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Evaluating species-specific responses to camera-trap survey designs

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Camera traps are widely used to collect information on the distribution and abundance of multiple species simultaneously. However, we still lack important guidance for designing camera-trap surveys to monitor multiple species, and the consequences of species-specific responses to survey design strategies are often overlooked. Using camera-trap data collected on ten medium-to-large North-American carnivores in northern Minnesota, USA, between 2016 and 2018 (23 337 active trap-days), we evaluated: 1) two different survey-design frameworks (random- versus road-based), 2) two different lure types (salmon oil versus fatty acid scent oil), 3) two different placement strategies (completely random versus randomly-selected sites with feature-based placement), 4) survey timing (spring versus fall) and 5) temporal trends in daily encounter probabilities. Using generalized linear mixed models, we found evidence of differential responses to all of these design strategies. For 9 out of 10 species, we found strong responses to survey design frameworks: red foxes *Vulpes vulpes*, coyotes *Canis latrans*, bobcats, *Lynx rufus*, striped skunks *Mephitis mephitis*, wolves *C. lupus* and gray foxes *Urocyon cinereoargenteus*, had estimated encounter frequencies that were 9- to 106-fold higher at unlured sites along secondary roads; black bears *Ursus americanus*, martens *Martes americana* and fishers *Pekania pennanti* had estimated encounter frequencies that were 15- to > 3600-fold higher at lured, randomly selected sites. For six species, salmon oil provided 2- to 4-fold more encounters than fatty acid scent oil, but feature-basedplacement only improved detections of fishers. Daily encounter probabilities differed between spring and fall for all species, and usually decreased slightly within each sampling period Our study confirms that even similar-sized or closely-related species respond differently to survey-design choices. To maximize encounter frequencies, we recommend that multi-species camera-trap studies use a mix of survey-design strategies and include these design features during statistical analysis.

Keywords: attractants, camera trapping, carnivores, detection survey, monitoring, site-selection, trail use, lure

Species status assessments are critical for conservation and management planning. Nevertheless, the high cost of field studies often limits the number of taxa that can be monitored for changes in distribution and abundance. The introduction of passive acoustic and visual sensors has revolutionized ecological field research; devices such as camera traps and acoustic sensors facilitate the collection of fine-resolution data on multiple species, with minimal or no increase in cost or effort compared to studies targeting individual species. Camera traps in particular have played a critical role in transitioning from single- to multi-species studies; almost two-thirds of the 266 camera-trap articles reviewed by Burton et al. (2015) collected and analyzed data on more than one species. Many camera-trap studies focus on a single, often endangered or charismatic, species (hereafter single-species studies); however, 'bycatch data' from these studies are frequently used to quantify community metrics or to infer relative abundance and distribution of other associated species (Scotson et al. 2017). A survey designed for a focal species may not be adequate for others, and thus, better understanding of the impacts of study design on various response metrics is critically important, especially for camera-trap studies that target multiple species (hereafter multi-species studies).

Survey design is a crucial component of any ecological study and can affect data quality and inferences (Johnson 2002, Albert et al. 2010). Survey designs should be tailored to specific research objectives (e.g. estimating population abundance, or assessing the impact of road traffic or other anthropogenic disturbance on habitat use), and different designs may be more or less appropriate for different inferential goals (Garton et al. 2004, Meek et al. 2014). When designing a camera-trap study, researchers have to decide

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among several design features, including the timing of the survey and its duration, the number of sampling sites, camera settings, whether to use attractants and if so, which ones. For single-species studies, several best-practice guidelines are available to tailor survey design choices to the biological traits of the focal species, such as their movement patterns, behaviour and home range size (Sunarto et al. 2013, Meek et al. 2014, Sun et al. 2014, Steenweg et al. 2016). Conversely, for multi-species camera-trap studies, recommendations are available only when the focus is on species richness and community composition (Tobler et al. 2008, Si et al. 2014, Kays et al. 2020), rather than relative abundance or distribution. Importantly, even similarly-sized or closely-related species might show differential responses to survey strategies (Harmsen et al. 2010). Although several authors have hinted at the importance of species-specific responses to survey-design choices (Tobler et al. 2008, Harmsen et al. 2010, Sunarto et al. 2013, Mann et al. 2015, Rocha et al. 2016), work in this area has been generally limited to a few aspects of survey design (camera array composition: Pease et al. 2016, Evans et al. 2019; response to attractants: Mills et al. 2019, Buyaskas et al. 2020, Holinda et al. 2020).

Accumulating enough encounter data to obtain robust and accurate descriptions of population distribution and trend is important, especially for species that have low encounter rates. Strategies for increasing numbers of encounters include use of more camera traps and longer duration of deployment, or increasing encounters per camera-trap day by using attractants, targeting specific features at the camera site, and choosing optimal times to survey (Meek et al. 2014). Convenience-based sampling using survey sites along secondary roads and trails can allow investigators to deploy and monitor cameras more efficiently but at the expense of completely random site selection, thus sacrificing the ability to generalize to a larger sampling frame (Anderson 2001, Wearn et al. 2013). Deploying cameras along anthropogenic linear features such as hiking, logging and skid trails or seismic lines, can also lead to higher number of encounters of the many carnivores that utilize these structures as traveling routes (Wearn et al. 2013, Mann et al. 2015). Targeting natural features such as fallen logs, game trails or natural funnels can improve the chance of photographing some species (Kolowski and Forrester 2017), but deploying cameras in such a fashion requires additional time and expertise, and might preclude participation by less-experienced individuals that might otherwise help expand the scope or intensity of the survey (e.g. in citizen-science projects such as Snapshot Wisconsin <https://dnr.wi.gov/topic/research/projects/snapshot/>). Attractants such as baits (food reward) and lures (non-food reward) are often used in carnivore studies to increase encounter events (Schlexer 2008). However, responses to attractants can vary greatly among species, making choice of attractants an important aspect of study design in multi-species studies (Du Preez et al. 2014, Ferreira-Rodríguez and Pombal 2019, Buyaskas et al. 2020, Holinda et al. 2020). Seasonal timing of the survey can influence inference regarding habitat use or activity patterns (Kays et al. 2020) and affect encounter frequencies, particularly for species that hibernate or exhibit seasonal differences in density (e.g. pre- versus post-birth pulse). Encounter probabilities can also change during a sampling session due to changes in species' behaviour (e.g. decreases in daily travel distances when denning), temporal variability in the responsiveness to attractants (Mills et al. 2019), or as a result of vegetation growth obscuring the field of view.

