Canadian Science Publishing | Canadian Journal of Zoology

Acoustic vs photographic monitoring of wolves: a methodological comparison of two passive monitoring techniques

Journal:	*Canadian Journal of Zoology*
Manuscript ID	cjz-2019-0081.R2
Manuscript Type:	Article
Date Submitted by the Author:	26-Aug-2019
Complete List of Authors:	Garland, Laura; University of Alberta, Biological Sciences Crosby, Andrew; University of Alberta, Biological Sciences Hedley, Richard; University of Alberta, Biological Sciences Boutin, Stan; University of Alberta, Department of Biological Sciences Bayne, Erin; University of Alberta, Biological Sciences
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	Autonomous recording units, bayesian occupancy, camera traps, Canis lupus, gray wolf

SCHOLARONE™
Manuscripts

Acoustic vs photographic monitoring of wolves: a methodological comparison of two passive monitoring techniques

LG, AC, RH, SB, EB

LG: Biological Sciences CW405, University of Alberta, T6G 2R3, CA, lgarland@ualberta.ca

AC: Biological Sciences CW405, University of Alberta, T6G 2R3, CA, crosby@ualberta.ca

RH: Biological Sciences CW405, University of Alberta, T6G 2R3, CA, rhedley@ualberta.ca

SB: Biological Sciences CW405, University of Alberta, T6G 2R3, CA, sboutin@ualberta.ca

EB: Biological Sciences CW405, University of Alberta, T6G 2R3, CA, bayne@ualberta.ca

Correspondence: Laura Garland, Biological Sciences CW405, University of Alberta, AB, CA

+1-080-3832-6698, (email lgarland@ualberta.ca)

Draft

Acoustic vs photographic monitoring of wolves: a methodological comparison of two passive monitoring techniques

Laura Garland, Andrew Crosby, Richard Hedley, Stan Boutin, Erin Bayne

Abstract

Remote camera traps are often used in large mammal research and monitoring programs because they are cost-effective, allow for repeat surveys, and can be deployed for long time periods. Statistical advancements in calculating population densities from camera trap data has increased the popularity of camera usage in mammal studies. However, drawbacks to camera traps include their limited sampling area and tendency for animals to notice the devices. In contrast, autonomous recording units (ARUs) record the sounds of animals with a much larger sampling area but are dependent on animals producing detectable vocalizations. In this study, we compared estimates of occupancy and detectability between ARUs and remote cameras for gray wolves (*Canis lupus,* Linnaeus 1758) in northern Alberta, Canada. We found ARUs to be comparable to cameras in their detectability and occupancy of wolves, despite only operating for 3% of the time that cameras were active. However, combining cameras and ARUs resulted in the highest detection probabilities for wolves. These advances in survey technology and statistical methods provide innovative avenues for large mammal monitoring that, when combined, can be applied to a broad spectrum of conservation and management questions, provided assumptions for these methods are rigorously tested and met.

Key words: Autonomous recording units, bayesian occupancy, camera traps, *Canis lupus*, gray wolf

Draft

Introduction

Apex predators are often a priority for natural resource management and conservation. As such, necessary aspects of predator management include understanding predator ecology, behavior, and distribution patterns. However, carnivores are a challenge to study, because they occur in low densities across vast geographic ranges (Ausband et al. 2014; Brassine and Parker 2015). With densities sometimes lower than 5/1000 km^2 in the northern limits of their range, and territories that can cover hundreds or even thousands of square kilometers, the gray wolf (*Canis lupus,* Linnaeus 1758), is a classic example (Fuller et al. 2003; Marquard-Petersen 2012).

Recent technological advances have improved our understanding of wolf ecology and distribution. However, these techniques can be expensive, logistically complex, inefficient, and may have negative effects on the health or behaviour of the animal (Mourão and Medri 2002; Brennan et al. 2013; Gable et al. 2018). Telemetry for example, requires an individual to be caught, fitted with a collar, and released, typically with the use of sedating drugs (Tuyttens et al. 2002). Aerial surveys on the other hand are expensive and often result in underestimates when applied to enumerating populations (Schlossberg et al. 2016). Both telemetry and aerial methods have been shown to have negative effects on the target species. Whether aerial surveys are done via drones or aircraft, target animals' stress often increases, and their behavior is altered, often up to several hours or days post-survey (Bleich et al. 1994; Fleming and Tracey 2008; Ditmer et al. 2015; Christie et al. 2016; Brambilla and Brivio 2018). For example, Eurasian lynx (*Lynx lynx*, Linnaeus 1758) and mule deer (*Odocoileus hemionus*, Rafinesque 1817) changed their movement patterns post-capture (Moa et al. 2001; Northrup et al. 2014). Howl surveys, which introduce foreign howls by people or playbacks to elicit vocal responses from nearby individuals

https://mc06.manuscriptcentral.com/cjz-pubs

or packs are labor-intensive and could disrupt the behavior and social interactions of canids and their neighbors (Suter et al. 2016).

Non-invasive passive survey techniques, such as camera trapping and bioacoustic detectors, may provide cost-effective and efficient alternatives for monitoring species that have low detection probabilities when surveyed using more traditional sampling methods (Diggins et al. 2016; Buxton et al. 2018; Steenweg et al. 2018). Currently, the most popular methods of passively monitoring large mammals is remote camera traps (Karanth 1995; Kelly and Holub 2008; Davis et al. 2018). Camera traps are used because of their ability to inexpensively survey a site continuously over a long time period and over large spatial extents simultaneously, with limited effects on the animals being studied (Burton et al. 2015; Newey et al. 2015). Camera data has been used to estimate occupancy, abundance, activity patterns, behavior, habitat use, and population density for several species, including wolves (Rowcliffe et al. 2008; Ausband et al. 2014; Gray 2018; Mattioli et al. 2018). One shortcoming of camera traps is they only survey a small area directly in front of the camera lens. Low detectability of the target species can therefore be problematic with camera trap data, especially for species with low densities and large home ranges such as wolves. Animals may also respond to the light or sound produced by cameras, which can bias detection probabilities (Meek et al. 2016).

Acoustic monitoring via autonomous recording units (hereafter ARUs) is rapidly emerging as a tool for monitoring a wide array of vocal taxa (e.g. whales (Mellinger et al. 2007), bats (Clement et al. 2014), birds (Charchuk and Bayne 2017), insects (Mankin et al. 2011)). Acoustic monitoring confers several advantages over traditional survey techniques, including a permanent data record, and reduced observer bias (Shonfield and Bayne 2017). Recent studies have proposed that acoustic monitoring could offer advantages over camera surveys for wolves

https://mc06.manuscriptcentral.com/cjz-pubs

(Suter et al. 2016; Papin et al. 2018). Wolf howls can be heard by neighboring wolves as well as humans at distances over 10 km, and recent estimates suggest they can be detected up to 4.6 km away by ARUs (Passilongo et al. 2015; Suter et al. 2016). However, ARUs have seldom been used to monitor wolves, presumably because of an assumed low howling rate and the time needed to process the data. Thus, it is not known how inferences regarding occupancy drawn from ARU data compare to those derived from cameras.

A crucial element of any occupancy study using passive monitoring devices is the definition of a sampling interval (Efford and Dawson 2012; Wilson and Schmidt 2015). Detectability estimates, and therefore estimated occupancy probabilities, may change depending on the length of time over which subsamples are divided, (e.g.: daily, weekly, or monthly intervals), regardless of what method is used (Efford and Dawson 2012; Steenweg et al. 2018). For example, if one detection at a single device occurs in 3 months of sampling, the naive detectability (and calculation of occupancy rates) will likely differ if the sample period is divided into days vs weeks vs months (1 detection in approximately 90 days (p=0.01, Ψ=0.34) vs 1 detection in 12 weeks (p=0.08, Ψ=0.32) vs 1 detection in 3 months (p=0.33, Ψ=0.31)). Researchers or managers may form monitoring conclusions without thinking about how different temporal survey intervals influence inference about occupancy rates. To our knowledge, comparing detection and occupancy estimates between cameras and ARUs at varying sub-sampling intervals has never been examined, despite the importance of this in defining what constitutes "occupancy" of a site, both at a spatial and temporal scale, for species monitoring and management (Efford and Dawson 2012).

