EVALUATION OF DESIGN AND ANALYSIS OF A CAMERA-BASED MULTI-SPECIES OCCUPANCY SURVEY OF CARNIVORES IN MINNESOTA

Fabiola Iannarilli[1], John Erb[2], Todd Arnold[1], and John Fieberg[1]

SUMMARY OF FINDINGS

Camera-based surveys are increasingly being used to monitor wildlife species across large areas and a diverse range of habitats. We initiated a study in a forested area of northern Minnesota to assess various design and analysis questions related to use of remotely-triggered cameras for simultaneously monitoring the occurrence of multiple species of carnivores. In spring and fall 2016, we deployed 100 cameras in an area equivalent to 20 townships, with 5 cameras placed in each 9.65- x 9.65-km township. To test different lures and strategies for camera placement, we conducted a 2 x 2 factorial experiment following a randomized complete block design: four cameras were placed at randomly selected locations within forested areas, and were assigned one of 2 lures (salmon oil or a liquid version of the fatty-acid scent used in tablet-form on the Minnesota Department of Natural Resources (MNDNR) scent-station survey) and one of 2 different placement strategies (on the closest suitable tree within 5 m from the randomly selected point, or at a user-chosen location within 90 m of the randomly selected point). We deployed an additional camera, without a lure, on a secondary road or trail within a forested area of each township. All cameras were active for a minimum of 6 weeks, and we recorded ~680,000 photos in the spring and ~370,000 in the fall. Among carnivores, black bears (*Ursus americanus*) and bobcats (*Lynx rufus*) were detected at a greater number of sites in spring than in fall, whereas coyotes (*Canis latrans*), red (*Vulpes vulpes*) and gray (*Urocyon cinereoargenteus*) foxes, martens (*Martes americana*), fishers (*Pekania pennanti*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) were detected more frequently in fall. Gray wolves (*C. lupus*) were detected at a similar number of sites in both seasons, whereas badgers (*Taxidea taxus*) and weasels (*Mustela spp.*) were detected only in the fall and at few sites. We also frequently detected several non-carnivore species, including white-tailed deer (*Odocoileus virginianus*), red squirrels (*Tamiasciurus hudsonicus*), snowshoe hares (*Lepus americanus*), and, more rarely, porcupines (*Erethizon dorsatum)* and moose (*Alces alces*). More detailed analysis of the data is pending.

INTRODUCTION

Monitoring programs designed to track the distribution and actual or relative abundance of carnivores can be important for determining population status and for quantifying the effects of harvest, habitat change, and environmental variability on populations. The Minnesota Department of Natural Resources (MNDNR) currently relies on 2 track-based surveys (scent station and snow-track surveys) to monitor trends in a suite of 14 carnivores/furbearers. The data from these surveys have provided rough estimates of trend for many species, although interpretation must always be qualified with acknowledgement of 2 key, but untested, assumptions, namely that detection rates do not exhibit significant temporal or spatial trends

[1] Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul.
[2] Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, Grand Rapids.

and that road-based surveys adequately represent population-wide trends. Logistical challenges with conducting these surveys have also increased in the last decade due to loss of survey collaborators from other natural resource agencies, increased traffic or paving/plowing of roads, and less reliable snow in early winter. In the past decade, several key carnivore species had declined (e.g., fishers, martens, bears) and management intensity had increased on wolves. Given the importance of monitoring these species, statistical uncertainties with existing surveys, and increasing logistical challenges, we felt it was an opportune time to consider alternative ways to monitor carnivore populations. Camera surveys are an attractive option because they provide a means to estimate detection rates with little if any additional field effort, are less dependent on specific environmental conditions, and are more amenable to use of 'citizen scientists' with little formal training (photos can be verified by trained staff). Thus, remote cameras are increasingly being used or considered for large-scale multi-species occupancy surveys (e.g., O'Brien et al. 2010, Pettorelli et al. 2010, Ahumada et al. 2011, Kays et al. 2011, Fisher and Burton 2012).

Camera-based surveys are not new to wildlife monitoring (Kays and Slauson 2008, Kucera and Barrett 2011), but the simultaneous development of improved remotely-triggered cameras, rigorous analytical methods, and reduced costs have bolstered their applied value. As evidenced by their use in monitoring a wide array of carnivores in different landscapes (e.g., see Table 5.1 in Kays and Slauson 2008), cameras are a non-invasive tool well-suited to detect species that may be difficult to trap and handle, occur at low densities, or have nocturnal and secretive habits.

Occupancy models (sensu MacKenzie et al. 2002, MacKenzie et al. 2006) are commonly used in wildlife monitoring programs, often in conjunction with camera traps, due to their flexibility, sound statistical framework, and close connection to population estimation. Taking advantage of repeated sampling (in space or time), occupancy models can provide unbiased estimates of occupancy probabilities that adjust for imperfect detection (i.e., failure to detect a species when it is present in a certain area). Failing to account for imperfect detection can lead to misleading estimates of spatial and temporal trends in occurrence (Guillera-Arroita et al. 2014a), and as a result, poor management and conservation decisions. While there are several important assumptions that must be met to apply occupancy models, the approach is not dependent on a specific tool or method to detect animals.

General survey design guidance for occupancy surveys is available (e.g., MacKenzie and Royle 2005, MacKenzie et al. 2006, Bailey et al. 2007, Guillera-Arroita and Lahoz-Monfort 2012, Guillera-Arroita et al. 2014b), but ideally study designs should be tailored to features of the target species and study area to avoid violation of model assumptions (e.g., independent detections and constant occupancy status), which can lead to biased estimators of detection and occupancy rates or require complex modelling approaches for sound statistical inference. Not surprisingly, occupancy modelling is an emerging and fast-moving field, and we expect new methods to be developed and guidance on their use to continually evolve in the coming years (Rota et al, 2016; Broms et al, 2016; Tobler et al, 2015; Ovaskainen et al, 2016).

Implementing a camera-based occupancy survey requires consideration of a variety of design and analysis options. While we do not delve into the details of each here, we highlight the following considerations: 1) camera selection and settings (Swann et al. 2004, Kays and Slauson 2008, Damm et al. 2010, Swann et al. 2011, Meek et al. 2012, Rovero et al. 2013, Weingarth et al. 2013, Wellington et al. 2013); 2) camera positioning; 3) whether to use baits/lures, and if so, which ones (Kays and Slauson 2008, Schlexer 2008, Du Preez et al. 2014); 4) time of year, which can affect species' behaviour and 'availability' as well as likelihood of meeting methodological assumptions (e.g., Kendall and White 2009, Rota et al. 2009); 5) number of cameras; 6) camera spacing and consideration of spatial correlation among sites (e.g., Sargeant et al. 2005, Hines et al. 2010, Magoun et al. 2010, Aing et al. 2011, Guillera-Arroita et al. 2011, Dorazio and Rodriguez 2012, Johnson et al. 2013); 7) whether or how best to discretize (e.g., hours, days, weeks) the temporally-continuous data from cameras into multiple survey occasions (e.g., Guillera-Arroita et al. 2011, Bischof et al. 2014); 8) site selection (e.g., random, systematic, convenience) and whether to allow flexibility in micro-site selection; and 9) approach to data analysis (e.g., single-species versus hierarchical community models; Dorazio and Royle 2005, Dorazio et al. 2006, Kery and Royle 2008, Zipkin et al. 2009, 2010, 2012, Giovanini et al. 2013, Pacifici et al. 2014).

