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ARTICLE

Emerging Technologies

Estimating wolf abundance from cameras

David E. Ausband[1] | **Paul M. Lukacs**[2] | **Mark Hurley**[3] | **Shane Roberts**[3] | **Kaitlyn Strickfaden**[2] | **Anna K. Moeller**[2]

[1]U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, Idaho, USA

[2]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, Montana, USA

[3]Idaho Department of Fish and Game, Boise, Idaho, USA

Correspondence
David E. Ausband
Email: dausband@uidaho.edu

Funding information
Idaho Department of Fish and Game

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Abstract

Monitoring the abundance of rare carnivores is a daunting task for wildlife biologists. Many carnivore populations persist at relatively low densities, public interest is high, and the need for population estimates is great. Recent advances in trail camera technology provide an unprecedented opportunity for biologists to monitor rare species economically. Few studies, however, have conducted rigorous analyses of our ability to estimate abundance of low-density carnivores with cameras. We used motion-triggered trail cameras and a space-to-event model to estimate gray wolf (*Canis lupus*) abundance across three study areas in Idaho, USA, 2016–2018. We compared abundance estimates between cameras and noninvasive genetic sampling that had been extensively tested in our study areas. Estimates of mean wolf abundance from camera and genetic surveys were within 22% of one another and 95% CIs overlapped in 2 of the 3 years. A single camera with many detections appeared to bias camera estimates high in 2018. A subsequent bootstrapping procedure produced a population estimate from cameras equal to that derived from genetic sampling, however. Camera surveys were less than half the cost of genetic surveys once initial camera purchases were made. Our results suggest that cameras can be a viable method for estimating wolf abundance across broad landscapes (>10,000 km^2).

KEYWORDS

abundance, camera, *Canis lupus*, density, monitoring, space-to-event, wolf

INTRODUCTION

Estimating the abundance and distribution of wildlife populations is a critical element of most wildlife population monitoring programs (Witmer, 2005). Long-term population monitoring that can be used to inform management and conservation requires several key elements. First, the monitoring program must track a population state variable that provides information to wildlife managers (Nichols et al., 2007). In Idaho, USA, for example, gray wolf (*Canis lupus*) abundance provides an important status metric for the population, a measure of the potential influence of wolves on prey populations, and a useful piece of public information to an engaged citizenry. Second, the monitoring must be based on a statistically defensible sampling and survey design (Nichols et al., 2007). Without a defensible design, the outcome of the monitoring program loses strength and interpretation of the results is left to the individual. Third, the monitoring method must be fiscally sustainable over time. Therefore, the cost of the program must be reasonable relative to the information gained. However, few field survey methods for large carnivores such as gray wolves fit all of the requirements listed above, and research continues to develop improved monitoring methods.

For over a decade, the use of motion-triggered trail cameras for wildlife sampling has increased (O'Connell et al., 2011). Camera-based sampling designs only require training on camera function and proper deployment techniques to be implemented. Cameras also capture images of nontarget animals, providing the potential to monitor multiple species with just one survey tool (Tobler et al., 2015). Additionally, cameras can be placed in the field and left unattended for long periods of time. This is particularly useful when using cameras to estimate abundance, because long field deployments provide the potential for multiple abundance estimates of the same species from a single field effort (Moeller et al., 2018). Few other field-sampling methods offer the ability to produce repeated estimates from a single field effort, although passive acoustic recorders (Sugai et al., 2019) could perform a similar function provided the area surveyed is estimated. Repeated estimates provide the opportunity to track changes in a population, such as migration or reproduction. Repeated estimates also provide a measure of reliability in the measurement. Similar estimates from different sets of data provide additional confidence in the estimates themselves. Yet, cameras also come with a large initial cost to purchase equipment (~$150–650/camera, USA) and a large data management and storage burden. There can be a large time investment in reviewing huge numbers of photos, although image recognition algorithms can shorten the time required for photo review (Tabak et al., 2019). Additionally, camera theft (Meek et al., 2016), damage from animals, wildfires, and wind may also reduce the usefulness of cameras.