Our goal was to compare the performance of ARUs and camera traps in estimating occupancy and detectability of gray wolves in northeastern Alberta under different sampling

https://mc06.manuscriptcentral.com/cjz-pubs

designs. Our objectives were: 1) compare camera and ARU data processing time and sampling effort 2) compare detectability between ARUs and cameras—examining how differences in detection estimates change given variations in the definition of a sampling occasion; as well as compare differences if methods are pooled or combined in a multi-method analysis and 3) we used these results to outline suggestions for a sampling framework that incorporates ARUs in long-term wolf monitoring.

Materials and methods

Study area

Our study area was in the northeastern region of Alberta, Canada, primarily covering the Interior Plains, an area approximately 163,350 km^2 in size with known wolf populations present. Specifically, our survey locations were north of Edmonton and east of the city of High Level (Figure 1). This region is characterized by a combination of boreal central mixedwood, upper and lower boreal highlands, and the Athabasca plain. Considered habitat generalists, gray wolves have a propensity to use both closed and open habitats throughout northeastern Alberta, including coniferous, deciduous, and mixed forests in addition to shrublands and wetlands (Benson et al. 2015; Uboni et al. 2017).

Study design

Working with the Alberta Biodiversity Monitoring Institute (hereafter the ABMI), we gathered camera and acoustic data during March 1st – June 30th of 2016 and 2017 (Figure 1). The ABMI primarily researches a variety of species in Alberta, therefore this particular study design was aimed at passively surveying amphibians, songbirds, and mammals with temporal and spatial replication. We paired cameras and ARUs at a station and a site consisted of four

https://mc06.manuscriptcentral.com/cjz-pubs

stations spaced 600 m apart in a square (Figure 2). We deployed sites in a systematic, 20 km grid across Alberta.

We used RECONYX Hyperfire 900 cameras (RECONYX, Holmen, WI). We programmed cameras to run 24 hours per day and cameras were motion-triggered to take photos continuously every second using an infrared trigger as long as the subject remained in the viewfinder. We placed the cameras approximately 1m high on trees with the lenses facing north to avoid glare in the photos during sunrise and sunset. If necessary, we cleared away vegetation that may have obstructed the camera viewfinder.

For ARU surveys, we used SongmeterSM3 and SM4 acoustic recorders (Wildlife Acoustics, Inc., Maynard, MA). We deployed ARUs with the camera traps approximately 1.5 m tall on trees. If necessary, we cleared away surrounding vegetation that may have obstructed or interfered with the ARUs' recording abilities. We did not place the ARUs in any type of weatherproofing due to weatherproofing being built into their designs. We set ARU units to record 38 minutes per 24 hours with a 44kHz sampling rate and no filtering. Continuous recordings occurred 30 minutes after sunrise for 13 minutes and for 6 minutes at noon to target songbirds, dusk for 6 minutes to record waterfowl and thrushes, and midnight for 13 minutes to target amphibians. Sunrise, dusk, and midnight hours are also times at which wolf vocal activity peaks year-round (McIntyre et al. 2017). As such, these recording schedules also allowed for spontaneous recordings of wolf vocalizations. SM4 units recorded in .wav and SM3 units in .wac, the latter being a type of lossless compression format.

Data selection

We created three datasets to compare ARU detectability with that of cameras. For the first dataset, we selected all cameras that were deployed in 2016 and 2017 that included at least

https://mc06.manuscriptcentral.com/cjz-pubs

one wolf detection to attain a baseline of camera detectability that we could then compare to ARUs. We constrained the sampling period of the cameras to that of the corresponding ARUs to only include detections during the time the ARUs were deployed, approximately March 1st – June 30th, across both years. If either the camera or paired ARU failed during the sampling period (i.e. stopped recording), we excluded all detections from the paired unit during the time of inactivity. We defined a “hit” as each unit’s first detection, and then the first photo or vocalization detected at least 12 hours since their last respective detection based on the minimum time between detections suggested by Rovero and Marshall (2009). This resulted in a total of 34 and 39 unique camera stations with a wolf hit in 2016 and 2017, respectively (Table 1).

The second dataset was comprised of stations where cameras had not detected a wolf, to allow for the possibility that an ARU might still detect one. We selected the same number of stations in each year (2016, n=34; 2017, n=39) where camera detections were zero, and processed the corresponding ARUs for wolf vocalizations (Table 2). The definition of a wolf “hit” remained the same as the previous comparison—a minimum of 12 hours between each detection.

Finally, we created a third dataset by randomly selecting one of the four stations at each of the sites represented in the first two datasets (N=69) (Figure 1). By ensuring each station was drawn from a different site in this dataset, we guaranteed each station was at least 20 km from all others.

Data processing

Camera trap species identification was done by technicians experienced in mammal identification and trained via a step-wise process according to tagging protocols established by the ABMI. Technicians recorded the scientific and common names of species in addition to the

https://mc06.manuscriptcentral.com/cjz-pubs

Draft

location identifier, camera identifier, date and timestamp, latitude, longitude, number of individuals, sex, and approximate age (if possible). Individuals were not identified using this method. For the purposes of our occupancy analysis, we considered photos taken 12 hours after the first photo to be independent samples, which is consistent with Rovero and Marshall (2009), who suggested a time of at least 60 minutes between capture events.

We used the program Sound eXchange (SoX) version 14.4.2 to process ARU data (Bagwell et al. 2013, SoX, http://sox.sourceforge.net). This program creates spectrograms from audio data based on the parameters specified by the user. To view wolf vocalizations, we used the *sox* function in the package 'seewave' in R version 3.3.1 (Sueur et al. 2008; R Core Team 2018), to convert raw audio files into 1-minute spectrograms. We truncated spectrograms from the original 44 kHz sampling rate to a 7 kHz sampling rate, and we used the standard colors provided by SoX to detect individual howls, responses, and choruses in each recording (Figure 3). We truncated the spectrograms because wolves have a low frequency howl, ranging approximately from 0.274 kHz (274 Hz) to 0.908 kHz (908 Hz) in fundamental frequency (Passilongo et al. 2010). All ARU data processing was completed by the same researcher. We built a call library, and the researcher was given a sample dataset from the call library to practice their identification skills. In cases where the identity of a vocalization was uncertain, the researcher listened to the recording to confirm species identification.

Processing time and sampling effort

To address our first objective to compare camera and ARU processing time and sampling effort, the researcher processing the audio data tracked the time it took to visually scan each station from the SoX output. We estimated the average time it took to scan all 146 stations and compared this processing time to the average camera processing time used by the ABMI.

Draft

Sampling effort

To examine how sampling effort between ARUs and cameras influenced our results, we used the stations from the first dataset that had known camera wolf detections (*n*=73) during March 1st – June 30th of 2016 and 2017. We did not match the exact dates of paired ARU and camera activity, instead viewing sampling effort based on the individual devices.

We defined a single "hit" for both cameras and ARUs as any wolf image or vocalization captured per minute between March 1st and June 30th, 2016 and 2017. For example, if three lone howls were detected in a single minute of ARU recording time, we counted that as a single detection. Additionally, if three images of a wolf were captured successively by a camera within the same minute, we also counted that as a single detection.

Occupancy analysis

To meet our second objective of comparing detection probabilities between ARUs and cameras, we used single season occupancy models (MacKenzie et al. 2002) using detection histories with varying sampling intervals.