Optimizing survey design becomes more complicated when multiple species with varying abundance and detection rates are involved. Biological characteristics of the species, such as home range size, movement patterns, and habitat preferences show large variation among carnivores (Boitani and Powell 2012). Consequently, a sampling design optimal for one species can violate important model assumptions for another. In the case of MNDNR surveys, where the suite of target species ranges from small to medium-sized mammals, such as skunks and martens, to large, roaming species like wolves and bears, design and analysis options that best account for or address this variability will be preferred. Recent attention has been given to design of camera-based occupancy surveys targeting a community of carnivores (Hamel et al. 2013, Shannon et al. 2014), but their conclusions may not extend beyond the specifics of the biological system and analysis approaches considered therein.

OBJECTIVES

The broad objectives of this project are to:

1. Compare effects of various survey design and analysis options on the magnitude and precision of estimates of detection and occupancy rate for multiple species.
2. Assess possible logistical constraints on implementing a large-scale multi-species camera survey in Minnesota; and
3. Compare the efficacy of camera surveys to the track surveys currently being used for monitoring carnivores in Minnesota.

As noted above, there is a large array of design and analysis questions to consider when conducting a multi-species occupancy survey with cameras. Hence, we decided to use an adaptive approach to survey design, focusing year 1 efforts on 4 specific design questions: 1) timing (spring versus fall survey; survey duration); 2) lure options (salmon oil versus fatty acid scent oil); 3) site selection (cameras on trails versus randomly selected sites); and 4) strategies for camera deployment (enhanced placement versus not enhanced). Our approach to analysis will also consider the effects of using daily versus weekly survey intervals and single- versus multi-species occupancy models. Additional comparisons and analysis will be undertaken next year after results of the first analyses are completed.

STUDY AREA

In spring and fall 2016, we implemented the first camera survey in one study area located in Itasca County, north-eastern Minnesota (Figure 1). This 1872 km^2 (48 x 39 km) area is mainly covered by forests and lakes and includes a high percentage of public land, including a portion of the Chippewa National Forest (SW portion of the study area), George Washington State Forest (NE portion), Scenic State Park (NC portion) and other state and county lands interspersed throughout.

METHODS

Based on our minimum camera specifications [i.e., passive infrared (PIR) cameras with intermediate to fast trigger (<0.7 s) and recovery (<1.7 s) speeds, multi-picture capability (minimum 3) per trigger event, “no-glow” (black LED) infrared flash, and of moderate cost (maximum $200 per camera)] and a competitive bid process, the camera model we deployed was the Bushnell Trophy Cam HD Aggressor No-Glow.

Survey Timing and Duration

We considered 4 objectives in selecting the timing of our camera surveys: 1) maximize the species richness of carnivores that would be ‘available’ for detection; 2) minimize the likelihood of violating the occupancy model assumption of species’ closure during the survey; 3) minimize logistic challenges with deploying cameras; and 4) maximize ‘biological relevancy’ and consistency with timing of existing surveys and annual management decisions. Although our experience has been that winter is a good time to conduct lure-based camera surveys for many carnivores, we concluded that several species would be undetectable (e.g., bears, skunks), ongoing harvest seasons for many species would increase risk of violating closure assumptions, and deep snow could pose logistic challenges. Although summer was a potential option, we believed that more rapid desiccation of lures and rapidly changing ‘availability’ of maturing offspring made it a less desirable option than spring and fall surveys. Hence, we chose to compare camera-based surveys conducted in the spring and fall, presumably reflecting spring ‘pre-breeding’ and fall ‘pre-harvest’ populations.

Our previous experience had been that few additional species are detected after 3–4 weeks of camera deployment. Although cameras can be left out indefinitely with only minimal additional financial cost related to personnel to review photos, long surveys increase risk of violating closure assumptions through mortality, immigration, or emigration. Hence, we chose to deploy cameras for 6 weeks during the first year, specifically May 1 to June 15 and September 1 to October 15.

Lure Selection

We concluded that use of a bait or lure was likely necessary to produce sufficient detection probability for many carnivore species, especially if cameras are to be deployed using a more desirable probabilistic sampling scheme. Similar to conclusions by Fisher and Burton (2012), we believed that olfactory lures will be preferred over baits and that all species of interest in this study can likely be attracted, albeit to varying degrees, with a more logistically-practical olfactory lure.

We decided to test 2 lures the first year, limiting our consideration to attractants that were likely to be not only effective for a suite of carnivore species, but also ones that could be reasonably standardized and were expected to be commercially available into the foreseeable future, easily applied, resistant to variable weather conditions, and could be purchased and distributed without significant secondary processing. There was a vast array of potential lures to consider. Based on our goals, personal experience, examination of the literature (e.g., Schlexer 2008), and consultation with a trapping lure manufacturer, we chose to compare commercial salmon oil with a liquid version of the synthetic fatty acid scent (FAS) that has been used (in tablet form) on a long-term multi-species track survey in Minnesota (Erb 2015). Details of the lure placement protocol are discussed below; here we simply note that at each site selected for salmon oil, we deployed 473 ml (16 oz), whereas for sites selected for FAS oil, we deployed a 237-ml (8 oz) bottle that consisted of 80% mineral oil and 20% liquid FAS.

Macro-Site Selection

In the first year, our focus was on evaluating the spatial sampling design in forested habitats. To identify suitable locations for camera deployment, we used Light Detection and Ranging (LiDAR) data (e.g., see Merrick et al. 2013) collected by the State of Minnesota in 2011 (http://www.mngeo.state.mn.us/chouse/elevation/lidar.html) to identify pixels (~ 20 X 20 m) with mean tree height >3 m (10 ft) and canopy cover >50% (Figure 2; details of this process will be incorporated in future reports). We then divided the study area into 20 contiguous blocks the size of townships (9.65 x 9.65 km). To ensure a minimum distance of 1.6 km (1 mi) between cameras both within and across blocks, we constrained the randomly selected points to lie within 4 equally-spaced sub-quadrats within each block (Figure 2). We then intersected the suitable locations (pixels) identified via LIDAR with the sub-quadrats and used the *Generate Random Points* tool in ArcGIS to select one random point falling within each of the 4 sub-quadrats in each block (Figure 2).

In addition, we deployed an un-lured camera placed on a secondary trail closest to the center of each township (hereafter, *trail camera*), provided the site was at least 400 m (0.25 mi) from all primary roads and at least 1.6 km (1 mi) from other cameras (Figure 2). We loosely defined secondary roads or trails as those that did not receive year-around maintenance and were accessed primarily on foot or with off-road vehicles. Our primary intent in deploying un-lured cameras along trails was to assess whether this type of convenience sampling was more likely to detect larger carnivores, such as wolves, that often use these trails and may be more wary of lured sites.

After selecting all locations and before deploying the cameras, each site was visualized on 2015 aerial photos to help ensure all requirements for deployment were likely met, including an additional requirement that each site was a minimum of 30 m (100 ft) from any non-forested edge.

