A comparison of passive monitoring methods for gray wolves (*Canis lupus*) in Alberta, Canada

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

University of Alberta

Abstract

Remote camera traps are often applied to large mammal conservation and management programs because they are cost-effective, allow for repeat surveys, and can be deployed for long time periods. Additionally, statistical advancements in calculating population metrics, such as density, from camera trap data has increased the popularity of camera usage in mammal studies. However, drawbacks to camera traps include their limited spatial coverage and tendency for animals to notice the devices. In this study, we compared autonomous recording units (ARUs) to cameras in their detectability of gray wolves (*Canis lupus*) through a paired study design in northeastern Alberta. The use of ARUs to survey for large, low-density predators, like wolves, is just now emerging as a viable passive monitoring method, but to our knowledge, a comparison of ARU and camera detectability for wolves has never been done. We also tested the random encounter and staying time model (REST), a new means of estimating the density of an unmarked population, using human volunteers and simulated camera surveys. We found ARUs to be comparable in their detectability of wolves to cameras, despite only operating a fraction of the time that cameras were active. We also found the REST method to produce unbiased estimates of density, regardless of changes in human abundance, movement rates, home range sizes, or simulated camera effort. These advances in surveying technology and statistical methods provide innovative avenues of large mammal monitoring that have the potential to be applied to a broad spectrum of conservation and management studies, provided assumptions for these methods are rigorously tested and met.

Preface

This thesis is an original work by Laura Garland. The data were provided by the Alberta Biodiversity Monitoring Institute. The research questions were conceptualized by Erin Bayne, Stan Boutin, and Laura Garland. Erin Bayne and Stan Boutin provided input and feedback on analysis and writing. Richard Hedley and Andrew Crosby assisted with coding for analysis in Chapter 2. Eric Neilson assisted with coding for analysis in Chapter 3. The Research Ethics Office at the University of Alberta granted approval for using human volunteers for the data collection conducted in Chapter 3, application No. Pro00075181.

Acknowledgements

Funding for this research was provided by the University of Alberta Thesis-Based Master's Scholarship and CREATE-Environmental Innovation graduate scholarship. Extensive in-kind field and technician support was provided through the Bioacoustic Unit and the Alberta Biodiversity Monitoring Institute. Thank you to the army of technicians that worked to deploy the cameras and ARUs during the summers of 2016 and 2017 all over Alberta, your efforts are greatly appreciated. I would like to personally thank my committee members and supervisors Erin Bayne, Stan Boutin, and thank you Mark Boyce for being my external on short notice. Thank you Erin and Stan for accepting me as a master's student and for providing endless feedback, meetings, and pushing me to think critically as I tackled my thesis questions. I hope I have become a better researcher and thinker under both of your guidance. Thank you, Ainsley Sykes and Hedwig Lankau who helped me navigate life as a graduate student when I first joined the U of A. Thank you also to Alex MacPhail for his patience with this Californian as he showed me how not to die in the Canadian boreal forest.

Thank you also to all members of the Bayne and Boutin labs, without whom I would have been lost as a graduate student. Thank you in particular to Richard Hedley, Andrew Crosby, Eric Neilson, and Elly Knight for all of your help with R code, introducing me to Bayesian statistics, and for reading and commenting on very rough, rough drafts of my writing. Thank you also to my basement-dwelling officemates: Connor, Nick, Jocelyn, Emily, Jill, and Carrie-Ann for the shenanigans and science talks we had. Thank you especially to Jill, with whom I spent many hours discussing wolves, ARUs, cameras, and frogs, and who helped keep me sane during this entire process.

Christine, Derek, and Kenny, even though we are thousands of miles apart, I could not have asked for better friends and moral supporters through these last two and half years. Thank you, Christine, for patiently listening to all my complaints and every detail of my thesis, no matter how small. Thank you especially to Derek and Kenny for those long video chats explaining code and math concepts; you blew me away with your helpfulness. Lastly, thank you Mom, Dad, and Sarah for putting up with and supporting me for all these years.

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Chapter 1: General Introduction

Predator roles in the Canadian boreal forest

Canadian apex carnivores have been points of both management and conservation concern for decades. Balancing conservation efforts of keystone species while managing human expansion on a finite landscape and reducing human-wildlife conflict are just a few of the priorities of ecologists and researchers in the 21st century (Boertje et al. 2010, Latham et al. 2011, Venier et al. 2014). These interests have resulted in a suite of technological and statistical advancements aimed at answering ecological questions related to predator distributions across geographic areas, predator-prey cycling, top-down cascades, the landscape of fear, and several other research topics (Mourão and Medri 2002, Borchers and Efford 2008, Rowcliffe et al. 2008). In Alberta, Canada, the gray wolf (*Canis lupus*) is of primary interest due to their high abundances within the province and their impacts on threatened woodland caribou (*Rangifer tarandus caribou*) (Hervieux et al. 2014, Leblond et al. 2016). As such, the need to have cost-efficient monitoring tools to manage wolf populations has been an area of methodological interest in recent years.

Technological monitoring advancements

Advancements in monitoring techniques have allowed researchers and managers to improve their data collection and assessments of predator statuses over the past decade. Popular methods include mark-recapture, radio telemetry, and aerial surveys to answer questions related to demographics, behavior, and distribution patterns (Kunkel and Mech 1994, Czetwertynski et al. 2007, Droghini and Boutin 2017). These methods are often accompanied by statistical programs that calculate desired variables such as abundance indices (Efford and Fewster 2013). However, major drawbacks of these methods include the intensive logistics, manpower, and time it takes to collect sufficient data. To alleviate some of the financial and logistic pressures of labor-intensive techniques while maintaining rigorous data collection, passive monitoring methods, the use of remote camera traps in particular, have increased markedly in recent years (Erb et al. 2012, Meek et al. 2016, Gray 2018). The ability to deploy camera traps for long time periods across large study areas in a relatively cost-efficient manner has made them many researchers' tool of choice, particularly for studying large, low-density predators (Burton et al. 2015). Additionally, recent statistical advances in calculating population metrics, such as species' density, from camera trap data has greatly increased interest in the use of cameras for population-level studies over other passive monitoring methods (Rowcliffe et al. 2008, Nakashima et al. 2017).

A new tool similar to cameras, aimed at passively capturing bioacoustic data has been gaining popularity. The use of autonomous recording units (ARUs) have received considerable traction due to the ability of ARUs to record their surrounding environments on pre-established schedules for long time periods, cover large detection areas, and quickly process large amounts of data. These attributes make ARUs comparable in their data collection benefits to cameras, and although thus far have primarily been used in marine mammal studies, are rapidly expanding into areas of amphibian, avian, and bat research (Shonfield and Bayne 2017, Van Wilgenburg et al. 2017, Sugai et al. 2018).

While advancements in the manipulation of camera data to obtain density estimates of unmarked populations has put cameras in the forefront of passive monitoring techniques, the ability of ARUs to collect similar data may render cameras less effective in terms of occupancy analysis. The recording capacities of ARUs makes them an ideal tool for studying vocal, terrestrial mammals. However, to date, few studies have examined the efficacy of this method, much-less attempted to compare ARU detectability to those of currently popular camera trap methods when they are applied to large, low-density carnivores, such as the gray wolf.

Thesis objectives

In this thesis we sought to compare ARUs to cameras as a viable means of passive monitoring for large vocal predators in Alberta using wolves as a test species. We compared camera and ARU detectability using a paired study design and Bayesian occupancy models. We compared discrepancies in detection probabilities as a function of the definition of a sampling interval as well as differences in the detection areas of both methods. We also compared camera and ARU hit rates from a technical standpoint of minutes of data collected versus the length of time the units were running, as well as technical adjustments that can be made to ARUs to target wolf vocal activity in future monitoring studies. Finally, we tested a recently developed method of mammal density estimation based on camera trap data developed by Nakashima et al. (2017), called the random encounter and staying time (REST) method. We used humans in a semi-realistic, controlled test to examine the effects of variation in human abundances, movement rates, home ranges sizes, and simulated camera trap effort on the precision and accuracy of the REST method. We discussed the limitations as well as applications of this method to future large mammal studies. General conclusions and implications for these methodological advancements are discussed in the conclusion chapter of this thesis (Chapter 4).

Chapter 2: Acoustic vs photographic monitoring of wolves: a methodological comparison of two passive monitoring techniques

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, often 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*), is a classic example (Marquard-Petersen 2012, Mech & Boitani, 2003).

Recent technological advances have improved our understanding of wolf ecology and distribution. However, these techniques are often costly in terms of finances, logistics, the time it takes to acquire data, and in some cases have negative effects on the health 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). Howl surveys, meanwhile, are labor-intensive and require the introduction of foreign howls by people or playbacks, which could disrupt the behavior and social interactions of canids and their neighbors (Suter et al. 2016).