The assumptions of a single-season occupancy model are occupancy of a site remains closed during the sampling season (i.e., individuals do not immigrate or emigrate from the sampling site during the sampling season), detection between sites are independent of each other, and the probability of occupancy and detection are equal across sites (MacKenzie et al. 2002). Our definition of a site was each group of four, paired cameras and ARUs spaced 600 meters apart, with our sampling unit constituting a single camera and a single ARU selected per site. We assumed site closure at the scale of wolf territories, because the detection zone for both cameras and acoustics is significantly smaller than a wolf's home range, we assumed at least one site was placed in a pack territory. We assumed that wolf occupancy of sites remained closed during the

https://mc06.manuscriptcentral.com/cjz-pubs

Draft

sampling period because wolves tend to occupy the same territories for long time periods, particularly during the pup-rearing season (spring-summer) (Jedrzejewski et al. 2001; Rio-Maior et al. 2018). Detectability between sites was not completely independent because wolves can travel up to 20 km in a day (Scurrah 2012; Ehlers et al. 2014; Latham et al. 2014). However, the sites were spaced far enough apart that if a wolf howled, it would not be detected by more than one ARU at a time (Passilongo et al. 2010). We expected wolf movement to be random relative to the camera-ARU site, therefore we did not expect strong biases in occupancy or detection estimates between sites (Kalan et al. 2015). The purpose of this paper was to examine the detectability of ARUs relative to cameras. Therefore, we were not overly concerned with the precision of the occupancy and detection probabilities as they apply to estimating wolf abundance or distribution, instead we focused on examining the similarity or differences in detection estimates based on the method employed.

Draft

We used the third dataset of 69 paired stations, where one station was randomly selected per site from the 146 processed stations to do this analysis. To understand how individual detection probabilities varied between ARUs and cameras, as well as how detectability changes with various sampling intervals, we ran occupancy models for each method separately using daily (120 survey events), weekly (17), and monthly (4) detection histories.

Additionally, we compared detection and occupancy estimates when the methods were pooled as well as through a multi-method approach. For the pooled analysis, we combined camera and ARU detections (given both units were functioning throughout the survey period), if either unit detected a wolf, it was entered as “1” for that sampling occasion. For example, if a camera had a detection history of {001} and the paired ARU had a detection history of {100}, the resulting combined detection history would be {101}.

We also combined both units' detection histories in a multi-method approach to assess an additional variable, θ_x, which is the probability of an individual being available for detection using method x, given an animal's presence. Therefore, a wolf that is detected by a camera will be within the detection zone of an ARU, but the reverse may not be true, which the multi-method approach accounts for. The multi-method approach also calculates ψ, as well as p_{xi}, or the probability of detecting an individual using method x in survey i. (Nichols et al. 2008).

Lastly, we examined how the efficacy of cameras and ARUs might change seasonally. We ran occupancy models for both cameras and ARUs at the weekly interval using week as a covariate of detection probability. Typically, the longer a unit is deployed, it is expected that their detection probabilities will increase (MacKenzie et al. 2002). However, when the Canadian boreal forest is transitioning from winter to spring and summer months, green up of the vegetation and summer rains may decrease the detection zone and impact detection rates due to false triggers (Norton et al. 2000; Efford and Dawson 2012).

Bayesian framework

We estimated occupancy and detectability using a Bayesian framework in JAGS version 4.3.0 (Plummer 2003) via the R package R2jags (Su and Yajima 2015). We used uninformative prior distributions for all estimated variables, where priors for occupancy and detection probabilities were uniformly distributed between 0 and 1, and the prior on detection coefficients was normally distributed between 0 and 0.01. We ran 3 chains, of 3,000 iterations, a burn-in of 500 iterations, and a thinning rate of 5. We assessed convergence of the MCMC chains using the Gelman and Rubin R-hat diagnostic (Brooks and Gelman 1998).[1]

Multi-method occupancy analysis

[1] See supplementary materials for model code.

https://mc06.manuscriptcentral.com/cjz-pubs

To examine multi-method occupancy and detectability, we used the program Presence version 12.23, as it integrates the methods proposed by Nichols et al. (2008). We collapsed the datasets by daily, weekly, and monthly intervals. In Presence, we ran a maximum likelihood occupancy model accounting for two detection methods at every survey interval, and estimated values for ψ, p_{xi}, and θ_x.

Results

Across the three datasets, we detected wolves at 111/146 (76%) of stations via ARUs and/or cameras. ARUs detected wolves at 46/73 (63%) of stations in the first dataset, which was drawn from stations at which cameras had detected a wolf. ARUs detected wolves at 38/73 (52%) of stations in the second dataset, which was comprised of stations at which cameras had not detected a wolf. ARUs detected wolves at 39/69 (57%) of stations in the third dataset, which was comprised of a mix of stations with and without camera detections.

Processing time

The average processing time for an ARU that recorded 38 minutes per day over 4 months (approximately 4500 one-minute spectrograms), varied depending if the recordings were made in .wac or .wav format. To create the spectrograms, .wac files first had to be converted to .wav, which typically increased the length of processing 1.5 times. However, opening R and initiating the SoX program per ARU took less than 2 minutes to complete. Creating 4500 1-minute spectrograms from .wav files took approximately two hours on an i-7 2400K at 3.40 Ghz with 16GB RAM computer running Windows 7 64-bit. Processing 4,500 1-minute spectrograms from a recording station took an experienced researcher less than an hour (52 ± 16 minutes). Researchers tagging camera photos were able to process about 2000 photos per hour, on average (Corrina Copp, personal communication, 2018). Since camera stations recorded an average of

https://mc06.manuscriptcentral.com/cjz-pubs

2349 photos per station over the deployment period, we estimate that processing one station would take slightly over one hour.

Sampling effort

Across 73 cameras deployed in 2016-2017, if every single unit was operating perfectly across the sampling period (i.e., 24 hour sampling effort), this would result in approximately 8906 days of continuous sampling. The actual days sampled (due to late start times or units failing early) was closer to 8064 days across both years. In contrast, if all 73 ARUs had been functioning perfectly during the sampling period, this would have resulted in 235 days of continuous sampling. (i.e. 38 minutes/24 hour sampling). Again, due to units failing early or being deployed late, the total days recorded between 2016-2017 were 222 days.

Throughout the sampling period from March 1st – June 30th, there were 254 wolf hits across 73 cameras and 309 wolf hits across the 73 ARUs (Table 3). Overall, 46/73 (63%) of the selected stations had at least one wolf vocalization recorded. Cameras had a hit rate of 0.029 hits/day, while ARUs had a hit rate of 1.440 hits/days, about fifty times higher than cameras.

Occupancy analysis and detectability for individual units

Detection probabilities derived from ARUs in the third dataset were comparable to detection probabilities from cameras, regardless of the temporal resolution of sampling. At the daily interval, camera and ARU detection probabilities were equal (p_{ARU}=0.033, 95% credible interval=0.022-0.047, p_{Camera}=0.030, 95% credible interval=0.024-0.050), but occupancy estimates from ARUs were double those of the cameras (Ψ_{ARU}=0.623, 95% credible interval=0.441-0.842, Ψ_{Camera}=0.304, 95% credible interval=0.165-0.561). At a weekly sampling interval, ARU detectability was higher than cameras (p_{ARU}=0.105, 95% credible interval=0.078-0.133, p_{Camera}=0.083, 95% credible interval=0.059-0.111), but both units' individual occupancy estimates were approximately equal (Ψ_{ARU}=0.652, 95% credible interval=0.499-0.913, Ψ_{Camera}=0.643, 95% credible interval=0.481-0.858). Lastly, at the monthly interval, ARU detectability was again higher than cameras (p_{ARU}=0.296, 95% credible interval=0.213-0.383, p_{Camera}=0.233, 95% credible interval=0.155-0.326), but their occupancy estimates were roughly equal (Ψ_{ARU}=0.752, 95% credible interval=0.569-0.945, Ψ_{Camera}=0.761, 95% credible interval=0.117-0.978). As the 95% credible intervals for ARU and camera detection probability always overlapped, neither method is statistically more significant in its ability to detect wolves.