Micro-Site Selection and Covariates

Another important decision, after selecting the camera macro-sites, was how much flexibility should be allowed in determining the exact placement of the camera. Although the use of lures effectively expands the area of camera 'coverage' well beyond the actual camera, within a given forest patch one can still potentially locate a microsite where the probability of carnivore use or detection will be higher. However, allowing flexibility in micro-site selection could introduce a source of heterogeneity in detection probabilities that may be difficult to quantify objectively. Using experienced biologists, we decided to test whether expert-based choices in fact increase detection rates. We accomplished this by dividing lured cameras into 2 camera placement strategies: 1) *not enhanced*, meaning the camera was placed on a tree within a 5-m (15-ft) radius from the randomly selected point; or 2) *enhanced*, meaning the operator actively looked for an optimal deployment location within a 90-m (300-ft) radius of the randomly selected point.

At all camera stations, we recorded several vegetation characteristics (tree species diameter and dominance, shrub cover, canopy cover) and presence of game trails, natural 'bottlenecks', and other features within approximately 15 m of the final deployment location that could increase probability of detecting a carnivore. We also took a digital photo of angular (45°) canopy cover in 4 directions around the base of the camera tree, parallel and perpendicular to the camera-lure axis. While walking to each camera site (usually < 3 km), we also recorded presence of indirect carnivore sign (tracks, scats, dens). For trail cameras, we recorded trail width, ease of access (e.g., walk, ATV, vehicle), an initial index of frequency of use by humans (which we will corroborate based on human-detections by the cameras), and vegetative coverage and height on the trail surface. Other variables (e.g., distance to main roads or water, landscape configuration metrics) will be measured using GIS. Although trail cameras were not designated an enhanced versus not enhanced treatment, we allowed flexibility in final deployment location of these cameras due to the need to position the camera on a tree at the desired angle and within sufficient distance of the trail to ensure trigger activation by animals; from the original coordinate, users were allowed a distance of 45 m (150 ft) in either direction down the trail to place the camera.

Experimental Design

To test different lures and placement strategies, we conducted a 2 x 2 factorial experiment following a randomized complete block design. Along with the trail camera, 4 lured cameras were placed within each block at sites selected using the processes described above in the macro- and micro-site selection sections. Cameras at each randomly chosen site were randomly assigned 1 of 2 lure types (salmon oil or fatty acid scent oil) and 1 of 2 camera placement strategies (not enhanced or enhanced, Figure 3).

Camera Deployment and Settings

In each camera session we deployed 100 passive infrared Bushnell Trophy Cam HD Aggressor No-Glow cameras, 80 at lured sites and 20 at un-lured trail sites. The general settings for all the cameras were based on pre-deployment testing. All cameras were attached to sturdy trees with bungee straps and placed about 75 cm (30 in) above the ground. The detection area in front of the cameras was cleared of vegetation (ferns, branches, leaves) that could obstruct the viewing area or cause false triggers, especially on windy days. At lured sites, we poured the lure on a tree located 4.5 to 9 m (15 to 30 ft) from the camera tree, with a preferred distance of 6 to 7.5 m (20 to 25 ft). We aimed trail cameras at a 45° angle to the main axis of the trail to ensure more opportunity to capture images of faster moving animals. We also aimed all cameras north (ranging from northeast to northwest) when possible to reduce false triggers and blurred photos from direct sunlight.

All the cameras were programmed to record 3 mega-pixel images (color during daylight and black/white during night), with 3 'rapid-fire' pictures per trigger event and a 2-second delay between subsequent triggers. Additionally, a set of 3 rapid-fire time-lapse pictures were taken twice a day (noon and midnight) to check the functioning of the cameras and to record regular measures of daily temperature at each site. Date, time, temperature and camera Id were printed on all the images and recorded in the image metadata.

Photo Processing and Analysis

Identification of species is done using experienced personnel following the protocol described in Niedballa et al. 2016, using the *camtrapR* package (Niedballa et al. 2017) in Program R (R Core Team 2015). We will use these data to compare detection rates for the 2 lures and the 3 camera placement strategies. In addition, we will calculate cumulative species richness curves to address questions related to survey duration and timing. Lastly, we will model occurrence and detection probabilities as functions of landscape features (e.g. bottlenecks, game trails) and forest characteristics (e.g. forest type, shrub cover) to provide information on species distribution and detectability. Further details of analysis methods will be presented in future reports.

RESULTS AND DISCUSSION

Camera Function

During the first year of sampling, cameras recorded ~680,000 pictures in the spring and ~370,000 in the fall. In the spring, 75 of the 100 cameras deployed remained operational for the full session (Figure 4); one was missing (site was logged), 4 malfunctioned, and bears altered camera positioning on approximately 20 cameras, though only 9 of these were moved to an extent that the lure tree was no longer visible. Insolation paired with lack of canopy cover during the first weeks of the spring survey and growing vegetation (especially ferns) in the later weeks resulted in a large number of false triggers and, in some cases, cameras that were no longer operable (e.g., when growing vegetation filled the detection area). In the fall, 93 of the 100 cameras remained operational (Figure 4); canopy cover appeared to reduce false triggering, all ground vegetation had sprouted and could be cut, and we added a second strap to secure the cameras and minimize bear disturbance to cameras. Bears were still the main reason for cameras becoming inoperable in the fall (5 out of 7), and the reduced number of bear-related problems could be due to a decrease in the number of bear visits in the fall.

Species Detections

Coyotes, red and grey foxes, raccoons, striped skunks, martens and fishers were detected at ≥ 2 times as many sites during the fall compared to spring (Figure 5). Conversely, bears were detected at >4 times the number of sites in spring compared to fall, and bobcats were detected at 42% more sites in the spring. Badgers and weasels were detected only in the fall, at 4 and 1 sites, respectively. Gray wolf was the only species that did not show a large difference in detections between the 2 sessions (Figure 5). In the spring, black bear was the most frequently detected species, followed by red fox and coyote. In the fall, grey foxes were the most frequently detected, followed by raccoons and coyotes (Figure 5). We also frequently detected white-tailed deer, red squirrels, snowshoe hares, and on occasion, porcupines, moose, and several species of birds.

Given the higher number of issues observed during the spring, which are still being considered prior to analysis, here we present more detailed results only for the fall survey. Fall cameras were active from approximately September 1 to November 2, for a total of 4,789 'trap-nights' ($\bar{x}$ = 48, SD = 11 trap-nights per camera). Most (n=60) cameras detected between 1 and 3 carnivores species (1 species, n=21; 2 species, n=20; 3 species, n=19); the maximum number of species detected was 7 (Figure 6).

Comparison of Lures and Site-Selection Strategies

Preliminary results suggest that coyotes, raccoons, and skunks may prefer salmon oil over liquid FAS, grey foxes were more likely to be detected at cameras deployed using the enhanced strategy, whereas Gray wolves were detected more often at sites with cameras deployed using the non-enhanced placement strategy (Table 1). Macro-site selection strategies indicated strong differences in the proportion of unlured on-trail versus lured random sites at which some species were detected (Table 1). In particular, preliminary analysis suggests that black bears, fishers, martens, and raccoons were more often detected at lured, randomly-selected sites compared to unlured trails, whereas wolves were more often detected at unlured trail sites (Table 1). A sample of the pictures collected during spring 2016 sampling is shown in Figure 7.