Passive monitoring methods using a variety of visual and acoustic sensors may provide cost-effective, non-invasive alternatives for monitoring predators (Nichols et al. 2008). Currently, one of the most popular methods of passively monitoring large mammals is via remote camera traps. Camera traps are used primarily because of their ability to inexpensively survey a site continuously over a long time period with limited effects on the animals being studied (Burton et al. 2015, Newey et al. 2015). Camera data has been used to produce occupancy, abundance, and population density estimates for several species, including wolves (Rowcliffe et al. 2008, Ausband et al. 2014, Gray 2018, Mattioli et al. 2018). One shortcoming of camera traps however 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. Animals also may respond to the light or sound produced by cameras, which also can bias detection probabilities (Meek et al. 2016). Acoustic monitoring via autonomous recording units (hereafter ARUs) is rapidly emerging as a useful tool for monitoring vocalizing species that could complement or possibly replace camera surveys (Suter et al. 2016, Papin et al. 2018). This is especially applicable to wolf howls, which can transmit over 10 kilometers and be heard by neighboring wolves as well as humans, and be detected up to 4.6 kilometers away by ARUs (Passilongo et al. 2015, Suter et al. 2016).

A potential advantage conferred by ARUs over cameras is that their detection areas are much larger, which may reduce the likelihood that the detected species will sense the recording unit and thereby avoid it. In contrast to cameras, however, ARUs have seldom been used to monitor carnivores because of an assumed low howling rate and data processing time. Thus, it is not known how inferences regarding occupancy drawn from ARU data compare to those derived from cameras.

Additionally, detectability estimates, and therefore occupancy probabilities, may change depending on the definition of a survey period, regardless of what method is used. Detecting the target species once out of hundreds of days sampling, versus once out of a dozen weeks of sampling affects the calculation of site occupancy probability. For example, if a species is detected once in 105 days, it would result in a naïve occupancy estimate of 0.010. However, if the survey period is defined in weeks, (ie: 15 weeks in this example), this results in a naïve occupancy estimate of 0.067. Whether a 0.057 difference in naïve occupancy estimation is biologically significant will depend on the monitoring goal. Researchers or managers may form monitoring conclusions without accounting for this bias produced by different survey periods. To our knowledge, comparing detection and occupancy estimates at varying sample intervals has never been examined, despite the importance of defining what constitutes "occupancy" of a site, both at a spatial and temporal scale, for species monitoring and management (Efford and Dawson 2012).

We use a paired ARU-camera design to directly compare inferences regarding the occupancy and detectability of gray wolves in Alberta, Canada. Our objectives were: 1) 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 2) compare camera and ARU sampling effort and data processing time 3) address how heterogeneity in detection areas influence estimates of detectability, and 4) outline suggestions for a sampling framework that incorporates ARUs in long-term wolf monitoring.

Methods

Study area

The northeastern region of Alberta, Canada where we concentrated our data collection, is approximately 163,350 km^2. Sites were located north of Edmonton and east of High Level (Figure 1.1). Vegetation patterns are relatively consistent throughout the landscape. Conifer, broadleaf, and mixed forests create a mosaic habitat interspersed with shrubland, water bodies, and grasslands (Norton et al. 2000). Considered habitat generalists, wolves have a propensity to use both closed and open habitats, including coniferous, deciduous, and mixed forests in addition to shrublands and wetlands (Uboni et al. 2017, Benson et al. 2015).

Study design

Data were gathered by the Alberta Biodiversity Monitoring Institute (hereafter ABMI) during the summers of 2016 and 2017 (Figure 1.1). Cameras and ARUs were paired at a station. Four stations spaced 600 m apart in a square (Figure 1.2). These sites were deployed in a systematic grid across Alberta in both terrestrial and wetland locations. Distances between sites was at least 20 km.

Cameras were programmed to run 24 hours a day and were motion-triggered to take photos as long as the subject remained in the viewfinder. ARUs were on a recording schedule of 38 minutes per 24 hours, with recordings occurring at dawn, midday, dusk, and midnight. Depending on the model of ARU deployed, recordings were done in either .wav or .wac, the latter being a type of lossless compression format (Wildlife Acoustics 2018). Recording length was ten minutes during the midnight hour and 7:00 or 8:00 AM, all other recordings were three minutes.

Data selection

We created three datasets to compare ARU detectability given camera detections, as well as ARU detectability given camera non-detections. For the first dataset, we selected all cameras that were deployed by the ABMI in 2016 and 2017 that included at least 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 hits during the time the ARUs were active, approximately March 1st – June 30th, across both years. If either the camera or paired ARU failed during the sampling period (ie: stopped recording), we excluded all detections from the paired unit during the time of inactivity. We defined a "hit" as the first photo or vocalization detected by either unit at least 12 hours since their last respective detection. This resulted in a total of 34 unique camera stations with a wolf hit in 2016 and 39 camera stations from 2017, for a total of 73 unique stations (Table 1.1).

The second dataset accounted for those stations where ARUs detected a wolf but cameras did not. We selected the same number of paired stations in northeastern Alberta between both years (2016, n=34; 2017, n=39) where camera detections were zero, and processed the corresponding ARUs for wolf vocalizations (Table 1.2). Defining 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 a single paired camera-ARU station per site deployed in northeastern Alberta based on the 146 stations used in the first two datasets (Figure 1.1). We chose a single station among the four deployed per site to avoid psuedoreplication within sites, for a total sample of 69 paired units.

Data processing

Camera trap species identification was done by technicians experienced in mammal identification and trained via a step-wise process according to the ABMI tagging protocols (ABMI User Guide).

We used the program Sound eXchange (SoX) version 14.4.2 to process ARU data. This program manipulates audio data and creates spectrograms based on the parameters specified by the user (SoX user manual 2013). To view wolf vocalizations, we used the *sox* function in the R package seewave (Sueur and Simonis 2008), version 3.3.1 (R Core Team 2018) to convert raw audio files into 1-minute spectrograms. Spectrograms were truncated from the original 44 kHz sampling rate to a 7 kHz sampling rate, and we used the standard colors provided by SoX to visualize individual howls, responses, and choruses in each recording (Figure 1.3). All ARU data processing was completed by the same researcher. Example vocalization patterns were studied, and the researcher was given a sample dataset 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.

Occupancy analysis

To compare detection probabilities between ARUs and cameras, we ran occupancy models using detection histories with varying sampling intervals. 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, weekly, and monthly detection histories.

Additionally, we compared detection and occupancy estimates when the methods were pooled using Bayesian methods, as well as through a multi-method approach. For the pooled analysis, we combined camera and ARU detections so that given both units were functioning normally within the same survey period, if one unit detected a wolf and the other did not, it was entered as "1" for that sampling occasion. 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}. This collapsing of both units' detection histories produces variables for detectability (p_i) and occupancy (ψ), with the exception that the probability of detection (p_i) is now dependent on the probability the target species is present within a camera-ARU detection zone *and* detection is conditional on the animal's presence (Nichols et al. 2008). Occupancy analysis with a single method is only dependent on the probability of the species being present within the detection zone of the device used (MacKenzie et al. 2002). 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. The multi-method approach also calculates ψ, as well as p^x_i, or the probability of detecting an individual using method x in survey i. (Nichols et al. 2008).

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 detectability is equal across sites, (MacKenzie et al. 2002). We assumed that wolf occupancy of sites remained closed during the sampling period because wolves tend to occupy the same territories for long time periods (Jedrzejewski et al. 2001, Rio-Maior et al. 2018). In this case, we assumed site closure at the scale of wolf territories instead of the detection areas of the cameras and ARUs, because it is unreasonable to assume that a wolf will remain in these detection areas for months at a time. 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 expect wolf movement to be random relative to the camera-ARU site, therefore we do not expect strong biases in occupancy or detection estimates between sites (Kalan et al. 2015). The purpose of this paper is to examine the detectability of ARUs relative to cameras. Therefore, we are not overly concerned with the precision of the occupancy and detection probabilities as they apply to estimating wolf abundance or distribution, instead we focus on examining the similarity or differences in detection estimates based on the method employed.

Bayesian framework

A maximum likelihood model, like the one available using the R package Unmarked, was unable to estimate occupancy and detection probability at the daily interval for our data, due to the low proportion of wolf detections by both cameras and ARUs. Therefore, we chose to estimate occupancy and detectability using a more flexible Bayesian framework in JAGS version 4.3.0 (Plummer 2003) via the R package R2jags (Yu-Sung & Yajima 2015), allowing us to estimate probability density distributions of our priors instead of single point estimates used in a frequentist approach (Nichols et al. 2008). The code used for these models is included in Appendix I. In occupancy estimates, where the outcome is a Bernoulli distribution of ones or zeroes, we selected priors that reflected a uniform distribution between 0 and 1 for both occupancy and detectability. Because all our models converged quickly (≤ 3,000 chains), we used uninformative, uniform priors to allow the data to determine the distribution of our posterior estimates. The potential of uninformative priors drifting to local minima was a non-issue in our approach because we used MCMC sampling to avoid this.

All occupancy models for individual and pooled units were run using 3 chains, 3,000 chain iterations, a burn-in of 500 chains, and thinning of every 5th chain. Convergence of each model was checked based on the R-hat values to ensure they fell between 1.000 and 1.100. All R-hat values were between 1.000 and 1.008. We also ran occupancy models for cameras, and ARUs for the weekly sampling interval, using the quadratic of week as a covariate on the detection probability, to test detectability as a function of time. We again used 3 chains, 3,000 iterations, a burn-in of 500 chains, and a thinning of every 5th chain. All R-hat values fell between 1.000 and 1.006 when week was used as a covariate of detectability.

Multi-method occupancy analysis

To examine multi-method occupancy and detectability, we used the program Presence v. 12.23, and 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, $p^{x}{}_{i}$, and θ^{x}.