The first abundance estimates using trail cameras were of tigers (*Panthera tigris*), and individuals were identified by their stripe patterns (Karanth & Nichols, 1998). Cameras have become a common tool for estimating abundance of animals that can be individually identified by natural or artificial marks. Additionally, there is a great interest in estimating abundance from unmarked populations, and a number of novel methods have been proposed in recent years, including the random encounter model (REM; Rowcliffe et al., 2008), spatial count (SC) model (Chandler & Royle, 2013), random encounter and staying time (REST) model (Nakashima et al., 2018), distance sampling (Howe et al., 2017), and space-to-event (STE) and time-to-event (TTE) models (Moeller et al., 2018). These models are varied in their advantages and disadvantages. For example, REM, REST, and TTE require precise estimates of animal movement, which are notoriously difficult to obtain (Seber, 1986). The SC model requires a dense grid of cameras to provide individuals with the potential to encounter more than one camera, making it expensive and time-consuming to employ at large spatial scales.

Newly developed space-to-event models show promise for estimating animal abundance using cameras (Loonam et al., 2021; Moeller et al., 2018). Genetic mark–recapture and SECR methods (spatially explicit capture recapture; Chandler & Royle, 2013) require high-density effort to get multiple detections of the same individual, creating major logistical challenges at large scales. Conversely, the STE model capitalizes on the relationship between animal density and detection rate to estimate abundance with lower-density effort. Logically, it follows that if there are more individuals in survey area A than survey area B, one should have to sample less space (i.e., fewer camera viewsheds) in survey area A to obtain a detection of the species of interest. Three key advantages of the STE model are as follows: (1) It does not require individual identification of animals; (2) it requires only the presence of the species and not a count of individuals; and (3) it is snapshot-based (instantaneous); therefore, movement of animals does not affect abundance estimates. The STE model relies on random sampling and builds on principles of statistical sampling (Cochran, 1977). Therefore, precision from a STE estimate is a function of the number of samples, not the density of samples. The relationship of precision to the number of samples allows the STE model and sampling to be scaled up to large areas in the same way that survey sampling can be scaled up, making it advantageous for large-scale sampling efforts.

While Moeller et al. (2018) and Loonam et al. (2021) found STE models useful for estimating the abundance of elk (*Cervus canadensis*) and mountain lions (*Puma concolor*), respectively, we do not know how well STE models work for low-density social species such as gray wolves. Wolf distribution can be influenced by human land use (DeCesare et al., 2018) as well as their inherent social nature, resulting in patchy distributions across large spatial scales such as an entire state (e.g., Idaho, USA). Wolf density is often in the range of 5–40 animals per 1000 km^2 (Fuller & Murray, 1998). Such low densities result in few encounters with wolves and, therefore, small sample sizes in typical data collection efforts. Despite these complications, social and political pressures frequently place a high value on understanding how many wolves exist across broad spatial areas. Thus, agencies that manage wolf populations often spend substantial personnel time and energy monitoring wolf populations.

Many methods exist for monitoring wolf populations including snow-tracking, harvest modeling, radio-collaring, and genetic sampling, to name a few (Ausband et al., 2014; Liberg et al., 2012; Patterson et al., 2004; Robichaud & Boyce, 2010; Stenglein et al., 2010). Most such methods require experienced personnel and are expensive to implement across large spatial scales, limiting their feasibility. Cameras do not necessarily require experienced personnel for deployment or great expense once the equipment is initially purchased. The use of camera approaches such as the STE model could provide a more efficient way to track wolf populations through time, yielding highly desired data for wolf management and conservation.

We examined the feasibility of using motion-triggered cameras and a STE model to estimate wolf abundance. We capitalized on intensive wolf research conducted in Idaho and tested cameras in locations with concurrent noninvasive genetic sampling. We focused on two considerations for evaluating the usefulness of the STE model: (1) an abundance estimate that agrees with an estimate derived from established independent genetic methods and (2) cost relative to genetic sampling.

METHODS

Field methods

Camera surveys

We deployed motion-triggered cameras in three study areas in Idaho during June–September 2016–2018 (Figure 1). The study areas were Idaho Department of Fish and Game (IDFG) game management units 4 (3188 km^2), 28 (3388 km^2), and the combination of 33/34/35 (3862 km^2). IDFG employees deployed one camera/50 km^2 (Hyperfire models PC900 and HC600, Reconyx, Inc., Holmen, WI) across each study area in a grid system. Cameras were deployed along roads or trails within 500 m of either historical wolf pack rendezvous sites (i.e., pup-rearing sites used in summer) or highly suitable predicted rendezvous site habitat (Ausband et al., 2010; Figure 1). Predicted rendezvous sites were mapped using a resource selection function (RSF) that incorporated habitat and landscape characteristics of historical sites (Ausband et al., 2010). Many cells contained multiple distinct areas of highly suitable rendezvous site habitat. In such cells, we deployed cameras in the largest contiguous patch of habitat that was distinct from habitat in neighboring cells. We violated the STE model assumption of random camera placement in part to ensure an adequate number of detections of a low-density animal. Using nonrandom camera placement and comparing the resulting estimate to one derived from independent genetic sampling allowed us to test the robustness of the STE model.