Although many preliminary findings are generally consistent with expectations, more complete and formal analyses will be conducted and presented in future reports. During year 2, protocols will remain the same with the exception that we are employing a crossover design with respect to lure choice (i.e., a site with salmon oil in 2016 will receive FAS lure in 2017). In addition, to partially avoid false triggers in the ongoing spring survey (2017), we decided to postpone the beginning of the sampling period for 2 weeks (from 1 May to 15 May) with the hope of allowing initial canopy growth (more shading) and initial growth of lower-growing herbaceous vegetation that could thus be seen and cut in the detection area at the time of camera deployment. Although reducing trigger sensitivity may also reduce false triggers, initially we were more concerned about potential loss of animal detections from reduced sensitivity.

ACKNOWLEDGEMENTS

Special thanks to Barry Sampson and Carolin Humpal for assistance with preparing, programming, and deploying cameras. We would also like to thank Michael Joyce for his assistance with processing and analysis of LIDAR data, and Jordan Schaefer, Perry Loegering, Mark Spoden, Jeff Hines, and Kevin Carlisle for logistical support during camera deployment. This project was funded in part by the Wildlife Restoration Program (Pittman-Robertson).

LITERATURE CITED

Ahumada, J. A., C. E. F. Silva, K. Gajapersad, C. Hallam, J. Hurtado, E. Martin, A. McWilliam, B. Mugerwa, T. O'Brien, F. Rovero, and others. 2011. Community structure and diversity of tropical forest mammals: Data from a global camera trap network. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2703-2711.

Aing, C., S. Halls, K. Oken, R. Dobrow, and J. Fieberg. 2011. A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear spatially correlated sites. Journal of Applied Ecology 48:1508–1517.

Bailey, L.L., J.E. Hines, J.D. Nichols, and D.I. Mackenzie. 2007. Sampling designing trade-offs in occupancy studies with imperfect detection: examples and software. Ecological Applications 17:281-290.

Bischof, R., S. Hameed, H. Ali, M. Kabir, M. Younas, K. A. Shah, J. U. Din, and M. A. Nawaz. 2014. Using time-to-event analysis to complement hierarchical methods when assessing determinants of photographic detectability during camera trapping. Methods in Ecology and Evolution 5:44-53.

Boitani, L. and R. A. Powell. 2012. Introduction: research and conservation of carnivores. In L. Boitani & R. A. Powell, eds. Carnivore Ecology and Conservation: A Handbook of Techniques. Oxford University Press, New York, pp. 1–7.

Broms, K. M., Hooten, M. B. and Fitzpatrick, R. M. 2016. Model selection and assessment for multi-species occupancy models. Ecology 97:1759–1770. doi:10.1890/15-1471.1

Damm, P. E., J. B. Grand, and S. W. Barnett. 2010. Variation in detection among passive infrared triggered-cameras used in wildlife research. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies 64:125–130.

Dorazio, R.M. and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of American Statistical Association 100:389–398.

Dorazio, R.M., J. A. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842–854.

Dorazio, R. M., and D. T. Rodriguez. 2012. A Gibbs sampler for Bayesian analysis of site-occupancy data. Methods in Ecology and Evolution 3:1093–1098.

Du Preez, B.D., A. J. Loveridge, and D. W. Macdonald. 2014. To bait or not to bait: A comparison of camera-trapping methods for estimating leopard *Panthera pardu*s density. Biological Conservation 176:153–161.

Erb, J. 2015. Carnivore scent station survey summary, 2015. Minnesota Department of Natural Resources, St. Paul.

Fisher, J.T. and Burton, C. 2012. Monitoring mammals in Alberta: Recommendations for remote camera trapping. Final Report. Alberta Biodiversity Monitoring Institute.

Giovanini, J., A. J. Kroll, J. E. Jones, B. Altman, and E. B. Arnett. 2013. Effects of management intervention on post-disturbance community composition: an experimental analysis using Bayesian hierarchical models. PLoS ONE 8:e59900.

Guillera-Arroita, G., B.J.T. Morgan, M.S. Ridout, and M. Linkie. 2011. Species occupancy modeling for detection data collected along a transect. Journal of Agricultural, Biological, and Environmental Statistics 16:301–317.

Guillera-Arroita, G., and J. J. Lahoz-Monfort. 2012. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. Methods in Ecology and Evolution 3:860–869.

Guillera-Arroita G, J. J. Lahoz-Monfort, D. I. MacKenzie, B. A. Wintle, and M. A. McCarthy. 2014a. Ignoring Imperfect Detection in Biological Surveys Is Dangerous: A Response to ‘Fitting and Interpreting Occupancy Models’. PLoS ONE 9(7): e99571. doi:10.1371/journal.pone.0099571

Guillera-Arroita, G., M. S. Ridout, and B. J. T. Morgan. 2014b. Two-stage Bayesian study design for species occupancy estimation. Journal of Agricultural, Biological and Environmental Statistics 19:278–291.

Hamel, S., S. T. Killengreen, J-A Henden, N. E. Eide, L. Roed-Eriksen, R. A. Ims, and N. G. Yoccoz. 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. Methods in Ecology and Evolution 4:105–113.

Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, A. M. Gopalaswamy, N. Samba Kumar, and K. U. Karanth. 2010. Tigers on Trails: Occupancy modeling for cluster sampling. Ecological Applications 20:1456–1466.

Johnson, D.S., P.B. Conn, M.B. Hooten, J.C. Ray, and B.A. Pond. 2013. Spatial occupancy models for large datasets. Ecology 94:801-808.

