

ESTIMATING POPULATION DENSITIES OF *PEROMYSCUS MANICULATUS*,
CLETHRIONOMYS RUTILUS, *LEPUS AMERICANUS*, AND *TAMIASCIURUS HUDSONICUS*
USING REMOTE CAMERAS IN THE BOREAL FOREST OF YUKON TERRITORY,
CANADA

by

PETRA MARY ANNE HOBSON VILLETTE

B.Sc., The University of British Columbia, 2011

A THESIS SUBMITTED IN PARTIAL FULLFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

December 2013

© Petra Mary Anne Hobson Villette, 2013

Abstract

Population density estimation of small mammals often involves live trapping, a procedure that can be stressful on the captured animals, time consuming, and expensive. Encounter or “hit” rates between animals and remote cameras have been suggested as a method for using remote cameras to estimate the population density of species when individuals cannot be identified; this method has not yet been tested on rodents.

Live trapping and filming of four species of small mammal was conducted in the boreal forest of Yukon Territory during the summers of 2010, 2011 and 2012 to determine if hit rates can be used to estimate the population density of deer mice (*Peromyscus maniculatus*), northern red-backed voles (*Clethrionomys rutilus*), snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*). *Microtus* spp. were also observed, but at numbers too low for analysis; density estimates and video counts are presented. The first objective was to determine if the hit window or protocol used to group videos suspected of being generated in the same encounter affects the correlation between hit rates and live-trapping-based population density estimates for these four species. Hit window duration had little effect on the correlation between hit rates and live-trapping-based population density estimates for deer mice, a moderate effect for northern red-backed voles, and major effects for snowshoe hares and red squirrels.

The second objective of this research was to determine if, given the “best” hit window for each species, hit rates and live-trapping-based population density estimates are correlated such that hit rates could be used in place of live trapping to estimate the population density of these species. Strong correlations between hit rates and trap-based density estimates suggest that remote cameras are an accurate and rapid non-invasive alternative to live trapping for estimating the population density of all four species.

Preface

All of the fieldwork reported here was conducted either at the Kluane Lake Research Station in Yukon Territory, Canada, or in the municipality of Mayo, Yukon Territory, Canada. The fieldwork was covered by UBC Animal Care Permit A09-0169, and Yukon Environment Wildlife Research Permit 0086.

Dr. Charles Krebs was responsible for the initial conception of this work; I was responsible for further development of the project, data collection and analysis, and manuscript preparation.

Table of Contents

Abstract.....	ii
Preface.....	iii
Table of Contents	iv
List of Tables	v
List of Figures.....	vi
Acknowledgments	viii
Chapter 1 : Introduction	1
<i>Remote Cameras</i>	1
<i>Population Density Estimation</i>	3
<i>Study Objectives</i>	5
Chapter 2 - Density Estimation of Northern Red-Backed Voles (<i>Clethrionomys Rutilus</i>) and Deer Mice (<i>Peromyscus Maniculatus</i>) Using Remote Cameras	10
Introduction	10
Materials and Methods	11
<i>Study Sites and Trapping</i>	11
<i>Remote Cameras</i>	13
<i>Statistics</i>	15
Results.....	17
Discussion	19
Chapter 3 - Density Estimation of Snowshoe Hares (<i>Lepus americanus</i>) and Red Squirrels (<i>Tamiasciurus hudsonicus</i>) Using Remote Cameras	30
Introduction	30
Materials and Methods	31
<i>Study Sites and Trapping</i>	31
<i>Remote Cameras</i>	34
<i>Statistics</i>	35
Results.....	37
Discussion	39
Chapter 4 - General Conclusions and Further Research.....	52
References	57

List of Tables

- Table 2.1. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*) by grid. Densities are animals/ha, with 95% confidence limits where applicable shown below in parentheses. 24
- Table 2.2. Linear regressions to predict live-trapping-based estimated densities from camera-based hit rates for northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*). Hit rates were calculated using a 90 minute hit window for both species, density is in animals/ha, and density and hit rate were square-root-transformed to achieve linearity. 27
- Table 3.1. Summary of video counts, filming effort, the number of individuals trapped (MNA or minimum number alive) and live-trapping-based density estimates for snowshoe hares (*Lepus americanus*) by grid. Densities are animals/ha and were calculated by dividing MNA by the effective trapping area of each grid (60 ha for Chitty, 56.6 ha for Silver, and 63.5 ha for Sulphur)..... 44
- Table 3.2. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for red squirrels (*Tamiasciurus hudsonicus*) by grid. Densities are animals/ha, with 95% confidence limits shown below in parentheses. 46
- Table 3.3. Linear regressions to predict trap-based population density estimates from camera-based hit rates for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*). Hit rates were calculated using 5 minute hit windows, density and hit rate were square-root-transformed to achieve linearity, and densities are in animals/ha. 48

List of Figures

- Figure 1.1. The Arctic Institute of North America's Kluane Lake Research Station (61°N, 138°W) is located on the southeastern shore of Kluane Lake in the southwestern corner of Yukon Territory, Canada. Live trapping grids used in this area are located east of the research station along the Alaska Highway (A), and on Jacquot Island (B). See Figure 1.2 for expanded views of A and B. 7
- Figure 1.2. Magnified view of the Alaska Highway east of the Arctic Institute of North America's Kluane Lake Research Station. Silver and Chitty mouse grids overlap with their respective hare grids but do not use the same trapping stations; Chitty and Sulphur squirrel grids are subsets of their respective hare grids. B. Magnified view of Jacquot Island. A and B are shown at the same scale and orientation. 8
- Figure 1.3. The Mayo study site (63°N, 136°W) is located in central Yukon Territory. Live trapping grids used in this area are located north of the town and are accessible via unpaved roads. 9
- Figure 2.1. R^2 values for linear regressions between live-trapping-based population density estimates and hit rates calculated with different hit window lengths for deer mice (*Peromyscus maniculatus*) and northern red-backed voles (*Clethrionomys rutilus*), Kluane Lake, 2010-2012. 26
- Figure 2.2. Relationship between hit rates and live-trapping-based density estimates for northern red-backed voles (*Clethrionomys rutilus*) using a 90 minute hit window. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2=0.59$), grey band indicates 95% prediction intervals. Error bars are 95% confidence intervals for density estimates. 28
- Figure 2.3. Relationship between hit rates and live-trapping-based density estimates for deer mice (*Peromyscus maniculatus*) using a 90 minute hit window. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2=0.84$), grey band indicates 95% prediction intervals. Error bars are 95% confidence intervals for density estimates. 29
- Figure 3.1. R^2 values for linear regressions between live-trapping-based population density estimates and hit rates calculated using different hit window lengths for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*), Kluane Lake, 2011-2012. 49

- Figure 3.2. Relationship between hit rates and live-trapping-based density estimates for snowshoe hares (*Lepus americanus*) at Kluane Lake. Hit rates were calculated using 5 minute hit windows. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2 = 0.90$), grey band represents 95% prediction intervals. 50
- Figure 3.3. Relationship between hit rates and live-trapping-based population density estimates for red squirrels (*Tamiasciurus hudsonicus*) at Kluane Lake. Hit rates were calculated using 5 minute hit windows. Each point represents a 2-day filming session followed by a 2-day live trapping session. Solid line indicates linear regression ($R^2 = 0.61$), grey band represents 95% prediction intervals. Error bars are 95% confidence intervals for density estimates. 51

Acknowledgments

I am grateful to my supervisor Dr. Charles Krebs for the opportunity to conduct this research as well as his advice and encouragement throughout this project; his support was invaluable.

I am grateful to Kate Broadley, Roslyn Johnson, Emily Lomax, Lucas Pavan and Nicole Warren for their dedication and enthusiasm – thank you for making field work awesome. I would also like to thank Rudy Boonstra, Liz Hofer, Virginia Mitford, Virginia Cobbett, and Mike Perry for their assistance in the field. I would like to thank Alice Kenney for teaching me the ways of data storage and management, and for her assistance in the field and enthusiastic support throughout this project. I am grateful to Tom Jung and the Yukon Fish and Wildlife Branch for the loan of their cameras.

I am grateful to the staff of the Kluane Lake Research Station, in particular Sian Williams, Lance Goodwin, and Bronwyn Goodwin; this project would not have been possible without you. Bill Harrower's insights into statistics and Jeff Werner's advice on all things were greatly appreciated.

I would like to thank the other members of my advisory committee, Dr. Roy Turkington and Dr. Kathy Martin, for their valuable insight and feedback throughout the project.

Funding for this project includes grants from NSERC and the Northern Scientific Training Program as well as the W. Garfield Weston Foundation, the University of British Columbia, and Dr. Charles Krebs.

Lastly, I would like to thank my family and friends whose support made the completion of this thesis possible: Helen and Gary Villette, Lexa Villette, Joan Hobson, Riya Sharma, Diane Gold, and Julia Maddison.

Chapter 1 : Introduction

Estimating population density of small mammals is of interest within the field of ecology because small mammals often exhibit dramatic fluctuations in density that can have widespread and drastic impacts on coexisting species (Krebs et al. 2001; Marcstrom et al. 1988; Marcström et al. 1989). Assessing small mammal density often relies on live trapping and mark-recapture techniques (Krebs et al. 2011). Live trapping is cause significant physiological stress responses in many species (Delehanty and Boonstra 2009; Fletcher and Boonstra 2006). In addition, live trapping can be labour-intensive and therefore expensive. Cameras have been a part of the wildlife researcher's toolkit for almost 100 years, and represent a possible alternative to live trapping for estimating small mammal densities.

Remote Cameras

Cameras were developed in the 19th century and photographing wildlife proved to be an appealing past time, but early wildlife photography required manual operation of the shutter, obliging the photographer to be present. In 1878 Eadward Muybridge used a series of triggered by trip wires to photograph a horse as it galloped by, demonstrating that all four hooves come off the ground during a gallop. This was probably one of the first instances of an animal photographing itself (O'Connell et al. 2011), and set the stage for remote photography, or the collection of images or videos in the absence of a human camera operator.

Early remote camera set-ups relied on baited trip wires to attract animals and trigger the camera (Shiras 1913), and required manual reloading of the photographic medium (e.g. a glass plate) after every exposure. This, coupled with the danger and noise of the magnesium powder flashes used at that time, limited the use of cameras in rigorous scientific capacities. Chapman (1927) used trip wires placed across man-made paths to document the species present on the

island of Barro Colorado in Panama shortly after its establishment as a research island, but it wasn't until the development of electric light bulbs and camera units that could take multiple exposures without reloading, that remote cameras began to have more widespread use in wildlife research. The description of a portable and inexpensive camera unit for documenting wildlife by Gysel and Davis (1956) and Pearson's work on meadow vole (*Microtus californicus*) runway-use and activity patterns (Pearson 1959, 1960) illustrate the interest in remote cameras that was developing within the wildlife research community by the 1950's.

Since then, remote cameras have been used to address a wide variety of questions about wildlife. When Cutler and Swann (1999) reviewed the remote camera literature, they identified 107 peer-reviewed publications that used remote cameras to study wildlife. Most of these publications focused on birds, and more than half were investigations into feeding ecology, nesting behaviour and nest predation. For example, Grundel and Dahlsten (1991) photographed chickadees at nest boxes with light-beam triggered remote cameras and identified their insect prey, and Derksen (1977) used time-lapse photography to quantify aspects of nesting behaviour in Adelie penguins. More recent applications include assessing small mammal community diversity (De Bondi et al. 2010), and detecting rare species such as red fox in Australia (Vine et al. 2009).

Part of the appeal of using remote cameras in wildlife research is their ability to observe animals in a non-invasive capacity (Cutler and Swann 1999). In particular, being able to leave cameras in the field for extended periods of time and limiting the human presence in the study area have been cited as major advantages to using remote cameras over direct observation in many studies. The development of digital photography and high capacity memory cards has further contributed to this (McCallum 2013). In addition, camera units are now often waterproof

and capable of operating at sub-zero temperatures, further increasing their applicability in observing species that occupy remote or rough terrain. Infrared detectors, both “active” beams and “passive” field detectors, and infrared flashes have made cameras well suited for detecting rare, cryptic or shy species that are difficult to detect using conventional means such as track transects, visual surveys or live trapping (De Bondi et al. 2010; Trolle 2003). Remote cameras can also be a cheaper alternative to conventional means of observing wildlife because they can reduce the amount of time researchers need to spend in the field (Rovero and Marshall 2009).

There are, however, some limitations to remote cameras and their applicability in wildlife research. In general, remote cameras are complex and subject to mechanical failures (e.g. Bondi et al. 2010; Silver et al. 2004), and while the long-term cost of operating remote cameras can be less than other methods involving human observers, high start-up costs can be a barrier to their implementation (Rovero and Marshall 2009). An inadvertent consequence of the rapid advances in memory storage is that remote cameras are now capable of collecting thousands of images or hours of video before needing their memory cards changed. Processing these images or videos can be difficult and time consuming (Harris et al. 2010; McCallum 2013). As with any method, the usefulness of the photographs and videos obtained by remote cameras, and the validity of the subsequent inferences made using these data, is subject to the sampling design. For example, studies that aim to obtain presence/absence data need to account for the detectability of the focal species, and disperse the cameras across an appropriate spatial scale (Foster and Harmsen 2012).

Population Density Estimation

When McCallum (2013) reviewed the mammalian remote camera literature, he found that the predominant goal was to estimate population density. This trend can be attributed in part to Karanth’s landmark paper on tiger densities (Karanth 1995). Using 35mm film cameras and

infrared beam detectors, Karanth photographed tigers in Nagarahole National Park in India, identified individuals using their unique stripe patterns, and constructed “capture” histories analogous to those generated through live trapping and mark-recapture techniques. These capture histories could then be analyzed using the mark-recapture models developed to handle live trapping data and estimate densities. This method has subsequently been used to estimate tiger densities throughout their range (Karanth and Nichols 1998; O’Brien et al. 2003), and has undergone widespread adoption for monitoring other cat populations around the world, including jaguars (Maffei et al. 2004; Wallace et al. 2003), ocelots (Dillon and Kelly 2007; Trolle and Kéry 2003), pumas (Kelly et al. 2008), leopards (Wang and Macdonald 2009), snow leopards (McCarthy et al. 2008), and bobcats (Heilbrun et al. 2006).

The development of remote cameras as a tool for estimating population densities of species that do not feature individual unique markings, and for which capture histories cannot be reliably constructed, has been slower. Carbone (2001) used random walk computer simulations to suggest that encounter or “hit” rates between wildlife and remote cameras could be used as an index for density without the need to identify individuals. Rowcliffe et al. (2008) modelled hit rates using a random encounter model. They found that hit rates could be used in conjunction with average daily movement rates to accurately estimate the density of muntjac (*Muntiacus reevesi*), water deer (*Hydropotes inermis*) and red-necked wallabies (*Macropus rufogriseus*) in an enclosed setting.