Our study was motivated by a desire to inform design tradeoffs for a camera-trap survey being considered for medium-to-large sized carnivores occurring in Minnesota (USA). Minnesota hosts a diverse carnivore community that includes more than 16 species, from large-bodied carnivores such as American black bears *Ursus americanus* and wolves *Canis lupus* to small-bodied weasels (e.g. short-tailed weasels *Mustela erminea*), and it offers a good representation of the overall North American carnivore assemblage. The Minnesota Department of Natural Resources (MNDNR) currently uses scent-station and snow-track surveys to monitor trends in carnivore species (Sargeant et al. 2003, Erb 2016). Both of these surveys utilize a sampling framework of secondary roads and other linear features (i.e. transects are conducted along unpaved dirt roads or trails), which raises concerns about non-representative sampling if carnivores preferentially use or avoid these features. Camera trapping provides an attractive alternative to road-based surveys because it allows researchers to gather data over longer time periods and more representative spatial extents, and it is not dependent on specific road and traffic attributes (e.g. unpaved, low-traffic roads) or weather conditions (e.g. recent snow for snow-track surveys, or lack of rain for scent-station surveys). Camera traps have been used extensively to monitor terrestrial carnivores (Kelly et al. 2012, Mccallum 2013). However, guidance on camera-trap survey design when targeting multiple-species of carnivores can be further developed.

We quantified species-specific responses to two different sampling frameworks: 1) locations selected along secondary forest roads (road-based) versus 2) randomly-selected sites (random-based) baited with lures, where site indicates the location of a camera trap. We expected higher encounter probabilities along forest roads (compared to lured, random-based sites) for species that regularly use linear features as travel corridors (wolf: Dickie et al. 2017; coyote, *C. latrans*: Larrucea et al. 2007, Hinton et al. 2015; red fox, *Vulpes vulpes*, striped skunk, *Mephitis mephitis* and raccoon, *Procyon lotor*: Frey and Conover 2006) and we expected lower encounter probabilities for species that avoid these features (e.g. American marten, *Martes americana*: Robitaille and Aubry 2000). For random-based sites, we assessed two lures commonly used in carnivores studies (salmon oil versus fatty acid scent oil), and two placement strategies (randomly-selected with feature-based placement versus completely-random placement), where placement reflects the degree of flexibility afforded when choosing the exact location of the camera site. The lures we selected are both known to be multi-species attractants (Schlexer 2008), but they have not been formally compared for their efficacy at attracting carnivores. Targeting local features, such as natural topographic bottlenecks, proximity to creeks and other water sources, and animal trails (e.g. deer trails) or other signs of animal presence, usually increases encounter rates of carnivores (Trolle and Kéry 2005) and other mammals (Kolowski and Forrester 2017); we thus expected more encounters at feature-based sites compared to completely random locations. Each design feature was

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replicated in three spring and two fall sampling seasons, and we also assessed temporal trends in daily encounter probabilities for each species within each season. For most species, we expected marked differences between the two seasons due to post-birth increase in population size, and general decreasing trends in daily encounter probabilities during each sampling session as lures decreased in their attractiveness. Species-specific responses to sampling design might hinder the value of multi-species camera trapping; in our analysis, we evaluated species-specific responses by ten North-American carnivores to five aspects of sampling designs that are crucial in carnivore camera-trap studies.

Material and methods

Study area

We collected data in a 1872 km^2 (48 × 39 km) mixed-coniferous forested area located in northern Minnesota, USA (centered at 47°37′16.3″N, 93°26′25.6″W; Fig. 1A). This region is mainly covered by lakes and forests with a slight majority (51%) being public land, but on which management practices and intensity varied widely by agency (17, 16 and 18% managed by county, state and federal land management agencies, respectively). The remaining land was owned by private industrial timber companies (13%) and private individuals (36%). Most of the study area, including the private industrial forest, was open to most forms of public recreation; this included hunting and trapping, though these activities generally occurred outside of our survey sessions in spring and early fall. Forests consisted primarily of mixtures of aspen *Populus* spp., oaks *Quercus* spp., sugar maple *Acer saccharum*, birch *Betula* spp., pines *Pinus* spp., spruce *Picea* spp. and balsam fir *Abies balsamea*, in upland areas, and spruce, tamarack *Larix laricina*, cedar *Cedrus* spp. and black ash *Fraxinus nigra*, in lowlands (Itasca County Land Dept 2009), with timber extraction being common, but spatially variable in intensity, across the study area. The area was sparsely populated (~2 people km^{-2}) and had a low density of maintained roads (~0.22 km of road km^{-2}), though low or no maintenance forest trails (e.g. gated logging trails, ATV and snowmobile trails) were common in the study area. Carnivore species present included black bear, gray wolf, coyote, bobcat *Lynx rufus*, fisher *Pekania pennanti*, American marten, raccoon, striped skunk, gray fox *Urocyon cinereoargenteus*, red fox, American badger *Taxidea taxus*, North American river otter *Lontra canadensis*, mink *Neovison vison* and short-tailed, long-tailed (*M. frenata*) and least (*M. nivalis*) weasels (Hazard 1982).

Sampling design

We compared species-specific encounter frequencies at lured, randomly-selected sites (random-based) to those at unlured cameras placed along secondary roads or trails (road-based; Table 1). We loosely defined secondary forest roads or trails as those that did not receive year-round maintenance and were accessible primarily on foot or with off-road vehicles (e.g. logging or forest roads, ATV or snowmobile trails). At the random-based sites, we further compared two lure types and two placement strategies using a 2 × 2 factorial experiment following a randomized complete block design.