Kays, R.W., and K.M. Slauson. 2008. Remote cameras. Pages 110-140 in Long, R., P. Mackay, J. Ray, and W. Zielinski (eds). Noninvasive Survey Methods for Carnivores. Island Press, Washington, DC.
Kays, R., S. Tilak, B. Kranstauber, P. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, J. Eggert, and Z. He. 2011. Camera traps as sensor networks for monitoring animal communities. International Journal of Research and Reviews in Wireless Sensor Networks 1:19-29.
Kendall, W.L. and G.C. White. 2009. A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. Journal of Applied Ecology 46:1182–1188.
Kery, M., and J. A. Royle. 2008. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. Journal of Applied Ecology 45:589–598.
Kucera, T., and R.H. Barrett. 2011. A history of camera trapping. Pages 9-26 in O'Connell, A., Nichols, J.D., Ullas-Karanth, K. (eds). Camera traps in ecology. Springer. London, UK.
MacKenzie, D.I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248–2255.
MacKenzie D.I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.
MacKenzie, D.I., J. D. Nichols, J.A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, Oxford.
Magoun, A. J., J. C. Ray, D. S. Johnson, P. Valkenburg, F. N. Dawson, and J. Bowman. 2007. Modeling wolverine occurrence using aerial surveys of tracks in snow. Journal of Wildlife Management 71:2221–2229.
Meek, P., G. Ballard and P. Fleming. 2012. An introduction to camera trapping for wildlife surveys in Australia. PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.
Merrick, M. J., J. L. Koprowski, and C. Wilcox. 2013. Into the third dimension: Benefits of incorporating LIDAR data in wildlife habitat models. U.S. Dept. of Agriculture, Forest Service, RMRS-P-67.
Niedballa, J., R. Sollmann, A. Courtiol, and A. Wilting. 2016. camtrapR: An R package for efficient camera trap data management. Methods in Ecology and Evolution 7(12):1457-1462.
Niedballa J., Courtiol A., and Sollmann R. 2017. camtrapR: Camera trap data management and preparation of occupancy and spatial capture-recapture analyses. R package version 0.99.7. http://CRAN.R-project.org/package=camtrapR.
O'Brien, T.G., M.F. Kinnaird, and H.T. Wibisono. 2010. Estimation of species richness of large vertebrates using camera traps: an example from an Indonesian rainforest. pp. 233-252 in O'Connell, A.F., J.D. Nichols, and K.U. Karanth, eds. Camera traps in ecology. Springer, London.
Ovaskainen, O., N. Abrego, P. Halme, and D. Dunson. 2016. Using latent variable models to identify large networks of species-to-species associations at different spatial scales. Methods in Ecology and Evolution 7:549–555.
Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry and A. DeWan. 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecology and Evolution 4:877-888.
Pettorelli, N., A. L. Lobora, M. J. Msuha, C. Foley, and S. M. Durant. 2010. Carnivore biodiversity in Tanzania: Revealing the distribution patterns of secretive mammals using camera traps. Animal Conservation 13:131-139.
R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Rota, C.T., R. J. Fletcher, R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46:1173-81.

Rota, C.T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A multispecies occupancy model for two or more interacting species. Methods in Ecology and Evolution. doi:10.1111/2041-210X.12587.

Rovero, F., F. Zimmerman, D. Berzi, and P. D. Meek. 2013. Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. Hystrix: Italian Journal of Mammalogy 24:9–17.

Sargeant, G., M. Solvada, C. Slivinski, and D. Johnson. 2005. Markov chain Monte Carlo estimation of species distributions: a case study of the swift fox in western Kansas. Journal of Wildlife Management 69:483–497.

Schlexer, F.V. 2008. Attracting animals to detection devices. Pages 263-292 in Long, R., P. Mackay, J. Ray, and W. Zielinski (eds). Noninvasive Survey Methods for Carnivores. Island Press, Washington, DC.

Shannon, G., J. S. Lewis, and B. D. Gerber. 2014. Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. PeerJ 2:e532; DOI 10.7717/peerj.532.

Swann, D.E., C. C. Hass, D. C. Dalton, and A. Wolf. 2004. Infrared-triggered cameras for detecting wildlife: an evaluation and review. Wildlife Society Bulletin 32:357–365.

Swann, D.E., K. Kawanishi, and J. Palmer. 2011. Evaluating types and features of camera traps in ecological studies: guide for researchers. In: O'Connell AF, Nichols JD,
Karanth KU (eds). Camera traps in animal ecology: methods and analyses. Springer, New York.

Tobler, M. W., A. Zúñiga Hartley, S. E. Carrillo-Percastegui, and G. V. N. Powel. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. Journal of Applied Ecology 52:413–421. doi:10.1111/1365-2664.12399

Weingarth, K., F. Zimmermann, F. Knauer, and M. Heurich. 2013. Evaluation of six digital camera models for the use in capture-recapture sampling of Eurasian Lynx (Lynx lynx). Waldo¨kol Landsch Forsch Naturschutz 13:87–92.

Wellington, K., C. Bottom, C. Merrill, and J. A. Litvaitas. 2013. Identifying performance differences among trail cameras used to monitor forest mammals. Wildlife Society Bulletin; DOI: 10.1002/wsb.425.

Zipkin, E. F., A. DeWan, and J. A. Royle. 2009. Impacts of forest fragmentation on bird species richness: a hierarchical approach to community modelling. Journal of Applied Ecology 46:815–822.

Zipkin, E.F., J.A. Royle, D.K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation 143:479-484.

Zipkin, E.F., E.H. Campbell Grant, and W.F. Fagan. 2012. Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. Ecological Applications 22:1962-1972.

Table 1. Number of fall 2016 camera sites in Itasca County, MN at which each species was detected based on a) lure type, and b) micro-site selection strategy. For macro-site selection, we report the percentage of sites where each species was detected to better compare the visitation at on-trail cameras (n=20) versus random lured sites (n=80).

	BADGER	BLACK BEAR	BOBCAT	COYOTE	FISHER	GREY FOX	MARTEN	RACCOON	RED FOX	SKUNK	WEASEL	WOLF
Lure type												
Fatty acid scented oil	2	6	3	7	12	9	10	10	5	6	0	7
Salmon oil	1	4	3	16	16	13	13	16	8	17	0	5
Micro-site selection												
Non enhanced	0	5	3	12	12	8	14	14	7	11	0	9
Enhanced	3	5	3	11	16	14	9	12	6	12	0	3
Macro-site selection (%)												
On-trail	5.0	5.0	5.0	45.0	10.0	60.0	5.0	20.0	25.0	45.0	5.0	50.0
Random	7.5	25.0	15.0	57.5	70.0	55.0	57.5	65.0	32.5	57.5	0.0	30.0