Results

Occupancy analysis and detectability for individual units

Detection probabilities derived from ARUs were equivalent to or higher than detection probabilities from cameras, regardless of the resolution of sampling (Table 1.3). At the daily interval, camera and ARU detectability was equal ($p_{ARU} = 0.033$, $p_{Camera} = 0.030$), but occupancy estimates from ARUs were double those of the cameras ($\Psi_{ARU} = 0.623$, $\Psi_{Camera} = 0.304$). At a weekly sampling interval, ARU detectability was higher than cameras ($p_{ARU} = 0.105$, $p_{Camera} = 0.083$), but both units’ individual occupancy estimates were approximately equal ($\Psi_{ARU} = 0.652$, $\Psi_{Camera} = 0.643$). Lastly, at the monthly interval, ARU detectability was again higher than cameras ($p_{ARU} = 0.296$, $p_{Camera} = 0.233$), but their occupancy estimates were roughly equal ($\Psi_{ARU} = 0.752$, $\Psi_{Camera} = 0.761$).

Occupancy analysis and detectability for pooled and multi-method units

Pooled estimates were higher than either individual unit’s~~’~~ probabilities, but were lower compared to the multi-method estimates that accounted for individual unit detectability given animal presence and availability for detection (Table 1.4). The pooled estimates were as follows: daily ($p_{Pooled} = 0.047$, $\Psi_{Pooled} = 0.548$), weekly ($p_{Pooled} = 0.153$, $\Psi_{Pooled} = 0.766$), and monthly ($p_{Pooled} = 0.443$, $\Psi_{Pooled} = 0.782$). Multi-method estimates, particularly detection probabilities, were higher than the pooled estimates, but occupancy probabilities were similar at both the weekly and monthly intervals. At the daily interval, the units' multi-method detectability increased ($\theta_{Multi} = 0.267$), as did their occupancy estimates ($\Psi_{Multi} = 0.742$), relative to pooled methods. The multi-method detectability at the weekly interval was higher than the pooled units ($\theta_{Multi} = 0.698$), but both occupancy estimates were similar ($\Psi_{Multi} = 0.757$). The multi-method monthly detectability was again higher than the pooled estimates, but their occupancy estimates were again, similar, ($\theta_{Multi} = 0.829$, $\Psi_{Multi} = 0.800$).

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 and used in the multi-method analysis. The greatest discrepancy occurred between weekly and monthly sampling intervals when detectability 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 1.4) over time. For every additional week cameras were deployed, their detectability decreased linearly by 0.0013% (R^2 = 0.996), while ARU detectability decreased exponentially (R^2 = 0.998).

Sampling effort

The comparability of the estimates given by the ARUs compared to cameras is surprising given that the cameras were operating 24 hours a day, whereas the ARUs were on a recording schedule of only 38 minutes per day. To examine how sampling effort between ARUs and cameras influenced our results, we used the stations from dataset one that had known wolf detections on the cameras (n=73). We constrained all hits between March 1st – June 30th of 2016 and 2017. These are the approximate dates during which the ARUs and cameras overlapped in their activity. We did not match the exact dates of paired ARU and camera activity, instead viewing sampling effort on an individual unit basis.

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 hit. 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.

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 12,824,640 minutes of sampling. The actual minutes sampled (due to late start times or units failing early) was closer to 11,612,160 minutes across both years. In contrast, if all 73 ARUs had been functioning perfectly during the sampling period, this would have resulted in 338,428 recording minutes (ie: 38 minutes/24 hour sampling). Again, due to units failing early or being deployed late, the total minutes recorded between 2016-2017 were 319,054 minutes.

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 1.5). We note that because our selection of these stations was initially dependent on camera detections, not every paired ARU recorded a wolf vocalization. 46/73 (63.01%) of the selected stations had at least one wolf vocalization recorded. Cameras had a hit rate of 0.00002 hits/minute, and ARUs had 0.001 hits/minute. While both methods return low hit rates, the ARU hit rate was fifty times higher than cameras. This translates to approximately 0.029 hits/day or 0.202 photos/week for cameras, and 1.440 hits/day or 10.080 recordings/week for ARUs. Long-term studies of wolf behavior typically report howling activity at the monthly scale (Nowak et al. 2007, McIntyre et al. 2017), but the ability to passively capture howls at daily or weekly intervals provides details about wolf acoustic patterns that have previously been unavailable.

Finally, among those 73 stations we sampled where cameras did not detect a wolf in dataset two, we found that approximately 50% of the ARUs deployed at both the station and site level (38/73 stations; 29/57 sites), did detect a wolf (Table 1.2).

Processing time

The average processing time for an ARU that recorded 38 minutes per day over 4 months (approximately 4,500 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. Creating 4,500 1-minute spectrograms from .wav files took approximately two hours on a Windows 7 computer with a 64-bit operating system and 16 GB of RAM.

Processing the spectrogram output was comparable to, if not faster than, scanning and tagging camera photos for similar data. Distinguishing wolf vocalizations from other species is an initial step to working with audio data. However, once the researcher is comfortable identifying different vocalization types, 4,500 spectrograms can be scanned, tagged, and even occasionally listened to in order to confirm species' identification in under one hour ($\bar{x}$ = 52 minutes; SD 16 minutes).

The ABMI estimates that scanning and tagging camera photos using their protocol allows the researcher to tag a maximum of 2,000 photos per hour (the ABMI, personal comm.). However, additional species were identified using this approach. While the visual evaluation of spectrograms could be done for multiple species, there are far too many species making sounds to make visual scanning a viable method for recording all vocalizing species at the same time.

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 and other vocal mammals. The discrepancy in occupancy estimates may be explained in part due to the differences in the detection radii of the methods, with cameras having a much smaller detection area than ARUs. Reconyx advertise their cameras as having a 30 m detection radius and 42° interior angle (Reconyx 2017), for an approximate detection area of 0.00033 km^2. Work completed by Suter et al. (2016) found that harmonics of captive wolf howls were easily detected from a recording distance of 3.60 km, and trace howls were still detectable from a recording distance of 4.62 km on ARUs. A conservative detection radius of 3.00 km results in a detection area of approximately 28.00 km^2 for ARUs. Given this discrepancy, the probability of a wolf being detected by a camera, given that it is moving, and thereby "occupying" the camera site, is much lower than that of a howl being detected by an ARU, given that the wolf is vocalizing.

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 hindering the transmission of sound waves (Yip et al. 2017). Additionally, ARUs are more vulnerable than cameras to weather variables, especially wind in open areas, decreasing the acoustic detection areas, and therefore potentially including a negative bias in occupancy analysis if not accounted for. Because of this, the detection areas of ARUs may be highly variable depending on the habitat they are placed in. However, 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 also be approximated from an ARU based on noise level. 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, can have drastic impacts on estimates of occupancy. Therefore, because both methods are influenced 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).

Both ARUs and cameras decreased in their individual probabilities of detection for each additional week the units were operating. This decline in detectability may be explained in part due to the decrease in movement and vocal activity by wolves post-breeding after the winter, when pups are at dens during the late spring and early summer (Finďo and Chovancová 2004, McIntyre et al. 2017). Green-up of vegetation as the summer progresses also might influence camera and ARU detectability both visually and acoustically, although vegetation may affect ARU detectability more so than cameras, causing the exponential decline in detectability we found for ARUs in this study.

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 seem to be an improved reflection of 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 more accurate for long-term wolf monitoring to maximize detectability. This aligns with the current popularity of multi-method approaches to monitor rare species or trends in biodiversity patterns across regions (O'Connell et al. 2006, Nichols et al. 2008).

We observed a decrease in both detectability and occupancy of wolves as our sampling intervals increased (i.e., more samples per unit time). 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 will draw different conclusions of detection rates if the surveys are defined as daily or collapsed into weekly intervals. 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 should be considered.

Technical ARU adjustments

By adjusting ARU sampling rate, bit rate, and compression formats, there is potential for ARUs to record at a daily rate similar to cameras. SM4 units produced by Wildlife Acoustics can record compressed audio recordings that double, triple, or quadruple recording time per level. These three formats respectively are: W4V-8, W4V-6, and W4V-4 (Wildlife Acoustics SM4 user manual).

The noise floor of the recordings is increased using these compressed formats, but according to the Wildlife Acoustics' user manual, the change is typically not detectable between an uncompressed WAV, W4V-8, and W4V-6 file. We briefly tested this using two recordings of a wolf chorus and lone howl made in the uncompressed WAV format from SM4 units. We compressed both recordings at each level available (WAV, W4V-8, W4V-6, and W4V-4) in Kaleidoscope Viewer. We listened to the uncompressed recordings and then each of the compressed versions. We did not detect a difference in our ability to hear and classify the vocal types from these sample recordings, but additional vocalizations should be tested to ensure the distance over which an animal can be detected is comparable.

In addition to compressing the file formats, there is also the option to change the bit rate and sampling rate in ARUs. Bit rate is defined as the amount of data, or bits, that are transferred per unit time, typically measured in seconds. Larger 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, as frequencies are 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). As such, the lowest sampling rate of 8 kHz would suffice for recording wolf howls, which could further reduce data storage needs.

The Wildlife Acoustics' user manual and SM4 Configurator software 2.1.1B estimates the number of hours different size SD cards can record with different sampling rates. Using a sampling rate of 8 kHz to hypothetically record wolf howls, at the highest compression level (W4V-4), using two, 16 GB cards, one could record for 93, 12-hour days, or 46, 24-hour days. To record every minute for a full year would require two, 128 GB cards, but external batteries would be required in this scenario (Wildlife Acoustics user manual 2018). Alternatively, it is possible to record 5 minutes every hour from dusk to dawn for one year without using external batteries.