We divided the study area into 20 contiguous 9.65 × 9.65 km blocks (Fig. 1A). Then, we delineated four equally-spaced and equally-sized subquadrats within each block to ensure a minimum of 1.6 km between camera locations both within and across blocks, thereby minimizing the chance of cross contamination (e.g. via wind transference of scent; Fig. 1B). Using ~20 × 20 m resolution light detection and ranging (LiDAR) data collected by the State of Minnesota in 2011 (<www.mngeo.state.mn.us/chouse/elevation/lidar.html>; Fig. 1), we restricted site selection to forested areas with mean tree height > 3 m and canopy cover > 50% to account for the habitat preferences of the target species (predominantly forest carnivores) and avoid selection of sites in lakes, wetlands or recently logged areas. We intersected the forest areas identified via LiDAR with the subquadrats and used the generate random points tool in ArcGIS (ESRI 2011) to select one random forested location within each subquadrat (Fig. 1B). We randomly assigned the four combinations of lure type (salmon oil versus fatty acid scent oil) and placement strategy (completely random versus random but feature-based) to the four sites within each block. Camera locations (and thus, placement strategies) were kept constant across all study periods, but we employed a crossover design with respect to lure choice starting in spring 2017 (i.e. sites with salmon oil in 2016 received the fatty acid scent oil in 2017 and 2018, and vice versa). In each block, we deployed an additional unlured camera on the secondary road or trail closest to the centre of each block, provided the site was at least 400 m from all primary roads and at least 1.6 km from other cameras (Fig. 1B).

In each sampling session, we collected data from 100 sites (20 unlured, road-based and 80 lured, random-based). At each site, we deployed a passive infrared camera (Bushnell 119776). We conducted five bi-annual (spring and fall) six-week surveys from spring 2016 through spring 2018. Cameras were deployed from 1 May to mid-June in spring 2016; however, in 2017 and 2018, we postponed deployment until 15 May to reduce the occurrence of false triggers resulting from growing vegetation or the interaction between insolation and shadow movement due to lack of canopy cover. In the fall, we deployed cameras starting on 1 September. Additional details regarding the sampling design and camera settings are provided in the Supplementary information.

Lure type

We opted for using scent lures as an attractant. Following a literature review (Schlexer 2008) and preliminary field testing, we narrowed our choice to two options commonly used in carnivore studies: salmon oil (Salmon) versus fatty acid scent oil (FAS), a liquid version of the synthetic fatty-acid tablets used by the MNDNR in their current scent-station survey and in many similar surveys throughout North America (Gese 2001, Erb 2016). Depending on the randomly assigned lure type, we deployed either 473 ml of Minnesota Brand salmon oil (Minnesota Trapline Products, Pennock, MN, USA) or a 237 ml bottle that consisted of 80% mineral oil and 20% liquid FAS (USDA Pocatello Supply Depot, Pocatello, ID, USA). We poured the lure on a tree located

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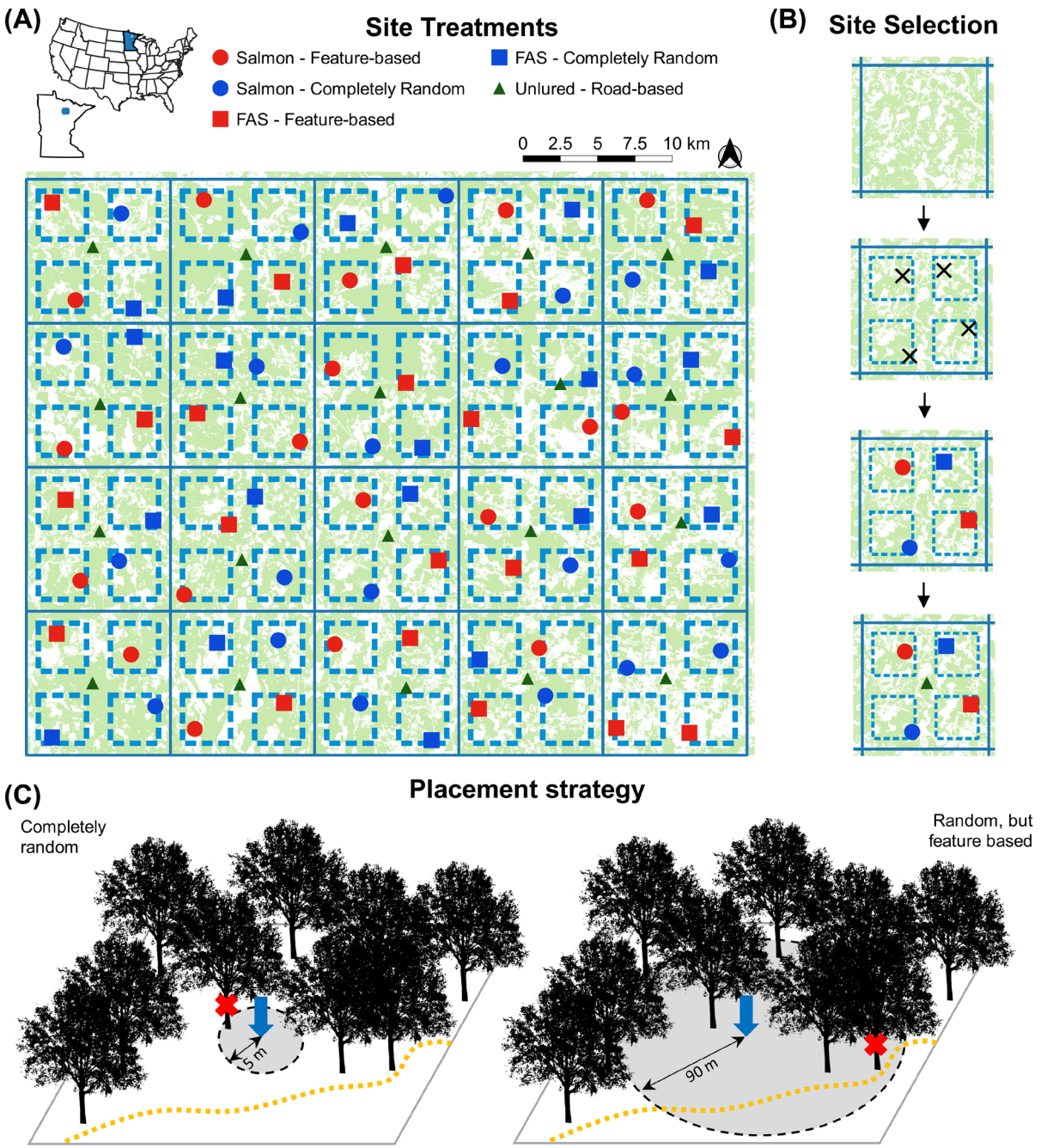


Figure 1. (A) Schematic of the study area and treatments assigned at each site during spring 2017. Green-shaded areas represent forest; solid and dashed lines delineate blocks and subquadrats within blocks, respectively. (B) In each block, we first identified the forested areas using LIDAR data, and randomly selected one site (black cross) within each subquadrat. Then, we randomly assigned a combination of lure type and placement strategy to each of the four sites. Finally, we identified a fifth site on the secondary road closest to the centre of the block to deploy the unlured, road-based camera. (C) Placement strategy: we placed cameras (red cross) assigned to the completely random treatment on a tree within a 5-m radius from the randomly selected location (blue arrow). For cameras assigned to the feature-based treatment, we opportunistically selected a tree at or facing a feature that might increase carnivore encounters (e.g. deer trails: dotted orange line) within a 90-m radius from the randomly selected location.