Occupancy analysis and detectability for pooled and multi-method units

Pooled estimates were higher than either individual unit's individual probabilities, but were lower compared to the multi-method estimates that accounted for individual unit detectability given animal presence and availability for detection. The pooled estimates were as follows: daily (p_{Pooled}=0.047, 95% credible interval=0.034-0.062, Ψ_{Pooled}=0.548, 95% credible interval=0.388-0.727), weekly (p_{Pooled}=0.153, 95% credible interval=0.125-0.180, Ψ_{Pooled}=0.766, 95% credible interval=0.650-0.807), and monthly (p_{Pooled}=0.443, 95% credible interval=0.362-0.525, Ψ_{Pooled}=0.782, 95% credible interval=0.651-0.905). Multi-method estimates, particularly detection probabilities, were higher than the pooled estimates, but occupancy estimates were similar at both the weekly and monthly intervals. At the daily interval, the units' multi-method detectability increased (θ_{Multi}=0.267, 95% confidence interval=0.092-0.569), as did their occupancy estimates (Ψ_{Multi}=0.742, 95% confidence interval=0.641-0.838), relative to pooled methods. The multi-method detectability at the weekly interval was higher than the pooled units (θ_{Multi}=0.698, 95% confidence interval=0.228-0.948), but both occupancy estimates were similar (Ψ_{Multi}=0.757, 95% confidence interval=0.624-0.855). The multi-method monthly detectability was again higher than the pooled estimates, but their occupancy estimates were again, similar

Draft

(θ_{Multi}=0.829, 95% confidence interval=0.360-0.977, Ψ_{Multi}=0.800, 95% confidence interval=0.635-0.902).

Variation in detectability based on survey period

ARUs and cameras increased their detectability and occupancy estimates as the survey period length increased from daily to monthly, both individually and when the methods were pooled or used in multi-method analysis. The greatest discrepancy occurred between weekly and monthly sampling intervals when detectability more than doubled for individual units, increased by 29% for the pooled methods, and increased by 20% in the multi-method analysis. Occupancy estimates also increased by approximately 10% across all comparisons between weekly and monthly estimates. The differences in detectability and occupancy estimates between daily and weekly intervals was much smaller across the board, except for cameras doubling in their occupancy estimates between daily and weekly periods.

When week was included as a continuous covariate of detection probability at the weekly sampling interval, we observed a decrease in detectability in both cameras and ARUs (Figure 4) over time. Cameras were 0.747 (95% credible interval=0.006-0.999) times as likely to detect a wolf for every additional week they sampled while ARUs were 0.999 times as likely to detect a wolf per week (95% credible interval=0.978-0.999).

Discussion

We found that ARUs had equivalent or higher detection probabilities than cameras, regardless of the sampling interval used, even though ARUs recorded on a far sparser schedule. This indicates that ARUs may be a viable passive alternative to monitoring wolf populations. The discrepancy in occupancy estimates is explained in part by differences in the detection area of the methods, with cameras having a drastically smaller detection area than ARUs. Under ideal

https://mc06.manuscriptcentral.com/cjz-pubs

conditions, (ie: open habitat, no inclement weather), Reconyx advertises their cameras as having a 30 m detection radius and 42° interior angle (Reconyx 2017), for an approximate sampling area of 0.00033 km^2 for a single camera. Work completed by Suter et al. (2016) found that harmonics of captive wolf howls were easily detected from a recording distance of 3.6 km and trace howls were still detectable from a recording distance of 4.62 km on ARUs. A conservative detection radius of 3 km results in a detection area of approximately 28 km^2 for a single ARU. Given this discrepancy, the probability of a wolf being detected by a camera in an area it is occupying is much lower than the same wolf being detected by an ARU. Granted, the detection area for the ARU is dependent on habitat type and the distance of the wolf from the ARU. Increasing distance from the ARU lowers detectability, in addition to dense forest or vegetation also altering the transmission of sound waves (Yip et al. 2017). Additionally, detection rates from ARUs may be more vulnerable than cameras to weather variables, especially wind and rain, decreasing the acoustic detection areas during certain weather events, and therefore potentially resulting in lower detection rates depending on survey length. Overall, the detection areas of ARUs is likely to be more variable than cameras depending on the habitat they are placed in but this requires further investigation. These limitations are similar to cameras in their ability to capture images within the range of the viewfinder, dependent on animal positioning relative to the camera and the surrounding vegetation influencing detectability (Efford and Dawson 2012; Burton et al. 2015). Wind speeds can be approximated from an ARU based on noise level and thus corrected for or alternatively, they can be included as detection variables in occupancy modeling. Efford and Dawson (2012) point out that undefined or varying detection areas of passive recording devices, coupled with unknown or varying home range sizes of the target species, will have important impacts on estimates of occupancy. Therefore, because both methods are influenced

Draft

by weather and vegetation variables, further comparisons of absolute versus the relative error of these detection methods should be done. If passive methods like cameras and ARUs are to be applied to monitoring programs, it is necessary that detection areas be considered, particularly how detection areas are influenced by variables such as vegetation, weather, and background noise that may affect detectability and therefore estimates of occupancy (Efford and Dawson 2012).

ARUs, and to a lesser extent cameras, decreased in their individual probabilities of detection for each additional week the units were operating. This decline in detectability is likely explained in part by decreased movement and possibly vocal activity post-breeding (Find'o and Chovancová 2004; McIntyre et al. 2017). Decreased movement during the summer is primarily attributed to the presence of pups at dens or rendezvous sites, and to a lesser degree because wolves do not need to range as far in search of prey. (Find'o and Chocancová 2004). Wolves are known to vocalize more often in the months leading up to breeding, with a drop-off in vocal activity observed in the months following when pups are born. This drop in vocalization may be the result of decreases in hormone levels in wolves that resulted in increased aggression and howling behavior pre-breeding and during the breeding season. (Kreeger 2003; McIntyre et al. 2017). Green-up of vegetation as the summer progresses also might influence camera and ARU detectability both visually and acoustically. Although the reason for the change in detection probability is unknown in our dataset, it seems that if resources are constrained, monitoring should be conducted early in the season (March-April), as this is when wolves were most efficiently detected, and because these months indicate a higher vocalization rate before dropping in the later spring and early summer months (McIntyre et al. 2017).

Draft

Given that ARUs and cameras did not have perfect detectability at every site, when the methods were combined in the multi-method occupancy estimates, the resulting detection probabilities resulted in improved wolf detectability across each site. Therefore, despite ARUs performing slightly better in terms of their detectability of wolves over cameras, a multi-method approach would likely be the most accurate for long-term wolf monitoring. Additionally, the incorporation of spatial modeling of pack territories and seasonality of pack movement would greatly improve our predictions of when and where on the landscape wolves are. This would allow for improved precision and accuracy in our occupancy analyses using passive monitoring methods. This aligns with the current popularity of multi-method approaches to monitor rare species or trends in biodiversity patterns across regions (O'Connell Jr. et al. 2006; Nichols et al. 2008).

Draft

We observed an increase in both detectability and occupancy of wolves as the length of our sampling intervals increased. The greatest differences were seen in the multi-method estimates, with detectability increasing by 43% between daily and weekly intervals, and 13% between weekly and monthly periods. The variation in detectability seen across the three sampling intervals can affect monitoring and management conclusions made by researchers, depending on the goal of their projects. For example, detecting a wolf at a camera-ARU site twice in two weeks or 14 times in two weeks may result in different conclusions if the surveys are defined as daily or collapsed into weekly intervals. This is particularly important when comparing across studies. To simply determine species presence-absence, the heterogeneity across survey periods may not pose an issue. However, if the goal is to determine long-term trends in habitat use, species' distributions, or species' abundance, then determining the appropriate temporal scale of the sampling interval needs careful consideration.

Technical ARU adjustments

There are several adjustments that can be made to ARUs to increase their recording capacity and better target wolf vocal activity. These include compressing the audio formats to allow for increased storage of audio data and lowering the bit rate and sampling rate of the recordings. Bit rate is defined as the amount of data, or bits, that are transferred per unit time, typically measured in seconds. Higher bit rate, although it increases the quality of the recording, also increases the file size, thus increasing the space taken up per SD card. Therefore, we suggest a 16-bit rate for recording wolf vocalizations in long-term studies as this can maximize available memory space. Additionally, the sampling rate, or the number of samples taken per second of an audio recording, can be adjusted based on the vocal frequency of the target species. In ARUs, the sampling rate can be as low as 8 kHz, with frequencies recorded up to half of the sampling rate. Free ranging wolf howls range from approximately 0.274 kHz (274 Hz) to 0.908 kHz (908 Hz) in fundamental frequency (Passilongo et al. 2010). Therefore, 8 kHz would suffice for recording wolf howls while reducing storage needs.

