 2002; Allen 2012; Güthlin *et al.* 2013). More recently, faeces sampling has been used in concert with molecular genetic analyses in order to obtain absolute abundance estimates (Kohn *et al.* 1999; Bhagavatula and Singh 2006; Kruckenhauser *et al.* 2009). The use of faeces sampling in carnivore studies is forecast to increase due to the logistical ease of field sampling and low costs when compared with more invasive methods, such as animal capture (Long *et al.* 2008; Dempsey *et al.* 2014), and recent advancements in landscape and conservation genetics (Storfer *et al.* 2010; Lampa *et al.* 2013) that are becoming increasingly cost effective (Long *et al.* 2008; Stenglein *et al.* 2010; Lampa *et al.* 2013).

Faeces sampling for carnivores has often been conducted on or alongside roads or trails (Kohn *et al.* 1999; Farrell *et al.* 2000; Allen 2012; Allen and Leung 2012). Such use is likely due to several factors including logistical ease of sampling, documented road use by the species of interest, off-road restrictions (i.e. restrictions on military bases, wilderness areas, or areas containing sensitive vegetative communities), and their commonality in many landscapes.

Most carnivore investigations using road-based faecal sampling either assume or ignore that in order for roads or trails to be unbiased, animals must be randomly distributed across the landscape and not change their behaviour/movements near roads (Kohn *et al.* 1999; Harrison *et al.* 2002; Dodge and Kashian 2013; Dempsey *et al.* 2014).

There may be several additional forms of bias when using road-based faeces sampling that have not been addressed. First, road characteristics (i.e. road width, road type (gravel or two-track)) may impact the likelihood that an observer will detect an individual faeces (hereafter faeces detection rate). For example, the size of grains constituting a road's substrate (hereafter particle size: Blott and Pye 2012) could influence faeces detection probabilities, with larger grains resulting in reduced faeces detection probabilities. Such a relationship would result in a lower number of faeces being collected on 'gravelly' than 'dirt' roads, even if an equal number of faeces are deposited on each road type. Another potential form of bias is faecal size. If a positive relationship between faeces size and faeces detection rate occurs, counts of 'small' faeces deposited on road transects could be underestimated within a sample. Seemingly, research endeavors that violate a methodological or modeling assumption that faeces detection is perfect or constant across survey roads or across species used run a risk of introducing bias into research findings. Despite the aforementioned, the relationship between road characteristics, faeces size, and faeces detection probabilities is an unexplored area.

In this study, we addressed questions pertaining to faeces detection probabilities on roads for a small carnivore – the kit fox (*Vulpes macrotis*) – and a mesocarnivore – the coyote (*Canis latrans*). Road-based faeces deposition surveys have been employed to estimate and monitor relative abundance of coyotes (Clark 1972; Stoddart 1984; Dodge and Kashian 2013) and have been determined to be an effective survey method for kit foxes (Thacker *et al.* 1995; Dempsey *et al.* 2014). Using a 'blind' test along faeces deposition transects with known locations of faeces, our objectives were to (1) test whether faeces detection probabilities vary by species (coyote versus kit fox), and (2) test whether road characteristics influence faeces detection probabilities. Our evaluation was considered a 'blind' test since the technicians did not know the locations of the placed faeces along the transects surveyed.

Materials and methods

Data collection

Our study area (hereafter DPG) was located on 879 km^2 of the eastern portion of the USA Army Dugway Proving Grounds, Utah, USA, and the adjoining land managed by the Bureau of Land Management (Fig. 1). DPG was located ~128 km south-west of Salt Lake City, in Tooele County, Utah. Elevations ranged from 1302 m to 2137 m. The study site was in the Great Basin Desert and was characterised as a cold desert. Winters were cold, summers were hot and dry, with most precipitation occurring in the spring. DPG consisted of predominately flat playa punctuated with steep mountain ranges. A combination of military testing and training activities, the range of topography, and selective road maintenance resulted in a heterogenic road network. Roads were used as a primary location of transects for wildlife surveys due to military restrictions and the logistical ease of road-based surveys (Dempsey 2013).

Kit fox faeces were collected at active kit fox den sites and coyote faeces were collected from areas of high coyote use in the southern and north-eastern portions of DPG, respectively; Dempsey *et al.* (2014) found that kit foxes did not occur in the north-eastern portion of DPG, while coyotes occurred throughout DPG (Kozlowski *et al.* 2008). We were able to locate active kit fox den sites and determine areas of high coyote activity in the north-eastern portion of DPG by monitoring radio-collared animals of both species. We attempted to collect recently deposited faeces (i.e. faeces that had not been bleached white by the sun and had not begun to deteriorate: Godbois *et al.* 2005), but ultimately we could not determine how long faeces had been in the environment before collection. Upon collection, faeces were frozen until they were used for placement in this study. Faeces were placed on 15 5-km transects that were distributed randomly along available non-paved roads with the constraints of being as linear as possible and having year-round access (limitations included military closures and low-lying seasonally inundated greasewood areas). We used the Hawths tools extension in ArcGIS 9.4 (ESRI, Redlands, CA) to select random faeces placement sites along survey transects. Random points were exported into a Wide Area Augmentation System enabled GPS unit (Archer Rugged Field PC, Juniper Systems, Logan, UT) in order to locate known faeces placement sites in the field. At each faeces placement site we randomly selected the faeces type (i.e. kit fox or coyote), the road edge on which the faeces was placed (i.e. north or south, east or west), and the distance (i.e. 0.25, 0.5, 0.75, 1.0, 1.25. or 1.5 m) that the faeces was placed from the road edge. We defined 'road edge' as either the conspicuously marked line left by a road grader or the congruence of vegetation and substrate along each road. Any naturally occurring deposited faeces within 5 m of a known placed faeces were removed and collected. For each faeces, we measured and recorded the length and maximum diameter.