4.3–9.1 m in front of the camera, with a preferred distance of 5–7 m (mean ± SD: 6.3 ± 0.97).

Placement strategy

At the lured cameras, we compared two placement strategies: completely random (CR) versus random, but feature-based (Feature; Fig. 1C). At completely random sites, we placed the camera on a tree within a 5-m radius from a predefined randomly-selected location. At feature-based sites, the operator, an experienced biologist, actively looked for an optimal placement location (e.g. animal trail, proximity to water, movement 'bottleneck' or high quality denning or foraging features) within a 90-m radius of a randomly selected point (Fig. 1C).

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Table 1. Treatments applied to camera-trap sites. In each of the 20 blocks in the study area, we deployed a camera on the secondary road closest to the centre of the block and four other cameras at randomly-selected locations, to which we randomly assigned the four combinations of lure type (two levels) and placement strategy (two levels). During each sampling session, 20 camera sites were allocated to each of the five treatments. We tested for differences between survey-design strategies using the contrasts specified below. α_ω represents the estimated coefficient for each treatment, with: $\omega = 1$: unlured, road-based; $\omega = 2$: salmon oil with feature-based placement; $\omega = 3$: salmon oil with completely-random placement; $\omega = 4$: FAS with feature-based placement; $\omega = 5$: FAS with completely-random placement.

	Coefficient estimates for specific sampling strategy	Contrast
Survey framework		$\frac{\alpha_2+\alpha_3+\alpha_4+\alpha_5}{4}-\alpha_1$
Random	$(\alpha_2+\alpha_3+\alpha_4+\alpha_5)/4$	
Road-based	α_1	
Lure type		$\frac{\alpha_2+\alpha_3}{2}-\frac{\alpha_4+\alpha_5}{2}$
Salmon oil (Sal)	$(\alpha_2+\alpha_3)/2$	
Fatty acid scent oil (FAS)	$(\alpha_4+\alpha_5)/2$	
Placement strategy		$\frac{\alpha_3+\alpha_5}{2}-\frac{\alpha_2+\alpha_4}{2}$
Completely random (CR)	$(\alpha_3+\alpha_5)/2$	
Random, feature-based (Feat)	$(\alpha_2+\alpha_4)/2$	

Photo processing

We collected > 2 300 000 images over 23 337 active trap-days. Following the protocol described in Niedballa et al. (2016), we used the open access photo manager software Digikam to add species ID to the EXIF metadata of each image. This information, along with date and time the image was taken, were then extracted using the *camtrapR* package (Niedballa et al. 2016) in program R (<www.r-project.org>). For morphologically similar species (i.e. wolf–coyote, marten–fisher and red–gray fox at night), we assigned an image (or sequence of images) to a certain species only when the majority of at least three observers agreed on the classification. Most images were of solitary individuals, but if an image contained multiple individuals (e.g. female bear with cubs), the group was recorded as a single observation.

Statistical analysis

For each species, we assessed the effect of treatments on the number of independent encounter events using a daily observation window. To determine the minimum time interval needed to assure independence among subsequent images, we constructed lorelograms (Heagerty and Zeger 1998, Iannarilli et al. 2019) to quantify correlation at time lags of 1–60 min using the R-package *lorelogram* (Iannarilli and Fieberg 2019), pooling data across years for each combination of species and season (Supplementary information). Based on the lorelograms, we defined two subsequent images of the same species at the same site as independent events if they were ≥ 30 min apart, and applied this threshold to extract the number of independent events within each day using the *camtrapR* R-package (Niedballa et al. 2016). For most species, serial independence was reached at short intervals (e.g. < 20 min in black bears); however, we used a more conservative threshold of ≥ 30 min to accommodate species that lingered for a longer time at the site (e.g. raccoons in the fall; Supplementary information).

For each species, we fit a negative binomial generalized linear mixed model (GLMM) to the number of independent events per day C_{ijkt} at site i within block j during day t and season k to test for effects of Treatment (ω, with 5 levels: $\omega = 1$: unlured, road-based; $\omega = 2$: salmon oil with feature-based placement; $\omega = 3$: salmon oil with completely-random placement; $\omega = 4$: FAS with feature-based placement; $\omega = 5$: FAS with completely-random placement; Table 1), number of days since deployment/30 (Day), Season (a factor with two levels, spring = 1 or fall = 0), and the interaction between Season and Day to allow temporal changes to vary by season:

$$C_{ijkt} \quad \text{NegativeBinomial}\left(\mu_{ijkt}, \theta\right)$$

$$\log(\mu_{ijtk}) = \alpha_{\omega(ijk)} + \beta_1 \times \text{Season}_k + \beta_2 \times \text{Day}_t + \beta_3 \times \text{Season}_k \times \text{Day}_t + \varphi_j + \gamma_{ij}$$

$$\varphi_j \quad \text{Normal}\left(0, \sigma^2_\varphi\right)$$

$$\gamma_{ij} \quad \text{Normal}\left(0, \sigma^2_\gamma\right)$$

where θ is the dispersion parameter of the negative binomial distribution. We included block φ_j and site-within-block γ_{ij} as design-based random effects to account for the hierarchical structure of the data (i.e. repeated measures at sites within blocks). We fit models using the R-package *glmmTMB* (Brooks et al. 2017) and applied post hoc pairwise comparisons (Table 1) to test for main-effect differences between survey strategies (lured-random versus unlured, road-based design framework; salmon oil versus FAS; completely-random versus randomly selected sites with feature-based placement) using the R-package *emmeans* (Lenth 2020). For example, we can contrast the effect of salmon oil versus FAS using the following contrast: $\frac{\alpha_2+\alpha_3}{2}-\frac{\alpha_4+\alpha_5}{2}$ (Table 1). To visualize seasonal trends in encounter frequencies during the spring and fall, we used the fitted models