By adjusting ARU sampling rate, bit rate, and compression formats, there is potential for ARUs to record at a daily rate similar to cameras. Although this would produce many hours of data that would be impractical to sort manually, automated processing methods may be helpful (Knight et al. 2017).

Wolf monitoring framework incorporating ARUs

Monitoring programs frequently rely on multi-method approaches to achieve their management or conservation goals (O'Connell Jr. et al. 2006; Ausband et al. 2014; Buxton et al. 2018). Already, camera traps and ARUs are being compared for their efficacy to monitor deer, whales, and elephants (Enari et al. 2017; Rayment et al. 2017; Wrege et al. 2017), and these

https://mc06.manuscriptcentral.com/cjz-pubs

methods are also used to assess human impact on several species (Horton et al. 2015; Robinson et al. 2015). This expansion into multi-method monitoring practices using both cameras and acoustics opens up several avenues of research questions ranging from development of hardware (e.g. improving the range of camera detection zones or ARU microphones), software (e.g. automated recognition programs for both methods), as well as animal ecology (e.g. seasonality of movement and vocal activity, predator-prey interactions).

With our comparison of ARU detectability to cameras in a Bayesian occupancy framework, in addition to the adjustments that can be made to ARU settings and an efficient way to process the audio data via SoX, it is feasible to use paired cameras and ARUs for additional studies, such as behavior, habitat use, and possibly even to measure breeding status of wolves (Palacios et al. 2016). Additionally, there are a lack of detailed studies assessing wolf howl rates (McIntyre et al. 2017), despite the importance of vocalizations as a form of communication for both inter- and intra-pack interactions (Nowak et al. 2007; Palacios 2016). The ability to passively capture daily and weekly howling behavior to answer questions related to vocal rates is now possible with ARU technology. Seasonal behavior as well, based on monthly howl rates, allows researchers to now map long-term trends in howling activity.

Research in recent years has established that the number of howling members in wolf packs can be counted based on individual vocalizations (Passilongo et al. 2015; Palacios et al. 2016). With this information, combined with year-round recording capabilities using both cameras and ARUs, there is the potential to answer several questions ranging from individual morphology and identification, density estimates, howling rates, habitat use, community-level interactions, establishing trends in behavior, and breeding status are all possible, without the need for invasive techniques.

https://mc06.manuscriptcentral.com/cjz-pubs

Draft

Acknowledgements

We gratefully acknowledge the University of Alberta and Natural Sciences and Engineering Research Council of Canada (NSERC) CREATE-EI scholarships for their financial support during this study. Additionally, we thank the Alberta Biodiversity Monitoring Institute for their support both financial and logistic during the 2016-17 field seasons. We would also like to thank the many field technicians that assisted in deploying and retrieving the equipment. Finally, thank you to the associate editor and two anonymous reviewers for their helpful comments and feedback on earlier versions of this manuscript. The authors declare no competing interests in this study.

Draft

References

Ausband, D.E., Rich, L.N., Glenn, E.M., Mitchell, M.S., Zager, P., Miller, D.A.W., et al. 2014. Monitoring gray wolf populations using multiple survey methods. J. Wildl. Manage. **78**(2): 335-346. doi:10.1002/jwmg.654.

Bagwell, C., Sykes, R., and Giard, P. 2013. SoX. Version 14.4.2. http://sox.sourceforge.net.

Benson, J.F., Mills, K.J., and Patterson, B.R. 2015. Resource selection by wolves at dens and rendezvous sites in Algonquin Park, Canada. Biol. Conserv. 182: 223-232. doi:10.1016/j.biocon.2014.12.010.

Bleich, V.C., Bowyer, R.T., Pauli, A.M., Nicholson, M.C., and Anthes, R.W. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. Biol. Conserv. **70**(1): 1-7. doi:10.1016/0006-3207(94)90292-5.

Brambilla, A., and Brivio, F. 2018. Assessing the effects of helicopter disturbance in a mountain ungulate on different time scales. Mamm. Biol. 90: 30-37. doi:10.1016/j.mambio.2018.02.001.

Brassine, E., and Parker, D. 2015. Trapping elusive cats: using intensive camera trapping to estimate the density of a rare African felid. PloS One, **10**(12): 1-16. doi:10.1371/journal.pone.0142508.

Brennan, A., Cross, P.C., Ausband, D.E., Barbknecht, A., and Creel, S. 2013. Testing automated howling devices in a wintertime wolf survey. Wildl. Soc. Bull. **37**(2): 389-393. doi:10.1002/wsb.269.

Brooks, S.P., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. J. Comp. Graph. Stat. **7**(4): 434-455. doi:10.1080/10618600.1998.10474787.

Burton, A.C., Neilson, E., Moreira, D., Ladle A., Steenweg, R., Fisher, J.T., Bayne, E., and

Draft

Boutin, S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. **52**(3): 675-685. doi:10.1111/1365-2664.12432.

Buxton, R., Lendrum, P., Crooks, K.R., and Wittemyer, G. 2018. Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. Global Ecol. Conserv. 16: 1-9. doi:10.1016/j.gecco.2018.e00493.

Charchuk, C., and Bayne, E.M. 2017. Avian community response to understory protection harvesting in the boreal forest of Alberta, Canada. For. Ecol. Manage. 407: 9-15. doi:10.1016/j.foreco.2017.10.033.

Christie, K.S., Gilbert, S.L., Brown, C.L., Hatfield, M., and Hanson, L. 2016. Unmanned aircraft systems in wildlife research: current and future applications of a transformative technology. Front. Ecol. Environ. **14**(5): 241-251. doi:10.1002/fee.1281.

Clement, M.J., Rodhouse, T.J., Ormsbee, P.C., Szewczak, J.M., and Nichols, J.D. 2014. Accounting for false-positive acoustic detections of bats using occupancy models. J. Appl. Ecol. **51**(5): 1131-1467. doi:10.1111/1365-2664.12303.

Davis, C.L., Rich, L., Farris, Z.J., Kelly, M.J., Di Bitetti, M.S., Blanco, Y.D., et al. 2018. Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. Ecol. Lett. 21: 1401-1412. doi:10.1111/ele.13124.

Diggins, C.A., Gilley, L.M., Kelly, C.A., and Ford, W.M. 2016. Comparison of survey techniques on detection of Northern flying squirrels. Wildl. Soc. Bull. **40**(4): 654-662. doi:10.1002/wsb.715.

Draft

Ditmer, M.A., Vincent, J.B., Werden, L.K., Tanner, J.C., Laske, T.G., Iaizzo, P.A., Garshelis, D.L., and Fieberg, J.R. 2015. Bears show a physiological but limited behavioral response to unmanned aerial vehicles. Curr. Biol. **25**(17): 2278-2283. doi:10.1016/j.cub.2015.07.024.

Efford, M.G. and Dawson, D.K. 2012. Occupancy in continuous habitat. Ecosphere. **3**(4): 32. doi:10.1890/ES11-00308.1.

Ehlers, L.P.W., Johnson, C.J., and Seip, D.R. 2014. Movement ecology of wolves across an industrial landscape supporting threatened populations of woodland caribou. Landsc. Ecol. **29**(3): 451-465. doi:10.1007/s10980-013-9976-8.

Enari, H., Enari, H., Okuda, K., Yoshita, M., Kuno, T., and Okuda, K. 2017. Feasibility assessment of active and passive acoustic monitoring of sika deer populations. Ecol. Indic. 79: 155-162. doi:10.1016/j.ecolind.2017.04.004.

Find'o, S., and Chocancová, B. 2004. Home ranges of two wolf packs in the Slovak Carpathians. Folia Zool. **53**(1): 17-26. doi:10.1007/s10980-013-9976-8.

Fleming, P.J.S., and Tracey, J.P. 2008. Some human, aircraft, and animal factors affecting aerial surveys: how to enumerate animals from the air. Wildl. Res. 35: 258-267.

Fuller, T.K., Mech, L.D., and Cochrane, J.F. 2003. Wolf population dynamics. *In* Wolves: behavior, ecology, and conservation. *Edited by* L.D. Mech and L. Boitani. University of Chicago Press, Chicago. pp. 163-191.