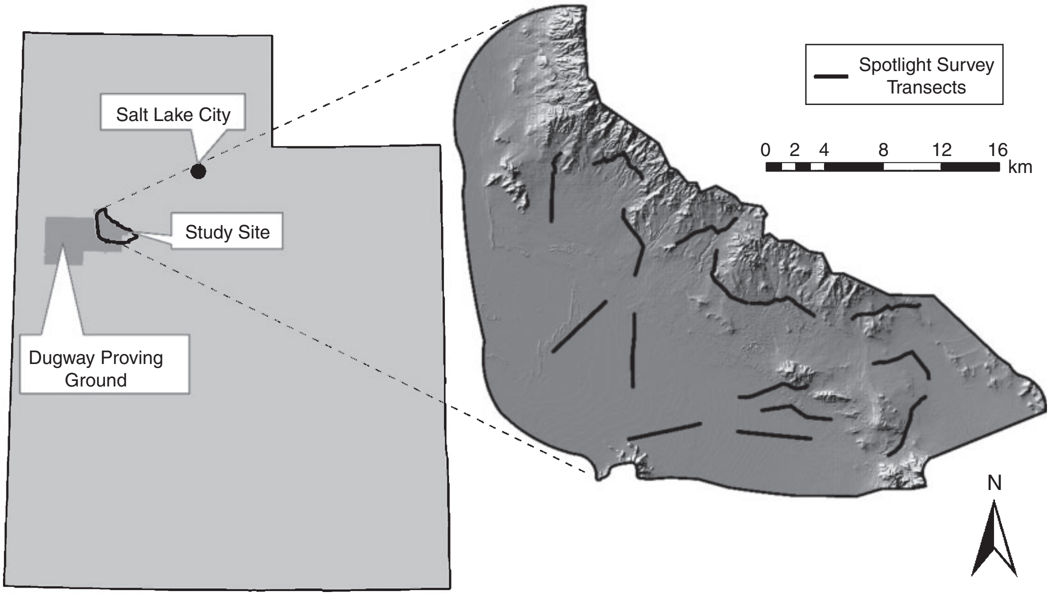

Fig. 1. Map of Utah (USA) showing location of study area and road transects available for carnivore faeces placement within and adjacent to the Army Dugway Proving Ground, Utah, 2012–13.

From November 2012 to August 2013 we placed 178 faeces at known locations on road transects. At each known faeces location we measured road width as the distance between road edges. We used a modified line–point–intercept method (Herrick *et al.* 2005) at 0.25-m intervals to determine the composition of road surface types at faeces placement locations. We initially classified surface type as either particle (e.g. silt, sand, gravel: Blott and Pye 2012) or plant matter. We defined 'plant matter' as alive or dead woody and non-woody vegetative material. We measured the maximum diameter of each particle encountered along the line using a digital caliper. Particles >2 mm were classified as gravel and particles <2 mm were considered sand, silt or clay (Blott and Pye 2012). We combined all sand, silt and clay particles into a single surface type (hereafter SSC) due to the difficulty of accurately measuring particles <2 mm in the field. Hence, at each faeces placement site we had a measure of road width and the composition of surface types (plant matter, gravel, and SSC) across a line that intersected the faeces and was perpendicular to the survey road edges. All human tracks left during faeces placement and measuring roads were removed with a straw broom.

Within 24 h of placing faeces we conducted two-person blind faeces deposition surveys on road transects where faeces had been placed. Following recommendations of Knowlton (1984) and Schauster *et al.* (2002), observers started at opposite ends of each road transect and walked on opposite sides of each transect in order to increase faeces detection probabilities. Detection probabilities could not be calculated using this method because observers collected faeces as they were detected; both observers did not have the opportunity to detect faeces because the first observer to encounter the faeces collected it. Surveyors were trained to search for faeces at a pace of 4.5 km h^{-1} and to search a 2.5-m cross-section of the road. Surveyors were trained to distinguish between kit fox and coyote faeces by size, shape, and odour (Knowlton 1984; Elbroch 2003; Ralls and Smith 2004). Faeces placement and faeces deposition surveys were blind (i.e. surveyors did not place faeces and had no knowledge of faeces locations). Upon locating a faeces, surveyors recorded the location and species, and collected the faeces. This design allowed us to readily ascertain faeces detection probabilities for known placed faeces and determine whether faeces were identified correctly. We attempted to collect faeces that were not detected by faeces surveyors within 12 h of faeces surveys; faeces that were not located were noted as lost.

Data analyses

We tested for differences in faeces misidentification by species of origin and lost faeces by species of origin using Fisher's Exact Tests (Zar 2010) at a significance level of $\alpha = 0.05$. We tested for differences in diameter, length, and size (diameter × length) for coyote and kit fox faeces using analysis of variance (ANOVA) (Zar 2010) at a significance level of $\alpha = 0.05$. Next we developed generalised linear models (GLMs) using faeces detection as the binomial response variable, and faeces size (i.e. faeces diameter × length), road width (continuous variable), and the percentage of the SSC surface type (continuous variable) as continuous predictor variables. We removed percentage plant and percentage gravel as predictor variables because we detected high levels of collinearity with percentage SSC by calculating the Pearson's correlation using $r > 0.6$ as a threshold for removal (collinearity can severely distort model estimation and subsequent predictions: Dormann *et al.* 2013). We censored lost faeces observations ($n = 5$) from the GLMs and detection probability calculations because we had no way of determining whether faeces were still on the transect when the faeces detection survey took place.