One of the fundamental questions that underlie the use of hit rates as estimators of density is how to define a hit. When Rowcliffe et al. (2008) developed their random encounter model, they defined a hit as an encounter between an animal and the camera, but recognized that multiple photos could be generated during a single encounter, and recommended grouping

photos suspected of being of the same encounter. When Rovero and Marshall (2009) applied a random encounter model to camera data to estimate the density of wild Harvey's duiker (*Cephalophus harveyi*), they used a convention that I will here refer to as a hit window; photos that were taken within 60 minutes (within a 60 minute hit window) were not considered independent, and were grouped as a single hit. When Manzo et al. (2011) used the random encounter model approach to assess European pine marten (*Martes martes*) densities in Italy, they utilized a 5-minute delay setting on their cameras to reduce the chances of multiple photos being taken during single encounters. In these three cases, it is unclear if the delay, hit window, or grouping used was the "best"; that is, if a different protocol for defining hits would have had a significant impact on the density estimates obtained.

Study Objectives

In the research described here I tested the applicability of motion-detecting remote cameras for observing small mammals by filming deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys rutilus*), red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hares (*Lepus americanus*) in Yukon Territory, Canada, and estimating the correlation between camera hit rates and live-trapping-based mark-recapture estimates of density. The boreal forest in the Kluane Lake region has been the location of intense investigation into the dynamics of snowshoe hare populations and their influence on the entire ecosystem for over 35 years, with the monitoring of mice, vole and red squirrel densities an integral part of that research (Boonstra et al. 2001). Vole and deer mouse densities have been monitored through live trapping in the boreal forest around the village of Mayo since 2004 as part of the Yukon Community Ecological Monitoring program. With the infrastructure necessary for trapping small mammals already in place in both of these locations, I decided to address the use of remote cameras on small

mammals at the Arctic Institute of North America's Kluane Lake Research Station (Figures 1.1 and 1.2), and in the Mayo region (Figure 1.3).

I used remote cameras equipped with passive infrared detectors to film deer mice, red-backed voles, red squirrels, and snowshoe hares as they interacted with live traps used for estimating their densities through mark-recapture methods, to address the following two questions. First, does the protocol one uses for defining 'hits' affect the relationship between hit rate and estimates of population density? Specifically, is there a hit window duration that maximizes the correlation between hit rate and live-trapping-based density estimates? Secondly, given the "best" hit window, can I use hit rates to estimate the population density of *Peromyscus maniculatus*, *Clethrionomys rutilus*, *Lepus americanus* and *Tamiasciurus hudsonicus*?

This research is divided into two chapters presenting the results of my investigations, delineated by species (*Peromyscus* and *Clethrionomys* data were collected concurrently on relatively small grids with an approx. effective trapping area of 3.4 ha, while *Lepus* and *Tamiasciurus* data were collected on larger grids with an approx. effective trapping area of 60 ha and 16.5 ha). In Chapter 2 I present how hit window duration affects the correlation between hit rates and live-trapping-based density estimates of *Peromyscus* and *Clethrionomys*, and discuss the applicability of the "best" correlations between hit rates and live-trapping-based density estimates as a means of estimating density for these two species. In Chapter 3 I present how hit window duration affects the correlation between hit rates and live-trapping-based density estimates of *Lepus* and *Tamiasciurus*, and discuss the applicability of the "best" correlations between hit rates and live-trapping-based density estimates as a means of estimating density for these two species. I summarize my main findings in Chapter 4 where I also suggest areas for future research.

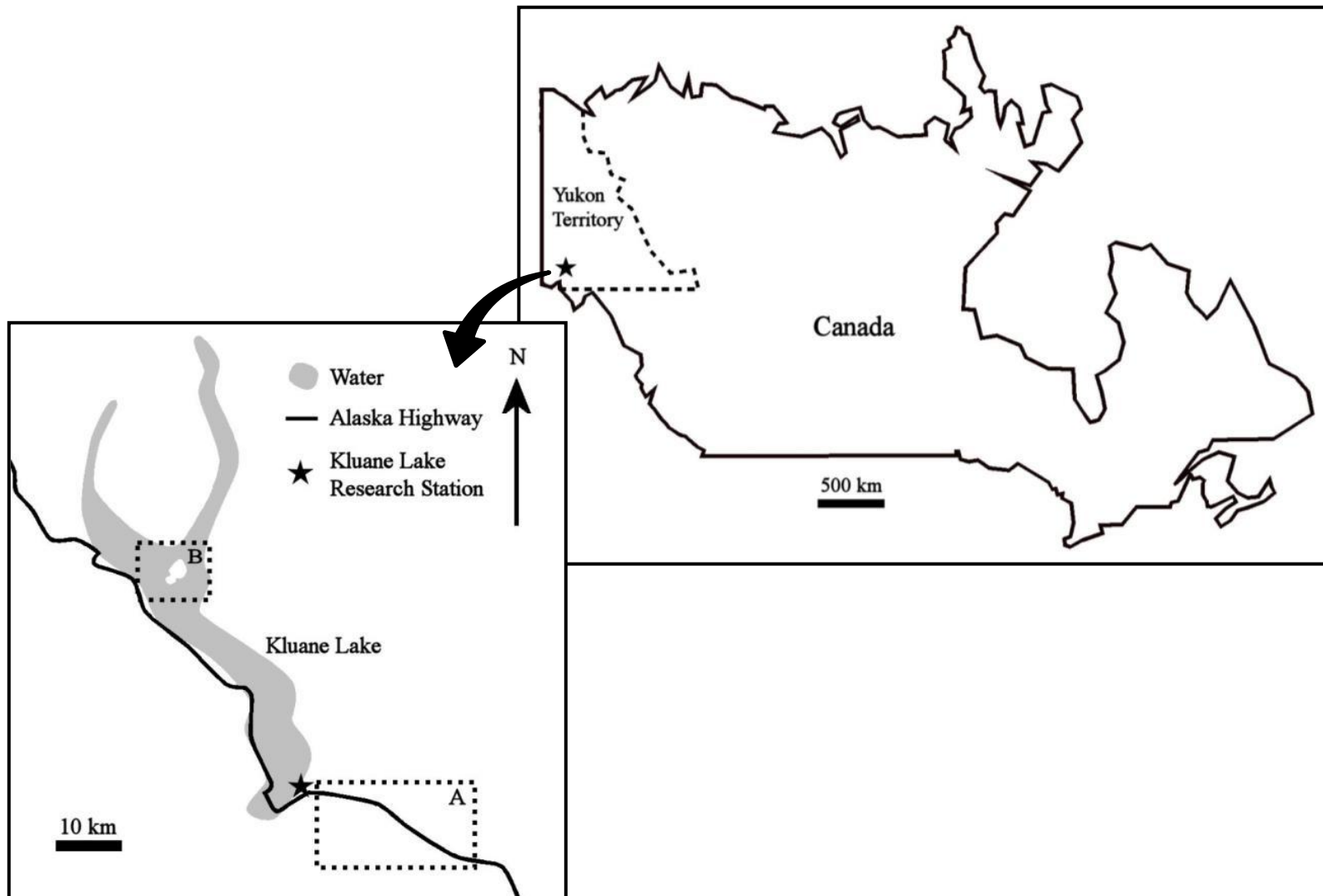


Figure 1.1. The Arctic Institute of North America’s Kluane Lake Research Station (61°N , 138°W) is located on the southeastern shore of Kluane Lake in the southwestern corner of Yukon Territory, Canada. Live trapping grids used in this area are located east of the research station along the Alaska Highway (A), and on Jacquot Island (B). See Figure 1.2 for expanded views of A and B.

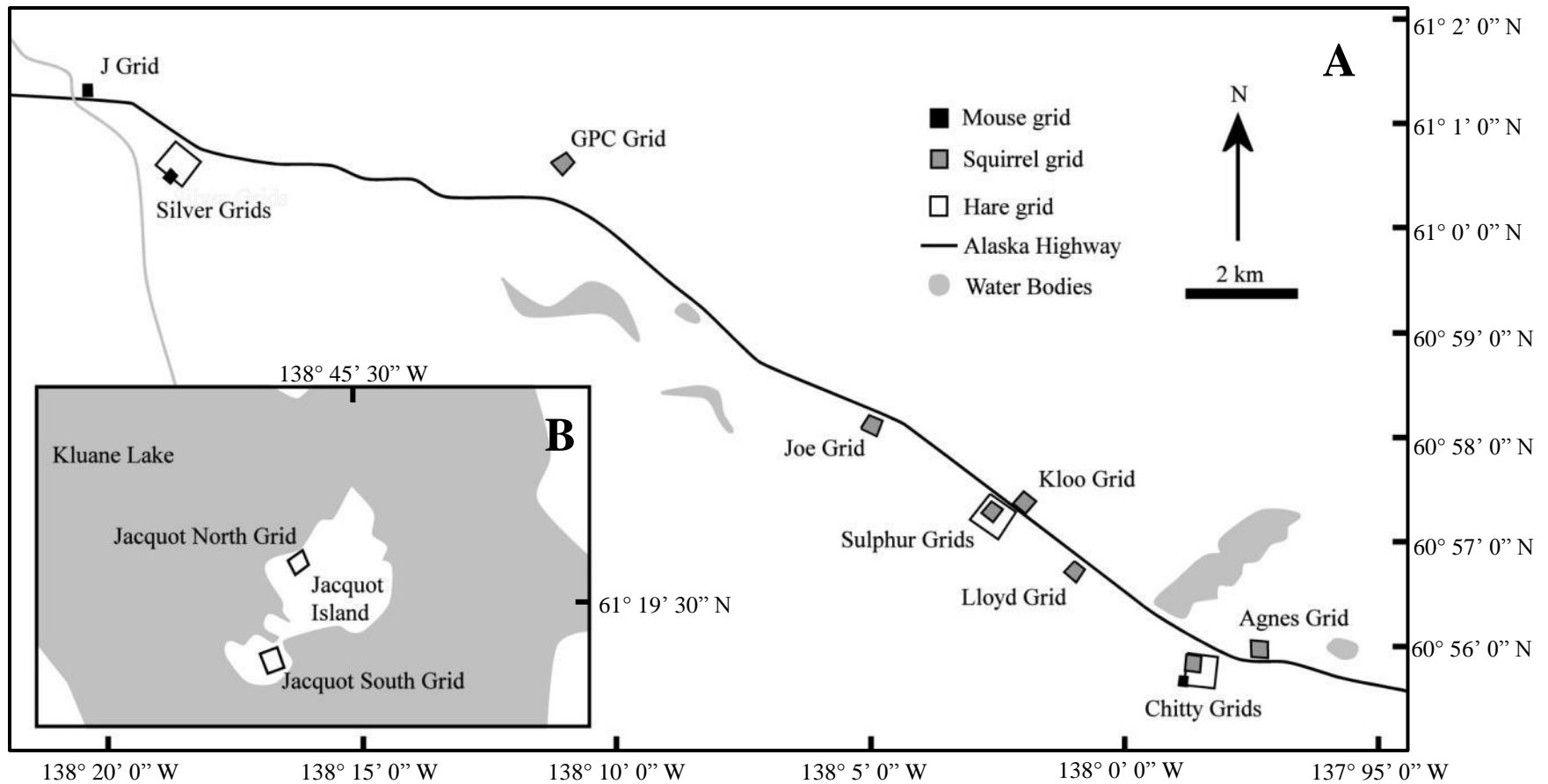


Figure 1.2. Magnified view of the Alaska Highway east of the Arctic Institute of North America's Kluane Lake Research Station. Silver and Chitty mouse grids overlap with their respective hare grids but do not use the same trapping stations; Chitty and Sulphur squirrel grids are subsets of their respective hare grids. B. Magnified view of Jacquot Island. A and B are shown at the same scale and orientation.

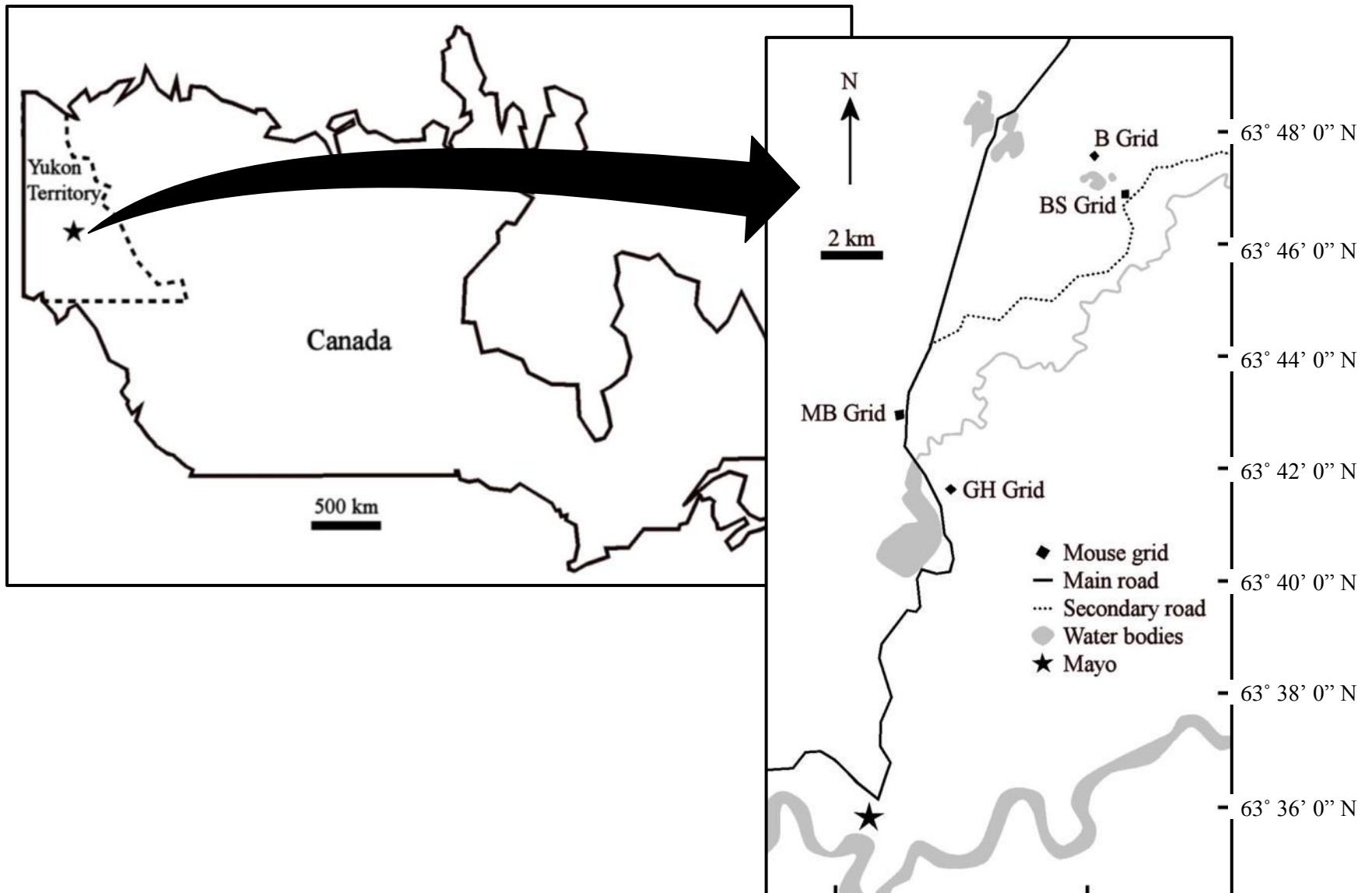


Figure 1.3. The Mayo study site (63°N, 136°W) is located in central Yukon Territory. Live trapping grids used in this area are located north of the town and are accessible via unpaved roads.