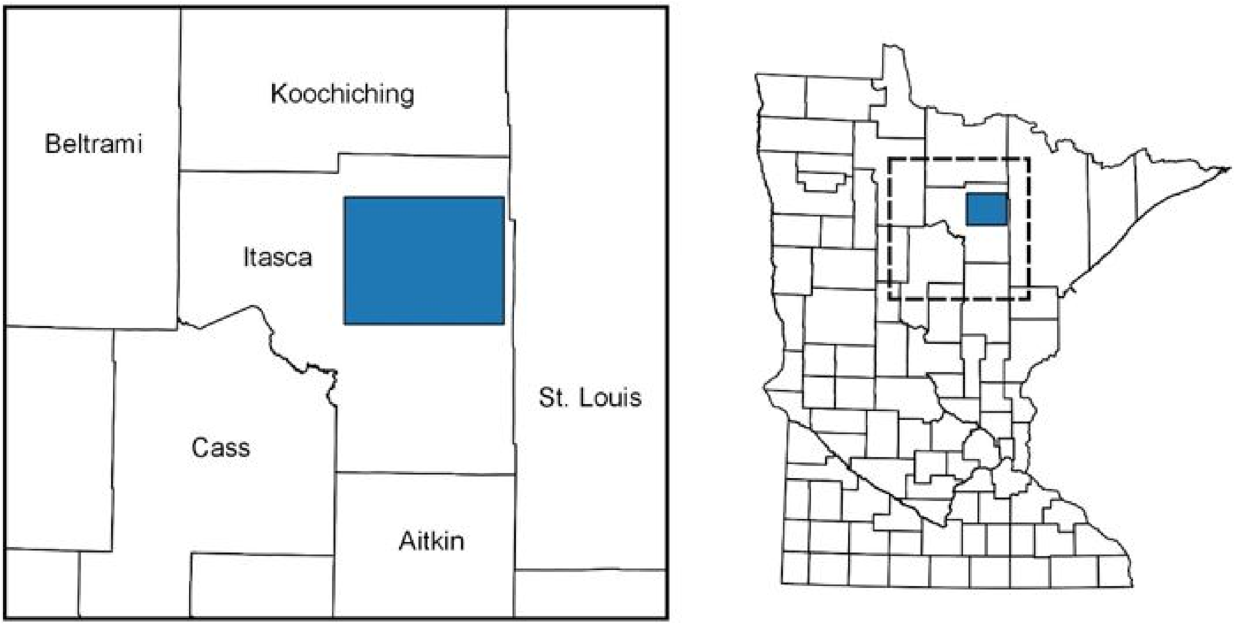
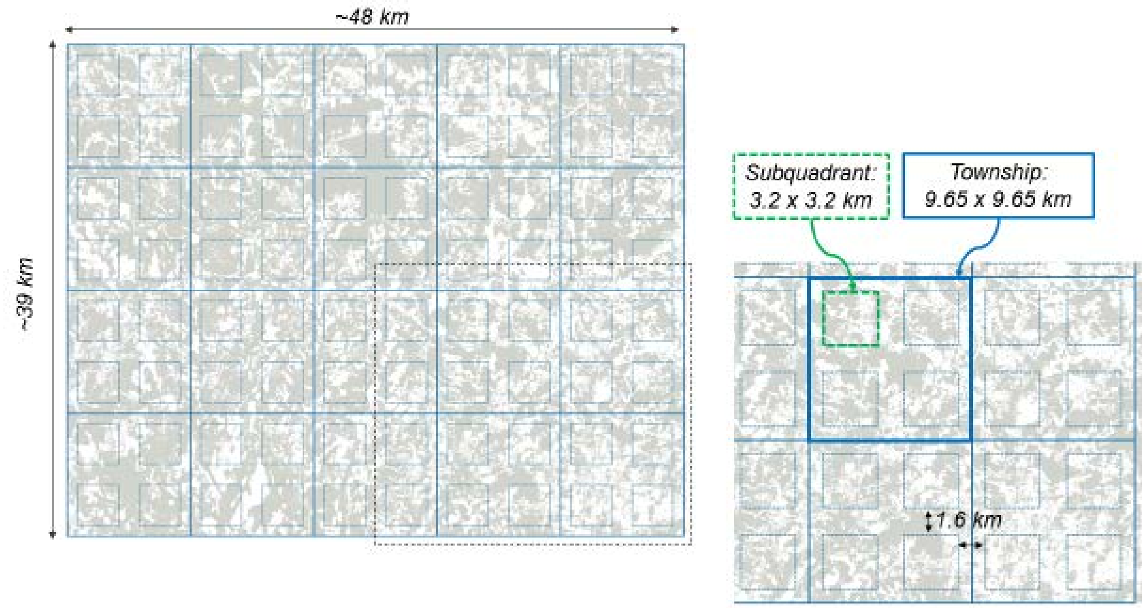


Figure 1. Location of the 2016-17 carnivore camera survey in the north-eastern portion of Itasca County, Minnesota.



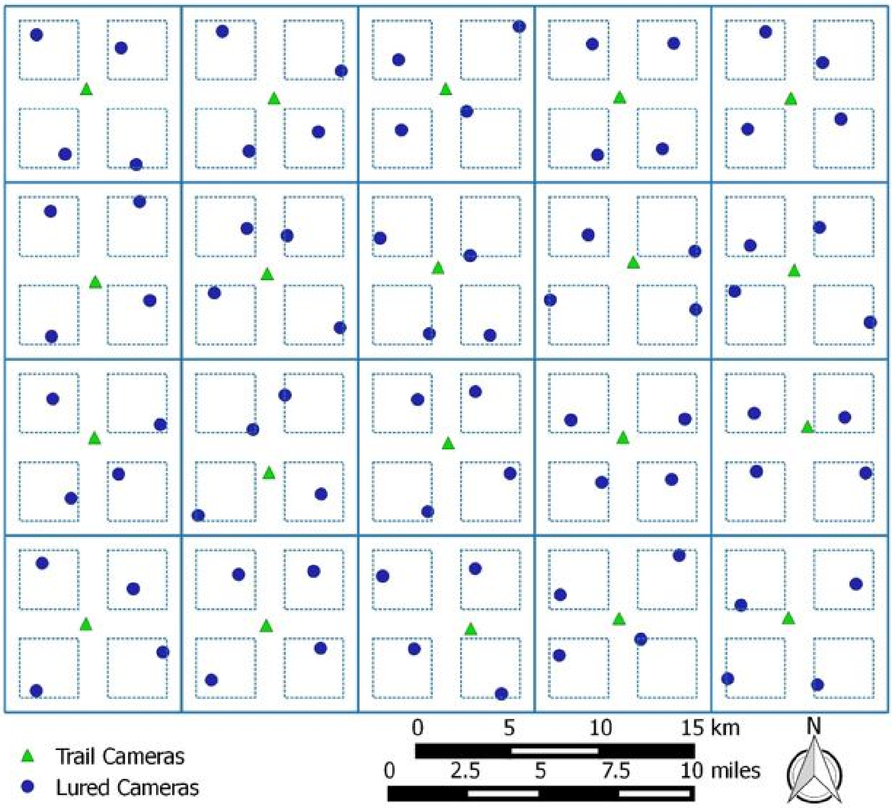


Figure 2. *Top*: Graphic of the Itasca County, MN study area showing forested habitat meeting our macro-site selection criteria in 2016 (*top:* gray areas). In each township (solid blue lines; 9.65 x 9.65 km) we defined four 3.2 x 3.2 km sub-quadrats (green dotted lines). The spacing between adjacent sub-quadrats ensured a minimum distance of 1.6 km (1 mi) between cameras subject to different treatments. *Bottom:* One location for a lured camera was then randomly selected from the suitable area within each sub-quadrat. A fifth un-lured camera was placed outside the quadrats and on a trail nearest the center of the township.