The higher cost of larger storage cards (i.e. 128 GB) used in ARUs is offset given the fact that cameras are spatially limited in their ability to capture wolves. ARUs have the benefit of covering a larger spatial area than cameras, making them more cost-effective from a spatial coverage perspective.

Wolf monitoring framework incorporating ARUs

Monitoring programs frequently rely on multi-method approaches to achieve their management or conservation goals (O'Connell et al. 2006, Ausband et al. 2014, Buxton et al. 2018). 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 even breeding status (Palacios et al. 2016). Our suggestions for a framework of monitoring that incorporates ARUs includes the following:

If we adjust ARUs to record for 12 hours a day, using a 16-bit rate, 8 kHz sampling rate, and the highest compression level, W4V-4, it is possible to obtain daily estimates of wolf vocal activity. Depending on the number and size of SD cards used, these settings would provide a researcher with anywhere from 3 months to over a year of data. With a focus on night recording sessions, as night, dawn, and dusk are indicated as the times during which most wolf activity occurs (Theuerkauf et al. 2003, Nowak et al. 2007, McIntyre et al. 2017), patterns of vocal behavior could be easily obtained. Research in recent years has established that the number of howling members in wolf packs can be counted based on their vocalizations (Passilongo et al. 2015, Palacios et al. 2016). With this information, combined with year-round recording capabilities, establishing trends in wolf behavior, habitat use, and breeding status are entirely possible, without the need for invasive techniques.

Understanding predator distribution patterns is a fundamental element of predator-prey ecology and management. While advances in invasive techniques have filled several knowledge gaps, passive methods, particularly cameras, have also heavily contributed to estimates of predator occupancy, distribution, and abundance. Due to drawbacks in camera usage, particularly the potential bias of animals detecting the units due to light or sound emissions, in addition to their limited spatial coverage (Meek et al. 2016), we sought to compare the detectability of ARUs to cameras in a paired study. ARUs have the benefit of a larger detection area, given that the target species vocalizes, therefore decreasing the probability that animals may detect the unit. We found that ARUs had equal or higher detection probabilities to cameras when compared in a

Bayesian occupancy framework, despite only being active a fraction of the time that cameras were operating. This suggests that ARUs can monitor wolves similarly to cameras, but also allows for the opportunity to collect behavioral and count data previously unavailable from camera data. The potential for future studies using ARU technology to estimate precise howling rates, breeding statuses, and even population densities is a fundamental step towards improving methods of wolf management and conservation.

Figures

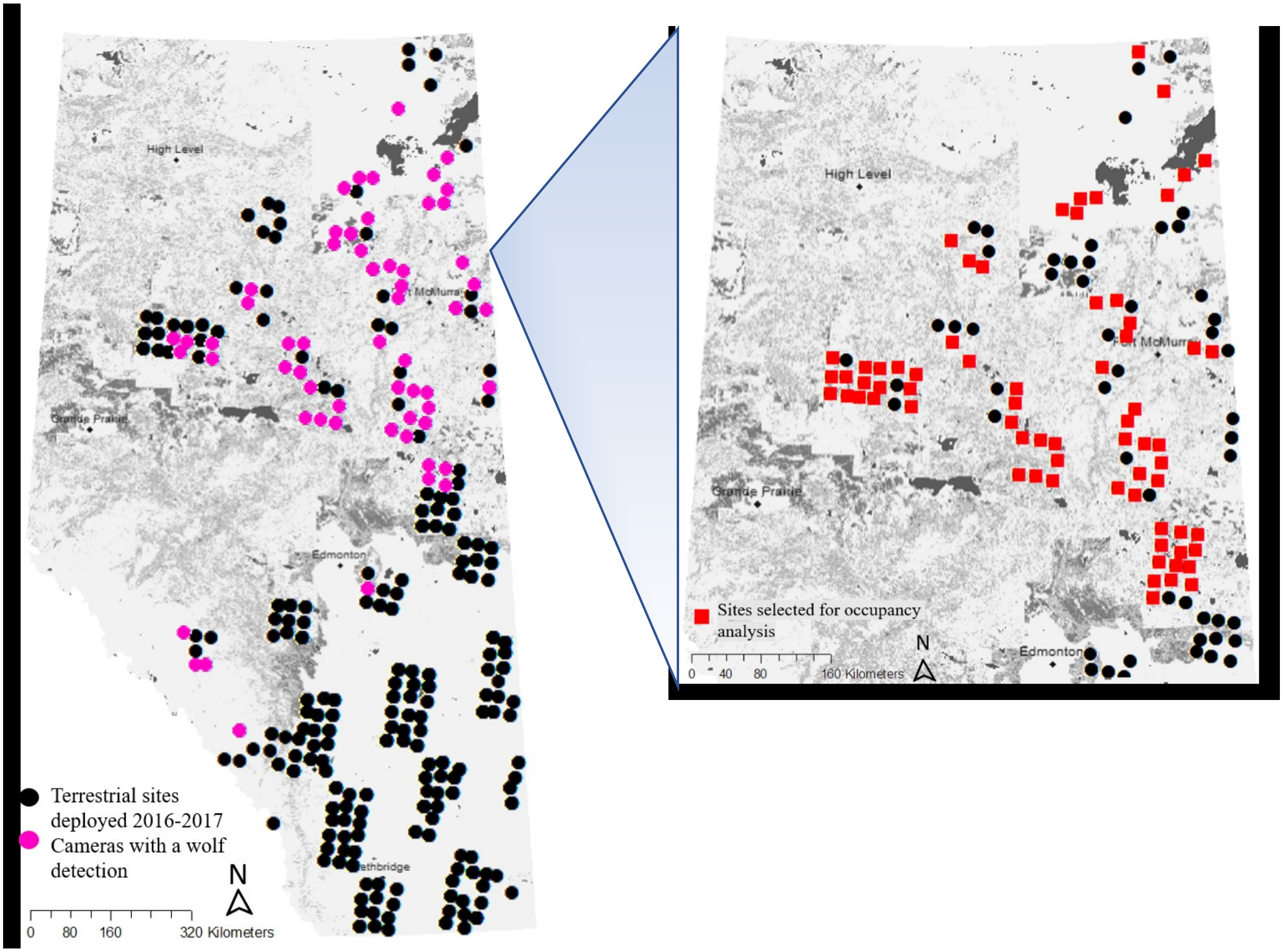

Figure 1.1. Terrestrial sites deployed by the ABMI between the summers of 2016 – 2017. Each black circle represents a site, with pink indicating a camera wolf detection at that site between March 1st – June 30th, 2016-2017. The inset depicts the northeastern sites that were randomly selected for occupancy analysis. These site locations are based on the publicly available latitude and longitudes produced by the ABMI, and do not represent actual locations.