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to calculate $\hat{p}_t$, the probability of encountering a species at least once during day t at a 'typical site' (i.e. one with all random effects set to 0; Fieberg et al. 2009):

$$p_t = 1 - p_t(0)$$

where $p_t(0)$, the probability of not encountering the species during day t, was calculated as $\left(\frac{\hat{\theta}}{\hat{\mu}_t + \hat{\theta}}\right)^{\hat{\theta}}$, with $\hat{\mu}_t$ equal to the model-based expected number of encounter events in day t, and $\hat{\theta}$ equal to the estimated overdispersion parameter. We used a parametric bootstrap with 2000 replicates to construct 95% confidence intervals around $\hat{p}_t$, facilitated by the bootMer function in R-package *lme4* (Bates et al. 2015). As a form of sensitivity analysis, we re-analysed the data with models that also included fixed year effects. All the analyses were performed in R ver. 4.0.0 (<www.r-project.org>). Data and code are available at <https://conservancy.umn.edu/handle/11299/217465>.

We use the term 'encounter' to stress that our response variable (counts of species at each site) captures animals that pass within the camera's triggering window, and is thus influenced by species traits (e.g. body size, home-range size), animal abundance and movement rates. Species must also be correctly identified in the photos, and factors such as camera model and settings, weather conditions, clarity of the images captured, use of attractants, vegetation density and other features of the camera sites can influence species counts (Hofmeester et al. 2019 for a more exhaustive list of factors). We attempted to minimize systematic (non-random) variation in these factors as much as possible, for example using the same camera model at all locations and standardizing the amount of lure applied.

Results

Encounter events

We restricted our analysis to 10 species with ≥ 75 independent encounter events over the entire study period. This included American black bears (1041 events), gray foxes (637), raccoons (584), gray wolves (535), striped skunks (357), red foxes (285), coyotes (253), fishers (245), American martens (161) and bobcats (76; Fig 2A), but excluded badgers (19), weasel spp. (9) and otters (1). Ignoring zeroes, the number of independent encounter events per day ranged between 1 and 7 (mean ± SD: 1.17 ± 0.53) but was usually 1 (Fig. 2B).

Sampling framework

For all species except raccoon, the potential effect sizes in response to site-selection strategies were extremely large, with estimated contrasts having a median of ±4 units on the log scale, representing 55-fold variation in frequency of encounters on the real parameter scale (Fig. 3A). Canids, bobcats and skunks were encountered more frequently along roads, although effect sizes for both fox species were imprecise, with confidence intervals that broadly overlapped zero; conversely, bears, fishers and martens were encountered less frequently at sites along roads (Fig. 3A).

Lure type

Six species (wolf, striped skunk, marten, gray fox, fisher and coyote) were encountered more frequently when using salmon oil relative to fatty acid scent oil, with estimated effect sizes on the log scale ranging between 0.63 and 1.46, which equates to ~1.9- to 4.3-fold more encounters per day when using salmon oil (Fig. 3B). Black bears were estimated to have ~1.3 times more encounters per day when using fatty acid scent oil relative to salmon oil, though the 95% confidence interval (0.95–1.72) for the rate ratio overlapped 1.

Placement strategy

We found little evidence that placing cameras at feature-based sites increased the chance of capturing images of carnivores, except for fishers which were estimated to have 3.32 (95% CI: 1.16–9.44) times more encounters per day at feature-based than at completely random sites (Fig. 3C).

Survey timing and temporal trends

The probability of encountering the species at least once during a day at a 'typical' camera site, $\hat{p}_t$, varied by season for all species (Fig. 4). Striped skunks, coyotes, fishers, gray foxes, martens and more weakly, wolves, raccoons, red foxes and bobcats had higher values of $\hat{p}_t$ during the fall survey; only black bears displayed higher values in the spring. Daily encounter probabilities were quite low for all species, as expected for carnivores, with the highest values ($\hat{p}_t \geq 0.02$) for black bear and wolf, the two largest species in our pool (Fig. 4). Further, $\hat{p}_t$ tended to decrease slightly throughout the sampling period for most species by season combinations, and decreased sharply for martens and fishers in the spring, and for black bears and skunks in the fall. By contrast, $\hat{p}_t$ increased slightly for black bears in the spring, and for the four canids in the fall (Fig. 4).

Estimated effect sizes for all survey-design features were robust to the inclusion of fixed year effects (Supplementary information).

Discussion

We concurrently assessed multi-species carnivore responses to multiple camera-trap design choices (lured, random versus unlured, road-based frameworks, multiple lures and placement strategies, and timing of surveys) using a model-based approach. Each of the ten carnivores species targeted in our survey showed strong, species-specific responses to one or more aspects of survey design. These findings illustrate how survey strategy can influence comparisons across time, space or species when assuming equal and constant detection probabilities (e.g. using relative abundance indices given by the number of capture events within a certain sampling period: Carbone et al. 2001, O'Brien et al. 2003).