We compared seven candidate models that included all additive combinations of predictor variables (Table 1). We used Akaike Information Criteria with a correction factor for small sample size (AIC_c) to select the most parsimonious model, the model with the minimum AICc; the models within two AICc units of the minimum AICc model were considered to be competitive models (Anderson and Burnham 2002). Next, we used likelihood ratio tests at a significance level of $\alpha = 0.05$ to test the effects of the predictor variables for our top model, as well as all possible two-way interactions. For our top model we used a predict function to interpret the influence of predictor variables on faeces detection probabilities. Analyses were performed using R 2.15.3 (R Development Core Team 2012).

Results

Overall faeces detection rate was 60% (103 of 173). Faeces were correctly identified to species by deposition surveyors at 95% (98 of 103) of placement sites. Of the five misidentified faeces, 60% ($n = 3$) were from coyotes and 40% ($n = 2$) were from kit foxes. There was no evidence that species misidentification varied by species ($P = 1.0$, d.f. = 1). The percentage of faeces that were not detected by deposition surveyors but were recovered within 12 h of the faeces detection survey (i.e. not lost) was 93% (65 of 70). There was no evidence that the number of lost faeces varied by species ($P = 0.706$, d.f. = 1). Mean faeces length differed ($F_{1,171} = 461.7$, $P < 0.001$) and were 11.2 (s.d. = 2.45) and 5.0 cm (s.d. = 0.90) for coyotes and kit foxes, respectively. Similarly, faeces diameters varied ($F_{1,171} = 380.0$, $P < 0.001$) and were 2.9 (s.d. = 0.54) and 1.7 cm (s.d. = 0.36) for coyotes and kit foxes, respectively. Mean faeces size also differed by species ($F_{1,171} = 414.1$, $P < 0.001$) and was 32.41 (s.d. = 10.41) and 8.30 (s.d. = 2.33) cm^2 for coyotes and kit foxes, respectively. Faeces detection probabilities were 45% (39 of 87) and 74% (64 of 86) for kit foxes and coyotes, respectively. Road width at faeces sites averaged 4.85 m (s.d. = 2.01) and ranged from 2.60 to 11.00 m. The percentage of occurrence (i.e. the number of faeces placement sites that contained the specific road surface type or the total number of faeces placement sites) for SSC, gravel, and plant matter across all faeces placement sites was 99% (170 of 172), 67% (116 of 172), and 38% (66 of 172), respectively. On average, the road surface at each faeces placement site comprised of 54% (s.d. = 28) SSC, 38% (s.d. = 31) gravel, and 8% (s.d. = 13) plant matter.

Linear models indicated that factors influencing faeces detection probabilities included faeces type (i.e. kit fox or coyote), road width, and the percentage of road SSC (Table 1).

Table 1. Model results for factors that influence faeces detection rates on roads within and adjacent to Dugway Proving Ground, Utah, 2012–13
K, no. of variables; ΔAICc, Akaike Information Criterion measure of each model relative to the best model; *w*, strength of evidence (i.e. Akaike weights)

Model	*K*	ΔAICc	*w*
Faeces size + road width + % SSC	3	0.00	0.81
Faeces size + % SSC	2	3.66	0.13
Faeces size + road width	2	5.78	0.05
Road width + % SSC	2	9.01	0.01
% SSC	1	11.90	<0.01
Road width	1	14.35	<0.01
Faeces size	1	18.37	<0.01

There were no significant interactions among predictor variables. Slope parameter estimates (β) for faeces detection increased with increasing SSC percentage ($\beta = 0.02$, s.e. = 0.01) and faeces size ($\beta = 0.04$, s.e. = 0.01) but decreased with increased road width ($\beta = -0.21$, s.e. = 0.10).

The relationship between predicted probability of faeces detection and road width was negative for both species (Fig. 2). Conversely, the predicted probability of faeces detection and SSC percentage was positive (Fig. 3).

Discussion

We presented a methodology that allows for identification of variable faeces detection probabilities based on species of origin and road characteristics. Our study indicated that species of origin (i.e. faeces size) influenced faeces detection probabilities, where kit fox faeces were more difficult to detect than coyote faeces. These findings may be attributed to factors associated with object recognition, a field of psychology (Ullman 2000). Three-dimensional object size has been shown to influence object recognition, where smaller objects are recognised less often or require more time to be identified (Keane *et al*. 2003; Favelle *et al.* 2006). Surveyors had a finite temporal window to detect faeces, as they walked at a constant pace. As a result, surveyors could not increase the level of attention needed to detect smaller faeces (e.g. kit fox faeces), which contributed to lower detection probabilities. Though we compared faeces detection probabilities from only two species of mammalian carnivores, we feel that a general positive relationship between faeces size and detection probabilities would be observed across these taxa and perhaps other taxa as well (i.e. herbivore faeces detection probabilities). Investigations that explore the effect of different temporal windows on faeces detection probabilities are needed. For example, studies focussed on collecting faeces for smaller taxa may require larger temporal windows (i.e. longer survey duration) to achieve adequate detection probabilities.