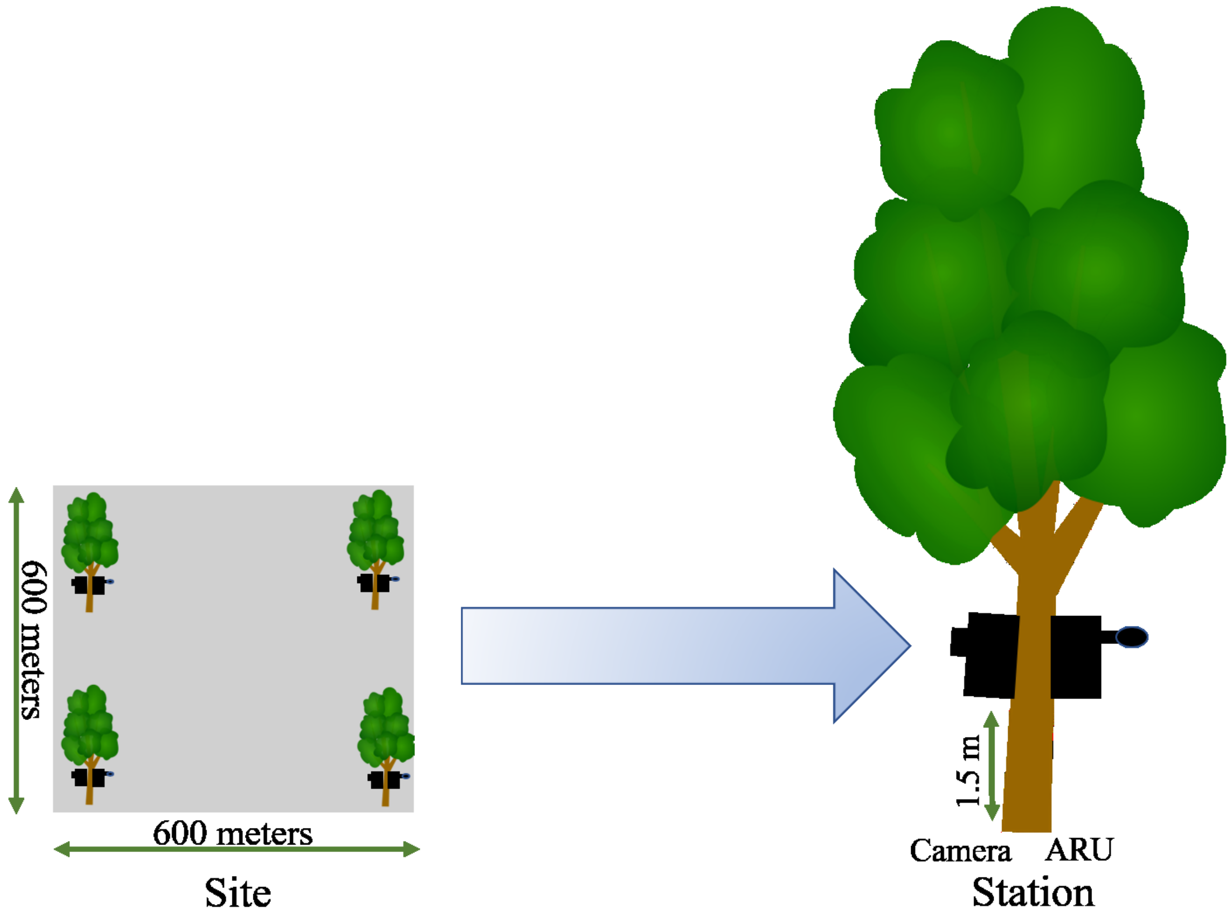

Figure 1.2. Sampling design of a site and station determined by the ABMI. Four, paired cameras and ARUs are deployed at a site, each pair making up a station. Each station is 600 meters distant in the shape of a polygon. Each site is at least 20 kilometers away from the nearest neighboring site.

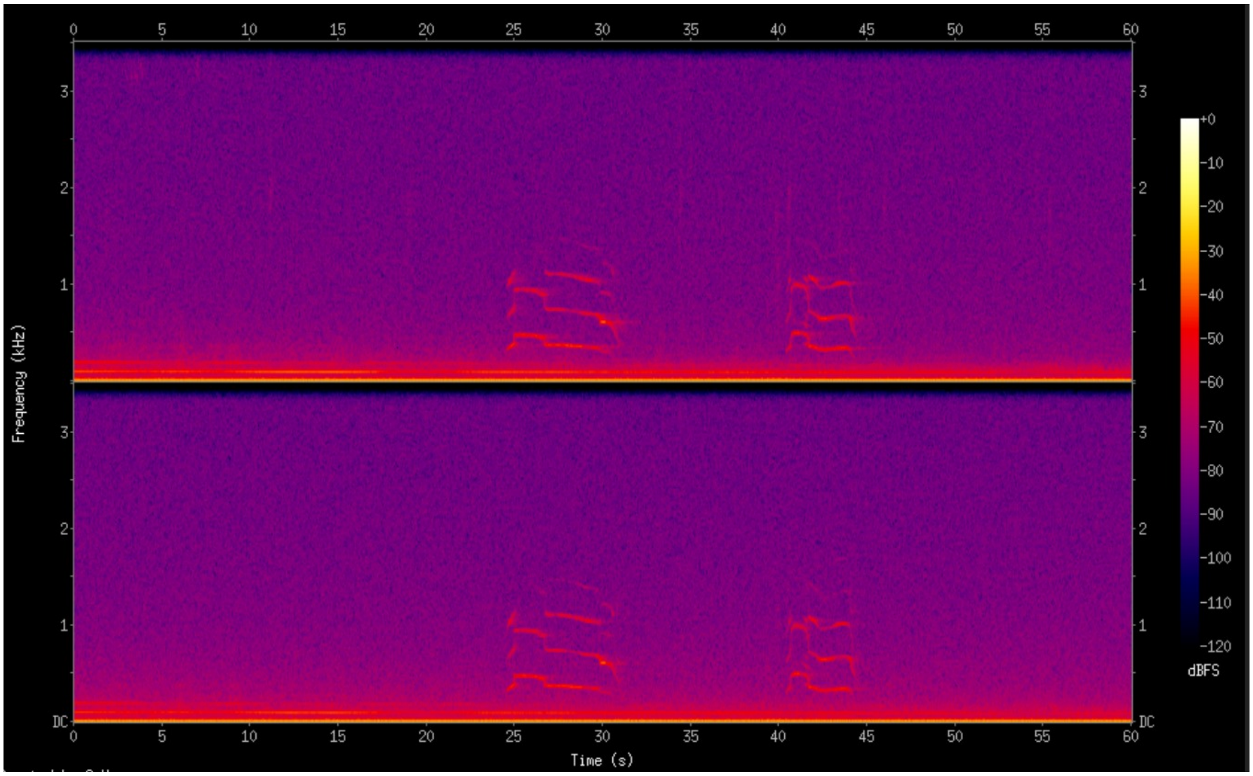

Figure 1.3. Example of an image output by SoX version 14.4.2. The y-axis is the frequency range in kHz, the top half representing the first channel and the bottom half the second channel from the ARU. The x-axis is marked in seconds, and the dBFs scale indicates the amplitude of the recording. The spectrogram itself shows a lone wolf howling twice approximately 10 seconds apart.

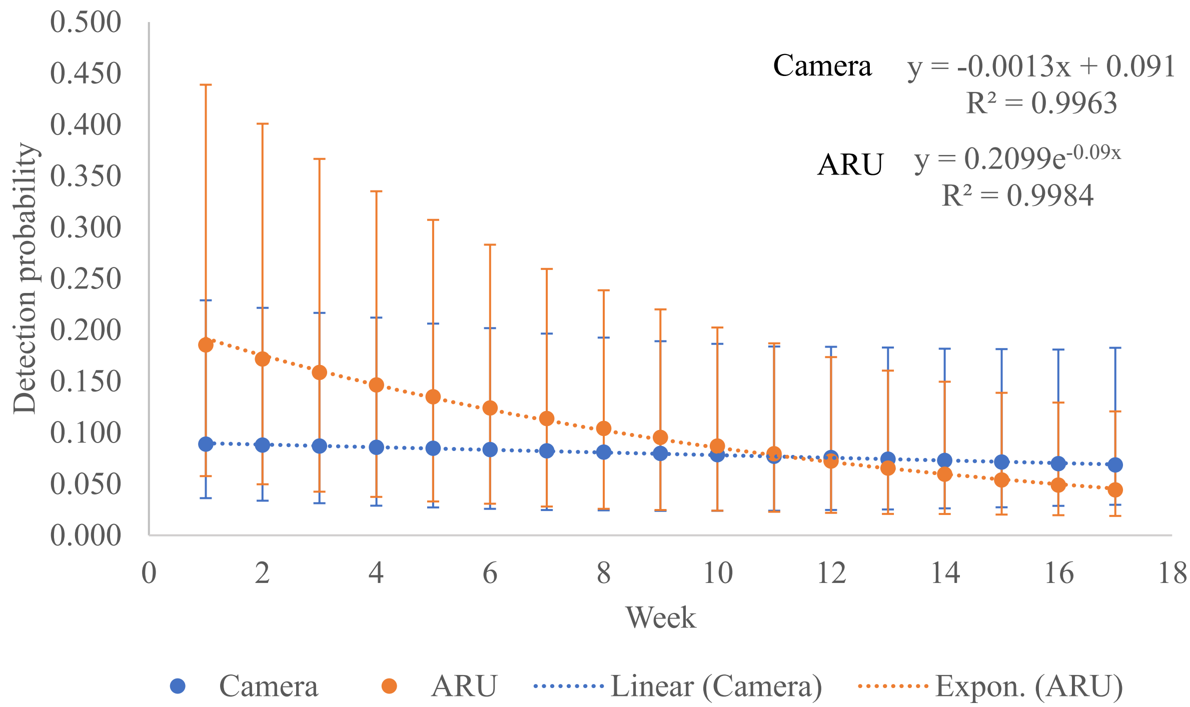

Figure 1.4. The effect of week on the probability of wolf detections for cameras and ARUs over 17 weeks of deployment in northeastern Alberta. Error bars represent 95% credible intervals.

Tables

Table 1.1. Total number of cameras deployed by the ABMI during the summers of 2016 and 2017 with at least one wolf detection between March 1st – June 30th. Paired ARUs at the same stations and their respective proportion of wolf detections.

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

Table 1.2. Comparison of ARU wolf detections at stations where cameras did not detect wolves between March 1st – June 30th 2016 and 2017.

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

Table 1.3. Occupancy and detectability estimates of cameras and ARUs using daily, weekly, and monthly detection intervals. 95% CI indicates the 95% credible intervals for each estimate.

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

Table 1.4. Comparison of detection and occupancy probabilities when camera-ARU stations were pooled as well as combined in a multi-method approach. The detectability estimates reported from the multi-method analysis are θ^x values, the probability of detection via camera and/or ARU given the wolf is present and available for detection.

Interval	Estimates	Pooled	95% Cred Int	Multi-method	95% Conf Int
Daily	p (detectability)	0.047	0.034, 0.062	0.267	0.092, 0.569
	Ψ (occupancy)	0.548	0.388, 0.727	0.742	0.614, 0.838
Weekly	p (detectability)	0.153	0.125, 0.180	0.698	0.228, 0.948
	Ψ (occupancy)	0.766	0.650, 0.807	0.757	0.624, 0.855
Monthly	p (detectability)	0.443	0.362, 0.525	0.829	0.360, 0.977
	Ψ (occupancy)	0.782	0.651, 0.905	0.800	0.635, 0.902

Table 1.5. Sampling effort between ARUs and cameras deployed by the ABMI during March 1st – June 30th, 2016-2017. 73 stations were selected based on those cameras with a known hit, ARUs were processed after for wolf hits.