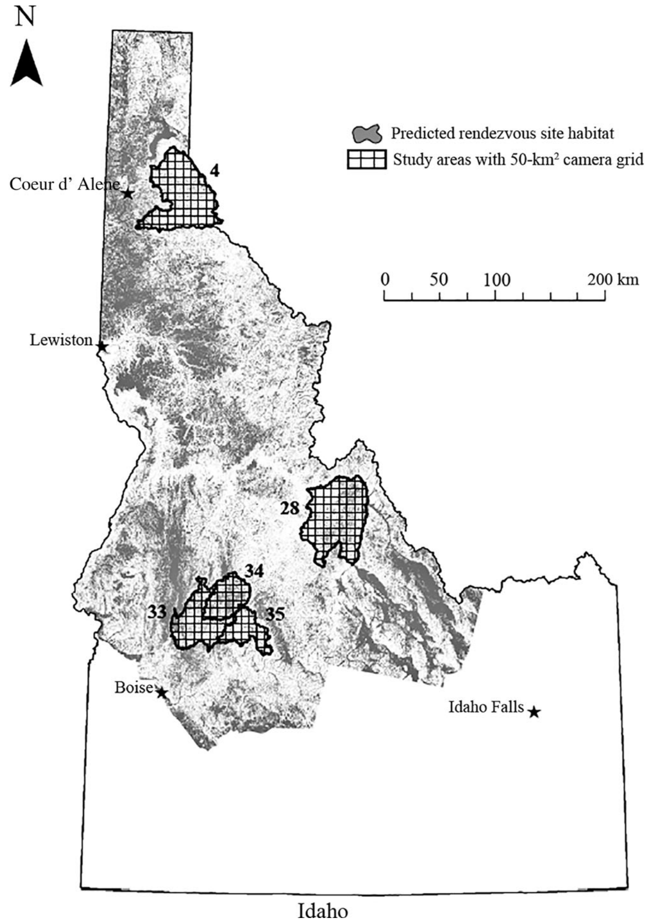

FIGURE 1 Study areas used to survey wolves with concurrent genetic and camera surveys in Idaho, 2016–2018. Shaded areas represent highly suitable wolf rendezvous site habitat from a resource selection function (Ausband et al., 2010). Grids represent 50 km^2 cells containing one camera

Cameras were mounted to trees >20 cm in diameter, at a height >2.4 m, and angled downward to capture movement on the road or trail below. In 2016, cameras were deployed at an angle <60° to the road or trail to capture movement of wolves approaching or leaving the camera. In 2017 and 2018, this protocol was altered in an attempt to increase wolf detections so that cameras were deployed perpendicular to the road or trail. In areas without suitable trees, fence posts or large sagebrush (*Artemisia* sp.) bushes were used. All obstructing vegetation was removed. Cameras were fit with a 32-GB memory card and set to: three pictures per trigger event, no delay between trigger events, RapidFire (<1 s) delay between images within each trigger event, high sensitivity, high resolution (3.1 megapixels), and balanced night mode. Once cameras were properly positioned, technicians used the "Walk Test" setting to measure and record the length of camera detection zones, although the overall area detected by the camera was not calculated. Cameras were then armed to take pictures and locked in place. Technicians also recorded a variety of site characteristics of the camera locations, including: UTM coordinates, habitat type, and percent canopy cover. All cameras remained untouched by IDFG employees until collection in mid-September.