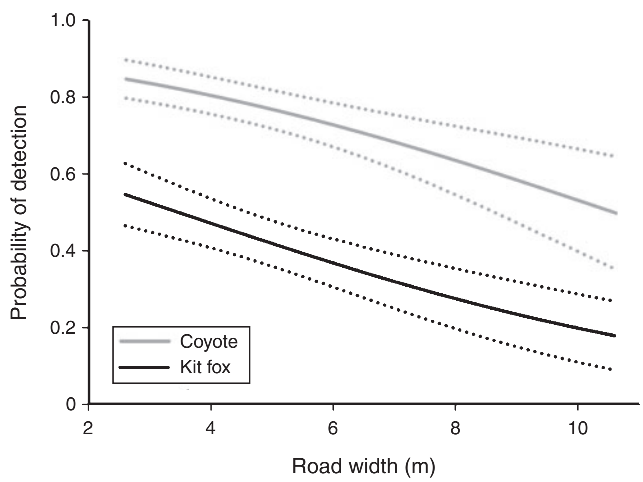

Fig. 2. Predicted probabilities (solid line) and pointwise standard errors (dashed lines) of coyote and kit fox faeces detection based on regression function of top linear model for road width when % SSC is held constant at 50% at the Dugway Proving Ground, Utah, and adjacent Bureau of Land Management land, 2012–13.

We found that road characteristics also influence faeces detection probabilities. The composition of the road surface influenced detection probabilities for both small and large faeces: roads containing low levels of SSC and high levels of gravel and or plant matter had lower detection probabilities. We attributed this to the various object settings, defined as the foreground and background where objects occur (Ullman 2000), on roads with high versus low amounts of gravel. We speculate that the object settings (i.e. faeces settings) on 'gravelly' roads created surveyor viewpoints less conducive to object identification (i.e. faeces detection) because the properties of faeces were more similar in dimensions and/or colour to gravel (Fig. 4*A*, *C*) than to sand, silt or clay (Fig. 4*B*, *D*) and thus were more easily missed. The phenomenon of similar sizes and textures of objects and object settings influencing viewpoint-dependent object recognition has been confirmed in laboratory settings (Peissig and Tarr 2007; de la Rosa *et al*. 2011). Road width also influenced detection probabilities, even though surveyors were trained to survey a uniform cross-section of road regardless of overall width. We speculate that, as road widths increased, surveyors were unable to fully focus their attention on the defined search area because the object setting was larger and altered surveyor viewpoint.

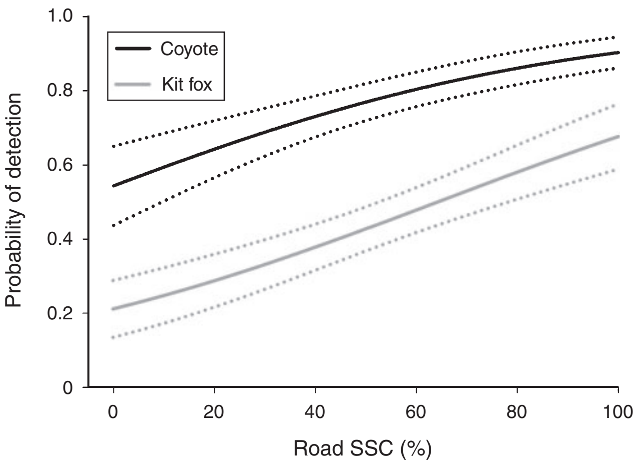

Fig. 3. Predicted probabilities (solid line) and pointwise standard errors (dashed lines) of detection of coyote and kit fox faeces based on regression function of the top linear model when road width is held constant at 4.85 m at the Dugway Proving Ground, Utah, and adjacent Bureau of Land Management land, 2012–13.

Though our findings are limited to two species, we speculate that a similar relationship between faeces detection probabilities, faeces size, and road characteristics would be observed for a host of species that are surveyed along roads. We also speculate that certain landscape and vegetative characteristics (e.g. slope, ground cover, vegetative cover, and vegetation height) may influence detection probabilities in a similar manner when survey routes are located on non-road substrates. Güthlin *et al.* (2014) found that slope and visibility influenced relative abundance estimates derived from red fox faeces counts, but most studies of faeces sampling using human observers have appeared to not address the issue of detectability (Stoddart 1984; Kohn *et al*. 1999; Harrison *et al*. 2002; Allen 2012).

