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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.

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 Manly 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

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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 1) higher for kit fox scats than coyote scats due to their smaller size, 2) higher at sites experiencing more frequent disturbance (higher traffic volumes), 3) higher along roads with a higher intensity of disturbances (larger roads facilitate increased traffic speeds), 4) highest for scats deposited in the tire tracks and lowest for those deposited on the shoulder and 5) 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.

Material and methods

Study area

The study was conducted on the US Army Dugway Proving Ground, USA, and neighboring lands (Fig. 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 1) two-lane gravel (large), 2) one-lane gravel (medium) and 3) two-track (small) roads, and then established three removal plots on roads representing each strata (Fig. 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 h 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,

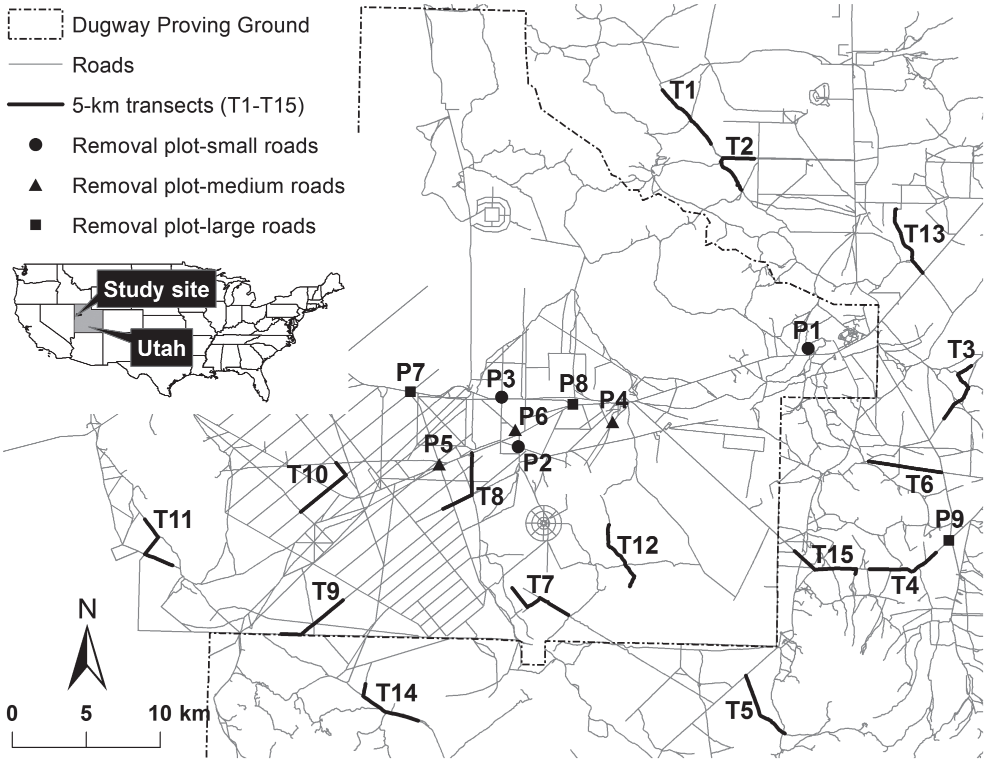

Figure 1. Locations of nine experimental plots (P1–P9) on two-lane (large) and one-lane (medium) gravel roads and two-track roads (small) used to estimate scat removal, and 15 scat survey transects (T1–T15) used to estimate relative abundance, for coyotes and kit foxes in western Utah, USA.

Oregon, USA) on eight plots. One plot (P9; Fig. 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. 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, <www.r-project.org>).

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, 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. 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. 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. 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, 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 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^{-1} 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 *Vulpes 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 ($\mathrm{AIC_C} = 1388.8$), but the Weibull model received similar support ($\mathrm{AIC_C} = 1389.8$). Log-normal ($\mathrm{AIC_C} = 1400.5$) and log-logistic ($\mathrm{AIC_C} = 1406.8$) 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 2). The second model included these same predictors plus season and was 2 $\Delta\mathrm{AIC_C}$ from the top model (Table 2), suggesting there was little support for this additional parameter or model (Arnold 2010). The next closest model was > 10 $\Delta\mathrm{AIC_C}$ from the top model, indicating relatively little or no support and the null model was among the models with the poorest fit (Table 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 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). Scats deposited in the median survived longer than those in the tracks; scats on the shoulder persisted the longest (Table 3). Scats on medium and small roads had 1.6 and 3.5 times longer survival, respectively, than scats on large roads (Table 3). Vehicle traffic was negatively associated with scat survival (Table 3).