Chapter 2 - Density Estimation of Northern Red-Backed Voles (*Clethrionomys Rutilus*) and Deer Mice (*Peromyscus Maniculatus*) Using Remote Cameras

Introduction

Remote cameras were first used to assess animal biodiversity in the 1920's (Chapman 1927), but since then remote cameras have become a valuable tool for studying wildlife (O'Connell et al. 2011). Within the mammalian remote camera literature, estimating population density is now the most common use of remote cameras (McCallum 2013).

Remote cameras are appealing because they are non-invasive compared to alternative methods for estimating population density like live trapping and mark-recapture, which can be stressful and disruptive for many species. (Fletcher and Boonstra 2006) observed symptoms of physiological stress (elevated corticosterone, blood glucose, and hematocrit concentrations) in live trapped *Microtus pennsylvanicus*, and live trapping can cause increased faecal glucocorticoid levels in *Peromyscus maniculatus* (Harper and Austad 2001). Even in species where live trapping does not appear to elicit a significant physiological stress response, the disruption of normal behaviours like nursing offspring can have long-lasting impacts on a population being live trapped, as maternal care is known to have a strong impact on the development of stress responses in rodents (Caldji et al. 2000).

The object of my study was to determine if camera-generated encounter or "hit" rates could be used to estimate densities of northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*) in Yukon boreal forest during the summer (snow-free) months. As described in Chapter 1, previous attempts to use remote camera hit rates to estimate population density of species have utilized hit windows, groupings, or delays to account for animal encounters with cameras that generate more than one image or video, but it is unclear

how these protocols influence any observed correlation between hit rates and independently obtained estimates of population density. To address this issue, I compared camera hit rates to population density estimates obtained through live trapping and mark-recapture methods, and asked the following two questions. First, does the protocol one uses for defining 'hits' affect the relationship between hit rates and estimated densities? Specifically, is there a hit window duration that maximizes the correlation between hit rate and live-trapping-based density estimates? Secondly, given the “best” hit window, can I use hit rates to estimate accurately the density of *Clethrionomys rutilus* and *Peromyscus maniculatus*?

Materials and Methods

Study Sites and Trapping

Live trapping and filming were conducted on three trapping grids in the Kluane Lake region (61°N, 138° W) in southwest Yukon Territory in May, June, July and August of 2010, 2011 and 2010, and on four grids near to the town of Mayo in central Yukon Territory (63°N, 136°W) in July of 2012. My general procedure was to conduct a 2-day filming session using 15-16 cameras on a grid, followed by a 3-day live trapping session on that grid. My experimental unit was one grid; a hit rate for a given filming session was calculated by pooling the footage from all of the cameras operating during that filming session together (see below).

The forest in the Kluane region is dominated by white spruce (*Picea glauca*) with some balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*). Gray willow (*Salix glauca*) is the predominant shrub, followed by bog birch (*Betula glandulosa*), *Potentilla fruticosa*, and soapberry (*Shepherdia canadensis*). Abundant herbaceous species include *Lupinus arcticus*, *Anemone parviflora*, *Mertensia paniculata*, and *Achillea millefolium* (Turkington et al. 2002). The three Kluane grids are located in slightly different habitat; Chitty grid and J grid are

located in open spruce forest, while Silver grid is located in denser spruce forest with considerable deadfall.

The boreal forest in the Mayo region features white spruce (*Picea glauca*), black spruce (*Picea mariana*), and trembling aspen (*Populus tremuloides*). Shrubs found in this area include willow (*Salix* sp.) and dwarf birch (*Betula glandulosa*), and ground cover species include kinnikinnick (*Arctostaphylos uva-ursi*), cranberries (*Vaccinium vitis-idaea*), blueberries (*Vaccinium* sp.), as well as various species of moss and lichen. MB grid is located in open forest with some shrub cover and abundant ground cover, GH grid is located in an area that was burned in 1990 and currently features abundant deadfall with some shrub cover and minimal groundcover. BS grid is located in open forest with minimal shrub cover and thick ground cover, and B grid is located in an area that was burned in 1972 and currently features abundant deadfall, dense shrub cover and dense ground cover. Data were collected in Mayo in an attempt to maximize the range of densities at which *Clethrionomys* and *Peromyscus* were trapped and filmed.

Each of the seven grids has 100 stations laid out in a 10x10 fashion, with 15 m between stations. The Kluane grids have a single Longworth live trap at every station, each covered by a wooden board to protect it from the elements, and placed inside a box or wire cage that allows for access by mice but not squirrels or larger animals. The Mayo grids have a single Longworth live-trap at every other station (A1, B2, A3, B4, etc.), covered with a small metal plate as protection from the elements. Live trapping sessions at both study sites consisted of 3 days of trapping, which were preceded by a 2-day prebait period during which a filming session was also conducted. . Longworth live traps were supplied with cotton for bedding and baited with seed oats in the afternoon or evening of the first day of the prebait period and left locked open. Cotton

was replaced where needed, oats were replenished, and apple slices were added to each trap in the evening of the first day of trapping, when the traps were set. Traps were checked the morning and evening of the second trapping day, and the morning of the third trapping day, at which time the oats and apple were removed and the traps locked open and left in position. Captured animals were tagged using numbered fingerling fish tags, and their mass, sex, and reproductive status were recorded. All live-trapping was carried out under protocols approved by the UBC Animal Care Committee and followed the standard animal care principles of the American Society of Mammalogists (Gannon and Sikes 2007).

Density estimates for each species for each trapping session were calculated using the DENSITY 4.4 program (<http://www.otago.ac.nz/density>) with a maximum-likelihood estimate of recapture distances when sample sizes were large. I used the default parameters for DENSITY 4.4 for all estimates and set the buffer width to 100 m. When sample sizes were small (<3 individuals) I used minimum number known alive (MNA) to estimate abundance and converted this to a density estimate by the use of an effective average grid area of 3.43 ha.

Remote Cameras

I used a total of 34 cameras of the following models: 3 Bushnell Trophy Cams (model 119455), 11 SG550 ScoutGuard cameras and 20 SG560 ScoutGuard cameras. All three models are equipped with a built-in passive infrared detector for detecting motion, and an infrared lamp for filming at night. 2GB memory cards of various brands were used in the Bushnell and SG550 ScoutGuard cameras, and 8GB memory cards of various brands were used in the SG560 ScoutGuard cameras.

Filming sessions took place during the prebait periods preceding trapping sessions; cameras were placed on a grid at the start of the prebait period, at random stations with

constraints such that, within a summer, a given trapping station on a grid was not filmed at twice. Additionally, cameras were never placed at adjacent trap stations during a filming session and were, therefore, always at least 30 m apart. 15-16 cameras were used for each filming session.

Wooden stakes were pounded into the ground 75 cm from the front of the trap, and the cameras were secured to the stakes approximately 15-20 cm above ground level pointing toward the front of the trap. Any obstructing vegetation was removed or pushed out of the way to give cameras a clear view of the traps. I angled the cameras downward using twigs or cones as wedges and for the SG550 ScoutGuard models I used a laser pointer held to the side of the cameras to aim them. The Bushnell and SG560 ScoutGuard were aimed without the aid of a laser pointer. All cameras were placed such that the mouth of the trap would appear in the upper half of the frame of the footage.

I set all of my cameras to record a 60-second video when triggered, and I set the delay option to the lowest possible setting for all cameras; in the ScoutGuard cameras this results in a delay of less than 1.2 seconds between videos and in the Bushnell cameras the delay is approximately 1 second. Motion sensitivity in all cameras was set to high, except for the following sessions, in which sensitivity was set to normal: Chitty 1, Chitty 2, J 1, J 2, Silver 2, and Silver 3. At this time cameras were often triggered by vegetation moving in the breeze, generating excessive amounts of uninformative footage that filled up memory cards before the end of the prebait period. Experimenting with the cameras in controlled settings suggested that changing the sensitivity from high to normal reduced the amount of non-animal-induced footage but had a minimal effect on the amount of animal-induced footage obtained.

Statistics

All statistical analyses were done in R version 2.14.2 (R Development Core Team 2012, www.R-project.org). To address my first question of whether hit window has an effect on the correlation between hit rates and live-trapping-based density estimates, I calculated hit rates for each filming session using different hit windows. The shortest hit window I used was 1 minute; this is equivalent to treating all videos as independent hits. Applying a longer hit window, for example, 5 minutes, involved grouping videos that were obtained at the same camera, featured the same species, and were taken within 5 minutes of each other, together as a single hit. I used hit windows of 5, 10, 30, 60, 90, 120, 150, 180, 210, 240, 720, and 1440 minutes. Hit rates for *Clethrionomys* and *Peromyscus* were calculated for each filming session as the total number of hits of the species obtained during the first 48 hours of the filming session, divided by the total effort in camera-days (the number of 24-hour periods each camera was operational for during that filming session, summed together). In instances in which a camera's memory card filled in less than 48 hours, the amount of time that camera was operational for was determined using the time stamp of the last video made by that camera.

Cameras that experienced lamp failures at any point during a filming session were excluded from that filming session's hit rate calculations. In addition, three cameras operating in two filming sessions (2 from Chitty 3 and 1 from Silver 6) were omitted from the *Clethrionomys* hit rate calculations and subsequent analysis due to suspected hit rate over-inflation. The number of videos these cameras obtained was high compared to the other cameras on the grid during their respective filming sessions, and the footage was predominantly of a vole sitting near the entrance of the live-trap, with little movement between videos, suggesting one individual was visiting the trap for an extended period of time. Counts and hit rates for *Clethrionomys* reported

in the results do not include data from these cameras. These omitted data comprised 1% of the total overall camera effort for all of the filming sessions

Microtine voles (*Microtus* spp.) were occasionally captured during live trapping and detected during filming; there are several species of the *Microtus* genus found in Kluane, but this genus is relatively rare compared to *Clethrionomys*. Pelt colour was the primary feature used to distinguish between *Clethrionomys* and *Microtus* in footage obtained during the day, but all three models of camera I used employed an infrared lamp to film at night, which results in black-and-white footage. In such footage, distinguishing between vole species was difficult to do with confidence. For the majority of filming sessions, in which no *Microtus* were identified in day-time footage, all night-time footage of voles was assumed to be of *Clethrionomys*. For the two filming sessions in which *Microtus* were observed in day-time footage (J 2 and Chitty 2), the ratio of *Clethrionomys*-to-*Microtus* day-time hits for that filming session was used to estimate the number of night-time hits of that filming session that were of *Clethrionomys* and *Microtus*. Low detection of *Microtus* by both trapping and filming did not result in sufficient data to conduct an analysis; *Microtus* are grassland voles, and all of the grids are located in forest habitat. Further investigation into *Microtus* would require filming and trapping in meadow habitat.

I used multiple linear regression to determine if live-trapping-based population density estimates could be predicted by hit rates for *Clethrionomys* and *Peromyscus*. Two additional candidate variables and the full complement of interaction terms were included in the preliminary models - the week of the year during which the live trapping session was conducted, and a weather rank variable based on the estimated amount of precipitation to fall during the trapping portion of the live trapping session. For Kluane grids, this was based on Environment

Canada precipitation data recorded at the Burwash airport and the Haines Junction airport; if the total precipitation for the three trapping days of the live trapping session averaged between the two stations was 0 the session was assigned a rank of 0, if between 0.1 and 10 mm a rank of 1, and >10 mm a rank of 2. For the Mayo grids, ranking was based on Environment Canada precipitation records for the Mayo airport. Grid and year were included as random factors. Both trap-based density estimates and hit rates were square-root transformed to achieve linearity for both species. Backwards stepwise model simplification was done using the stepAIC function of the MASS library (Venables and Ripley 2002), followed by manual backwards simplification using partial F-tests, for each species and each hit window. For models that did not simplify to a single explanatory variable, included variables were assessed for multicollinearity; where multicollinearity between hit rate and another variable was found, hit rate was retained in the model and the other variable removed.

Excluding cameras that were operational for less than 40 hours had no effect on the identity of the parameters included in the final models for all hit windows for *Clethrionomys* or *Peromyscus*, and no more than a 0.1% change in R^2 values for those models, therefore cameras that were not operational for a full 48 hours were retained in the analysis.

Results

Cameras were operational for a total of 582.5 days over the course of this investigation. Effort for a single filming session ranged from 17.6 to 29.5 camera-days (Table 2.1). Pooling across sites, a total of 1165 60-second videos of mice and voles were obtained during the filming sessions; 669 of these were of *Clethrionomys*, 28 videos were of *Microtus*, and 468 videos were of *Peromyscus*. *Clethrionomys* was filmed on every grid and *Peromyscus* was filmed only on Chitty, J, Silver and MB.

The maximum total number of 60-second *Clethrionomys* videos obtained in a single filming session was 116 (24 camera-days of filming effort); converting this to a hit rate using the various hit windows results in a hit rate ranging from 0.75 hits/camera-day (1440 minute hit window) to 4.83 hits/camera-day (1 minute hit window). The maximum total number of 60-second *Peromyscus* videos obtained in a single filming session was 127; converting this to a hit rate using the various hit windows results in a hit rate ranging from 0.78 hits/camera-day (1440 minute hit window) to 5.82 hits/camera-day (1 minute hit window). *Microtus* were filmed during Chitty 2, with a total count of 12 60-second videos, and J 2, with a total count of 16 60-second videos.