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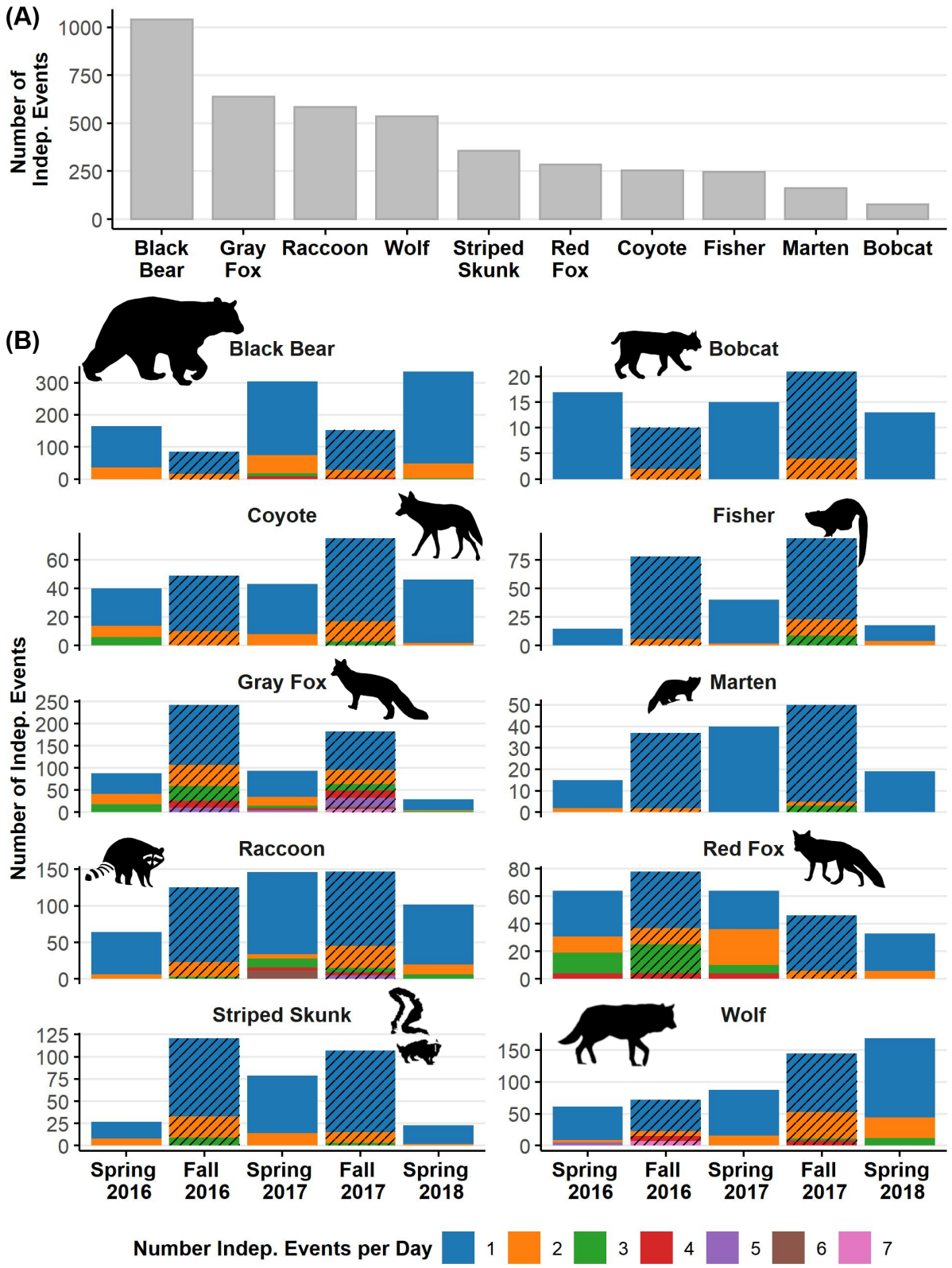


Figure 2. Overall number of independent encounter events by species (A) and species and session (B). Colours within bars in (B) highlight whether a specific event belonged to a day with one or more independent events (defined using a 30-min interval). Hatched bar: fall; otherwise: spring. Numeric ranges in y-axis differ by species.

Researchers should carefully consider species-specific responses to stimuli and survey-design strategies, and a hybrid, mixed survey strategy may be necessary to ensure adequate encounter probabilities when the objective is to simultaneously monitor trends of several species. For example, to monitor the medium-to-large carnivore species occurring in Minnesota, we recommend using a mix of road-based cameras and cameras at randomly-selected

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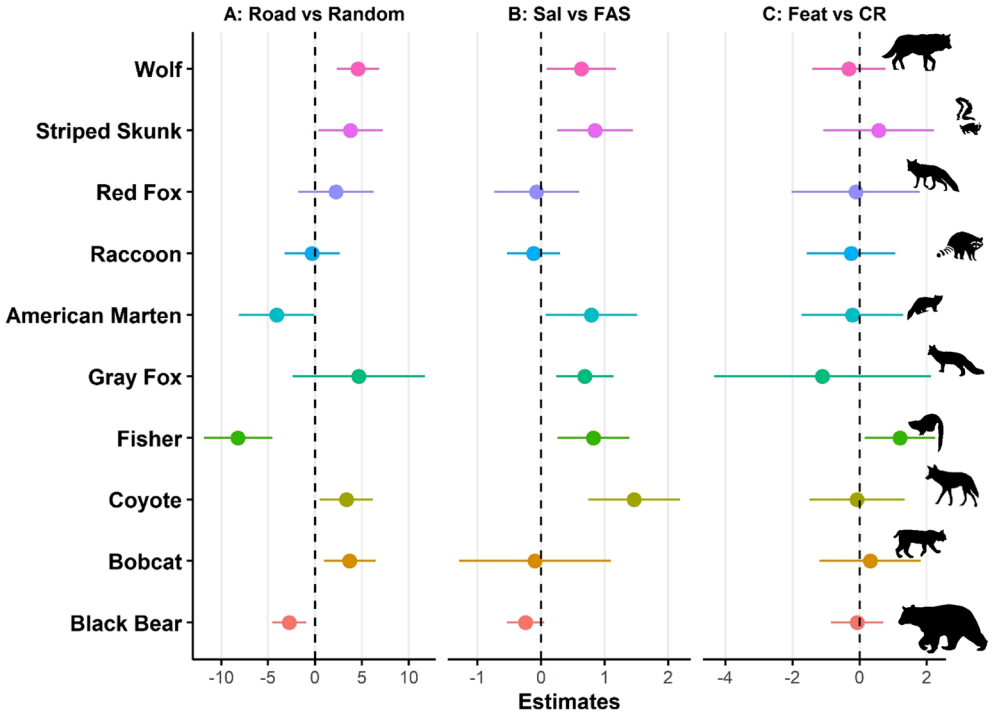


Figure 3. Estimated contrasts (mean and 95% confidence interval: dots and lines) comparing the log expected number of independent carnivore encounters per day under different camera-placement treatments. Note different scales for each treatment on x-axis; 1 unit represents an exp(1) ≈ 2.7-fold change in encounter frequencies. (A) Unlured cameras deployed along secondary forest roads (Road) versus lured cameras placed at random locations (Random). For cameras at random locations, we compared: (B) use of salmon versus fatty acid scent oil (FAS) as an attractant; (C) cameras opportunistically placed at local features that might enhance carnivore encounter (Feat) versus cameras deployed at completely random locations (CR). Wolves, striped skunks, coyotes and bobcats were more likely to be encountered at sites along forest roads; black bears, martens and fishers were more likely to be photographed at random, lured sites. For six out the ten species, salmon oil increased the number of independent encounter events compared to FAS. Placement strategy had little effect on frequency of encounter for most of the species; only fishers showed a ~3-fold increase at feature-based sites.