Genetic surveys

Field crews collected scats for genetic analysis at rendezvous sites of reproductively active wolf groups. Technicians also surveyed historical and highly suitable (≥70%) rendezvous sites predicted by a habitat model (Ausband et al., 2010). Because there were fewer radio-collared wolves present in our study site in 2017 and 2018 than in 2016, an increased number of rendezvous site surveys were required to locate wolves in 2017 and 2018. Once an active or recently active rendezvous site was found, technicians typically gathered 125–200 samples per group. DNA was extracted from scats at the University of Idaho Laboratory for Ecological, Evolutionary and Conservation Genetics and amplified at 18 microsatellite loci to identify individuals. Further detailed field and genetic analysis protocols can be found in Ausband et al. (2010), Stenglein et al. (2010, 2011), and Stansbury et al. (2014). Protocols and field sampling aligned with guidelines of the American Society of Mammalogists (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists, 2016).

Abundance analysis

Camera sampling

We analyzed wolf detections from trail cameras in a STE framework (Moeller et al., 2018) using the STE estimator implemented in *R* (R Core Team, 2019) with the package *spaceNtime* (Moeller & Lukacs, 2021). We used highly suitable rendezvous site habitat (i.e., top 30% predicted habitat) as the sampling frame for the analysis because camera locations were selected from those levels of the RSF (Ausband et al., 2010). Because the STE model in *spaceNtime* outputs a density estimate, we multiplied the estimate of wolf density by the area of highly suitable wolf rendezvous site habitat within the study areas to generate abundance. We did not estimate viewshed area during camera deployment; thus, we used a viewshed area based on expected performance of motion-triggered cameras. We assumed the cameras detected wolves within a 106-m^2, pie-slice shape area in front of the camera derived from standard field protocols and that the motion trigger detected all wolves that passed through the viewshed. Finally, we used a 2 s window every 30 s to generate detection histories. We developed capture histories using *spaceNtime* (Moeller & Lukacs, 2021). We estimated abundance using data from July and August each year. We focused on that time period because it represented the period of complete camera coverage across the study areas. Confidence intervals were based on a log-normal distribution as calculated in *spaceNtime*. Finally, we used a bootstrap procedure to select cameras at random with replacement and produce 100 estimates using 2018 data to assess the potential effects of influential cameras (i.e., those with and without many detections) on resulting population estimates.

Genetic sampling

After generating individual genotypes for each collected sample, we calculated recapture rates and estimated abundance across the three study areas using a two-innate rates model (Miller et al., 2005) in the R package *Capwire* (Pennell et al., 2013). This model allows for the heterogeneity in capture probabilities that are common to our data when sampling scats of pups and adults at wolf rendezvous sites. We then estimated density by dividing the abundance estimate by the size of the three study areas (km^2).

RESULTS

Motion-triggered cameras detected 13,219 wolves or groups of wolves from June 2016 through June 2018 pooled across the three study areas (Table 1). Of those detections, 8704 occurred during the 1 July to 31 August and were used in our STE model estimate. From the camera data, we estimated 196 (170–227, 95% CI) in 2016, 153 (130–179, 95% CI) in 2017, and 188 wolves in 2018 (162–218, 95% CI) in the three study areas combined. Total wolf density (wolves/1000 km^2) across the three study areas was 18.8 (16.3–21.7, 95% CI) in 2016, 14.7 (12.5–17.2, 95% CI) in 2017, and 18.0 (15.5–20.9, 95% CI) 2018. Our bootstrap estimate using sampling with replacement in 2018 yielded an estimate of 123 wolves (102–147, 95% CI), nearly identical to our genetic estimate that year. The camera survey cost $40,500 (USA) annually to deploy, retrieve, and process cameras and photos (i.e., crew of eight technicians to deploy and retrieve cameras for 6 weeks, three trucks, batteries, and 360 h of technician image processing time from our three

TABLE 1 Summary statistics for concurrent genetic and cameras surveys of wolves in Idaho, USA, 2016–2018

Survey type	Year	No. survey sites	No. wolf detections[a]
Genetic	2016	146[b]	142
Genetic	2017	281	153
Genetic	2018	310	89
Camera	2016	215[c]	4520 (3031)
Camera	2017	224[c]	4509 (2385)
Camera	2018	215[c]	4190 (3288)

[a]No. wolf detections for genetic surveys represent the number of individual consensus wolf genotypes, including recaptures. No. detections in parentheses indicates number of detections used in camera data analysis, 1 July–31 August.
[b]Genetic surveys in 2016 made use of multiple radio-collared wolves that were inactive in subsequent years. Increased surveys were required to locate rendezvous sites in 2017 and 2018.
[c]Not included in "No. survey sites" for cameras are 15, 3, and 14 cameras that failed due to theft, animal interference, fire, and user error in 2016, 2017, and 2018, respectively.