A total of 102 individual *Peromyscus* were live trapped over the course of this investigation, all but 5 of which were live trapped on either J grid or Chitty grid (Table 2.1). Live-trapping-based density estimates for this species ranged from 0 to 5.90 animals/ha. A total of 217 individual *Clethrionomys* were live trapped during this investigation; this species was live trapped during all trapping sessions on all grids. Estimated densities of *Clethrionomys* ranged from 0.29 to 9.21 animals/ha. A total of 32 *Microtus* individuals were live trapped during 12 of the 23 trapping sessions. Densities for this genus ranged from 0 to 2.77 animals/ha.

Hit rate was the best predictor of live-trapping-based density for all hit windows for both species; including week of the year and weather did not significantly improve the fit of any model for any hit window. Including grid or year as a random effect also did not significantly improve the fit of any of the models. The final model for each hit window for both species is therefore a simple linear regression of hit rate on live-trapping-based density estimates. Both variables were square-root transformed for linearity.

Peromyscus R^2 values changed only slightly from 0.81 to 0.84 over the range of hit windows, and the 90-minute hit window showed the maximum R^2 value (Figure 2.1). *Clethrionomys* R^2 values were more sensitive to the exact hit window chosen, and ranged from 0.48 to 0.59; increasing the duration of the hit-window improved model fit until the 90-minute window (Figure 2.1). The regressions for all of the hit windows were significant for the two species, but the 90-minute hit window regressions were chosen as the best based on model selection procedures suggested by Burnham and Anderson (2002).

The regression models for the 90-minute hit window were highly significant for both *Clethrionomys* ($F_{1,21} = 29.7$, $p < 0.001$, Figure 2.2; Table 2.3) and *Peromyscus* ($F_{1,21} = 111.4$, $p < 0.001$, Figure 2.3; Table 2.3). Slope estimates were highly significant for both *Clethrionomys* and *Peromyscus* ($t_{21}=5.45$, $p < 0.001$ and $t_{21}=10.55$, $p < 0.001$ respectively), while intercept estimates were not significant for either species ($t_{21} = 2.01$, $p=0.057$ and $t_{21}=1.01$, $p = 0.325$ for *Clethrionomys* and *Peromyscus* respectively).

Discussion

In this study I confirm that motion-detecting cameras are capable of detecting animals as small as mice and voles, and suggest that camera-generated hit rates may be an accurate means of estimating the density of these two species. This is the first attempt to use motion-detecting cameras to estimate small rodent densities. Cameras have been used to detect small (<1 kg) terrestrial mammals including anitchinus (Order Dasyuromorphia) and possums (Order Dirodontia) (De Bondi et al. 2010), squirrels (*Sciurus carolinensis* and *S. vulgaris*) and dormice (*Muscardinus avellanarius*) (Cerbo and Biancardi 2013). Cameras have also been used to estimate the density of some terrestrial mammals, with European pine marten (*Martes martes*)

being the smallest (1-2 kg) (Manzo et al. 2011). With an adult mass of less than 50 g, *Clethrionomys* and *Peromyscus* are considerably smaller than the European pine marten.

One would expect changing the hit window to have an effect when encounters with cameras are not always the same duration; if some animals spend more time around cameras than others, then the number of videos or photos obtained is no longer simply due to density, but is also due to individual behaviour. Such heterogeneity in behaviour around the cameras is especially likely in this study because I used bait to attract mice and voles to the live traps. Differences in food availability within home ranges could lead to some individuals spending more time around live traps eating the bait than others. An additional condition of my set-up that can contribute to variation in the number of videos produced during a single encounter is that once inside the live trap, the mouse or vole is hidden from the camera, and can therefore be near a camera but not generating footage. With two possible sources of behavioural variation (how an individual responds to the bait, and how long the individual chooses to be in the live trap), I expected hit window duration to have a large impact on the relationship between hit rate and density for both species.

The results for *Clethrionomys* support this expectation; goodness-of-fit of the relationship between hit rate and density was very sensitive to hit window duration (Figure 2.1). Conversely, hit window duration had little effect on the goodness-of-fit of the regression for *Peromyscus*. The implication here is that *Clethrionomys* exhibit more behavioural heterogeneity around cameras compared to *Peromyscus*, but such heterogeneity could be related to density itself. As density increases, there is a greater chance of a camera being placed near a burrow that could increase the number of hits that cameras obtain compared to cameras not located near active burrows. As *Peromyscus* were generally less abundant than *Clethrionomys* during this study, such a

phenomenon might not have been as important for this species, simply because there were so few active *Peromyscus* burrows on any given grid.

It is unclear why the 90-minute hit window is the “best” for both species; there are no instances in which a camera is continuously triggered for 90 minutes, and there are only three instances in which it appeared that a single individual was using the live trap extensively, and those were excluded from the analysis. One explanation is that voles encountering live traps with cameras may be spending considerable amounts of time around the trap, but not necessarily within the camera’s detection zone; individuals could be moving short distances away from traps, or entering the traps and disappearing from view. Because individuals cannot be identified, what might appear to be several different voles visiting a single live trap within 90 minutes could actually be a single vole, leading to hit rate inflation and a “decoupling” of hit rates from population density. Caching the bait for later consumption could generate this pattern of footage, and there were several instances in which voles were observed removing bait from the live trap without consuming it in front of the camera.

Using a 90-minute hit window, hit rates account for almost 60% of the variation in *Clethrionomys* live-trapping based density estimates. The scatter in the data is considerable, and of the 20 mark-recapture densities for which confidence intervals could be calculated, 6 such intervals do not encompass the model-predicted density. In general this suggests that hit rates may be appropriate for a general assessment of density for this species, but would not be an appropriate method for obtaining precise density estimates. Such discrepancies between predicted densities and live trap-based densities may be due to misidentification of voles in night-time footage. All vole footage obtained at night was assumed to be of *Clethrionomys* except during the two filming sessions in which *Microtus* were identified in day-time footage.

There were, however, 12 live trapping sessions in which *Microtus* were captured, 10 of which didn't obtain any *Microtus* day-time footage during their respective filming sessions. Using the ratio of live trapped *Clethrionomys*-to-*Microtus* to estimate the amount of night-time vole footage that was of *Clethrionomys* improves the correlation between live trap-based density estimates and hit rates calculated using a 90 minute hit window (R^2 increases from 0.59 to 0.61), but this improvement is small and suggests that misidentification of voles as *Clethrionomys* when they were in fact *Microtus* is not a major concern, at least at these densities. *Microtus* densities at Kluane can be much higher than those reported here (Krebs and Cowcill 2010) and not being able to distinguish between *Clethrionomys* and *Microtus* in night time footage may be a serious limitation for this method when *Microtus* are more abundant.

Another possible explanation involves the hit window itself. The 90-minute hit window is “best” when considering the entire data set, but may be severely misrepresenting the number of encounters that actually occurred at a camera or filming session level, leading to a reduced correlation between hit rate and density.

Hit rates calculated using a 90-minute hit window accounted for 84% of the variation in the *Peromyscus* live-trapping-based density estimates. The scatter in the *Peromyscus* data is less pronounced than in the *Clethrionomys* data, and of the 13 95% confidence intervals calculated for the mark-recapture densities, only 1 does not encompass the model-predicted density (Figure 2.3).

Further work is needed to increase the applicability of this method. Using bait to attract animals to the live traps during filming sessions is likely to have generated at least some of the variation that necessitated the use of a 90 minute hit window; determining if mice and voles are likely to pass in front of remote cameras without using bait or live traps to lure them there, and if

hit rates still correlate to density, could improve the applicability of this method by eliminating the cost of bait and the cost and effort of setting up live traps in front of remote cameras.

In addition, vole densities shown here do not represent the entire range of possible densities in these locations; historically, Kluane has had *Clethrionomys* densities as high as 30 animals/ha (Krebs et al. 2011) whereas the highest density observed during this study was 9.2 animals/ha. For this method to be applicable, determining the relationship between hit rate and density for the entire range of possible densities is necessary.

Differences between Kluane and Mayo were assumed to be negligible in this investigation, but because baits and live traps were used to lure animals in front of the cameras, the hit rates obtained are not only due to density, but also related to behaviour. Response to bait and live traps may differ within a species among different habitat types, and further work into determining if this is a significant effect would help to determine if the relationship between hit rate and density in one location can be applied to other locations with different habitats and community composition.

The effects of camera settings should also be explored. Determining if using the delay setting on the cameras would reduce the amount of footage to view without compromising the correlation between hit rate and density would be useful, and of interest in this case because the hit windows were applied to the *Clethrionomys* and *Peromyscus* data separately, and therefore the hit window is not analogous to the delay setting on the camera.

Overall, my results obtained in this study are encouraging because they indicate it may be possible to census small rodents with cameras, without the necessity of the more difficult and invasive effort of live trapping, marking, and releasing animals.

Table 2.1. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*) by grid. Densities are animals/ha, with 95% confidence limits where applicable shown below in parentheses.

	Chitty						J						
	1	2	3	4	5	6	1	2	3	4	5	6	7
	10-Jun-10	15-Jul-10	13-May-11	23-Jul-11	9-May-12	6-Aug-12	1-Jun-10	6-Jul-10	8-May-11	19-Jul-11	6-May-12	21-May-12	6-Aug-12
<u>Video counts</u>													
<i>Clethrionomys</i>	5	25†	0	15	6	64	2	67†	35	24	20	92	116
<i>Peromyscus</i>	14	13	23	109	15	127	18	34	17	63	1	9	11
<u>Filming effort</u>													
Camera-days	23.0	28*	24	26	20.0	23.7	26	26.9	26	28	24	28	24
Cameras	13	14*	12	13	11	13	13	14	13	14	12	14	12
<u>MNA</u>													
<i>Clethrionomys</i>	4	18	1	15	8	19	2	11	10	18	16	18	42
<i>Peromyscus</i>	3	8	5	19	8	17	6	15	5	12	3	2	10
<u>Estimated Density</u>													
<i>Clethrionomys</i>	0.36 (0.14, 0.97)	4.82 (2.89, 8.03)	0.29 -	3.18 (1.56, 6.48)	0.86 (0.40, 1.88)	3.03 (1.23, 7.47)	0.58 -	1.09 (0.57, 2.09)	1.77 (0.82, 3.83)	5.81 (3.61, 9.34)	3.27 (1.70, 6.29)	2.57 (2.00, 3.28)	9.21 (6.46, 13.11)
<i>Peromyscus</i>	0.65 (0.17, 2.40)	2.72 (1.27, 5.84)	1.26 (0.39, 4.08)	5.47 (3.32, 9.01)	1.38 (0.49, 3.89)	5.90 (9.93, 3.51)	1.84 (0.79, 4.24)	4.35 (2.19, 8.64)	0.52 (0.21, 1.33)	4.73 (2.54, 8.79)	0.63 (0.10, 2.40)	1.04 (0.20, 5.36)	3.12 (1.30, 7.46)

† Count consists of total number of day-time videos of *Clethrionomys*, as well as the number of night-time videos estimated to be of *Clethrionomys* using the ratio of day-time *Clethrionomys*-to-*Microtus* videos.

* Videos from two cameras excluded from the *Clethrionomys* counts shown due to suspected hit-rate inflation (filming effort of 23.6 camera-days).

Table 2.1 continued. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*) by grid. Densities are animals/ha, with 95% confidence limits where applicable shown below in parentheses.

	Silver						MB	GH	BS	B	Mean	Total
	1	2	3	4	5	6	1	1	1	1		
	22-May-10	20-Jun-10	29-Jul-10	1-Jun-11	27-Jul-11	9-Jun-12	12-Jul-12	12-Jul-12	16-Jul-12	16-Jul-12		
<u>Video counts</u>												
<i>Clethrionomys</i>	12	9	14	1	91	11	39	8	1	12	27.5	577
<i>Peromyscus</i>	0	0	1	0	5	0	8	0	0	0	20.3	468
<u>Filming effort</u>												
Camera-days	17.6	26.2	25.9	19.2	28	24.9**	28.3	27.4	27.9	29.5	25.2	582.5
Cameras	14	14	14	14	14	13**	15	14	14	15	13.4	309
<u>MNA</u>												
<i>Clethrionomys</i>	7	3	4	5	27	4	5	6	3	9	11.1	
<i>Peromyscus</i>	0	1	0	0	3	0	1	0	0	0	5.1	
<u>Estimated Density</u>												
<i>Clethrionomys</i>	0.87 (0.31, 2.47)	0.79 (0.23, 2.68)	0.87 (0.31, 2.47)	1.09 (0.41, 2.86)	7.87 -	0.37 (0.14, 1.00)	0.97 (0.25, 3.78)	1.73 (4.08, 0.73)	1.32 (0.18, 9.78)	1.89 (0.82, 4.34)	2.4	
<i>Peromyscus</i>	0 -	0.29 -	0 -	0 -	0.87 -	0 -	0.29 -	0 -	0 -	0 -	1.5	

** Videos from one camera excluded from the *Clethrionomys* count due to suspected hit-rate inflation (filming effort of 22.9 camera-days)

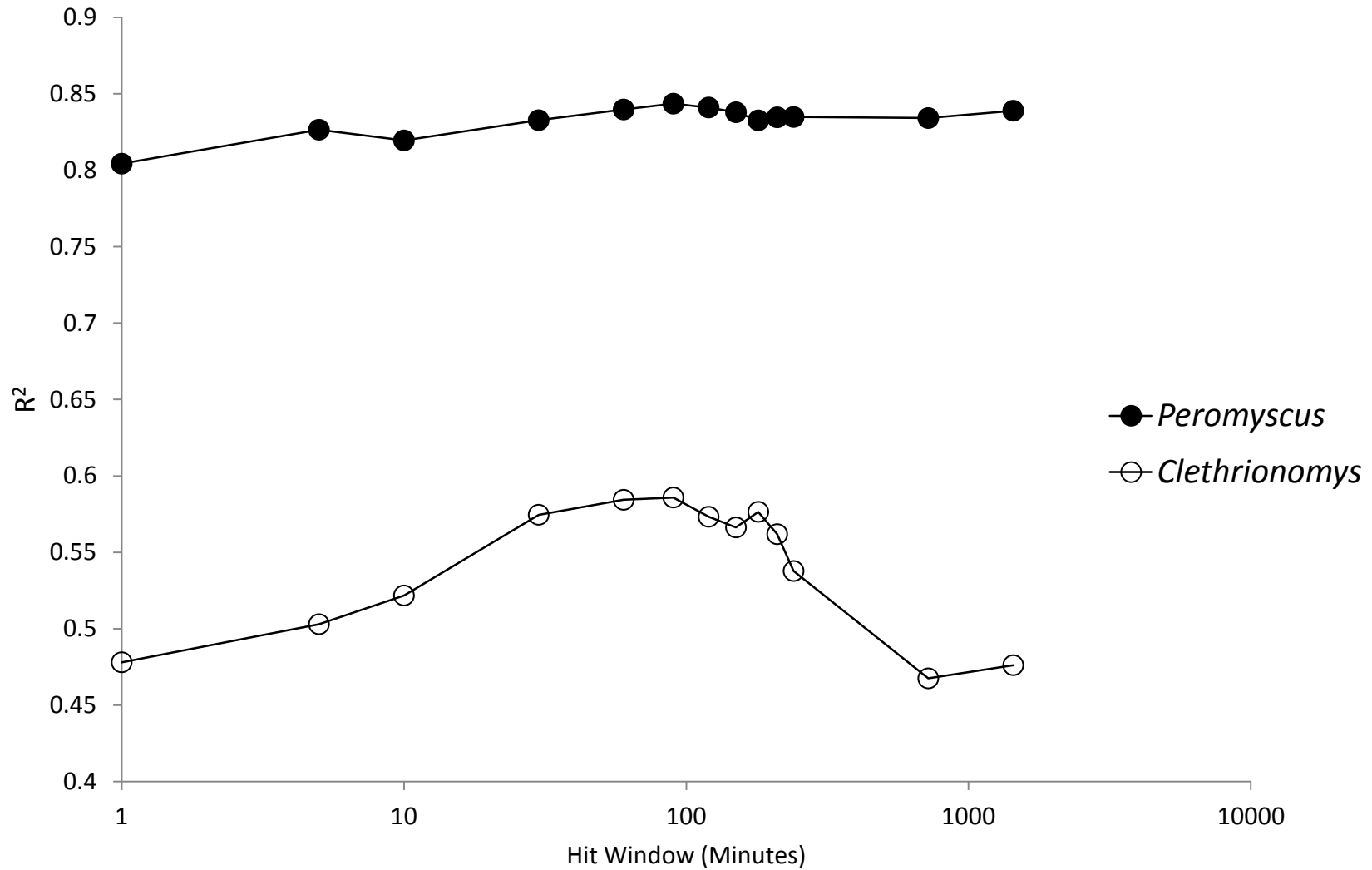


Figure 2.1. R² values for linear regressions between live-trapping-based population density estimates and hit rates calculated with different hit window lengths for deer mice (*Peromyscus maniculatus*) and northern red-backed voles (*Clethrionomys rutilus*), Kluane Lake, 2010-2012.