Applying coefficient estimates from the best model and a single overall mean traffic volume for each road type (Table 1), we calculated the estimated proportion of scats persisting over time for each combination of categorical predictors (Fig. 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. 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. 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). 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).

Table 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 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

Relative abundance estimation and correction

Six transects (2, 10, 11, 12, 14 and 15) contained two road types (Supplementary material Appendix 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 4, Supplementary material Appendix 1). Correcting relative abundance altered the rankings of transects for coyotes in both seasons (Table 4). In summer, corrected:uncorrected relative abundance ratios ranged from 1.8–91.2 (mean = 15.0 ± 6.4 SE) among transects (Table 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 4). We failed to detect kit fox on one transect in summer and six transects in winter (Table 4, Supplementary material Appendix 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 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 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 1).

Variation in corrected relative abundance was generally highest for transects characterized as large roads (Supplementary material Appendix 2 Table A3–A6). 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 (Supplementary material Appendix 2 Table A3–A6). As expected, the variance associated with corrected relative abundance values was low for both small and medium roads (Supplementary material Appendix 2 Table A3–A6), which received considerably less vehicle traffic than large roads.

Table 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

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. 2) and that time until removal was influenced by survey conditions (road type) and frequency of disturbance (traffic; Fig. 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 4).

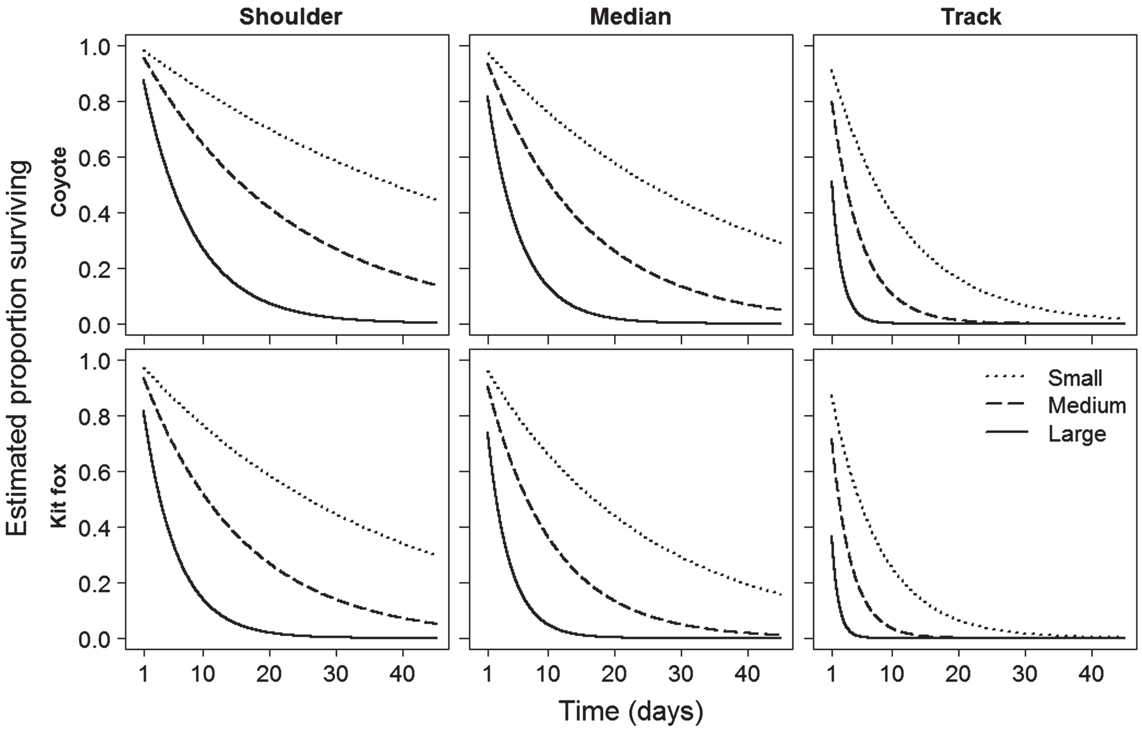

Figure 2. Estimated proportion of coyote and kit fox scats surviving over time on large (two-lane gravel), medium (one-lane gravel) and small (two-track) roadways when deposited in the median, track, or shoulder in western Utah, USA. Estimated survival was based on the exponential survival function assuming a mean daily traffic volume for each road type (large = 39.5; medium = 7.03; small = 0.54).