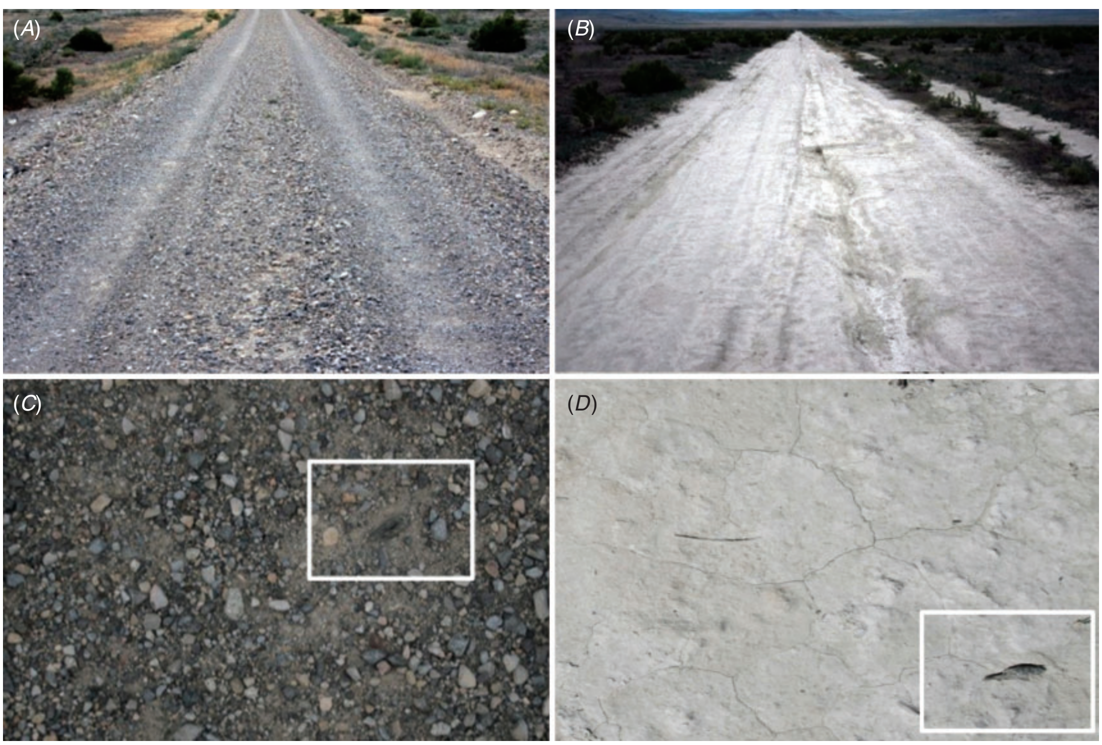

Fig. 4. Examples of kit fox faeces on roads dominated by gravel (*A*, *C*) and sand, silt or clay (*B*, *D*) within the study area at the Army Dugway Proving Ground, Utah, and adjacent Bureau of Land Management land, 2012–13.

Our faeces detection survey may not have accounted for several sources of bias. We collected faeces for the detection survey by collecting kit fox faeces at active kit fox dens and coyote faeces in areas of high coyote use where kit foxes were not detected during several years of monitoring at DPG (Dempsey *et al*. 2014). Nonetheless, misidentification of some faeces could have occurred at this stage because we did not verify species identification using molecular genetic approaches (Lampa *et al*. 2013). For this reason we advise that future faeces detection investigations validate faeces identification using genetic approaches. Second, we were unable to determine what factors were responsible for the small portion of lost faeces. These lost faeces may have been consumed or moved by various wildlife or displaced by abiotic factors (i.e. high winds). However, because the number of lost faeces did not vary by species of origin we feel that the impact of this factor on our faeces detection findings was negligible. Third, we did not quantify either the colour of faeces or the surface of roads, and these factors could have contributed to faeces detection. Despite this, we feel that our faeces detection findings are germane for several reasons. First, roads dominated by gravel or silt appeared to exhibit a clear dichotomy in colour. Second, faeces types were shown to significantly vary in size and faeces size was a contributing factor in our top model. Kit foxes and coyotes have been shown to have a large percentage of dietary overlap at DPG (Kozlowski *et al*. 2008), which likely leads to similar colours of faeces. We placed the faeces randomly on roads in an attempt to mimic defaecations of canids on roads. Because both kit foxes and coyotes defaecate for marking purposes (Feldhamer *et al*. 2003) it is possible that at least a portion of faeces deposited by kit foxes and coyotes are located in conspicuous, and in turn more detectable, locations on roads than random locations. To our knowledge, no investigations using road-based faeces deposition surveys have addressed this potential source of bias, but some species of carnivores (i.e. felids) are known to bury.

The importance of recognising and accounting for imperfect detection when developing estimates of abundance and occupancy, regardless of methodology or data type, is well established (Thompson 1998; Williams *et al*. 2002; White 2005). Despite this, previous investigations whose results hinge upon faeces counts collected from roads appear to ignore detection probabilities or assume it to be perfect (Stoddart 1984; Kohn *et al*. 1999; Harrison *et al*. 2002; Allen 2012). The use of faeces as a non-invasive sampling method for monitoring animal populations and distributions is forecasted to increase (Lukacs and Burnham 2005; Long *et al*. 2008; Storfer *et al*. 2010). As a result, measures should be taken to account for and increase detection probabilities. Researchers have found that utilisation of faeces detector dogs yields higher probabilities of detection than human observer–based surveys on road and non-road surfaces (Smith *et al*. 2005; de Oliveira *et al*. 2012), and that detection probabilities were not influenced by biological (i.e. species of origin) or environmental (i.e. slope) variables (Long *et al*. 2007). However, the high costs associated with using faeces detector dogs when compared with human observer–based surveys (Harrison 2006; de Oliveira *et al*. 2012) may prevent this survey type from completely supplanting human observer–based surveys.

The relationship between imprecision of population estimates and low capture/detection probability is well documented (Otis *et al*. 1978; Rosenberg *et al*. 1995); such imprecision diminishes the likelihood of detecting changes in population parameters and/or monitoring population trends over time (Williams *et al*. 2002; Link 2003). The use of faeces surveys as a non-invasive genetic sampling method for estimating and monitoring animal populations and distributions using a capture–recapture framework is forecast to increase (Lukacs and Burnham 2005; Storfer *et al*. 2010). As a result, measures should be taken to increase faeces detection rates. Models whose framework is based on the presence or absence of a species rather than individual animals (i.e. occupancy framework: Mackenzie *et al*. 2006) should not be as adversely affected by variable faeces detection rates, unless the species of interest is rare, detection rates are very low (<0.15), and the number of sampling occasions is low (<7) (Mackenzie *et al*. 2002).