Table 2.2. Linear regressions to predict live-trapping-based estimated densities from camera-based hit rates for northern red-backed voles (*Clethrionomys rutilus*) and deer mice (*Peromyscus maniculatus*). Hit rates were calculated using a 90 minute hit window for both species, density is in animals/ha, and density and hit rate were square-root-transformed to achieve linearity.

Species	Regression terms	Sample Size	Mean Squared Error	Slope Standard Error	R ²
<i>Clethrionomys</i>	$\sqrt{\text{estimated density}} = 1.61\sqrt{\text{hit rate}} + 0.41$	23	0.022	0.30	0.59
<i>Peromyscus</i>	$\sqrt{\text{estimated density}} = 1.89\sqrt{\text{hit rate}} + 0.11$	23	0.016	0.18	0.84

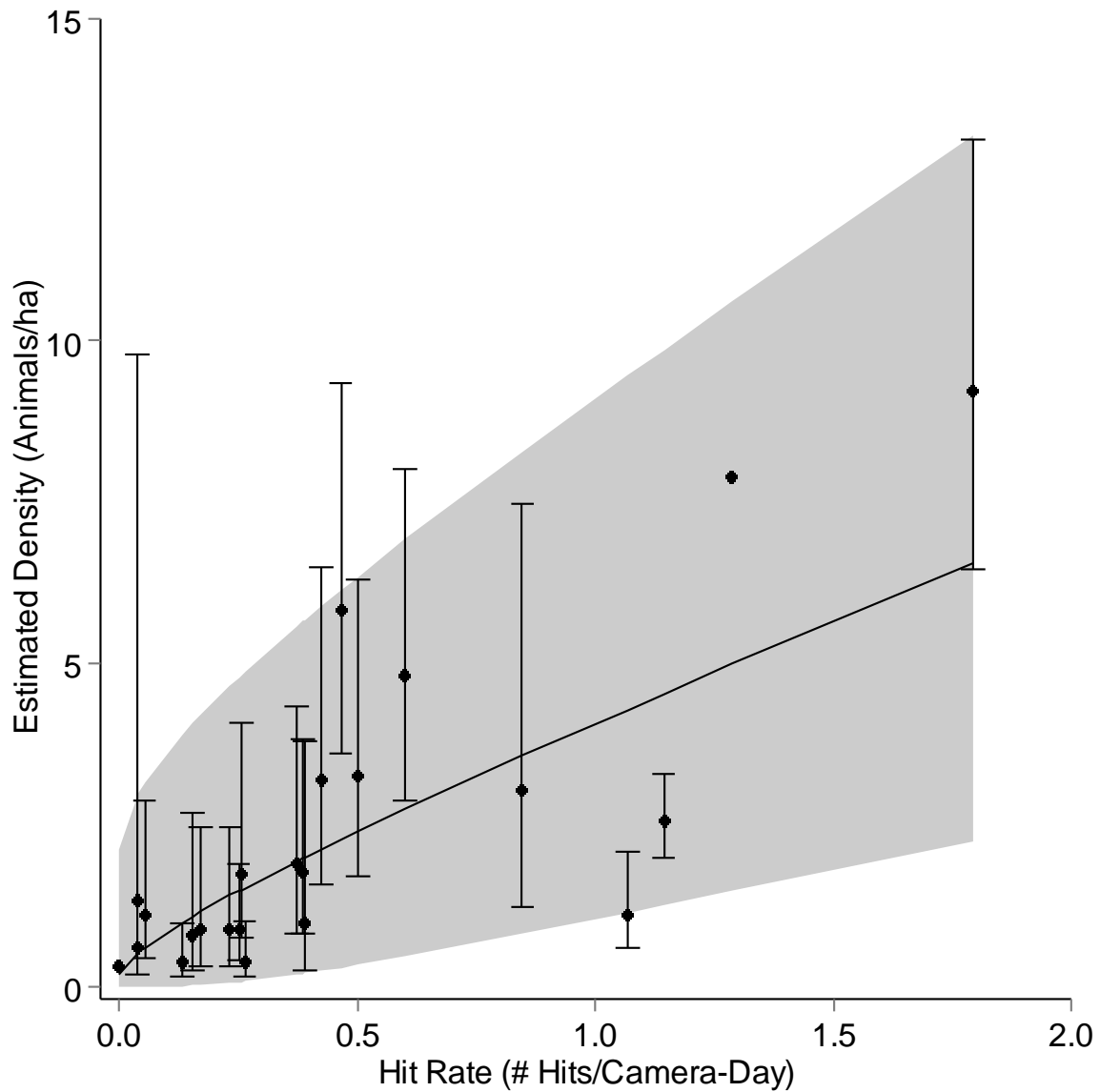


Figure 2.2. Relationship between hit rates and live-trapping-based density estimates for northern red-backed voles (*Clethrionomys rutilus*) using a 90 minute hit window. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2=0.59$), grey band indicates 95% prediction intervals. Error bars are 95% confidence intervals for density estimates.

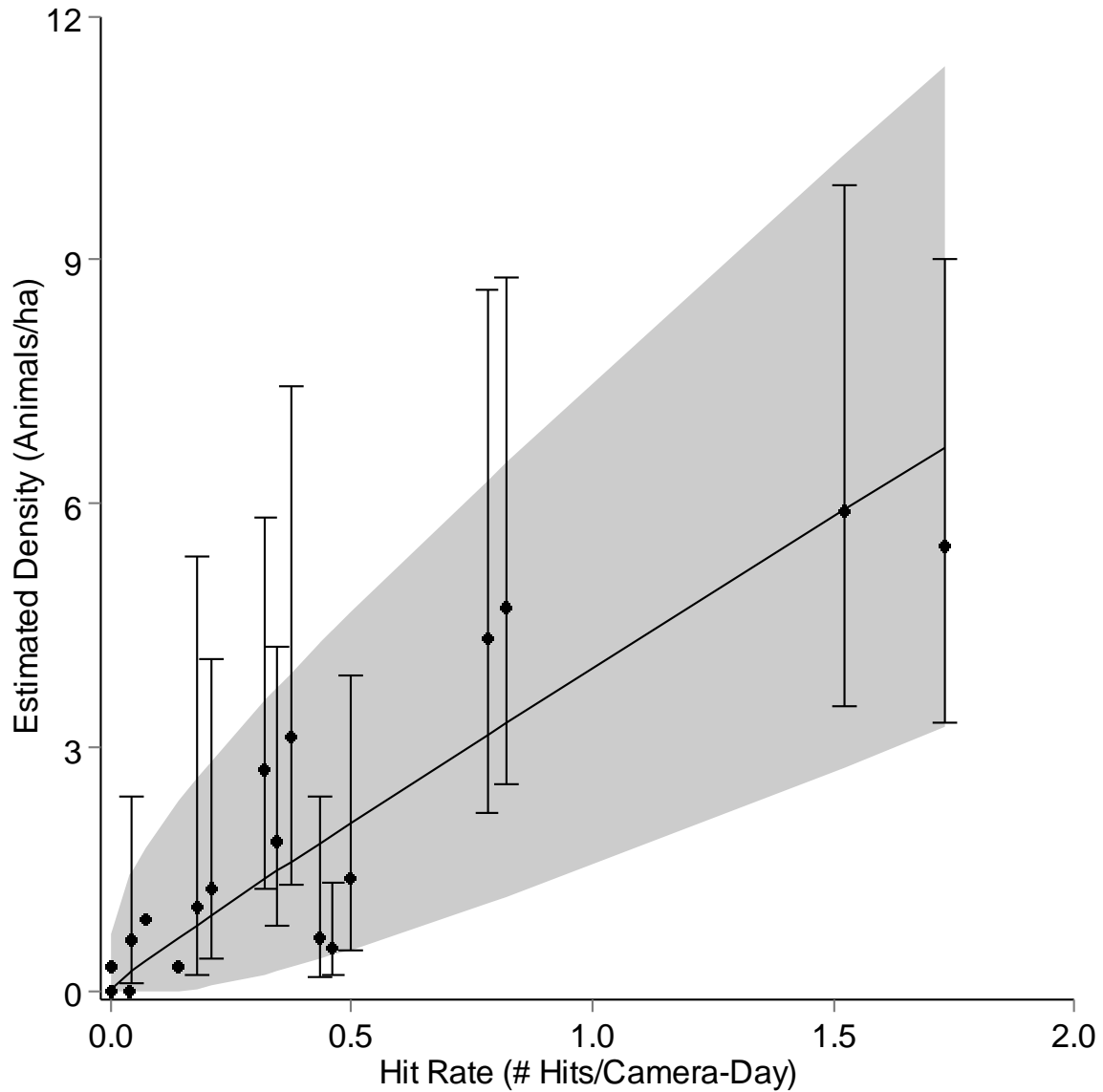


Figure 2.3. Relationship between hit rates and live-trapping-based density estimates for deer mice (*Peromyscus maniculatus*) using a 90 minute hit window. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2=0.84$), grey band indicates 95% prediction intervals. Error bars are 95% confidence intervals for density estimates.

Chapter 3 - Density Estimation of Snowshoe Hares (*Lepus americanus*) and Red Squirrels (*Tamiasciurus hudsonicus*) Using Remote Cameras

Introduction

Motion detecting cameras have been used to survey animal communities since the 1920's (Chapman 1927); within the past 15 years, the predominant use of mammalian remote camera investigations has been to estimate animal population density (McCallum 2013). Cameras are appealing for several reasons; photographing or filming animals is less invasive than techniques such as mark-recapture live trapping for estimating density. Additionally, cameras can be cheaper to operate in the long term by minimizing the amount of time in the field (Rovero and Marshall 2009), and cameras can operate in remote and extreme conditions (McCarthy et al. 2008).

Live trapping and mark-recapture methods are one of the more common ways of estimating small mammal density, but live trapping is known to cause significant physiological stress; Boonstra and Singleton (1993) documented elevated cortisol levels in live trapped snowshoe hares, and Boonstra and McColl (2000) reported elevated levels of blood cortisol in live trapped and handled ground squirrels and speculated that red squirrels experience a similar response to live trapping and handling. In addition, the effects of trapping are not limited to the animals being caught; trapping may disrupt nursing behaviour, which can be particularly serious for species such as snowshoe hares that only visit their litters once every twenty-four hours to nurse (Krebs et al. 2001). Stress induced by trapping may also negatively affect developing leverets prior to parturition; Sheriff et al. (2009) found that stress induced by non-lethal encounters with predators during pregnancy in snowshoe hares resulted in leverets that were smaller and lighter at birth.

The object of this study was to determine if camera-generated encounter or “hit” rates could be used to estimate densities of snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*) in the Yukon boreal forest during the summer (snow-free) months. As described in Chapter 1, previous attempts to use remote camera hit rates to estimate population density of species have utilized hit windows, groupings, or delays to account for animal encounters with cameras that generate more than one image or video, but it is unclear how these protocols influence any observed correlation between hit rates and independently obtained estimates of population density. To address this issue, I compared camera hit rates to population density estimates obtained through live trapping and mark-recapture models, and asked the following two questions. First, does the protocol one uses for defining 'hits' affect the relationship between hit rate and estimated population density? Specifically, is there a hit window duration that maximizes the correlation between hit rates and live-trapping-based population density estimates? Secondly, given the “best” hit window, can hit rates be used to estimate the population density of *Lepus americanus* and *Tamiasciurus hudsonicus*?

Materials and Methods

Study Sites and Trapping

Live trapping and filming for both species were conducted in the Kluane Lake region (61°N, 138° W) in southwest Yukon Territory in May, June, July and August of 2010, 2011, and 2012. The general procedure was to conduct a 2-day filming session using 15-16 cameras on a grid, followed by a 2- or 3-day live trapping session on that grid. My experimental unit was one grid; a hit rate for a given filming session was calculated using the footage from all of the cameras operating during that filming session pooled together (see below).

The forest in the Kluane region is dominated by white spruce (*Picea glauca*) with some balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*). Gray willow (*Salix glauca*) is the predominant shrub, followed by bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*) and soapberry (*Shepherdia canadensis*). Abundant groundcover plants include *Lupinus arcticus*, *Anemone parviflora*, *Mertensia paniculata*, and *Achillea millefolium* (Turkington et al. 2002).