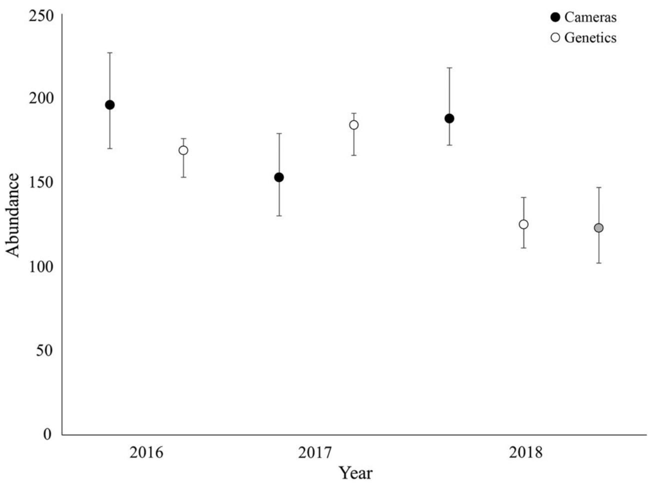

FIGURE 2 Estimated wolf abundance from concurrent camera and genetic surveys in three study areas (10,437 km^2) in Idaho, USA, 2016–2018. Error bars represent the 95% CI. A bootstrap estimate (gray dot) using sampling with replacement in 2018 yielded an estimate of 123 wolves (102–147, 95% CI)

study areas) after camera equipment was initially purchased. Cameras, cable locks, SD memory cards, and camera mounts cost $115,830.

In total, we genotyped 384 individual wolves captured 1–15 times pooled across the three study areas during 2016–2018 (Table 1). Estimated wolf abundance from DNA surveys was 169 (153–176, 95% CI) in 2016, 184 (166–191, 95% CI) in 2017, and 125 (111–141, 95% CI) in 2018 (Figure 2). Total wolf density (wolves/1000 km^2) across the three study areas was 16.2 (14.7–16.9, 95% CI) in 2016, 17.6 (15.9–18.3, 95% CI) in 2017, and 12.0 (10.6–13.5, 95% CI) in 2018. The genetic survey cost $89,500 (US) annually to conduct the wolf surveys and genotype collected scats.

DISCUSSION

We show that motion-triggered cameras and subsequent STE analyses can estimate the abundance of low-density, social species such as wolves. Our estimates of wolf abundance from cameras closely mirrored estimates from concurrent genetic sampling in 2 of 3 years. The genetic sampling approach we used had previously compared well to estimates of wolf abundance from aerial and ground telemetry-based surveys (Stansbury et al., 2014; Stenglein et al., 2010). Wolf density estimates derived from cameras (14.7–18.8 wolves/1000 km^2) also compared favorably to other systems with similar prey bases (e.g., elk, *Cervus canadensis*; deer, *Odocoileus* sp.; moose, *Alces alces*) in western North America (Fuller et al., 2003).

The confidence intervals of the genetic and camera estimates did not overlap in 1 year of our study, 2018, when the abundance estimate from genetic sampling was 34% lower than the camera estimate (Figure 2). One explanation for the difference between the two methods could be that we underestimated the population size using genetics in 2018. We sampled 50% fewer wolves in two of the three study areas in 2018 compared to the previous year. The scat sampling technique we used, however, has been tested extensively in areas of both low and high wolf density (Ausband et al., 2010; Stansbury et al., 2014; Stenglein et al., 2010), and we do not have reason to think that weather, observer error, or other such factors biased our sampling in 2018. Statewide harvest data from Idaho Department of Fish and Game indicated harvest did increase from 2017 to 2018, however. Genotyping of tissue samples from harvested wolves also indicated the harvest rate increased from 2016 to 2017 (11.2%) to the 2017–2018 season (25.5%; Ausband & Waits, 2020). The available data suggest there were indeed fewer wolves in our study areas in 2018 compared to previous years.