	Min Active/Unit/Day	Total Min Active (73 Units, ~122 Days)	Wolf Hits (1 Image/Min)	Hit Rate (Hits/Total Min Active)
ARU	38	319,054	309	0.001
Camera	1440	11,612,160	254	0.00002

Chapter 3: Testing the random encounter and staying time (REST) model using human participants

Introduction

The need to estimate and track animal densities is a critical element of wildlife monitoring and management. Whether populations are increasing, stable, cyclic, or declining can have major impacts on ecosystem function and therefore on decisions made by wildlife managers regarding species and community management (Kapota and Saltz 2018, Williamson et al. 2018). While management programs typically rely on indices of relative abundance, obtaining population densities is a more desirable metric for many studies. Until recently, this has proved challenging, with mammal density estimates typically encompassed by wide margins of error (Wilson et al. 2017, Lonsinger et al. 2018).

Current methods of obtaining density estimates rely on mark-recapture studies and/or estimating the home range sizes of species (Borchers and Efford 2008). Although accurate, these methods are also intensive in terms of logistics, manpower, and time (Efford and Fewster 2013, Mattioli et al. 2018). Rowcliffe et al. (2008) proposed the random encounter model (REM) to estimate densities of unmarked populations using remote cameras and animal movement based on the ideal gas model. The concept for this method is grounded in mechanistic physics models that describe rates of gas molecule collisions (Hutchinson and Waser 2007). For the purpose of density estimation, Rowcliffe adapted molecular movement to animal movement and molecular collision rates with camera encounter rates (Rowcliffe et al. 2008). The appeal of REM is that it does not require the use of marked individuals or estimates of home range sizes. However, the need to accurately define species' movement speed to use REM has been a drawback of the application of this method in field studies, due to the intensive data collection required to make this estimate. Nakashima et al. (2017) modified Rowcliffe's original method to instead account for the "staying time" of an animal within the detection area of remote cameras, without accounting for the animal's rate of movement. He referred to this model as the random encounter and staying time (hereafter: REST) method.

Nakashima et al. (2017) provided evidence for the robustness of the REST method via computer simulations and data collection of real duiker populations in Moukalaba-Doudou National Park, Gabon, Africa. In their computer simulations, they varied duiker movement patterns to include paired and solitary movement, as well as continuous movement and movement with resting. They found their computer simulations provided unbiased estimates in nearly every scenario. The estimates made using real duiker populations were comparable to those density estimates made via line transect surveys of the same study area.

We conducted controlled human trials in Edmonton, Alberta to test the effects of variation in human movement rates and home range sizes on the accuracy and precision of the REST method. Habitat type and simulated camera detection areas remained constant, but we varied human densities, movement rates, home range sizes, and simulated camera coverage. While Nakashima et al. (2017) used simulations and real populations, our goal was to test the method using individuals in a controlled population as an intermediate step between computer-simulated and real populations. We used humans as a proxy for non-territorial, terrestrial mammals as the focus of these tests, as it is easier to instruct people when and how to change their movement rates compared to non-humans.

Theory

The REST model calculates species' density as a function of the total residency time an animal spends in front of a camera. The equation is as follows, modified from Nakashima et al. (2017):

$$\hat{\rho} = \frac{\hat{N}}{A} = \frac{\sum_{i=1}^{n} t_i}{T \cdot \mathrm{n} \cdot \mathrm{a}},$$

where $\hat{\rho}$ is the estimated density, n is the number of cameras, and t_i is the total staying time of an individual at the i'th camera. $\hat{N}$ is the sum of each animals' residency time across each camera. The denominator (A) is determined by the duration of the study period (T), the number of cameras deployed (n), and the proportion of the study area covered per camera (a).

This method does not require estimates of animal movement speed, home range size, or individual identification. It also does not require closure of the study area in the sense that animals do not leave or enter the area, but only that immigration, emigration, births, and mortality are balanced during the study period. If multiple individuals are captured at the same time by the same camera, their residency time is calculated independently. If an individual leaves the detection area of the camera and returns, it is counted as the start of a new residency time. This eliminates the task of researchers defining a camera detection, instead simply summing the time individuals spend in front of each camera. This method is applicable to both territorial and non-territorial species, provided cameras are distributed either randomly or systematically, and that the scale is defined by the study area.

The REST model assumes that cameras are placed randomly relative to animal movement within the study area, and that cameras sample habitat proportional to their availability. The robustness of this method to animals that possess home ranges or territories relies on the assumption that there is an equal probability of a home range existing within the study area, in other words, the point-pattern of home range distributions is homogenous. Additionally, detectability within the detection zone of the cameras must be perfect (p=1). This method also assumes that animal behavior is not modified due to the detection device.

Methods

Study area

Our test took place at the Louise McKinney Riverfront Park in Edmonton, Alberta, 53°N 113°W. The study area was approximately 1.6 ha in size, and consisted of open grassy areas, walking paths, and a pavilion, all of which were accessible to the participants.

Park trials

The Research Ethics Office at the University of Alberta granted approval for using human volunteers in our test, application No. Pro00075181. A total of 12 volunteers were included—six participants on September 16th, 2017, and six participants on September 23rd, 2017. On both days, the area available to a participant was either the entire park, a home range of 1.6 ha, or half the park (0.80 ha). The park boundaries were roughly rectangular in shape. On September 16th, the park was divided in half length-wise, and on September 23rd it was divided in half width-wise. We measured these areas based on the area calculation function using a GPSMap78 unit, and halves were delineated with flags, so each participant was aware of their home range “boundaries”. Each participant was given either a GPSMap64 or a GPSMap78 unit to track their movements in one second intervals for the duration of each trial.

We conducted six trials, each lasting 16 minutes and each varying the home range size and movement rate of the participants (Table 2.1). The trials included participants jogging for 10 minutes and resting for 6 minutes, walking for 10 minutes and resting for 6 minutes, and walking for 16 minutes continuously. While participants moved independently of each other during each test, their movement rates were synchronized (ie: everyone moved and rested simultaneously). These trials were repeated to include the entire park as the home range, in addition to halving the park to include two, smaller home ranges with the same variation in movement rates.

We tracked the duration of each trial using a stopwatch and whistle signaling changes in movement rates and the end of each trial. Due to variation among participants in the time they took to start, stop, and save their individual tracks, each trial varied from exactly 960 seconds (16 min). The tracks over both days were merged according to trial in ArcMap v10.5.1 and clipped to the shortest duration of any given participant within trials to standardize the frequency of points per person per trial (Table 2.1). As such, trials averaged 932 s ± 19 s standard deviation. Polygons consisting of 800 cells were created around each trial based on the coordinates of the outermost tracks (Figure 2.1). Each cell was approximately 20 m^2. The number of points per cell were then summed for each trial. If a point fell on the border of two adjacent cells, whichever cell the majority of the point was in, we counted as belonging to that cell.

We assumed our park habitat was homogenous during this study, and detectability was perfect given that each participant was tracked via GPS units that never failed during the simulations. The potential bias of participant attraction to detection devices was not an issue because cameras were not actually deployed during the trials.

Analysis

We varied human densities to include 2, 6, and 12 people, and we varied the number of cells randomly chosen as deployments of 8, 20, 50, and 100 cameras. These camera densities resulted in 1%, 2.5%, 6.25%, and 12.5% coverage of the study area, respectively. We used 1000 bootstrap samples with replacement of camera effort in each scenario of movement speed, human densities, and home range area for a total of 72 different scenarios in R v.3.5.1 (R Core Team 2018).

Results

Each scenario provided accurate estimates of human density regardless of movement rate, home range area, camera effort, or number of participants (Figure 2.2). Density estimates were biased slightly negative when camera effort was 8 cameras, but accuracy increased with increases in camera coverage. Additionally, precision of the estimates increased as camera effort increased, with 100 camera deployments having an order of magnitude less error than scenarios with only 8 cameras deployed. Both movement rate and home range size did not affect the accuracy of estimates, although walking and resting and jogging and resting trials consistently had wider margins of error than those trials consisting of continuous walking speeds.

Effect of participant abundances on density estimates

In scenarios where true human densities were 2 people across 20, 50, and 100 camera deployments, we observed the least amount of error across all movement and home range size scenarios. In scenarios with 20 and 50 cameras, as human abundance in the park increased, so did our margins of error.

Effect of home range size and movement rate on density estimates

Among all variations in home range size and movement rate, the REST method accurately estimated human densities. We detected no difference in accuracy or precision of the REST method if home range sizes were large (1.6 ha) or small (0.80 ha). Continuous walking by the participants had the narrowest confidence intervals across all combinations of camera effort, human densities, and home range sizes. When movement rates were changed to include jogging and resting, as well as walking and resting, the accuracy of the estimates were not affected, but the margins of error were consistently wider between both movement rates than continuous walking.

Effect of camera effort on density estimates

Not surprisingly, the precision of the estimates increased as camera effort increased. When 100 camera cells were selected, the resulting confidence intervals were, on average, an order of magnitude smaller than when 8 camera cells were selected (Figure 2.2).