Hares were live trapped on five permanent grids; Jacquot North grid and Jacquot South grid are located on Jacquot Island, which is approx. 5 km² in area and located at the north end of Kluane Lake. Both Jacquot grids consist of 100 stations laid out in a 10x10 fashion, with stations 30 m apart. Single hare-sized tomahawk live traps were located at every other station (A1, B2, A3, B4 etc.) for a total of 50 trapping stations, and the traps were situated under trees for protection from the rain. The remaining three grids, Chitty grid, Sulphur grid and Silver grid, are located on the mainland, between 40 and 60 km southeast of Jacquot Island, along the Alaska Highway. These three grids consist of 400 stations laid out in a 20x20 fashion, with stations 30 m apart. Tomahawk live traps were located at alternating stations along the A, B, G, H, M, N, S, and T rows (A1, B2, A3, B4, etc.) and at D20, F20, I1, K1, P20 and R20 for a total of 86 trapping stations. Silver grid and Jacquot South are located in dense spruce forest with dense undergrowth and considerable deadfall; the remaining grids are located in open spruce forest with less undergrowth and deadfall.

Squirrels were live trapped on seven permanent grids; Agnes grid and Chitty grid are located in open spruce forest with little shrub cover, while Lloyd, Sulphur, Kloo, GPC and Joe are located in denser forest with considerable undergrowth and shrub cover. The Chitty and Sulphur squirrel grids are subset of their respective hare grids, and all seven squirrel grids are

located within 50-500m of the Alaska Highway. Each grid consists of 100 stations laid out in a 10x10 fashion, with stations 30m apart; 50 squirrel-sized tomahawk live traps were located at every other station (A1, B2, A3, B4, etc.), under trees for protection from the weather.

Hare live trapping sessions consisted of a 3 days of trapping, which were preceded by a 2-day prebait period during which a filming session was also conducted. Live traps were supplied with alfalfa cubes on the first day of the prebait period and left locked open; prebait was typically started in the afternoon or evening. Alfalfa was replenished where needed and a slice of apple was placed in every trap in the evening of the first day of trapping when the traps were set. Traps were checked the morning of the second trapping day and closed for the day to prevent red squirrels from getting trapped; traps were reset the evening of the second trapping day. Traps were checked again the morning of the third day, emptied of any bait and closed. Two sessions (Jacquot South 2 and Jacquot North 2) only had one night of trapping due to heavy rainfall.

Squirrel live trapping sessions consisted of 2 days of trapping, which were preceded by a 2-day prebait period during which a filming session was also conducted. Traps were baited with peanut butter and locked open the morning of the first day of prebait. Traps were re-baited with peanut-butter and set at 0700 the morning of the first day of trapping; traps were checked at 0830 and 1000, and again at 1130 at which time they were locked open. Trapping resumed on the second day at 7:00 at which time traps were re-baited and set. Traps were checked at 0830 and 1000 and emptied of peanut butter and closed during the last trap-check at 1130.

Captured animals were tagged using numbered fingerling fish tags, and their mass, sex, and reproductive status were recorded. All live trapping was carried out under protocols approved by the UBC Animal Care Committee and followed the standard animal care principles of the American Society of Mammalogists (Gannon and Sikes 2007).

All squirrel densities were calculated using the DENSITY 4.4 program (<http://www.otago.ac.nz/density>) with a maximum-likelihood estimate of recapture distances when sample sizes were large. I used the default parameters for DENSITY 4.4 for all estimates and set the buffer width to 100 m. The majority of hare live trapping sessions generated sample sizes too small to allow for maximum-likelihood estimation of recapture distances, so all hare densities were estimated using the number of individuals live trapped during a trapping session (hereafter referred to as minimum number alive or MNA) divided by the average effective grid area, calculated from historical live trapping. Effective grid areas were 56.6 ha for Silver, 63.5 ha for Sulphur, 60 ha for Chitty, and 16.5 ha for both Jacquot grids.

Remote Cameras

I used a total of 34 cameras: 3 Bushnell Trophy Cams (model 119455), 11 SG550 ScoutGuard cameras and 20 SG560 ScoutGuard cameras. All three models are equipped with a passive infrared detector for detecting motion and an infrared lamp for filming at night. 2GB memory cards of various brands were used in the Bushnell and SG550 ScoutGuard cameras, and 8GB memory cards of various brands were used in the SG560 ScoutGuard cameras.

Filming sessions were conducted during the prebait periods preceding trapping sessions; cameras were placed on a grid at the start of the prebait period at random stations with constraints such that, within a summer, a given trapping station on a grid was not filmed at twice. On squirrel grids, cameras were never placed at adjacent trap stations during a filming session and therefore were always at least 60 m apart. I used 15-16 cameras during each filming session. Cameras were secured with straps to trees 1-2 m from the trap entrance and 10-30 cm above ground; cameras were placed directly in front of the traps where possible, but when a clear view of the trap entrance was not possible, or when a trap could not be moved or rotated to face the camera without removing it from tree cover, the cameras were moved to the side.

All cameras were set to record a 60-second video when triggered, and the delay option was set to the lowest possible setting for all cameras; in the ScoutGuard this results in a delay of less than 1.2 seconds between videos and in the Bushnells the delay is approximately 1 second. Motion sensitivity in all cameras was set to high.

Statistics

All statistical analyses were done in R version 2.14.2 (R Development Core Team 2012, www.R-project.org). To address my first question of whether hit window has an effect on the correlation between hit rates and live-trapping-based population density estimates, I calculated hit rates for each filming session using multiple different hit windows. The smallest hit window I used was a 1 minute hit window; for the majority of the data set, in which each video is 1 minute in duration, this is equivalent to treating each video as an independent hit. There were 38 instances (17 during squirrel filming, 21 during hare filming) in which a camera malfunctioned and generated videos that were shorter than 60 seconds; applying a 1 minute hit window to videos obtained from these cameras is equivalent to treating videos that came from the same camera and feature the same species whose start times are within 1 minute of each other as a single hit. For 37 of these malfunctioning cameras, the number of “extra” videos obtained because of the malfunction is less than 5, but in one case 27 “extra” videos were obtained. Applying a hit window of longer duration (for example, 5 minutes) involves grouping videos that were obtained by the same camera, featured the same species, and were taken within 5 minutes of each other, together as a single hit. I used hit windows of 1, 5, 10, 30, 60, 90, 120, 150, 180, 210, 240, 720, and 1440 minutes. Hit rates for snowshoe hares and red squirrels were calculated for each filming session as the total number of hits of the species obtained during the first 48 hours of the filming sessions by all of the cameras, divided by the total effort in camera-days (the

number of 24-hour periods each camera was operational for during that filming session, summed together). In instances in which a camera's memory card filled in less than 48 hours, the amount of time that camera was operational for was determined using the time stamp of the last video made by that camera. Cameras that experienced lamp failures at any point during a filming session were excluded from that session's hit rate calculations.

Multiple linear regression was used to determine if live-trapping-based population density estimates could be predicted by hit rates for snowshoe hares and red squirrels. A weather rank variable based on the estimated amount of precipitation during the trapping session, as well as a hit rate – weather rank interaction term, were included in initial snowshoe hare models. For the two Jacquot grids, weather rank was based on Environment Canada precipitation data recorded at the Burwash airport; if the total precipitation for the three days of the trapping session was 0, the session was assigned a rank of 0, between 0.1 and 10 mm a rank of 1, and >10 mm a rank of 2. For all other grids, ranking was based on Environment Canada precipitation records averaged from the Burwash and Haines Junction airports. The week of the year during which the trapping session was conducted and a hit rate-week interaction term were included in the initial models used for the red squirrel data. Grid and year were included as random factors in hare and squirrel initial models. Both live-trapping-based population density estimates and hit rates were square-root transformed to achieve linearity for hares, and grid type (small or large) was also included as a random effect in initial hare models. Backwards stepwise model simplification was done using the stepAIC function of the MASS library (Venables and Ripley 2002), followed by manual backwards simplification using partial F-tests, for each species and each hit window. For models that did not simplify to a single explanatory variable, included

variables were assessed for multicollinearity; where multicollinearity between hit rate and another variable was found, hit rate was retained in the model and the other variable removed.

Results

A total of 573 videos of snowshoe hares were obtained in 432 camera-days of filming effort (Table 3.1). The number of hare videos obtained in a single filming session ranged from 0 to a maximum of 118, which, when converted to a hit rate using the various hit windows, results in a hit rate ranging from 0.65 hits/camera-day (1440 minute hit window) to 3.75 hits/camera-day (1 minute hit window). A total of 1349 videos of red squirrels were obtained in 361.3 camera-days of effort (Table 3.2). The minimum number of videos obtained in a single filming session was 9; converting this to a hit rate using the various hit windows generates a hit rate ranging from 0.01 hits/camera-day (1440 minute hit window) to 0.6 hits/camera-day (1 minute hit window). The maximum number of squirrel videos obtained in a single filming session was 149; this converts to a hit rate ranging from 0.9 hits/camera-day (1440 minute hit window) to 4.97 hits/camera-day (1 minute hit window). Filming effort for hare sessions ranged from 14.2 - 30 camera-days, and squirrel filming session effort ranged from 14 - 30 camera-days.

A total of 64 hares were live trapped in this study; the minimum number of individuals alive (MNA) ranged from 0 to 15, with densities ranging from 0 - 0.90 animals/ha (Table 3.1). A total of 361 individual red squirrels were live trapped, the minimum number of individuals alive on a grid ranged from 16 to 52, with densities ranging from 1.95 - 5 animals/ha (Table 3.2). There were no instances in which squirrels were filmed during a filming session but not live trapped and vice versa, but there were two instances in which hares were filmed during a filming session but not live trapped during the subsequent trapping session.

Hit rate was the best predictor of estimated population density for all hit windows for hares and red squirrels; including additional variables and interaction terms did not significantly improve fit for any of the hit windows for squirrels, and additional variables and interaction terms that did significantly improve fits for hares were also collinear with hit rate. Including grid or year as a random effect did not improve model fit for any hit window for hare or squirrels, and including grid type did not improve model fit for any hit window for hares. The final model for each hit window for squirrels is therefore a simple linear regression of hit rate on live-trapping-based population density estimates. The final model for hares for each hit window is a simple linear regression of hit rate on live-trapping-based population density estimates, both square-root transformed to achieve linearity.

For hares, hit window had some effect on goodness-of-fit; R^2 ranged from 0.72 to 0.90 (Figure 3.1). The highest R^2 value was obtained with a hit window of 5 minutes, but R^2 values for all hit windows between 1 and 240 minutes were similar. For red squirrels, R^2 values ranged from 0.33 to 0.61. A hit window of 5 minutes generated the highest R^2 value (Figure 3.1), but this does not differ much from the 1 minute hit window (R^2 of 0.57). The regressions for all of the hit windows were statistically significant for both hares and red squirrels; the 5 minute hit window was selected as the best model for both hares and red squirrels, based on model selection procedures suggested by Burnham and Anderson (2002).

The regression models were significant for hares ($F_{1,14}= 119.3$, $p < 0.001$, Figure 3.2, Table 3.3) and squirrels ($F_{1,12}=18.84$, $p < 0.001$, Figure 3.3, Table 3.3). Slope estimates were significant for hares ($t_{14} = 10.9$, $p < 0.001$) and squirrels ($t_{12}=4.34$, $p < 0.001$), and the intercept was significant for hares ($t_{14} = -2.8$, $p < 0.05$) but not for squirrels ($t_{12} = 2.0$, $p > 0.05$).

Discussion

In this study I confirm that motion-detecting cameras are capable of detecting animals as small as snowshoe hares and red squirrels, and suggest that camera-generated hit rates may be an accurate means of estimating the density of these two species. Motion-detecting cameras are capable of detecting animals as small as hares and squirrels, and suggest that camera-generated hit rates are an accurate means of estimating the population density of these two species. This is the first attempt to use motion-detecting cameras to estimate snowshoe hare and red squirrel densities. Investigations into the use of cameras to estimate densities of species without unique markings have been conducted with mustelids such as fishers (*Martes pennanti*) (Jordan et al. 2011) and the European pine marten (*Martes martes*) (Manzo et al. 2011) and small (<30kg) herbivores such as Harvey's duiker (*Cephalophus harveyi*) (Rovero and Marshall 2009), muntjac (*Muntiacus reevesi*), water deer (*Hydropotes inermis*) and red-necked wallabies (*Macropus rufogriseus*) (Rowcliffe et al. 2008).

The use of hit windows to group videos that occur within a short time frame should have an effect on the correlation between estimated population density and hit rates when there is heterogeneity in the amount of time individuals spend around traps. If some individuals spend more time around traps than others, then the number of videos generated in a set amount of time is due not only to population density, but also due to variation in behaviour. This is especially relevant to the investigation presented here because I used bait to lure the animals to the cameras; differences in food quality or food availability within home ranges could lead to some individuals spending more time around traps consuming bait than others. For this reason I expected hit rate to have a large impact on the relationship between hit rate and estimated population density for both snowshoe hares and red squirrels.

The results for hares do not support this expectation; the correlation between hit rates and live-trapping-based population density estimates was not particularly sensitive to hit window duration until the hit window exceeded 240 minutes in length. This could be an indication that there is little heterogeneity in how long hares are around traps which could be due to low heterogeneity in how individuals utilize the bait. Of the 45 adult hares captured, only 8 weighed less than 80% of their expected weight given their right-hind-foot length (Hodges et al. 1999). As these 8 are only 13% of the 64 hares captured, any hit rate inflation due to them spending more time at traps eating bait than the other hares would likely have to be considerable in order for hit windows to have a significant effect on the correlation between hit rates and population density.

Conversely, our expectations pertaining to the effects of hit window duration were met for red squirrels; the correlation between hit rate and population density was sensitive to hit window duration. The heterogeneity suggested by high sensitivity to hit window duration could be due to personality; Boon et al. (2008) observed that female squirrels that engaged in more risk-taking behaviours like exploration in a novel environment were live trapped more frequently than squirrels that engaged in less risk-taking behaviour. Variation in risk-taking behaviour that generates variation in trappability could also contribute to heterogeneity in how much time squirrels spend around traps. Decreasing correlation between hit rates and population density with longer hit windows may be due to the relatively high densities at which red squirrels were observed; it seems reasonable that more squirrels on a grid would increase the chances of more than one squirrel visiting a trap. Longer hit windows may group videos produced by different individuals together, under-representing the number of squirrels visiting the traps and reducing the correlation between estimated population density and hit rate.

Using a 5 minute hit window, hit rates account for 90% of the variation in snowshoe hare live-trapping based density estimates; there is considerable scatter in the data and one of the live-trapping-based population density estimates falls outside the model's 95% prediction intervals. Without the ability to generate confidence intervals for live-trapping-based population density estimates for very low density populations, it is difficult to compare the model predictions with live-trapping-based population density estimates, but in general, at these low densities hit rates calculated using a 5 minute hit window appear to be good predictors of live-trapping-based population density estimates for hares. The statistically significant negative intercept implies that at very low densities live trapping won't detect hares but cameras will, in which case the cameras are useful for obtaining presences-absence data.