Gable, T.D., Windels, S.K, and Bump, J.K. 2018. Finding wolf homesites: improving the efficacy of howl surveys to study wolves. PeerJ. 6: e5629. doi:10.7717/peerj.5629.

Gray, T.N.E. 2018. Monitoring tropical forest ungulates using camera-trap data. J. Zool. (Lond.) **305**(3): 173-179.

Horton, K.G., Shriver, W.G., and Buler, J.J. 2015. A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. Ecol. Appl. 25: 390-401.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., and Okarma, H. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Can. J. Zool. **79**(11): 1993-2004.

Kalan, A., Mundry, R., Wagner, O.J.J., Heinicke, S., Boesch, C., and Kühl, H.S. 2015. Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. Ecol. Indic. 54: 217-226. doi:10.1016/j.ecolind.2015.02.023.

Karanth, K.U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture methods. Biol. Conserv. **71**(3): 333-338. doi:10.1016/0006-3207(94)00057-W.

Kelly, M.J., and Holub, E.L. 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeast. Nat. **15**(2): 249-263. doi:10.1656/10926194(2008)15[249:CTOCTS]2.0.CO;2.

Knight, E.C., Hannah, K., Foley, G. Scott, C., Brigham, M., and Bayne, E.M. 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. Avian Conserv. Ecol. **12**(2): 14. Available from https://www.ace-eco.org/vol12/iss2/art14/ [accessed 18 February 2019].

Kreeger, T.J. 2003. The internal wolf: physiology, pathology, and pharmacology. *In* Wolves: behavior, ecology, and conservation. *Edited by* L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 192-217.

Latham, M.C., Latham, A.D.M., Webb, N.F., McCutchen, N.A., and Boutin, S. 2014. Can occupancy-abundance models be used to monitor wolf abundance? PLoS One, **9**(7): e102982. doi:10.1371/journal.pone.0102982.

Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology. **83**(8): 2248-2255. doi:10.2307/3072056.

Mankin, R.W., Hagstrum, D.W., Smith, M.T., Roda, A.L., and Kairo, M.T.K. 2011. Perspective and promise: a century of insect acoustic detection and monitoring. Am. Entomol. **57**(1): 30-44. doi:10.1093/ae/57.1.30.

Mattioli, L., Canu, A., Passilongo, D., Scandura, M., and Apollonio, M. 2018. Estimation of pack density in gray wolf (*Canis lupus*) by applying spatially explicit capture-recapture models to camera trap data supported by genetic monitoring. Front. Zool. 15: 38. doi:10.1186/s12983-018-0281-x.

Marquard-Petersen, U. 2012. Decline and extermination of an arctic wolf population in East Greenland. Arctic. **65**(2): 155-166. Available from https://www.jstor.org/stable/41638588 [accessed 13 October 2018].

McIntyre, R., Theberge, J.B., Theberge, M.T., and Smith, D.W. 2017. Behavioural and ecological implications of seasonal variation in the frequency of daytime howling by Yellowstone wolves. J. Mammal. **98**(3): 827-834. doi:10.1093/jmammal/gyx034.

Meek, P., Ballard, G., Fleming, P., and Falzon, G. 2016. Are we getting the full picture? Animal responses to camera traps and implications for predator studies. Ecol. Evol. **6**(10): 3216-3225. doi:10.1002/ece3.2111.

Draft

Mellinger, D.K., Nieukirk, S., Matsumoto, H., Heimlich, S., Dziak, B., Haxel, J.H., et al. 2007. Seasonal occurrence of North Atlantic Right Whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. Mar. Mamm. Sci. **23**(4): 856-867. doi:10.1111/j.1748-7692.2007.00144.x.

Moa, P., Negård, A., Overskaug, K., and Kvam, T. 2001. Possible effects of the capture event on subsequent space use of Eurasian Lynx. Wildl. Soc. Bull. **29**(1): 86-90. doi:10.2307/3783984.

Mourão, G., and Medri, I.M. 2002. A new way of using inexpensive large-scale assembled GPS to monitor giant anteaters in short time intervals. Wildl. Soc. Bull. 30: 1029-1032. Available from: https://www.jstor.org/stable/3784268 [accessed 23 September 2018].

Newey, S., Davidson, P., Nazir, S., Fiarhurst, G., Verdicchio, F., Irvine, R.J., and van der Wal, R. 2015. Limitations of recreational camera traps for wildlife management and conservation research: a practitioner's persepctive. Ambio. **44**(Suppl. 4): 624-635. doi:10.1007/s13280-015-0713-1.

Nichols, J.D., Bailey, L.L., O'Connell, A.F., Jr., Talancy, N.W., Grant, E.H.C., Gilbert, A.T., et al. 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. J. Appl. Ecol. 45: 1321-1329. doi:10.1111/j.1365-2664.2008.01509.x.

Northrup, J.M., Anderson, C.R., and Wittemyer, G. 2014. Effects of helicopter capture and handling on movement behavior of mule deer. J. Wildl. Manage. **78**(4): 731–738. doi: 10.1002/jwmg.705.

Norton, M.R., Hannon, S.J., and Schmiegelow, K.A. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography. **23**(2): 209-223. doi:10.1111/j.1600-0587.2000.tb00277.x.

Draft

Nowak, S., Jędrejewski, W., Schmidt, K., Theuerkauf, J., Mysłajek, W., and Jędrzejewska, B. 2007. Howling activity of free-ranging wolves (*Canis lupus*) in the Białowieża Primeval Forest and the Western Beskidy Mountains (Poland). J. Ethol. **25**(3): 231-237. doi:1007/s10164-006-0015-y.

O'Connell, A.F., Jr., Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R., and Gilbert, A.T. 2006. Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. J. Wildl. Manage. **70**(6): 1625-1633. doi:10.2193/0022-541X(2006)70[1625:ESOADP]2.0.CO;2.

Palacios, B., López-Bao, J.V., Llaneza, L., Fernández, C., and Font, E. 2016. Decoding group vocalizations: the acoustic energy distribution of chorus howls is useful to determine wolf reproduction. PLoS One, 11: e0153858. doi:10.1371/journal.pone.0153858.

Papin, M., Pichenot, J., Guérold, F., and Germain, E. 2018. Acoustic localization at large scales: a promising method for grey wolf monitoring. Front. Zool. 15: 11. doi:10.1186/s12983-018-0260-2.

Passilongo, D., Buccianti, A., Dessi-Fulgheri, F., Gazzola, A., Zaccaroni, M., and Apollonio, M. 2010. The acoustic structure of wolf howls in some Eastern Tuscany (Central Italy) free ranging packs. Bioacoustics. **19**(3): 159-175. doi:10.1080/09524622.2010.9753622.

Passilongo, D., Mattioli, L., Bassi, E., Szabó, L., and Apollonio, M. 2015. Visualizing sound: counting wolves by using a spectral view of the chorus howling. Front. Zool. 12: 22. doi:10.1186/s12983-015-0114-0.

Plummer, M. 2003. JAGS: a program for analysis of bayesian graphical models using gibbs sampling. *In* Proceedings of the 3rd International Workshop in Distributed Statistical Computing, Vienna, Austria, March 20-22 2003. Technische University, Vienna, Austria.

Draft

pp. 1-10.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/ [accessed 3 September 2018].

Rayment, W., Webster, T., Brough, T., Jowett, T., and Dawson, S. 2017. Seen or heard? A comparison of visual and acoustic autonomous monitoring methods for investigating temporal variation in occurrence of Southern Right Whales. Mar. Biol. 165: 12.

Reconyx. 2017. Hyperfire high performance camera instruction manual. Available from http://images.reconyx.com/file/HyperFireManual.pdf [accessed 10 September 2018].

Rio-Maior, H., Beja, P., Nakamura, M., and Álvares, F. 2018. Use of space and homesite attendance by Iberian wolves during the breeding season. Mamm. Biol. 92: 1-10. doi:10.1016/j.mambio.2018.03.014.

Robinson, W.J., Forcey, G.M., and Hooton, L.A. 2015. Developing an automated risk management tool to minimize bird and bat mortality at wind facilities. Ambio. 44: 557-571.

Rovero, F., and Marshall, A. 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46: 1011-1017. doi: 10.1111/j.1365-2664.2009.01705.x.