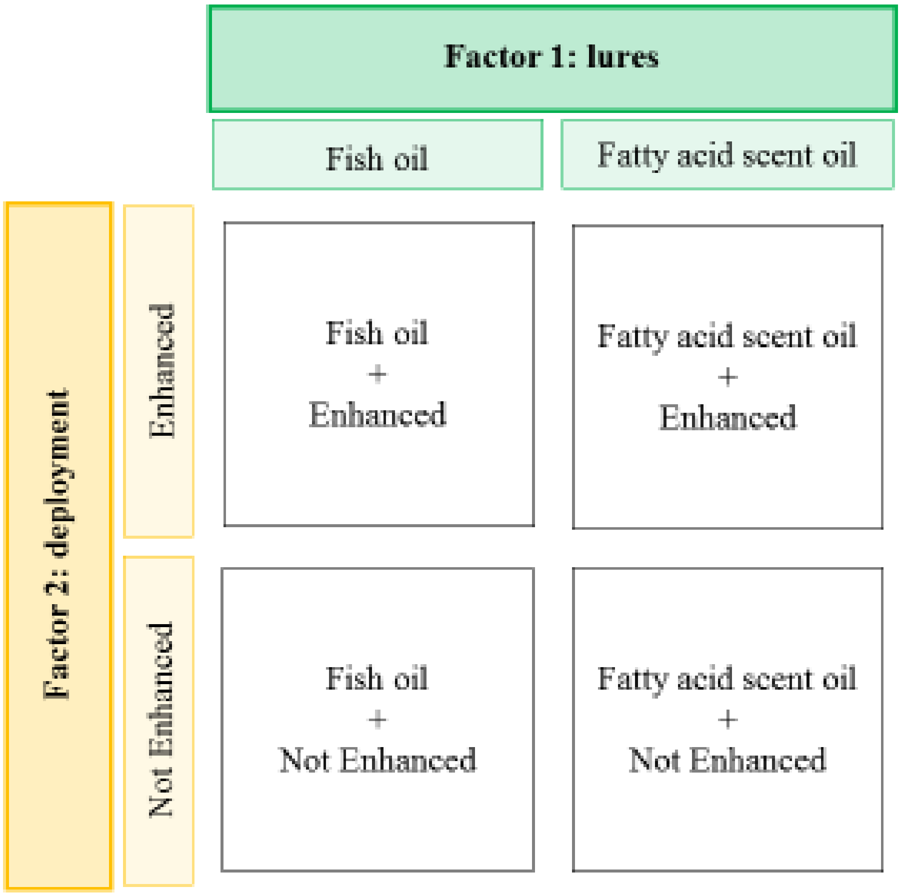


Figure 3. Factorial sampling design, 2016-17. In each of 20 townships in Itasca County, MN, 4 cameras were randomly assigned to one of 4 different treatments given by the intersection between 2 factors: lure type and camera deployment strategy. The lure factor had 2 levels: *fatty acid scent oil* and *fish oil*; the second factor, camera deployment strategy, also had 2 levels: *not enhanced* (i.e., camera placed on nearest tree to the randomly selected UTM location) and *enhanced* (i.e., camera placed at a presumably optimal location within 90 m of the randomly selected point to increase carnivore detection).

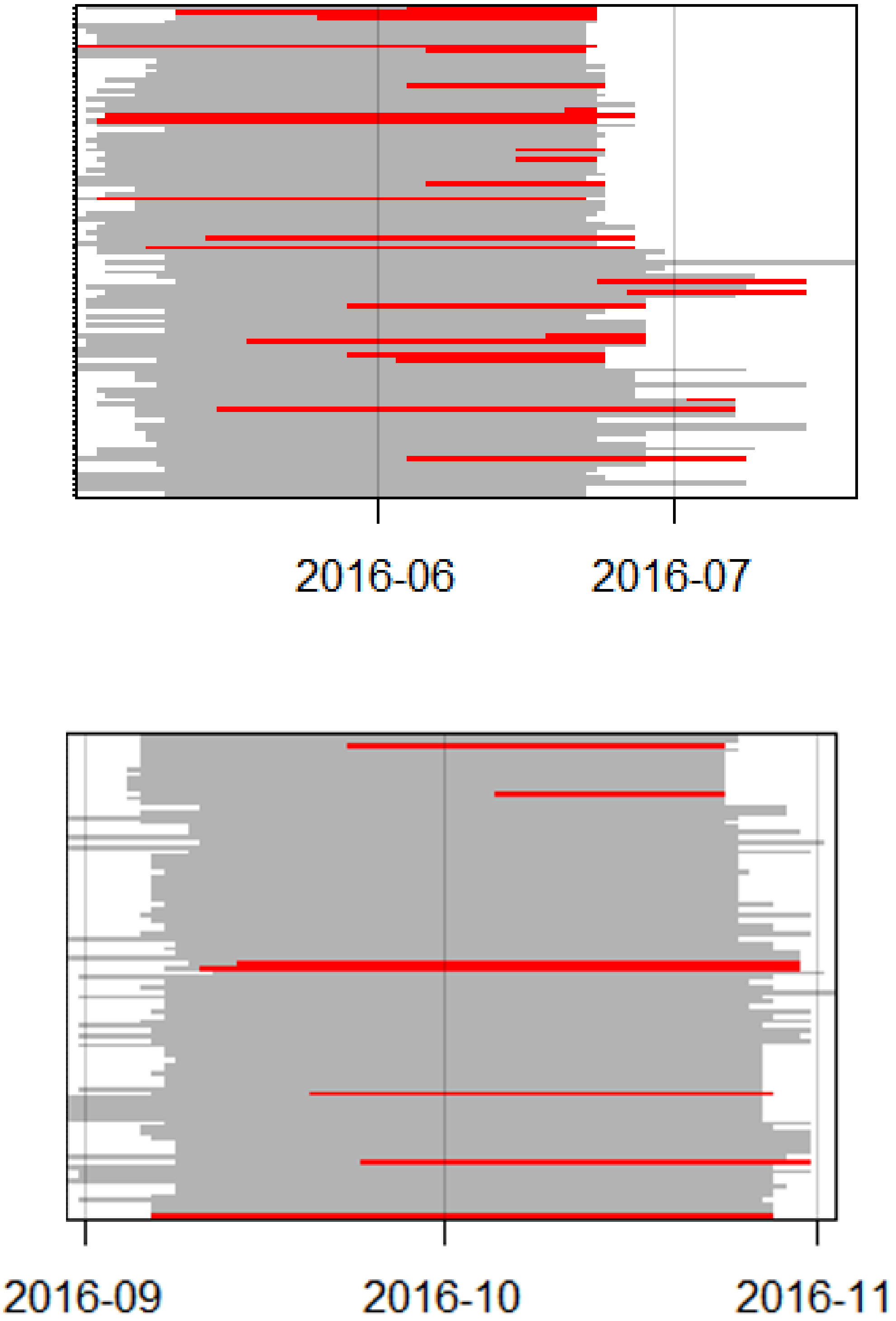
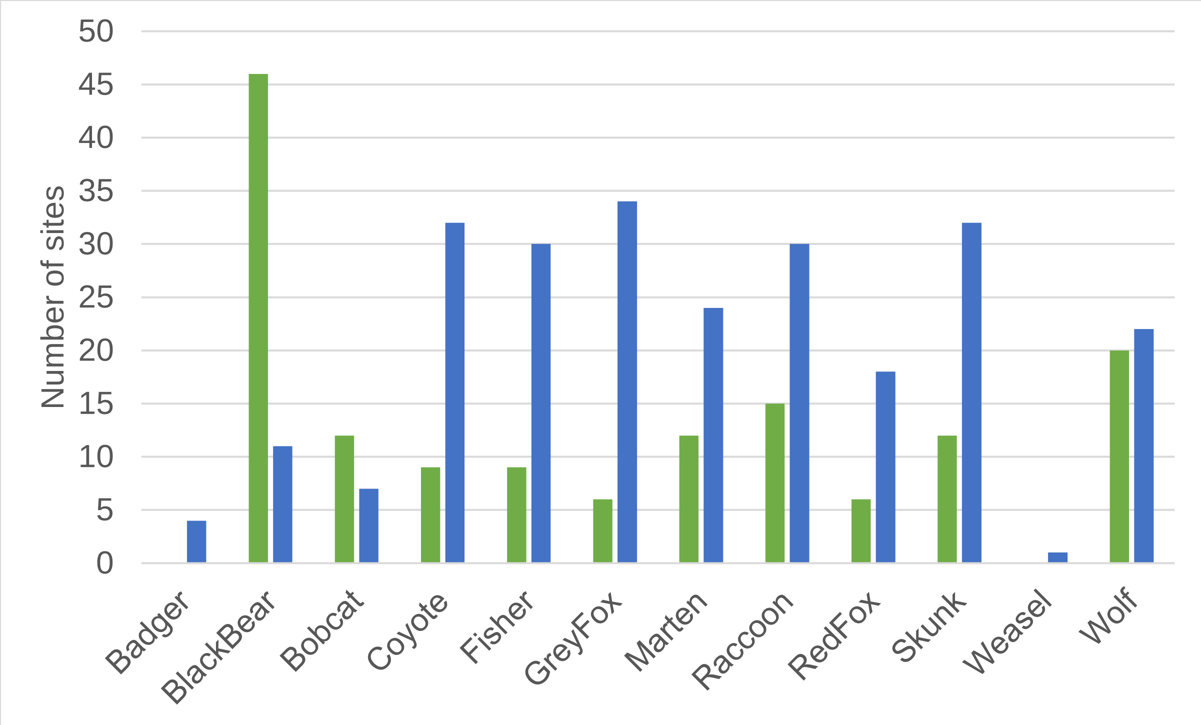