Using a 5 minute hit window, hit rates account for 61% of the variation in red squirrel live-trapping based density estimates. While there is considerable scatter in the data, the model-predicted densities for each hit rate fall within their respective live-trapping-based population density estimate's 95% confidence interval, and the 95% prediction interval of the model encompasses most of the 95% confidence intervals of the live-trapping-based population density estimates (Figure 3.1). Why only 61% of the variation can be accounted for by hit rates may be related to the hit window itself; using a 5 minute hit window for the entire data set assumes that the 5 minute hit window is the "best" way to account for hit rate inflation caused by prolonged visits for all filming sessions on all grids. But, as suggested above, heterogeneity in trap visitation behaviour in squirrels may be related to population density; longer hit windows may group different visits together on high-density grids, but may be less likely to do this on lower-density grids because fewer squirrels are present to visit traps.

Further work is needed to develop this method. The densities at which snowshoe hares were detected (0 to 0.9 animals/ha) represent the lower end of possible densities in the Kluane area; snowshoe hares have historically reached densities as high as 4.4 animals/ha at the peak of their population cycle in this region (Krebs et al. 2013), and determining if hit rates and densities correlate along the entire range of possible densities would increase the applicability of this method. The squirrel densities observed during this investigation (1.95 to 5.0 animals/ha) are fairly representative of the range of densities that have been observed in this region, but densities have gotten as low as 0.33 animals/ha and collecting additional footage and trapping data at lower squirrel densities would be prudent.

Jacquot Island hare data and mainland hare data were analyzed together in this investigation; I assumed that grid size would have no effect on hit rates. In a theoretical treatment of hit rate data, Rowcliffe et al. (2008), who used gas models to approximate how often animals encounter cameras when moving across a landscape, suggested that sampling area would not affect the rate of encounters between animals and cameras. It should be noted that there is low overlap in densities between Jacquot Island and the mainland; densities from the mainland ranged from 0 to 0.15 animals/ha, while densities on the island ranged from 0.18 to 0.9 animals/ha. Collecting additional data from both grid sizes such that there is greater overlap in densities between the two sites would allow for the confirmation that sampling area does not have a significant effect on hit rates.

In addition, determining if the relationship between hit rates and population density found in Kluane can be applied to different areas in the boreal forest is vital. Calibrating relationship between hit rates and estimated population density at each location in which one wishes to collect population density information would be cost prohibitive in many cases,

therefore determining if the models I have presented here can be applied to camera data collected in other habitats is critical.

The use of bait should also be further explored. I used bait here to increase the chances of animals encountering cameras, but also to increase the chances of trapping individuals. Determining if animals are likely to pass in front of cameras without using bait or traps to lure them there, and if the resulting hit rates still correlate with estimated population density, could improve the applicability of this method by eliminating the cost of bait and the effort of setting up traps in front of cameras, and perhaps reducing the chances of hit rate inflation due to consuming the bait.

In summary, I suggest the following two studies are needed to validate this approach. First, the effects of bait and traps in front of cameras need to be assessed; are relationships between hit rates and population density obtained for these two species when bait and traps are not used similar to those presented here? Secondly, do the relationships presented here extend linearly for the whole possible range of hare and squirrel densities?

The results obtained in this study are encouraging because they indicate it may be possible to census small mammals with cameras, without the necessity of the more difficult and invasive effort of live trapping, marking, and releasing animals.

Table 3.1. Summary of video counts, filming effort, the number of individuals trapped (MNA or minimum number alive) and live-trapping-based density estimates for snowshoe hares (*Lepus americanus*) by grid. Densities are animals/ha and were calculated by dividing MNA by the effective trapping area of each grid (60 ha for Chitty, 56.6 ha for Silver, and 63.5 ha for Sulphur, 16.5 ha for Jacquot North and Jacquot South).

	Chitty				Silver		Sulphur			
	1	2	3	4	1	2	1	2	3	4
	29-Jun-11	12-May-12	14-Jun-12	12-Aug-12	13-Aug-11	6-Jun-12	31-Jul-11	15-May-12	16-Jun-12	12-Aug-12
<u>Video Counts</u>	2	14	8	43	3	0	22	3	8	15
<u>Filming Effort</u>										
Camera-Days	28	30	28	28	14.2	30	30	26	24	24
Cameras	14	15	14	14	12	15	15	13	12	12
<u>MNA</u>	0	3	0	9	1	0	5	1	2	3
<u>Estimated Density</u>	0	0.05	0	0.15	0.02	0	0.08	0.02	0.03	0.05

Table 3.1 continued. Summary of video counts, filming effort, the number of individuals trapped (MNA or minimum number alive) and live-trapping-based density estimates for snowshoe hares (*Lepus americanus*) by grid. Densities are animals/ha and were calculated by dividing MNA by the effective trapping area of each grid (60 ha for Chitty, 56.6 ha for Silver, 63.5 ha for Sulphur, 16.5 ha for Jacquot North and Jacquot South).

	Jacquot North			Jacquot South			Mean	Total
	1	2	3	1	2	3		
	20-Jun-11	7-Aug-11	1-Aug-12	22-Jun-11	7-Aug-11	3-Aug-12		
<u>Video Counts</u>	117	34	101	54	31	118	35.8	573
<u>Filming Effort</u>								
Camera-Days	30	28	28	28.5	26	29.3	27.0	432.0
Cameras	15	14	14	15	13	15	13.9	222.0
<u>MNA</u>	15	3	4	11	3	12	4.5	
<u>Estimated Density</u>	0.90	0.18	0.24	0.67	0.18	0.73	0.21	

Table 3.2. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for red squirrels (*Tamiasciurus hudsonicus*) by grid. Densities are animals/ha, with 95% confidence limits shown below in parentheses.

	Agnes		Chitty		GPC		Joe		Kloo	
	1	2	1	2	1	2	1	2	1	2
	7-Jun-11	8-Jul-12	18-May-11	20-May-12	17-May-11	5-Jun-12	13-Jun-11	8-Jul-11	6-Jul-11	28-Jun-12
<u>Video Counts</u>	149	109	9	92	18	83	117	143	95	118
<u>Filming Effort</u>										
Camera-Days	30.0	29.7	15.0	22.1	14.0	29.6	28.9	29.8	28.0	28.0
Cameras	15	15	8	13	7	15	15	15	14	14
<u>MNA</u>	50	45	21	23	16	17	34	52	31	35
<u>Estimated Density</u>	4.68	3.80	2.09	2.94	1.95	2.12	3.81	4.87	2.68	3.42
	(3.53, 6.22)	(2.81, 5.15)	(1.34, 3.27)	(1.84, 4.70)	(0.64, 5.91)	(1.20, 3.74)	(2.64, 5.49)	(3.65, 6.48)	(1.88, 3.83)	(2.46, 4.79)

Table 3.2 continued. Summary of video counts, filming effort, the number of individuals trapped (or minimum number alive, MNA) and mark-recapture density estimates for red squirrels (*Tamiasciurus hudsonicus*) by grid. Densities are animals/ha, with 95% confidence limits shown below in parentheses.

	Lloyd		Sulphur		Mean	Total
	1 6-Jul-11	2 4-Jul-12	1 2-Jul-11	2 24-Jun-12		
<u>Video Counts</u>	120	129	84	74	95.7	1340
<u>Filming Effort</u>						
Camera-Days	23.4	27.1	26.2	29.5	25.8	361.3
Cameras	12	14	14	15	13.3	
<u>MNA</u>	32	36	32	35	32.8	
<u>Estimated Density</u>	3.26	5.00	2.48	2.97	3.29	
	(2.29, 4.64)	(3.02, 8.27)	(1.70, 3.60)	(2.12, 4.18)		

Table 3.3. Linear regressions to predict trap-based population density estimates from camera-based hit rates for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*). Hit rates were calculated using 5 minute hit windows, density and hit rate were square-root-transformed to achieve linearity, and densities are in animals/ha.

Species	Regression terms	Sample Size	Mean Squared Error	Slope Standard Error	R ²
<i>Lepus</i>	$\sqrt{\text{density}} = 0.13\sqrt{\text{hit rate}} - 0.14$	16	0.007	0.28	0.90
<i>Tamiasciurus</i>	$\text{density} = 0.79\text{hit rate} + 1.06$	12	0.067	0.18	0.61

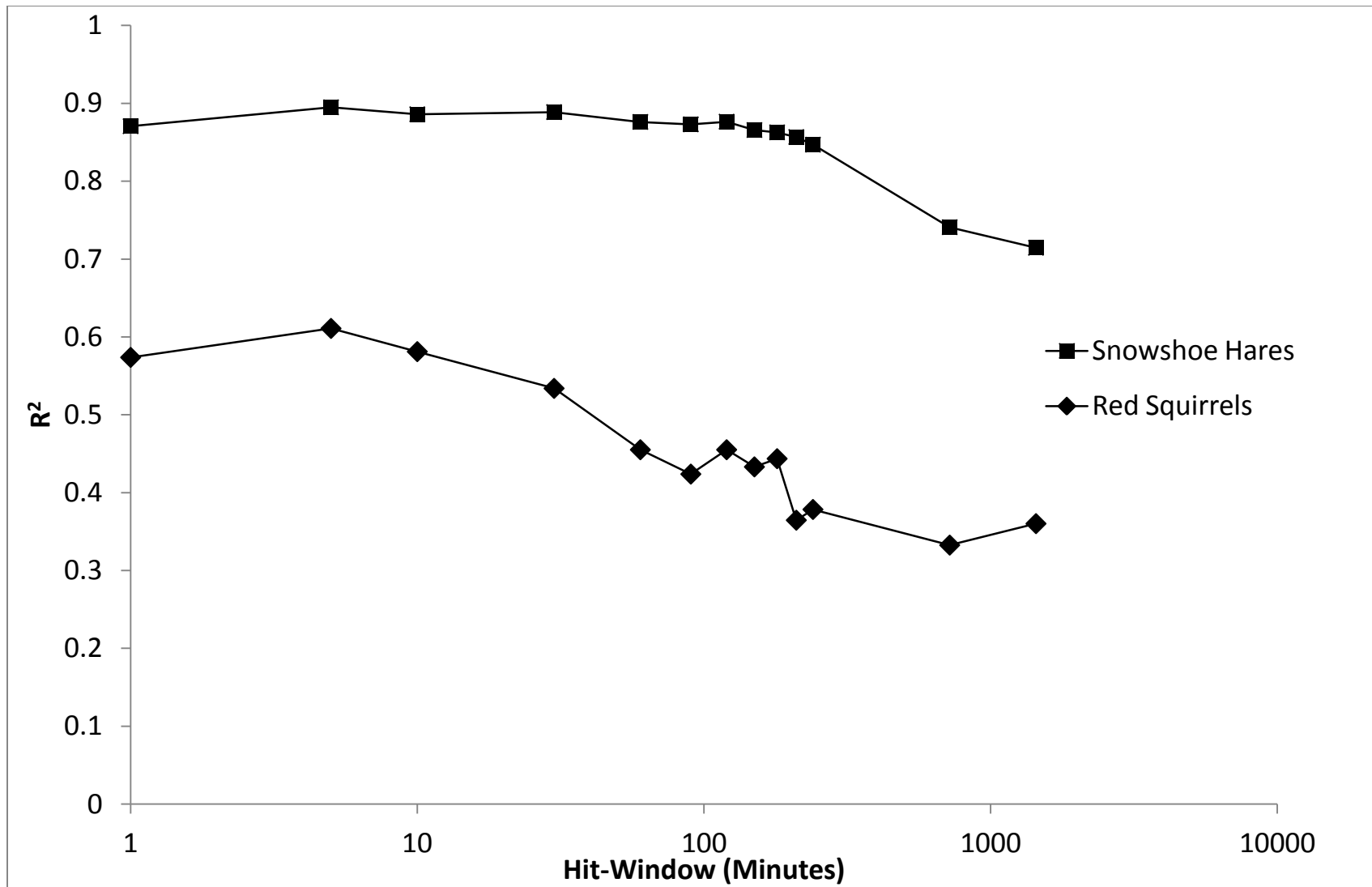


Figure 3.1. R^2 values for linear regressions between live-trapping-based population density estimates and hit rates calculated using different hit window lengths for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*), Kluane Lake, 2011-2012.

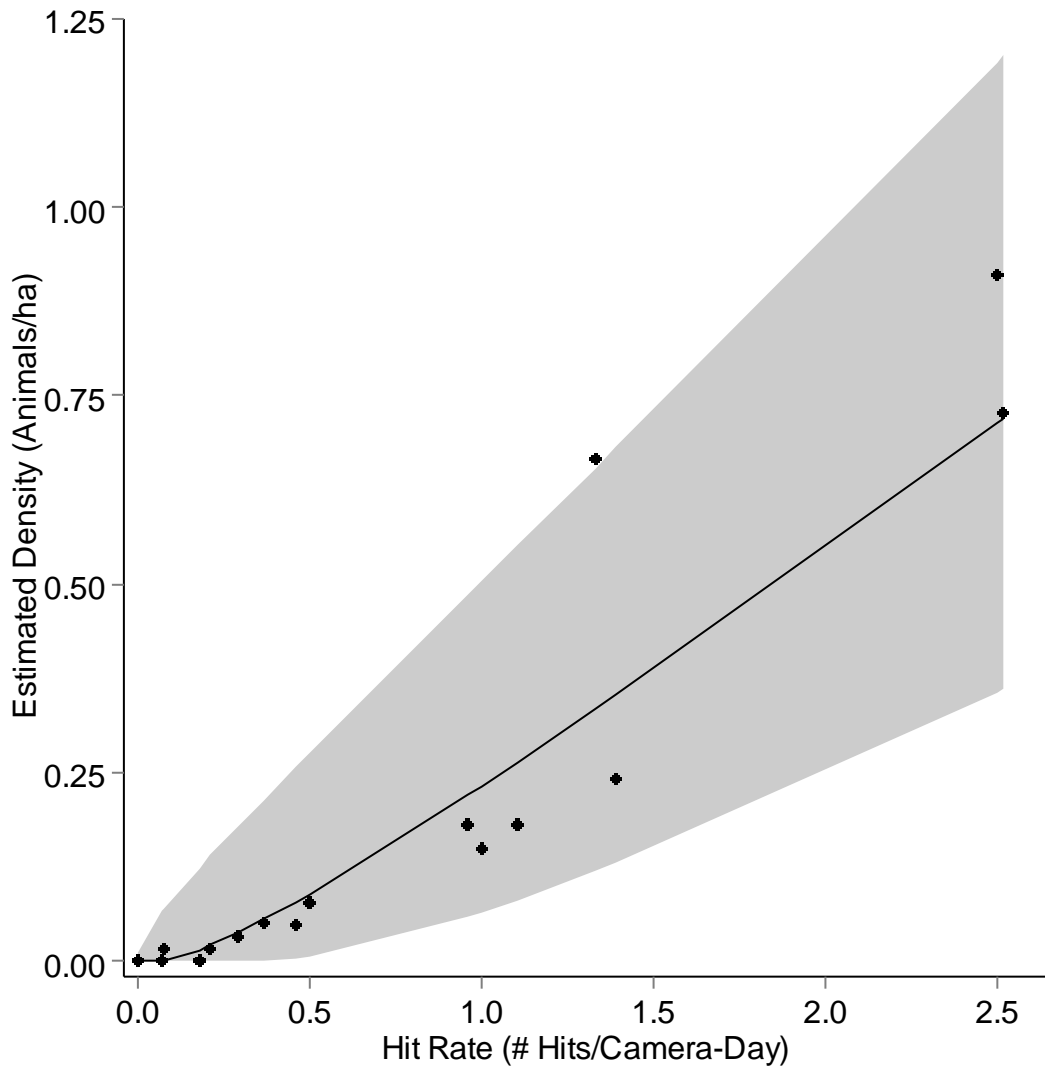


Figure 3.2. Relationship between hit rates and live-trapping-based density estimates for snowshoe hares (*Lepus americanus*) at Kluane Lake. Hit rates were calculated using 5 minute hit windows. Each point represents a 2-day filming session followed by a 3-day live trapping session. Solid line indicates linear regression ($R^2 = 0.90$), grey band represents 95% prediction intervals.