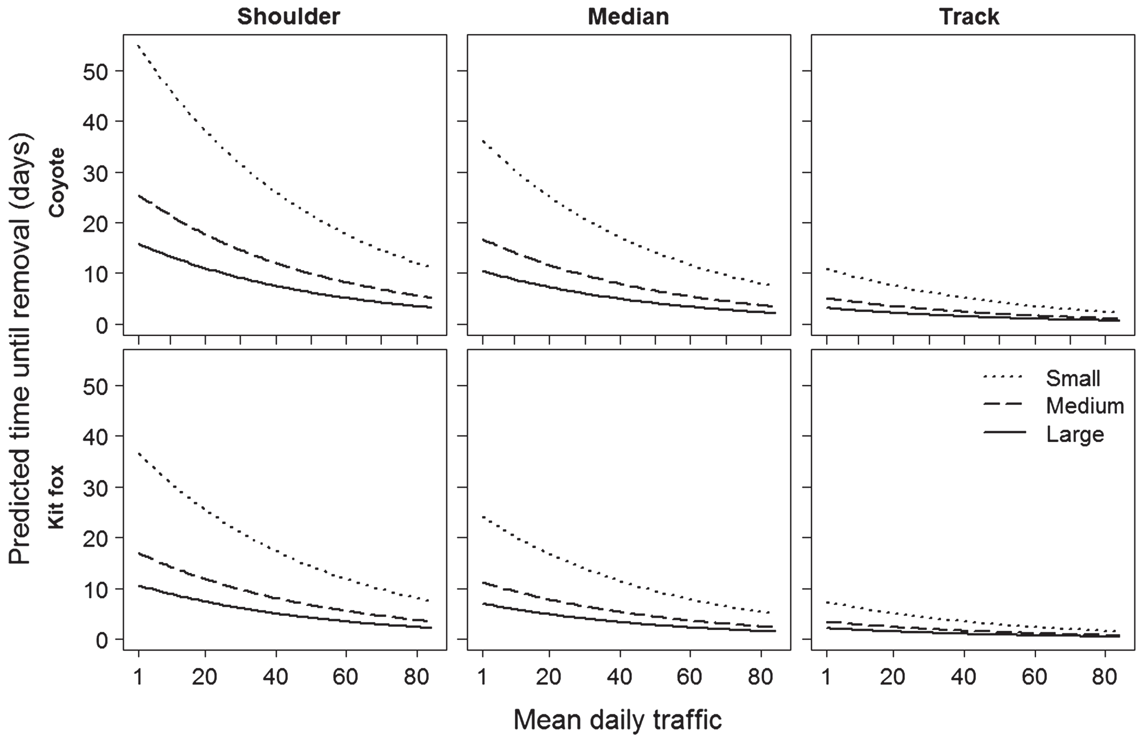

Figure 3. Predicted time until removal for coyote and kit fox scats as a function of mean daily vehicle traffic on large (two-lane gravel), medium (one-lane gravel) and small (two-track) roadways when deposited in the median, track or shoulder in western Utah, USA.

Table 4. Relative abundance (RA), corrected relative abundance (cRA), and ratio (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. Transect road types, traffic, and scat positions are available in Supplementary material (Appendix 1 Table A1–A2).

	Coyote						Kit fox					
	Summer 2013			Winter 2014			Summer 2013			Winter 2014		
Tran	RA	cRA	Ratio	RA	cRA	Ratio	RA	cRA	Ratio	RA	cRA	Ratio
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

Factors influencing scat removal

Species had a significant influence on scat survival, with kit fox scats being removed more rapidly (Fig. 2, 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. 2). When traffic volumes were held constant across road types, models predicted that time until removal increased with decreasing road size (Fig. 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. 2). Across road types, scats positioned in tracks had more similar removal rates (Fig. 2) and persistence times (Fig. 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 five 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. 2, 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). Indeed, traffic has been implicated for false-negatives, where scat surveys failed to detect swift foxes *Vulpes 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 4). Although season was not identified as an important predictor, vehicle traffic was important and was typically higher in summer than winter (Table 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 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. 2, 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 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 4, Supplementary material Appendix 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 4, Supplementary material Appendix 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 (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 1) conduct pilot studies to elucidate patterns and rates of scat deposition and removal, 2) minimize variation in removal among surveys during the design phase of studies and 3) and avoid surveys along transects with extremely high levels of disturbance and removal.

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