Rowcliffe, J.M., Field, J., Turvey, S.T., and Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. 45: 1228-1236. doi:10.1111/j.1365-2664.2008.0.

Schlossberg, S., Chase, M.J., and Griffin, C.R. 2016. Testing the accuracy of aerial surveys for large mammals: an experiment with African Savanna Elephants (*Loxodonta africana*). PLoS One, **11(**10): e0164904. doi:10.1371/journal.pone.0164904.

Draft

Scurrah, F.E. 2012. Gray wolf (*Canis lupus*) movement patterns in Manitoba: implications for wolf management plans. M.Sc. thesis, School of Environment and Sustainability, University of Manitoba, Winnipeg, M.B.

Shonfield, J., and Bayne, E.M. 2017. Autonomous recording units in avian ecological research: current use and future applications. Avian Conserv. Ecol. **12**(1):14. doi:10.5751/ACE-00974-120114.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., and McKelvey, K. 2018. Sampling scales define occupancy and underlying occupancy-abundance relationships in animals. Ecology. **99**(1): 172-183.

Su, S.Y., and Yajima, M. 2015. R2jags: using R to Run 'JAGS'. R package version 0.5-7. Available from https://CRAN.R-project.org/package=R2jags [accessed 15 September 2018].

Sueur, J., Aubin, T., and Simonis, C. 2008. Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics. 18: 213-226.

Suter, S.M., Giordano, M., Nietlispach, S., Apollonio, M., and Passilongo, D. 2016. Non-invasive acoustic detection of wolves. Bioacoustics. **26**(3): 237-248. doi:10.1080/09524622.2016.1260052.

Tuyttens, F.A.M., MacDonald, D.W., and Roddam, A.W. 2002. Effects of radio-collars on European badgers (*Meles meles*). J. Zool. (Lond.) **257**(1): 37-42. doi:10.1017/S0952836902000638.

Uboni, A.D., Smith, D.W., Stahler, D.R., and Vucetich, J.A. 2017. Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. Ecosphere. **8**(4): e01705. doi:10.1002/ecs2.1705.

Wildlife Acoustics. 2011. Songscope software 4.0 users manual. Wildlife Acoustics, Maynard, Massachusetts, USA.

Wilson, T.L., and Schmidt, J.H. 2015. Scale dependence in occupancy models: implications for estimating bear den distribution and abundance. Ecosphere. 6: 1-13.

Wrege, P.H., Rowland, R.D., Keen, S., and Shiu, Y. 2017. Acoustic monitoring for conservation in tropical forests: examples from forest elephants. Methods Ecol. Evol. 8: 1292-1301.

Yip, D.A., Bayne, E.M., Sólymos, P., Campbell, J., and Proppe, D. 2017. Sound attenuation in forest and roadside environments: implications for avian point-count surveys. Condor **119**(1): 73-84. doi:10.1650/CONDOR-16-93.1.

Draft

Table 1. Total number of cameras deployed by the Alberta Biodiversity Monitoring Institute (ABMI) in northeastern Alberta, Canada during the summers of 2016 and 2017 with at least one gray wolf (*Canis lupus*) detection between March 1st – June 30th, as well as the paired autonomous recording unit (ARU) detections that were processed retrospectively (*n*=73).

2016	**Unique Stations**	**Unique Sites**	**Hits**
Camera	34	27	55
ARUs with wolf detections	19	15	39
Proportion (ARU/Camera)	0.558	0.571	0.709
2017	**Unique Stations**	**Unique Sites**	**Hits**
Camera	39	31	71
ARUs with wolf detections	27	24	97
Proportion (ARU/Camera)	0.692	0.774	1.366

Draft

Table 2. Comparison of stations deployed between March 1st – June 30th in 2016 and 2017 by the Alberta Biodiversity Monitoring Institute (ABMI) where autonomous recording units (ARU) detected wolves (*Canis lupus*) but cameras did not (n=73).

	Unique Stations	Unique Sites
Total	73	57
ARUs with wolf detections	38	29
Proportion	0.521	0.509

Draft

Table 3. Occupancy (*Ψ*) and detectability (*p*) estimates of gray wolves (*Canis lupus*) from cameras and ARUs deployed by the Alberta Biodiversity Monitoring Institute in northeastern Alberta between March 1st – June 30th in 2016 and 2017 using daily, weekly, and monthly detection intervals and 95% credible intervals.

Interval	Estimates	Camera	95% Cred Int	ARU	95% Cred Int
Daily	*p*	0.030	0.024, 0.050	0.033	0.022, 0.047
	Ψ	0.304	0.165, 0.561	0.623	0.441, 0.842
Weekly	*p*	0.083	0.059, 0.111	0.105	0.078, 0.133
	Ψ	0.643	0.481, 0.858	0.652	0.499, 0.813
Monthly	*p*	0.233	0.155, 0.326	0.296	0.213, 0.383
	Ψ	0.761	0.117, 0.978	0.752	0.569, 0.945

Draft

Figure 1. Terrestrial sites deployed by the ABMI in Alberta, Canada, between the summers of 2016 – 2017 mapped using ArcMap v10.4.1 (Environmental Systems Research Institute, Redlands, CA, USA). Each black triangle represents a site composed of four, paired camera-ARU stations deployed by the ABMI between March 1st – June 30th, 2016-2017. Gray circles indicate those sites that we randomly selected for occupancy analysis (N=69). These site locations are based on the publicly available latitude and longitudes produced by the ABMI, and do not represent actual locations.

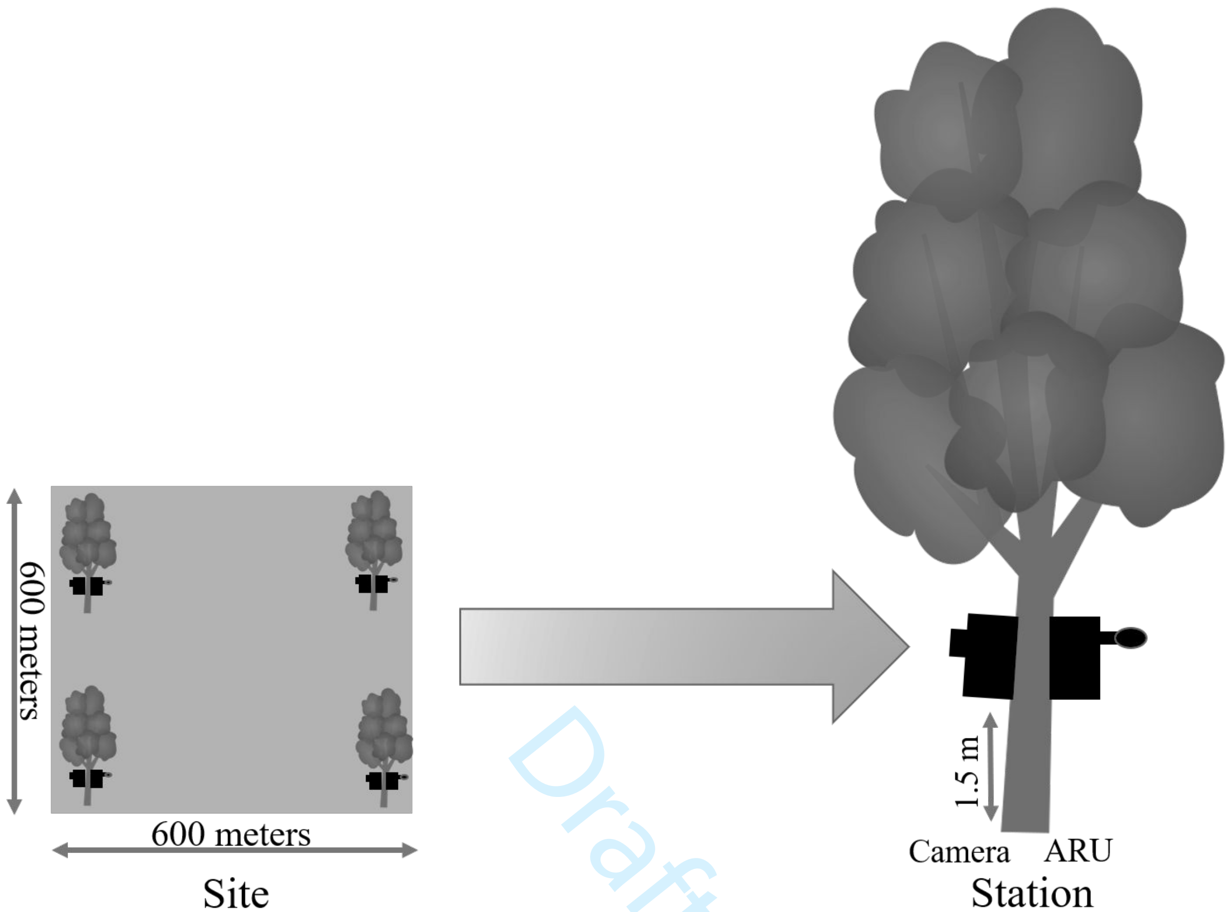
Figure 2. Sampling design of a site and station deployed in Alberta, Canada between March 1st – June 30th 2016 and 2017, determined by the Alberta Biodiversity Monitoring Institute (ABMI). Four, paired cameras and autonomous recording units (ARUs) are deployed at a site, each pair making up a station. Each station is 600 meters distant in the shape of a polygon to create a site. Each site is at least 20 kilometers away from the nearest neighboring site.