Discussion

We found the REST method accurately estimated human densities regardless of movement rate, home range size, and camera coverage in these tests. Density estimates had the widest range of error with the lowest camera coverage (8 cameras) and with higher human abundances. While variations in movement rate and home range size did not affect overall density estimates, the least precise trials were those that involved jogging and resting and walking and resting. Increased precision when participants were moving at slower paces continuously as opposed to moving and resting may be indicative of the robustness of this method to slower moving animals, which would theoretically allow for longer residency times per camera, and therefore more precise estimates. Nakashima et al. (2017) noted that the REST method may not be robust to species that have long periods of inactivity. Our human experiment partially accounted for this potential bias by incorporating resting in which participants did not move from their locations for approximately 38% of the survey period during two of the trials. Despite this lack of movement, the REST method was still able to estimate density in those scenarios, however the estimates were less precise than other movement rates. Further testing of the effects of animals with long periods of inactivity may be warranted.

Nakashima et al. (2017) also suggested that cameras have sensitive sensor settings, no delay period between photos, or alternatively, take video recordings, and that the effective detection area be tested in situ according to methods proposed by Rowclifffe et al. (2011). For the purpose of this simulation, we addressed the concern of delays in camera capture rate as well as the possibility of imperfect detections within the detection zones by having each participant tracked every second. The cumulative number of tracks in each cell, if that cell was designated as a camera, would then be perfectly detectable. However, in field settings when real cameras are used, camera sensitivity, detection areas, and photographic capture rate should all be tested and accounted for.

The potential of environmental factors and variation in target species' attributes may influence detectability. Dense vegetation and inclement weather will decrease the effective detection areas of cameras, leading to overestimates of animal densities. While weather is an uncontrollable factor, it is common practice in camera trap studies to clear thick understories that block the view of the camera, or to place cameras in less dense areas (Rowcliffe et al. 2011, Rovero et al. 2013, Villette et al. 2016). Regardless of where cameras are placed, it is necessary that the effective detection area of each camera be tested in the field to accurately measure animal densities (Nakashima et al. 2017).

Variation in body size may affect detectability and therefore capture rates of different species, such as smaller animals that may be missed by the camera, despite being present in the detection area (Rovero et al. 2013, Kolowski and Forrester 2017). This bias would lead to underestimates of mammal density (Nakashima et al. 2017). Our human trials did not test the effect of body size on detectability. Therefore, the REST method should be applied to multiple species to quantify these potential biases (Nakashima et al. 2017).

The application of the REST method to camera trap studies may have the potential to improve monitoring efforts for several species, provided assumptions are met. This method offers a cost-effective, unbiased means by which animal densities can be estimated from camera trap data without the use of marked individuals or estimates of home range sizes. Nakashima et al. (2017) applied the REST model to computer simulated and real data of red and blue duikers (*Cephalophus natalensis* and *Philantomba monticola*), in which they found the model to accurately estimate simulated and real duiker densities with even lower camera coverage (<1%) than we simulated in these park trials. While further testing of this method on other species remains to be completed, the effectiveness of REST on a controlled human test provides evidence of the potential application of this method to future mammal monitoring and management programs.

Figures

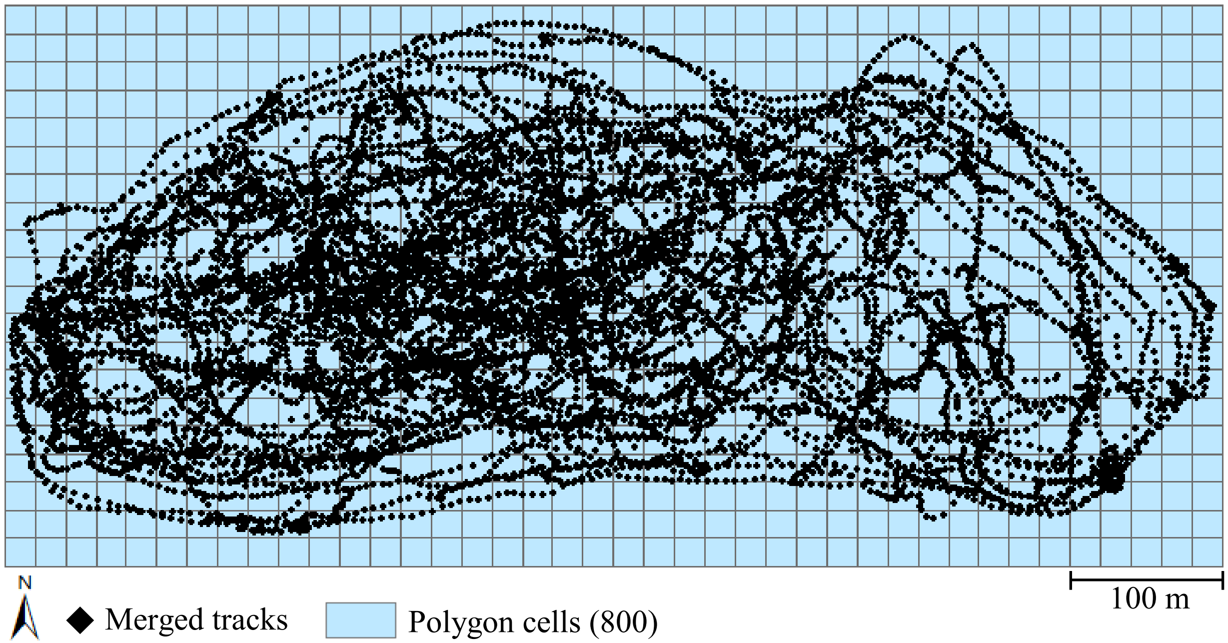

Figure 2.1. Merged tracks of all 12 participants in the 800 cell polygon from trial 5. In this trial, the entire Louise McKinney Riverfront Park was available to everyone, and the movement rate was walking for a total of 10 minutes, and resting (no movement) for a total of 6 minutes.

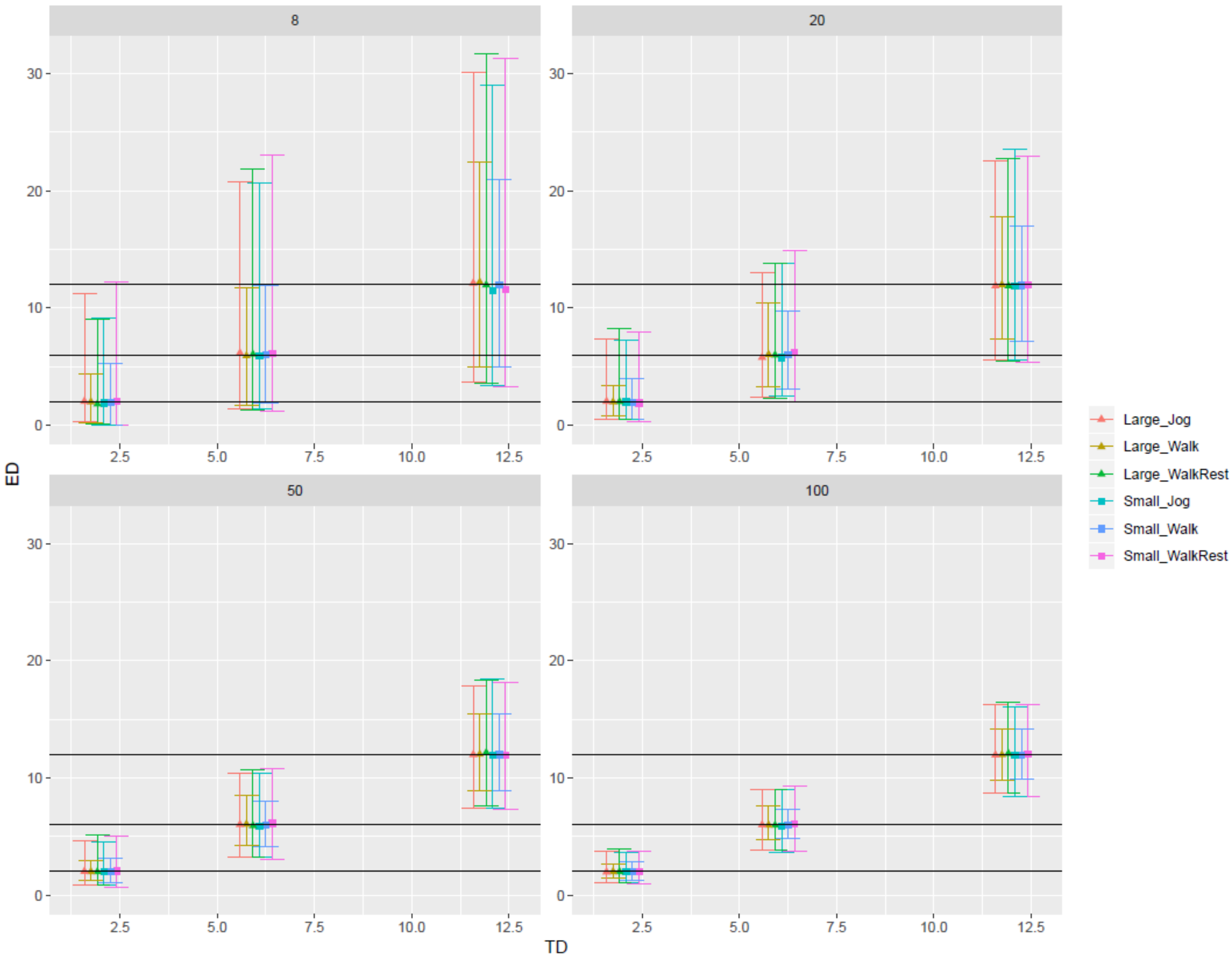

Figure 2.2. Bootstrapped mean estimates and 95% confidence intervals of human densities including 2, 6, and 12 people with camera trap effort varying from 8, 20, 50, and 100 cameras across all six trials of movement rate and home range size. TD is the true density of each scenario while ED is the estimated density. Black, horizontal lines indicate what the true density was in each scenario.