locations lured with salmon oil. Limiting the survey to only cameras deployed along secondary roads would have resulted in many fewer encounters of fishers, martens and black bears, and using only cameras deployed at lured, random forest sites would have resulted in fewer encounters of wolves and other species that tend to use linear features. Historically, many multi-species carnivore monitoring projects have relied on recorded tracks or signs of animal presence along roads (Gese 2001). Our results suggest that road-based camera surveys likely lack statistical power for detecting trends in the relative abundance of species like fisher, marten and black bear that limit their use of roads. Ultimately, however, survey designs need to be tailored to meet specific study objectives, and a stratified design might be needed to ensure representative habitats are sampled while also allowing for certain areas to be oversampled. Pilot studies can help assess species-specific responses to different sampling strategies, verify that any proposed sampling design will be able to meet study objectives, and help determine whether it will be important to include survey design features as covariates when analysing survey data (as also suggested by Hofmeester et al. 2019).

Encounter frequencies at unlured sites along forest roads and trails were dramatically higher than at lured, randomly-selected locations for red foxes (9-fold average increase), coyotes (28-fold), bobcats (39-fold), striped skunks (43-fold), wolves (96-fold) and gray foxes (106-fold), although effects were less precise for the two fox species. Canids and striped skunks exploit secondary roads and other linear features to efficiently traverse the landscape and increase their search area for prey (Frey and Conover 2006, Larrucea et al. 2007, Hinton et al. 2015, Dickie et al. 2017). Camera-trap studies focused on felids often use road-based surveys (Hines et al. 2010, Blake and Mosquera 2014). Bobcats, the only felid in our pool of species, were more frequently encountered at cameras placed along forest roads, where the species might benefit from the forest-edge habitat provided by these openings to ambush its prey (McNitt et al. 2020); secondary trails, some of which were related to logging, might also be correlated with dense, early successional habitat that bobcats may prefer (Kapfer 2012). By contrast, black bears, martens and fishers were 15, 60 and > 3600 times, respectively, more likely to be encountered at lured, randomly-selected sites than at unlured locations on forest roads. Black bears are extremely sensitive to human use of secondary roads (Ditmer et al. 2018), tend to use these structures only when human traffic is low (Switalski and Nelson 2011, Buyaskas et al. 2020) and only during certain periods (e.g. outside bear-hunting season: Brody and Pelton 1989). American martens and fishers prefer forested areas with overhead cover and complex physical structure near the ground (Powell et al. 2003), characteristics not present on secondary roads or trails, and martens also show higher frequency of habitat use in forested areas away from roads

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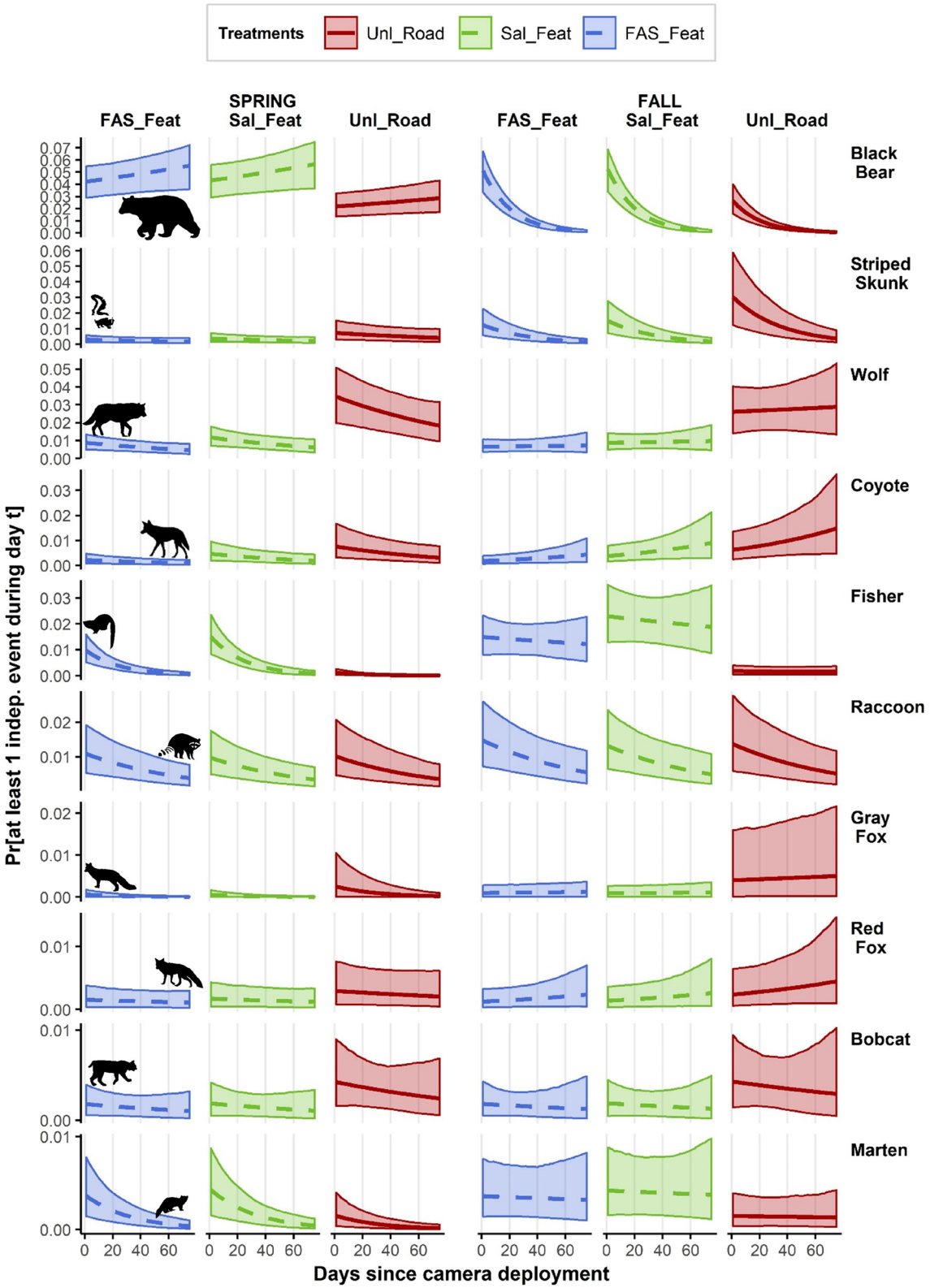