Our study identified several sources of bias for road-based faeces deposition surveys, but there are others that should be considered when this survey type is used to estimate or monitor carnivore populations or distributions. Roads may not have allowed for random sampling of kit foxes or coyotes, as animals may have altered behaviour/movements when near roads. San Joaquin kit foxes, a species closely related to kit foxes, did not avoid roads (Cypher *et al*. 2009), and predicted kit fox distributions at DPG based on road-based faeces deposition surveys were similar to those based on radio-telemetry data (Dempsey 2013). In concert, these findings suggest that faeces deposition surveys may be appropriate for determining the distribution of kit foxes at DPG. However, for a landscape in which roads are scarce in relation to land area, road-based surveys may be inadequate for kit foxes because survey routes would not cover large portions of kit fox habitat. Güthlin *et al*. (2012) found that red fox faeces sampling on trails was less precise than randomly placed transects, and trail sampling encompassed less potential habitat than random transects. Other species of carnivores, such as wolves (*Canis lupus*) have been shown to both avoid (Kaartinen *et al*. 2005) and select (Whittington *et al*. 2005) for roads. Further, some species may defaecate on roads, but bury their faeces (i.e. felids: Feldhamer *et al*. 2003), making detection more difficult or impossible. Taken as a whole, these findings suggest that the utility of roads for faeces deposition surveys is both species and site specific. Second, faeces deterioration rates (i.e. the amount of time a faeces remains detectable in the environment: Godbois *et al*. 2005) may influence detection probabilities. For our faeces detection study, bias from deterioration rates seemed minimal because of the short and constant temporal window (e.g. <24 h) between faeces placement and faeces deposition surveys and the low traffic volume on roads, but faeces deterioration may have a larger impact on traditional faeces deposition surveys that 'clear' roads of faeces and then return one to several weeks later to resurvey. Faeces deterioration may vary by spatial (e.g. study site), temporal (e.g. season), biological (e.g. diet: Godbois *et al*. 2005) and anthropogenic (e.g. road traffic volume) factors. As a result, the impact of faeces deterioration and the other factors mentioned above warrant further attention.

In conclusion, we advise wildlife researchers to acknowledge and account for imperfect and variable observer-based faeces detection probabilities for carnivores. This may be especially important when investigations take a multispecies approach or the species of interest, and its respective faeces, is small (i.e. kit fox). Other factors that may bias faeces detection findings and resultant inferences should be carefully considered. Detection probabilities can be improved during the sampling design phase by sampling on roads that contain surface type compositions of 'high' SSC particles (e.g. >75%) and relatively 'narrow' road widths (e.g. <5 m), as long as such roads allow for the population of interest to be randomly sampled. If not accounted for during the sampling design phase, models used to estimate absolute or relative population state variables should take into account factors that may influence faeces detection probabilities and bias findings.

Acknowledgements

Funding and logistical support was provided by the Department of Defense, USA Army Dugway Proving Ground, Environmental Programs, Dugway, Utah, and the USA Department of Agriculture, Wildlife Services, National Wildlife Research Center, Utah State University, Logan, Utah. Additional funding was provided by the Quinney College of Natural Resources, Utah State University, Logan, Utah, and the Endangered Species Mitigation Fund of the Utah Department of Natural Resources, Division of Wildlife Resources, Salt Lake City, Utah. We thank R. Knight for providing continual support for the project, J. Fasig, W. Knowlton, W. Wright, C. Perkins, S. McEachin, J. DeCotis, and M. Richmond for field assistance, and R. Knight for review of the manuscript.

References

Anderson, D. R., and Burnham, K. P. (2002). Avoiding pitfalls when using information theoretic approaches. *Journal of Wildlife Management* **66**, 912–918.

Allen, B. L. (2012). Scat happens: spatiotemporal fluctuation in dingo scat collection probabilities. *Australian Journal of Zoology* **60**, 137–140. doi:10.1071/ZO12038

Allen, B. L., and Leung, L. K. P. (2012). Assessing predation risk to threatened fauna from their prevalence in predator scats: dingoes and rodents in arid Australia. *PLoS One* **7**, e36426. doi:10.1371/journal.pone.0036426

Bhagavatula, J., and Singh, L. (2006). Genotyping faecal samples of Bengal tiger *Panthera tigris tigris* for population estimation: a pilot study. *BMC Genetics* **7**, 48. doi:10.1186/1471-2156-7-48

Blott, S. J., and Pye, K. (2012). Particle size scales and classification of sediment types based on particle size distributions: review and recommended procedures. *Sedimentology* **59**, 2071–2096. doi:10.1111/j.1365-3091.2012.01335.x

Clark, F. W. (1972). Influence of jackrabbit density on coyote population change. *Journal of Wildlife Management* **36**, 343–346.

Cypher, B. L., Bjurlin, C. D., and Nelson, J. L. (2009). Effects of roads on endangered San Joaquin kit foxes *Journal of Wildlife Management* **73**, 885–893.

de la Rosa, S., Choudhery, R. N., and Chatziastros, A. (2011). Visual object detection, categorization, and identification tasks are associated with different time courses and sensitivities. *Journal of Experimental Psychology. Human Perception and Performance* **37**, 38–47. doi:10.1037/a0020553

de Oliveira, M. L., Norris, D., Ramirez, J. F. M., Peres, P. H. D., Galetti, M., and Duarte, J. M. B. (2012). Dogs can detect scat samples more efficiently than humans: an experiment in a continuous Atlantic Forest remnant. *Zoologia* **29**, 183–186. doi:10.1590/s1984-46702012000200012

Dempsey, S. J. (2013). Evaluation of survey methods and development of species distribution models for kit foxes in the Great Basin desert. M.Sc. Thesis, Utah State University, Logan, UT.