Tables

Table 2.1. Details of each trial: home range sizes paired with varied movement rates for each trial conducted at Louise McKinney Riverfront Park. The cell area (m^2) refers to the approximate cell size per trial.

Trial	Home range (ha)	Movement rate	Duration (s)	Point freq (s)	Cell area	Total area (m^2)
1	0.75	Jog 5 min, rest 3 min (2x)	11424	952	20	16,000
2	0.75	Walk 5 min, rest 3 min (2x)	11184	932	19	15,200
3	0.75	Walk continuously (16 min)	11268	939	20	16,000
4	1.5	Jog 5 min, rest 3 min (2x)	11208	934	20	16,000
5	1.5	Walk 5 min, rest 3 min (2x)	10752	896	20	16,000
6	1.5	Walk continuously (16 min)	11244	937	20	16,000

Chapter 4: General Conclusions

Summary

The goal of this study was two-fold: to compare the use of ARUs to remote cameras to monitor vocal predators in Alberta, using the gray wolf as a test species, and to assess a new method of estimating unmarked mammal densities from camera traps. We found ARUs to be comparable to cameras in their detectability of wolves in this paired study. We also found the density estimation method to produce unbiased estimates of density in a controlled test using humans as a proxy for wild animal movement.

In our camera-ARU comparison, at the site-level, ARUs detected wolves at approximately 59% of selected sites (68/115), while cameras detected wolves at approximately 50% of selected sites (58/115). Additionally, when we selected 73 stations where every station had a wolf detection via camera, while approximately 60% of the paired ARUs detected a wolf, ARUs had a higher per minute hit rate than cameras out of the total time each unit was active (ARU = 0.001 hits/min, Cam = 0.00002 hits/min). We found that ARUs had slightly higher detectability than cameras, and that occupancy and detectability estimates from daily and weekly sampling intervals were comparable (Table 1.3). However, daily and weekly estimates were much lower than monthly intervals, regardless of the method employed. Additionally, detectability estimates from the multi-method approach were generally higher than estimates made from simply pooling the data, without accounting for individual detection probabilities of each method (Table 1.4). Lastly, we found both camera and ARU detectability decreased for every additional week they were active, although ARUs decreased exponentially while cameras decreased linearly (Figure 1.4). This may be due to green-up of the vegetation as the summer progressed, decreasing both camera and ARU detectability.

The second goal of this thesis was to test the random encounter and staying time (REST) model (Nakashima et al. 2017). We did this using human volunteers in Louise McKinney Riverfront Park in Edmonton, Alberta. We tested the effects of different human abundances, movement rates, home range sizes, and simulated camera effort on the precision and accuracy of the REST method. The different combinations of these variables resulted in 72 scenarios, each of which we estimated using 1000 parametric bootstrap samples with replacement. For every scenario, the REST method produced unbiased estimates of human density, although precision was the most variable in scenarios where movement rates incorporated resting, camera effort was lowest (1% coverage) and when human densities were highest (12 people). Our most precise estimates were consistently those where movement rates were constant, regardless of human densities or camera effort. Home range size had no effect on our density estimates.

Inclusion of ARU technology in wolf monitoring

The use of ARUs to collect wolf data is a technological advancement that may further our ability to monitor wolves passively. Recent studies have suggested that individual wolves can be identified based on their vocal signature, which allows the number of howling wolves per pack to be counted from spectral data, opening up avenues of mark-recapture studies based solely on vocalizations (Root-Gutteridge et al. 2014, Passilongo et al. 2015). The applicability of analyses such as occupancy, abundance estimates, and potentially even density estimates to ARU data allows for the diversification of monitoring methods that can be used for target species, such as wolves.

Limitations and implications

Although passive monitoring methods have become ubiquitous in recent years, and our study provided evidence for the applicability of ARUs for gray wolf monitoring in Alberta, certain limitations and assumptions of these methods should be accounted for. While ARUs, on average, have much larger detection areas than cameras, both methods are limited by the environments in which they are placed. Dense vegetation, inclement weather, and background noise will decrease the detectability of these devices (Efford and Dawson 2012, Yip et al. 2017). In the cases of occupancy and density, this decrease in detection areas, or miscalculation of true detection areas, may inflate both estimates unless properly accounted for. Therefore, researchers should make every effort to quantify the detection areas of these devices when they are in the field in order to reduce biased estimates as much as possible (Rowcliffe et al. 2011, Nakashima et al. 2017).

In the case of ARUs sampling vocal predators, detectability is highly dependent on the vocal activity of the target species. Wolves are known to howl year-round, but studies have indicated that peak howling activity occurs in the fall and winter (Hennelly et al. 2017, McIntyre et al. 2017). Therefore, to effectively incorporate ARUs into wolf monitoring programs, focusing ARU recording activity during night, dawn, and dusk hours during seasons of high wolf howling activity will likely yield the most data (Passilongo et al. 2010).

Our human test of the REST method provided evidence for the model's robustness, given that assumptions were met. However, variables such as animal body size and variation in camera detection areas were not tested in this study. Nakashima et al. (2017) suggested that small animals may be missed more often by cameras, effectively underestimating densities. Additionally, if cameras are not placed proportionally according to habitat availability, this will bias estimates of density. However, knowing *a priori* a species' use of habitat, and placing cameras accordingly, may be more difficult to estimate, and therefore may influence density estimates using the REST method. As such, we suggest continued testing of the REST method using different species and the effects of accuracy and precision in heterogenous habitat.

In conclusion, this thesis provided strong evidence for the viability of using ARUs to monitor vocal, low-density predators in a fashion similar to currently popular camera methods. We additionally provided support for the robustness of the REST method in estimating densities of unmarked populations. The potential to estimate gray wolf howling rates, behavior, and identify individuals from passive methods may contribute to the conservation and management efforts for species of interest in Alberta. Additionally, the applicability of the REST method to estimate densities of unmarked populations is a valuable advancement of the use of camera trap data in wildlife monitoring studies. Having the ability to accurately estimate density is a highly desirable but until now, labor-intensive management goal. The use of passive surveying methods, in addition to advancements in statistical and mathematical applications to these types of data, no doubt provide researchers with tools to not only better understand predator ecology but to also implement effective management strategies.

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Appendix I

Appendix I. Bayesian model using JAGS version 4.3.0 for camera and ARU occupancy models. Bolded lines are those that estimate weekly detectability as a function of the quadratic week. Non-bolded lines indicate occupancy models without covariates.

```
y <- read.csv("CamARUDay69Wide.csv", fileEncoding = "UTF-8-BOM")   #y (detection
history)
y <- data.matrix(y, rownames.force = NA)
nsite <- nrow(y)  #nsite (number of sites/rows)
nsurv <- ncol(y)  #nsurv (number of columns in y)
week <- c(1:17)
week <- week/100
week2 <- week^2
week <- as.numeric(week)
#Model
library(R2jags)
sink("model.txt")
cat("
   model{
   # Priors
   psi ~ dunif(0, 1) # The prior on occupancy probability
   p ~ dunif(0, 1)  # The prior on detection probability
   alpha.p ~ dnorm(0, 0.01)
   beta.p ~ dnorm(0, 0.01)
```

beta.p2 ~ dnorm(0, 0.01)

Likelihood

for(i in 1:nsite){

z[i] ~ dbern(psi) # The occupancy state of site i (z[i]) is distributed bernoulli with probability psi

for(j in 1:nsurv[i]){

y[i, j] ~ dbern(eff.p[i, j]) # Detection during survey j at site i (y[i, j]) is distributed bernoulli with probability p*z, where z is 1 or 0

eff.p[i, j] <- z[i]*p

logit(p[i, j]) <- alpha.p + beta.p*week[j] + beta.p2*week2[j]

}

}

 # Generated quantities

for(j in 1:nsurv){

lp.week[j] <- alpha.p + beta.p*week[j] + beta.p2*week2[j]

}

}

",fill=TRUE)

sink()

#Bundle data

win.data <- list(y=y, nsite=nsite, nsurv=nsurv)

win.data <- list(y=y, nsite=nsite, nsurv=nsurve, week=week, week2=week2)

#Function to generate starting values

```
zst <- apply(y,1,max)

inits <- function(){list(z=zst,psi=runif(1,0,1), p=runif(1,0,1))}

inits <- function(){list(z=zst,alpha.p=rnorm(1,0,1), beta.p=rnorm(1,0,1),

beta.p2=rnorm(1,0,1))}

#Parameters to estimate

params <- c("psi", "p")

params <- c("psi", "alpha.p", "beta.p", "beta.p2", "lp.week")

#MCMC Settings

nc <- 3

nb <- 500

ni <- 3000

nt <- 5

#Start Gibbs sampler

out <- jags(win.data, inits, params, "model.txt", n.chains=nc, n.iter=ni, n.burn=nb, n.thin=nt)
```