Figure 4. Operating time for each of the 100 cameras deployed in the spring (top) and fall (bottom) 2016, Itasca County, MN. Red segments represent times when cameras were not operable. At the time of the retrieval, 93 cameras were still operating in the fall, whereas only 75 were still operable in spring.



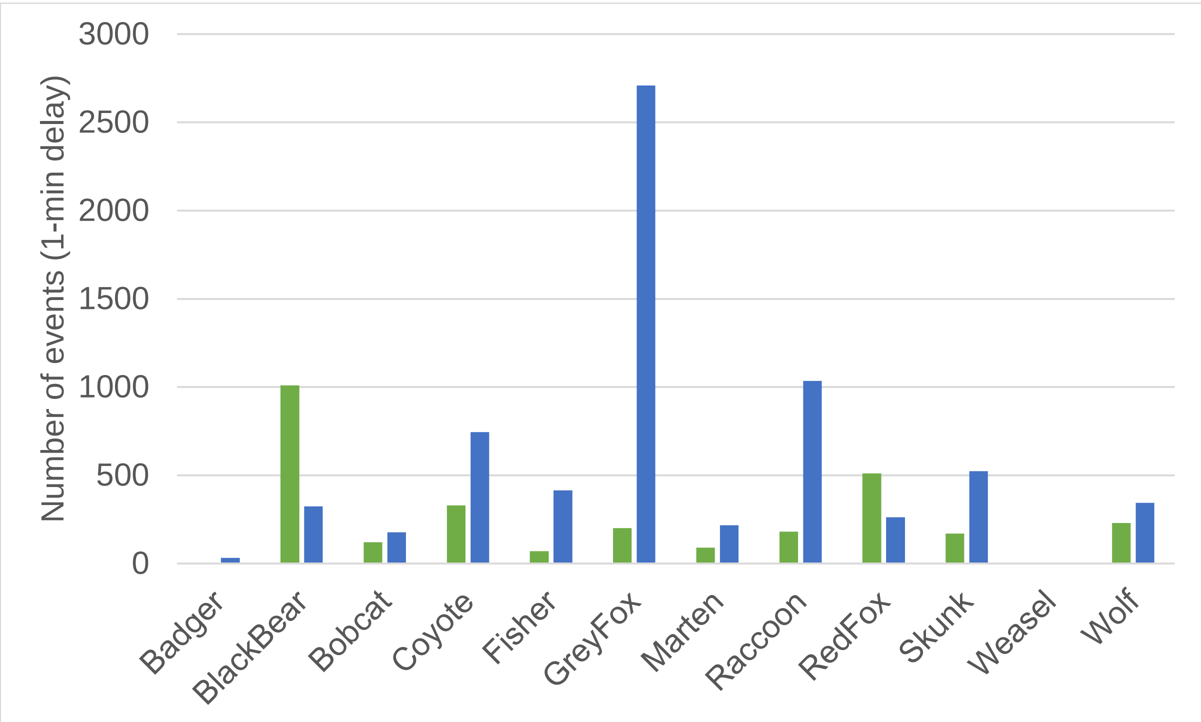


Figure 5. Number of events (bottom) and number of sites (top) at which each species was detected during spring (green bar) and fall (blue bar) 2016 survey, Itasca County, MN. An event was defined as a detection with at least 1 minute delay from the previous picture of the same species at the same site.

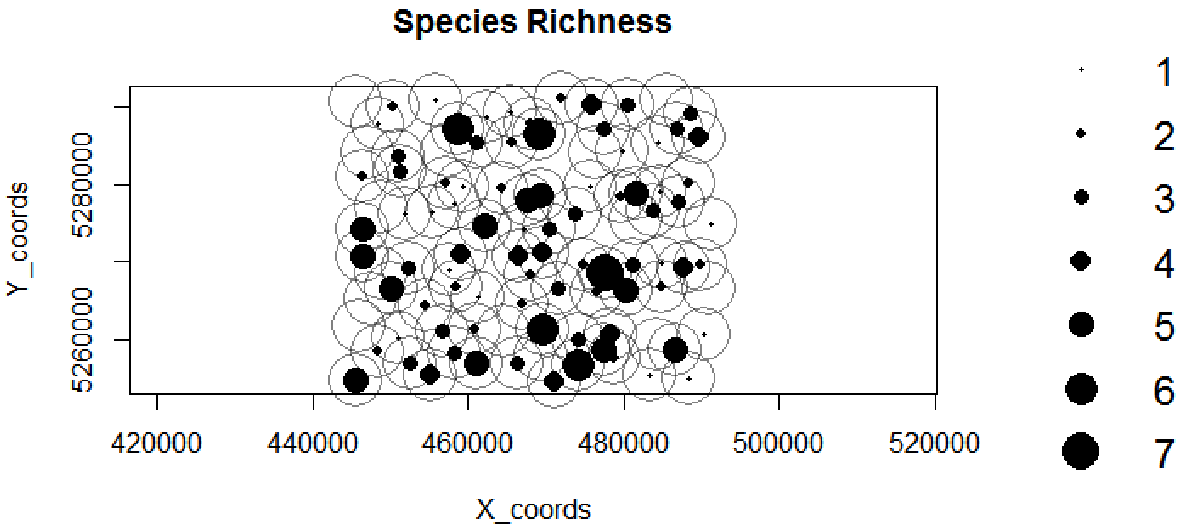


Figure 6. Species richness at each camera location during fall 2016, Itasca County, MN. Most of the cameras detected from 1 to 3 carnivore species.

Figure 7. Example of images collected during the spring 2016 survey, Itasca County, MN. From top-left to bottom-right: gray wolf, red fox, bobcat, bear with two cubs, fisher, raccoon, striped skunk, and coyote.