Dempsey, S. J., Gese, E. M., and Kluever, B. M. (2014). Finding a fox: an evaluation of survey methods to estimate abundance of a small desert carnivore. *PLoS One* **9**, e105873. doi:10.1371/journal.pone.0105873

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Gudrun, C., Carré, G., Garcia Marquéz, J. R., Gruber, B., Lafourcade, B., Leitao, P. J., Munkemuller, T., McClean, C., Osborn, P. E., Reineking, B., Schroder, B., Skidmore, A. K., Zurell, D., and Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46. doi:10.1111/j.1600-0587.2012.07348.x

Dodge, W. B., and Kashian, D. M. (2013). Recent distribution of coyotes across an urban landscape in southeastern Michigan. *Journal of Fish and Wildlife Management* **4**, 377–385.

Elbroch, M. (2003). 'Mammal Tracks and Sign: a Guide to North American Species.' (Stackpole Books: Mechanicsburg, PA.)

Farrell, L. E., Romant, J., and Sunquist, M. E. (2000). Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology* **9**, 1583–1590. doi:10.1046/j.1365-294x.2000.01037.x

Favelle, S. K., Palmisano, S, Burke, D, and Hayward, W. G.. (2006). The role of attention in processing configural and shape information in 3-D novel objects. *Visual Cognition* **13**, 623–642. doi:10.1080/13506280544000228

Feldhamer, G. A., Thompson, B. C., and Chapman, J. A. (2003). 'Wild Mammals of North America: Biology, Management, and Conservation.' (Johns Hopkins University Press: Baltimore, MD.)

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. In 'Carnivore Conservation'. (Eds J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne.) pp. 372–396. (Cambridge University Press: Cambridge.)

Gittleman, J. L., Funk, S. M., Macdonald, D. W., and Wayne, R. K. (2001). Why 'carnivore conservation'? In 'Carnivore Conservation'. (Eds J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne.) pp. 1–7. (Cambridge University Press: Cambridge.)

Godbois, I. A., Conner, L. M., Leopold, B. D., and Warren, R. J. (2005). Effect of diet on mass loss of bobcat scat after exposure to field conditions. *Wildlife Society Bulletin* **33**, 149–153. doi:10.2193/0091-7648(2005)33[149:EODOML]2.0.CO;2

Güthlin, D., Kroschel, M., Kuchemhoff, H., and Storch, I. (2012). Faecal sampling along trails, a questionable standard for estimating red fox (*Vulpes vulpes*) abundance. *Wildlife Biology* **18**, 374–382. doi:10.2981/11-065

Güthlin, D., Storch, I., and Kuchenhoff, H. (2013). Landscape variables associated with relative abundance of generalist mesopredators. *Landscape Ecology* **28**, 1687–1696. doi:10.1007/s10980-013-9911-z

Güthlin, D., Storch, I., and Kuchenhoff, H. (2014). Toward reliable estimates of abundance: comparing index methods to assess the abundance of a mammalian predator. *PLoS One* **9**, e94537. doi:10.1371/journal.pone.0094537

Harrison, R. L. (2006). A comparison of survey methods for detecting bobcats. *Wildlife Society Bulletin* **34**, 548–552. doi:10.2193/0091-7648(2006)34[548:ACOSMF]2.0.CO;2

Harrison, R. L., Barr, D. J., and Dragoo, J. W. (2002). A comparison of population survey techniques for swift foxes (*Vulpes velox*) in New Mexico. *American Midland Naturalist* **148**, 320–337. doi:10.1674/0003-0031(2002)148[0320:ACOPST]2.0.CO;2

Herrick, J. E., Van Zee, J. W., Havstad, K. M., Burkett, L. M., and Whitford, W. G. (2005). Monitoring manual for grassland, shrubland and savanna ecosystems. Pages 9–15. USDA-ARS Jornada Experimental Range.

Kaartinen, S., Kojola, I., and Colpaert, A. (2005). Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici* **42**, 523–532.

Keane, S. K., Hayward, W. G., and Burke, D. (2003). Detection of three types of changes to novel objects. *Visual Cognition* **10**, 101–127. doi:10.1080/713756672

Kelly, M. J., Betsch, J., Wultsch, C., Mesa, B., and Mills, L. S. (2012). Noninvasive sampling of carnivores. In 'Carnivore Ecology and Conservation: A Handbook of Techniques'. (Eds L. Boitani and R. A. Powell.) pp. 47–69. (Oxford University Press: Oxford.)

Knowlton, F. F. (1984). Feasibility of assessing coyote abundance in small areas. Final report, Denver Wildlife Research Center, Denver, CO.