Draft

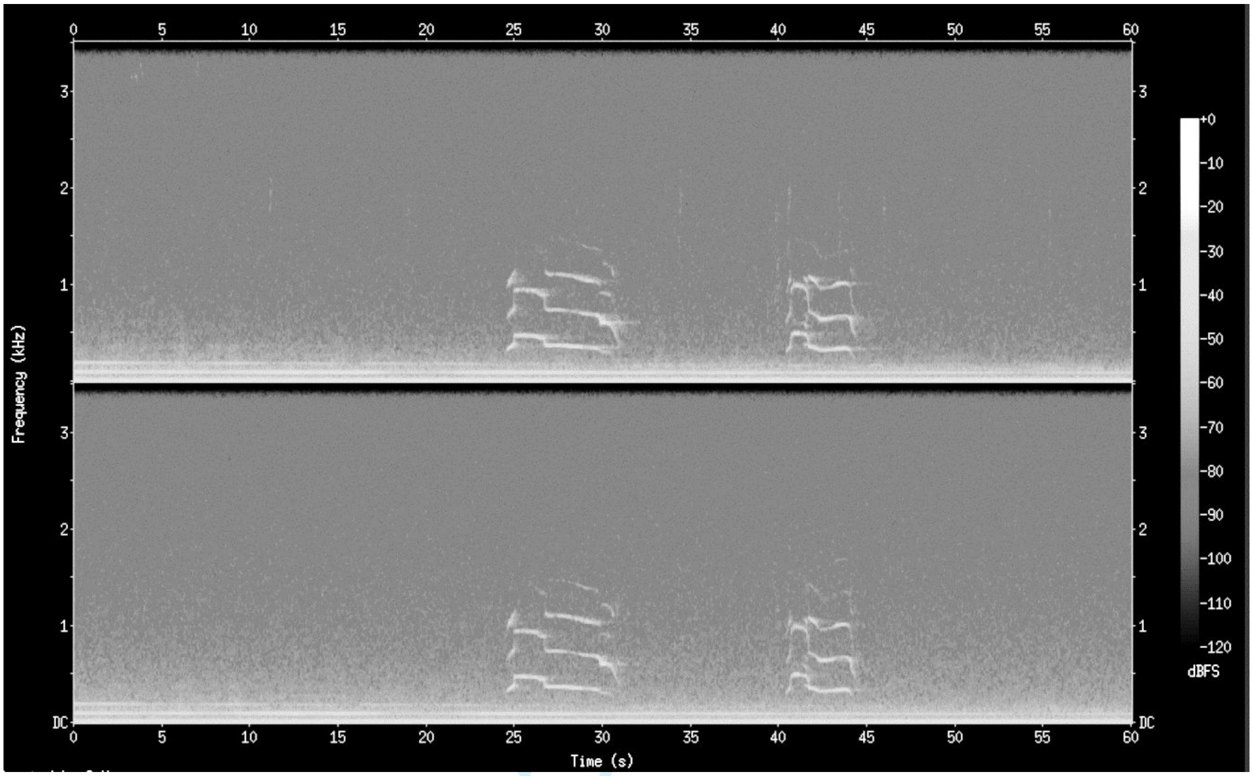
Figure 3. Example of a gray wolf (*Canis lupus*) vocalization image output by SoX version 14.4.2. The *y*-axis is the frequency range in kHz, the top half representing the first channel and the bottom half the second channel from the ARU. The *x*-axis is marked in seconds, and the dBFs scale indicates the amplitude of the recording. The spectrogram itself shows a lone wolf howling twice approximately 10 seconds apart.

Figure 4. The effect of week on the probability of gray wolf (*Canis lupus*) detections for cameras and autonomous recording units (ARUs) over 17 weeks of deployment in northeastern Alberta, Canada between March 1st – June 30th 2016 and 2017. Error bars represent 95% credible intervals.

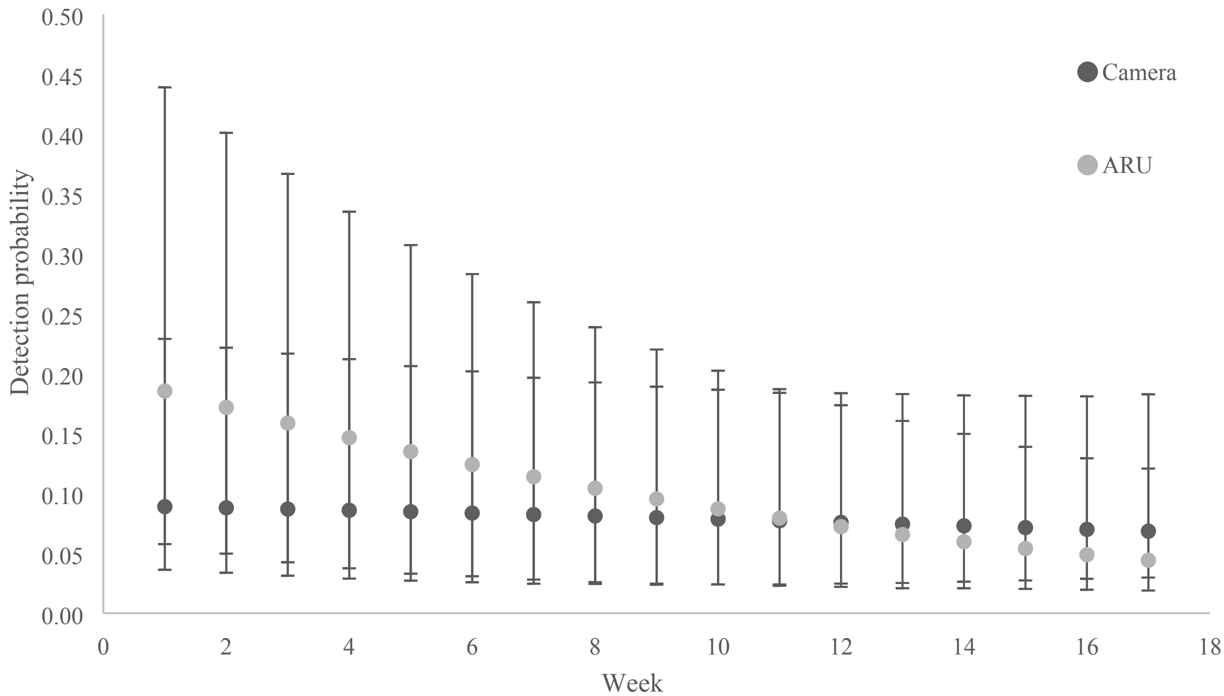

N
0 100 200 400 km
Legend
ABMI Sites
Occupancy Sites
0 30 60 120 km
Powered by Esri | App by Tesera |, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors



Draft



Draft


Camera
ARU
Detection probability
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
2
4
6
8
10
12
14
16
18
Week

Draft