A second explanation for the disparity in estimates in 2018 could be that cameras overestimated population size. Wolf abundance at cameras can be biased high if (1) the camera viewshed is underestimated (Cusack et al., 2015; Rowcliffe et al., 2008), (2) use of highly suitable habitat changes during the survey period (Chandler & Royle, 2013), or (3) through random chance present in 1 year but not others, wolf behavior causes individuals to be captured on cameras at very high rates (e.g., camera at a den site). We do not believe viewsheds were consistently underestimated because of our camera deployment protocol, nor did habitat use change; high detections at just a few cameras, however, could have biased estimates slightly high in some years. Indeed, a single camera in 2018 had 2101 detections. Excluding this camera from analyses reduced the camera abundance estimate from 188 to 78 wolves (62–98, 95% CI). We sampled high-quality habitat to ensure we obtained detections of a low-density species, but note that such sampling may yield a large number of detections at just a few cameras, thus biasing estimates high. We assessed the influence of such potential outlier cameras on our estimate in 2018. Our bootstrap estimate in 2018 was nearly identical to our genetic estimate (123 vs. 125 wolves; Figure 2). One might consider using a bootstrapping procedure when sampling yields cameras with too few or too many detections.

We chose to use STE for our camera surveys because it does not require movement information or accurate counts of animals in groups, and it can be implemented at a large spatial scale. First, random encounter models and TTE require detailed information about movement of animals of interest (Rowcliffe et al., 2014) and inaccurate estimates of movement can lead to biased estimates of abundance. Because STE uses snapshots of the landscape in time, the results are not affected by animals moving at different speeds. Removing assumptions about animal movement substantially reduces risk from assumption violations and data needs. Second, STE uses presence/absence of the species or interest instead of group counts. Many other camera estimation methods require accurate group counts in every photo (e.g., random encounter models, distance sampling, instantaneous sampling), which can be difficult if weather or time of day affect photo quality or if animal behavior makes it challenging to see each individuals (Moeller et al., 2018). Third, STE is an unbiased estimator regardless of camera density or spatial scale, and it can be implemented at large spatial extents cost-effectively. In contrast, SECR models require multiple cameras per animal activity center to estimate the size of the movement area, so cameras must be deployed at a particular camera density (Chandler & Royle, 2013). To scale up to a large study area such as ours (10,438 km^2), the number of cameras required to meet this assumption greatly increases the cost and effort for a survey, making SECR models inefficient for large areas.

The use of snapshot sampling with the STE model may lead to inefficiencies with data collection if cameras are set to record motion-triggered images. Motion-triggered images potentially produce a less accurate STE estimate because we must assume that the cameras captured every wolf that entered the viewshed. However, the use of only snapshots from motion-triggered cameras greatly reduces the number of photos that need to be reviewed because the large number of motion-triggered photos need not be examined unless desired for other studies. This trade-off can improve turnaround time from field implementation to actionable information.

We deployed our cameras largely on mountainous public land and in conifer forests. Additionally, we assumed that high-quality rendezvous site habitat predicted by Ausband et al. (2010) was available for wolves to use in our study areas. Because we sampled large blocks of contiguous public land, this assumption was very likely met. If predicted habitat is not likely to be used, however, such areas (e.g., developed private land) should be removed from the sampling frame to avoid extrapolating density from camera viewsheds to unused area and biasing estimates high.

We recommend the viewshed of each camera be measured explicitly to ensure the most accurate estimates are obtained. This can be done by testing the motion trigger at varying distances from the camera and recording the maximum distance of a detection. Alternatively, flagging could be placed at a fixed distance in front of the camera within the detectable range. Only wolves detected within the flagged distance would be considered in the analysis. Cameras should also be set to take time-lapse photos. Time-lapse photos ensure that the same instance in time is sampled by all cameras. Time-lapse photos also provide a measure of confidence that a camera was functioning throughout its entire deployment.

We have shown that abundance estimates from camera data and an STE model match well with estimates from an established method (genetic sampling) for a low-density, social species of great management interest. Management questions may still require use of alternate survey methods in some situations (e.g., genetic surveys to look at diversity in a population). For density and abundance estimation, however, the STE model has many advantages over other methods, which may make it more economical and sustainable for use in wildlife management and conservation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

DNA recapture data (Ausband, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5659015 and camera detection data (Ausband, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5659308.

ORCID

David E. Ausband https://orcid.org/0000-0001-9204-9837

Anna K. Moeller https://orcid.org/0000-0001-9102-6959

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