Kohn, M. H., York, E. C., Kamradt, D. A., Haugt, G., Sauvajot, R. M., and Wayne, R. K. (1999). Estimating population size by genotyping faeces. *Proceedings. Biological Sciences* **266**, 657–663. doi:10.1098/rspb.1999.0686

Kozlowski, A. J., Gese, E. M., and Arjo, W. M. (2008). Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of Utah. *American Midland Naturalist* **160**, 191–208. doi:10.1674/0003-0031(2008)160[191:NOARPB]2.0.CO;2

Kruckenhauser, L., Rauer, G., Daubl, B., and Haring, E. (2009). Genetic monitoring of a founder population of brown bears (*Ursus arctos*) in central Austria. *Conservation Genetics* **10**, 1223–1233. doi:10.1007/s10592-008-9654-6

Lampa, S., Henle, K., Klenke, R., Hoehn, M., and Gruber, B. (2013). How to overcome genotyping errors in non-invasive genetic mark–recapture population size estimation – a review of available methods illustrated by a case study. *Journal of Wildlife Management* **77**, 1490–1511. doi:10.1002/jwmg.604

Link, W. (2003). Nonidentifiability of population size from capture–recapture data with heterogeneous detection probabilities. *Biometrics* **59**, 1123–1130. doi:10.1111/j.0006-341X.2003.00129.x

Long, R. A., Donovan, T. M., Mackay, P., Zielinski, W. J., and Buzas, J. S. (2007). Effectiveness of scat detection dogs for detecting forest carnivores. *Journal of Wildlife Management* **71**, 2007–2017. doi:10.2193/2006-230

Long, R. A., MacKay, P., Zielinski, W. J., and Ray, J. C. (2008). 'Noninvasive Survey Methods for Carnivores.' (Island Press: Washington, DC.)

Lukacs, P. M., and Burnham, K. P. (2005). Review of capture–recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* **14**, 3909–3919. doi:10.1111/j.1365-294X.2005.02717.x

Mackenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy probabilities when detection probabilities are less than one. *Ecology* **83**, 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Mackenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2006). 'Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence.' (Academic Press: Burlington, MA.)

Otis, D. L., Burnham, K. P., and White, G. C. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**, 135.

Peissig, J. J., and Tarr, M. J. (2007). Visual object recognition: do we know more now than we did 20 years ago? In 'Annual Review of Psychology'. pp. 75–96. (Annual Reviews: Palo Alto, CA.)

Proulx, G., Cattet, M. R. L., and Powell, R. A. (2012). Humane and efficient capture and handling of carnivores. In 'Carnivore Ecology and Conservation'. (Eds L. Boitani and R. A. Powell.) pp. 70–129. (Oxford University Press: Oxford.)

Purvis, A., Mace, G. M., and Gittleman, J. L. (2001). Past and future carnivore extinctions: a phylogenetic perspective. In 'Carnivore Conservation'. (Eds J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne.) pp. 11–34. (Cambridge University Press: Cambridge.)

R Development Core Team (2012). 'R: a Language and Environment for Statistical Computing.' (Foundation for Statistical Computing: Vienna.)

Ralls, K., and Smith, D. A. (2004). Latrine use by San Joaquin kit foxes (*Vulpes macrotis mutica*) and coyotes (*Canis latrans*). *Western North American Naturalist* **64**, 544–547.

Rosenberg, D. K., Overton, W. S., and Anthony, R. G. (1995). Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management* **59**, 252–261. doi:10.2307/3808938

Schaller, G. B. (1996). Introduction: carnivores and conservation biology. In 'Carnivore Behavior, Ecology, and Evolution'. (Ed. J. L. Gittleman.) pp. 1–10. (Cornell University Press: Ithaca, NY.)

Schauster, E. R., Gese, E. M., and Kitchen, A. M. (2002). An evaluation of survey methods for monitoring swift fox abundance. *Wildlife Society Bulletin* **30**, 464–477.

Smith, D. A., Ralls, K., Cypher, B. L., and Maldonado, J. E. (2005). Assessment of scat-detection dog surveys to determine kit fox distribution. *Wildlife Society Bulletin* **33**, 897–904. doi:10.2193/0091-7648(2005)33[897:AOSDST]2.0.CO;2

Stenglein, J. L., Waits, L. P., Ausband, D. E., Zager, P., and Mack, C. M. (2010). Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. *Journal of Wildlife Management* **74**, 1050–1058. doi:10.2193/2009-305

Stoddart, L. C. (1984). Relative abundance of coyotes, lagomorphs, and rodents on the Idaho National Engineering Laboratory. Annual report on predator ecology and behavior project. Idaho Falls, ID.

Storfer, A., Murphy, M. A., Spear, S. F., Holderegger, R., and Waits, L. P. (2010). Landscape genetics: where are we now? *Molecular Ecology* **19**, 3496–3514. doi:10.1111/j.1365-294X.2010.04691.x

Thompson, W. L. (1998). 'Monitoring Vertebrate Populations.' (Academic Press: San Diego, CA.)

Thacker, R. K., Flinders, B. H., Blackwell, B. H., and Smith, H. D. (1995). Comparison and use of four techniques for censusing three sub-species of kit fox. Utah Division of Wildlife Resources, Salt Lake City, Utah.

Treves, A., and Bruskotter, J. (2014). Tolerance for predatory wildlife. *Science* **344**, 476–477. doi:10.1126/science.1252690

Ullman, S. (2000). 'High Level Vision: Object Recognition and Visual Cognition.' 3rd edn. (Massachusetts Institute of Technology: Cambridge, MA.)

White, G. C. (2005). Correcting wildlife counts using detection probabilities. *Wildlife Research* **32**, 211–216. doi:10.1071/WR03123

Whittington, J., St. Clair, C. C., and Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* **15**, 543–553.

Williams, B. K., Nichols, J. D., and Conroy, M. L. (2002). 'Analysis and Management of Animal Populations.' (Academic Press: San Diego, CA.)

Zar, J. H. (2010). 'Biostatistical Analysis,' 5th edn. (Prentice Hall: Upper Saddle River, NJ.)