Figure 4. Daily probability of encountering a species at least once during a certain day of sampling at a 'typical site' (i.e. a site with all random effects equal to zero) as a function of days since camera deployment and season based on treatments (unlured, road-based: Unl_Road; feature-based sites lured with salmon (Sal_Feat) or FAS (FAS_Feat) oil). Completely-random sites exhibited trends similar to feature-based sites. For all species, daily probabilities were low and changed over time and across seasons. Numeric ranges in y-axis differ by species. Shaded areas represent 95% confidence intervals constructed from a parametric bootstrap.

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(Robitaille and Aubry 2000). Furthermore, Buyaskas et al. (2020) found that the use of attractants was important for detecting martens and fishers; the combination of lures and placement of cameras away from roads and trails proved effective for detecting these two species in our study.

We found that salmon oil, compared to FAS, quadrupled encounters of coyotes, doubled those of wolves, gray foxes, American martens, fishers and striped skunks, and was at least as effective for attracting bobcats, raccoons and red foxes. Black bears were the only species for which encounter frequencies tended to be higher at sites lured with FAS, but this result was fairly weak (about 1.3 times higher at FAS sites), not statistically significant, and black bears already had the highest encounter probabilities of any species. The use of lures and other attractants has often been criticized because it could affect individuals' movement and behaviour patterns (Balme et al. 2014), but studies have shown that attractants do not always influence movement patterns (Du Preez et al. 2014, Stewart et al. 2019) or alter distance travelled (Braczkowski et al. 2016); more research is needed to determine the general extent and magnitude of these effects. Further, the importance of lure effects on movements will depend on the study's objectives and may be more important when estimating density than when attempting to quantify species distribution patterns at coarser scales. Also, the efficacy of lures in attracting carnivores usually decreases over time (Mills et al. 2019); the diminishing effect of lures can be modelled by including a variable that measures time since deployment. The lessening potency of lures during our six-week sampling periods might also explain the declines in daily encounter probabilities that we observed for most species (Fig. 4). Anecdotally, we have found that lures generally increased the number of images per encounter event. This can be extremely helpful in multi-species studies because it greatly improves the chance of correctly identifying species with similar morphology (e.g. wolf–coyote, marten–fisher, red–gray fox in our study). Similarly, in mark–recapture studies, a higher number of pictures per event can facilitate the identification of individuals (Du Preez et al. 2014).

Contrary to other studies (Cusack et al. 2015, Kolowski and Forrester 2017), we found that targeting local features (e.g. game trails) in the vicinity (within 90 m) of a randomly-selected location did not increase encounter frequencies. It is possible the use of a lure masked any potential advantages of feature-based placement (i.e. because lures may draw an animal to a site regardless of other features). Fishers represented the only exception, showing a 3.3-fold increase in encounters at feature-based sites. Our comparison of placement strategies suggests that there is little benefit to exclusively depending on the expertise of trained biologists (versus citizen scientists) for camera placement, at least when using lures. Hence, monitoring programs may benefit from engaging citizen scientists in camera placement to extend the spatial scale and camera density of a study (McShea et al. 2016). Feature-based placement may be more beneficial when not using lures.

Sampling in fall instead of spring led to higher daily probabilities of encounter for fishers, martens and striped skunks, and slightly higher probabilities for raccoons and the four canids. Black bear was the only species showing higher encounter probabilities in spring than in fall, possibly due to a stronger attraction to lures after first emergence from dens in spring and a decrease in use of roads and lured sites in response to hunting in the fall (Brody and Pelton 1989, Candler et al. 2019). Seasonal differences in movement rates due to different foraging opportunities or reproductive activities (e.g. reduced movements during the denning period in fishers in the spring: Powell et al. 2003) might also result in seasonal differences in encounter probabilities. The two largest species, black bear and wolf, had the highest daily encounter probabilities. Others have also found that larger-sized species tend to have more encounters (Tobler et al. 2008, Rowcliffe et al. 2011, Anile and Devillard 2016). These results may be explained, in part, by differences in detection probabilities resulting from commonly used camera heights (~75 cm above the ground) and angles (parallel to the ground). Smaller species may be less likely to trigger the camera, and they may be more difficult to identify in blurry pictures compared to larger-body animals. These issues may partially explain the lower encounter probabilities of martens in our study. Alternatively, lower encounter probabilities may be tied to lower densities or movement extents of smaller species. The low daily encounter probabilities of coyote, the third largest species in the study, may be a result of lower density in our study area due to the presence of interspecific competitors like wolves (Palomares and Caro 1999, Levi and Wilmers 2012), or potentially more wariness of humans and cameras (Séquin et al. 2003).

The current rate of biodiversity loss is exacerbating the need to assess species status and distribution over broad spatial scales (Dirzo et al. 2014). Camera traps, paired with the engagement of citizen scientists in camera deployment and species identification, have extended the spatio–temporal scale of ecological studies (Steenweg et al. 2017) and facilitated the development of broad-scale networks aimed at monitoring large assemblages of species (e.g. TEAM Network: Jansen et al. 2014; Snapshot Safari: <https://lioncenter.umn.edu/snapshot-safari/>; eMammals: McShea et al. 2016). However, localized, model-based and standardized research like ours will facilitate comparative analyses and development of much needed guidelines for applied monitoring programs. We recommend that monitoring programs seeking to collect information on a diverse range of species rely on a mix of standardized, consistently-applied survey strategies to maximize data collection for as many of the target species as possible. Pilot testing of several survey options could help inform future design choices and analysis, and, in turn, have a positive impact on the quality and quantity of the data collected and used to inform wildlife management decisions.

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Supplementary information (available online as Appendix wlb-00726 at <www.wildlifebiology.org/appendix/wlb-00726>).

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