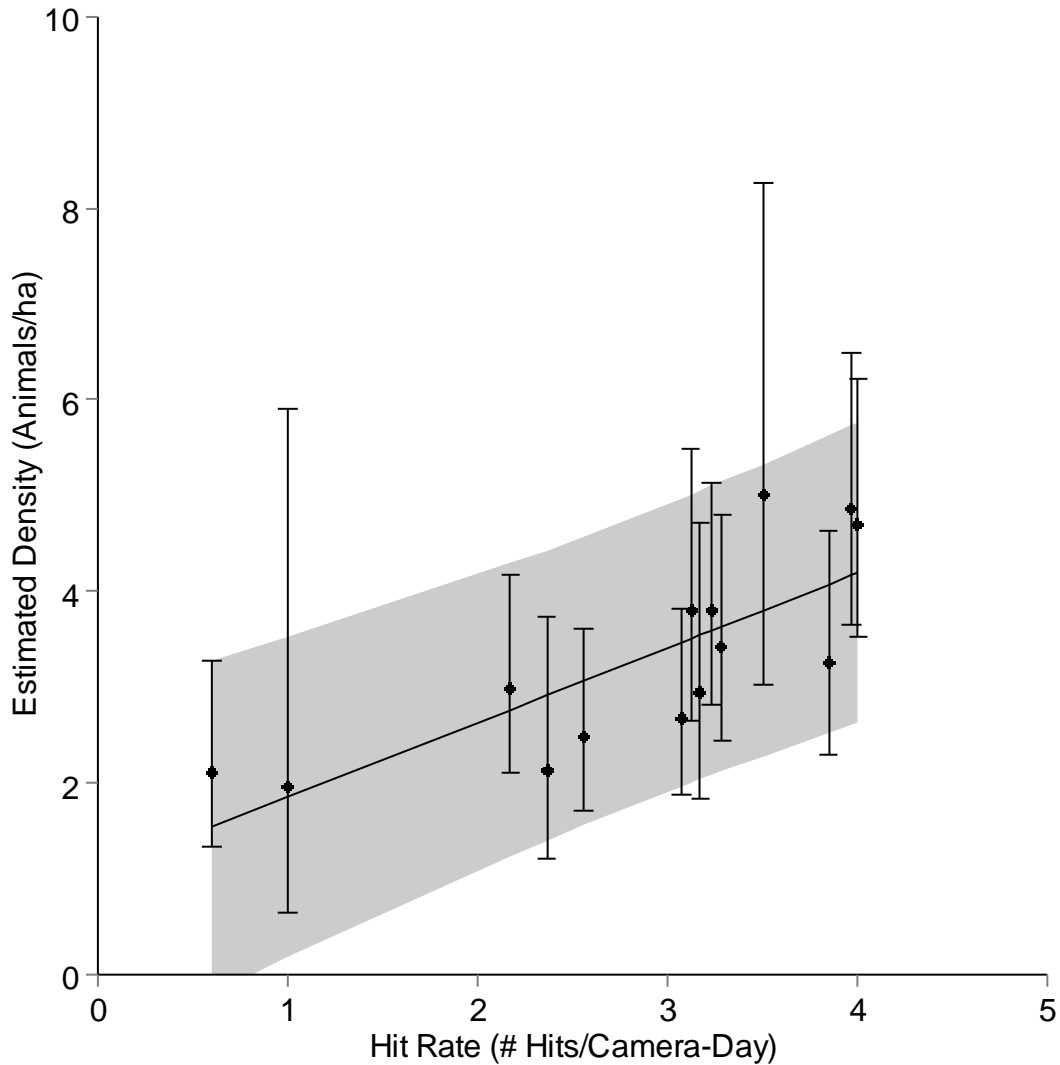


Figure 3.3. Relationship between hit rates and live-trapping-based population density estimates for red squirrels (*Tamiasciurus hudsonicus*) at Kluane Lake. Hit rates were calculated using 5 minute hit windows. Each point represents a 2-day filming session followed by a 2-day live trapping session. Solid line indicates linear regression ($R^2 = 0.61$), grey band represents 95% prediction intervals. Error bars are 95% confidence intervals for density estimates.

Chapter 4 - General Conclusions and Further Research

The objectives of this investigation were to assess the impact of hit window duration on the correlation between hit rates and live-trapping-based population density estimates of deer mice (*Peromyscus maniculatus*), northern red-backed voles (*Clethrionomys rutilus*), snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*), and to determine if, given the “best” hit window, hit rates could be used to estimate population density of these species.

The major findings of this investigation were the following:

- 1) Hit window duration does not have a major impact on the correlation between hit rates and live-trapping-based population density estimates for deer mice (*Peromyscus maniculatus*); R^2 ranged from 0.81 to 0.84, with a 90 minute hit window generating the highest R^2 value. Model-predicted densities and 95% prediction intervals were similar to live-trapping-based density estimates and their respective 95% confidence intervals, suggesting that hit rates can be used to estimate population density for this species.
- 2) The correlation between hit rates and live-trapping-based population density estimates was sensitive to hit window duration for northern red-backed voles (*Clethrionomys rutilus*); R^2 values ranged from 0.48 to 0.59, with a 90 minute hit window generating the largest R^2 value. Model-predicted densities did not always fall within trapping-based confidence intervals, and 95% prediction intervals for the model tended to be larger than trapping-based 95% confidence intervals. This suggests that hit rates might be useful for rapidly assessing general trends in density

- for this species, but further refinement is necessary in order for hit rates to be useful in estimating density precisely and accurately for this species.
- 3) Hit window duration has a moderate impact on the correlation between hit rates and live-trapping-based population density estimates for snowshoe hares (*Lepus americanus*). R^2 ranged from 0.72 to 0.9, with a hit window of 5 minutes generating the strongest correlation, but the correlation is similar for all hit windows between 1 and 240 minutes in length and only declines with longer hit windows. Without 95% confidence intervals for the live-trapping-based density estimates it is difficult to compare model predictions to live-trapping estimates, but in general the strong correlation between live-trapping-based density estimates and hit rates suggests that hit rates can be used to estimate population density for this species.
 - 4) The correlation between hit rates and live-trapping-based population density estimates was sensitive to hit window duration for red squirrels (*Tamiasciurus hudsonicus*). R^2 ranged from 0.33 to 0.61, with a 5 minute hit window generating the highest R^2 value. Model-predicted densities and 95% prediction intervals were similar to live-trapping-based density estimates and their respective 95% confidence intervals, suggesting that hit rates can be used to estimate population density for this species.

In general, I suggest that remote cameras can be used to assess the population density of deer mice, northern red-backed voles, snowshoe hares, and red squirrels. This is encouraging, as remote cameras can be less labour-intensive to operate compared to live trapping, and are less invasive. Cost and logistical constraints often limit the scale, both temporal and spatial, at which ecological studies are conducted, and the development of economical methods for observing

wildlife will hopefully contribute to an increased understanding of the natural world by allowing for longer and larger studies to occur.

Given the above findings, I recommend the following general questions for future research:

- 1) Can the regressions presented here be used in other locations or habitat types?

Calibrating the relationship between hit rates and estimated population density at each location in which one wishes to collect population density information would be cost prohibitive in many cases, therefore determining if the models I have presented here can be applied to camera data collected in other habitats is critical.

- 2) Do hit rates correlate with live-trapping-based population density estimates for the entire range of densities for these species? The regressions presented here are based on data collected at the lower end of the range of possible densities for deer mice, red-backed voles and snowshoe hares; determining if hit rates correlate linearly with trap-based population density estimates for the entire range of possible densities of these species would improve the applicability of this method.

- 3) Do hit rates correlate with trapping-based population density estimates for these species in the absence of live traps or bait? Live traps are costly and setting them up to house bait in locations that are not already live-trapped would be a labour-intensive and cost-prohibitive endeavor in many cases; not needing live traps and/or bait would improve the applicability of using remote cameras to estimate small mammal densities.

- 4) What is the minimum effort required for hit rates and live-trapping-based population density estimates to correlate for these species? Specifically, how many cameras are needed, and for how long should they operate?
- 5) Can cameras be used to monitor multiple species at once? Snowshoe hares and red squirrels were occasionally filmed during mouse filming sessions, and mice and voles were occasionally filmed during squirrel and hare filming sessions. Identifying a camera set-up (height and orientation) as well as an appropriate spatial scale that would allow for the simultaneous monitoring of all four species would be of great interest.

In addition, there is the potential for monitoring other species in the boreal forest using remote cameras; I obtained footage of bears (*Ursus arctos* and *Ursus americanus*), moose (*Alces alces*), arctic ground squirrels (*Uroditellus parryii*) and several species of birds during my filming sessions, using camera set-ups meant to maximize observations of small mammals. Determining if this footage of non-target species can be used in some way (e.g. assessing the distribution, habitat selection, or behaviour of these species), and developing remote camera set-ups and protocols that target these species, are both areas that should be explored.

Live trapping data and footage of *Microtus* were insufficient for performing an in-depth analysis here. Misidentification of *Microtus* individuals as *Clethrionomys* in black and white footage does not appear to have been a serious problem here, but it illustrates a limitation of the cameras in this community, and further work to determine if this limitation reduces the applicability of the cameras for estimating *Clethrionomys* densities when *Microtus* are more abundant would be prudent.

Finally, developing a protocol or set of standards for storing camera data and accompanying metadata (camera model used to obtain the photographs or videos, detection equipment used, GPS coordinates of camera location, duration of observation or camera-effort, etc.) could greatly facilitate the sharing of camera data.

References

- BOON, A., D. REALE AND S. BOUTIN. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–1328.
- BOONSTRA, R. AND C. J. MCCOLL. 2000. Contrasting stress response of male arctic ground squirrels and red squirrels. *The Journal of Experimental Zoology* 286:390–404.
- BOONSTRA, R. AND G. SINGLETON. 1993. Population declines in the snowshoe hare and the role of stress. *General and Comparative Endocrinology* 91:126–143.
- BURNHAM, K. P. AND D. R. ANDERSON. 2002. *Model Selection and Multi-Model Inference : A Practical Information-Theoretic Approach*. 2nd edition. Springer-Verlag, New York, New York.
- CALDI, C., J. DIORIO AND M. J. MEANEY. 2000. Variations in maternal care in infancy regulate the development of stress reactivity. *Biological Psychiatry* 48:1164–74.
- CERBO, A. R. AND C. M. BIANCARDI. 2013. Monitoring small and arboreal mammals by camera traps: effectiveness and applications. *Acta Theriologica* 58:279–283.
- CHAPMAN, F. 1927. Who treads our trails. *The National Geographic Magazine*:330–345.
- CUTLER, T. AND D. SWANN. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27:571–581.
- DE BONDI, N., J. G. WHITE, M. STEVENS AND R. COOKE. 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research* 37:456–465.
- DELEHANTY, B. AND R. BOONSTRA. 2009. Impact of live trapping on stress profiles of Richardson's ground squirrel (*Spermophilus richardsonii*). *General and Comparative Endocrinology* 160:176–82.
- DERKSEN, D. 1977. A quantitative analysis of the incubation behavior of the Adelie Penguin. *The Auk* 94:552–566.
- DILLON, A. AND M. J. KELLY. 2007. Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* 41:469–477.
- FLETCHER, Q. E. AND R. BOONSTRA. 2006. Impact of live trapping on the stress response of the meadow vole (*Microtus pennsylvanicus*). *Journal of Zoology* 270:473–478.
- FOSTER, R. J. AND B. J. HARMSSEN. 2012. A critique of density estimation from camera-trap data. *The Journal of Wildlife Management* 76:224–236.

- GANNON, W. L. AND R. S. SIKES. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GRUNDEL, R. AND D. DAHLSTEN. 1991. The feeding ecology of mountain chickadees (*Parus gambeli*): patterns of arthropod prey delivery to nestling birds. *Canadian Journal of Zoology* 69:1793–1804.
- GYSEL, L. AND E. DAVIS. 1956. A simple automatic photographic unit for wildlife research. *The Journal of Wildlife Management* 20:451–453.
- HARPER, J. M. AND S. N. AUSTAD. 2001. Effect of capture and season on fecal glucocorticoid levels in deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*). *General and Comparative Endocrinology* 123:337–44.
- HARRIS, G., R. THOMPSON, J. CHILDS AND J. SANDERSON. 2010. Automatic storage and analysis of camera trap data. *Bulletin of the Ecological Society of America* 91:352–360.
- HEILBRUN, R., N. SILVY, M. PETERSON AND M. TEWES. 2006. Estimating bobcat abundance using automatically triggered cameras. *Wildlife Society Bulletin* 34:69–73.
- HODGES, K. E., C. I. STEFAN AND E. A. GILLIS. 1999. Does body condition affect fecundity in a cyclic population of snowshoe hares? *Canadian Journal of Zoology* 77:1–6.
- JORDAN, M. J., R. H. BARRETT AND K. L. PURCELL. 2011. Camera trapping estimates of density and survival of fishers *Martes pennanti*. *Wildlife Biology* 17:266–276.
- KARANTH, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* 71:333–338.
- KARANTH, K. U. AND J. D. NICHOLS. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- KELLY, M., A. NOSS, M. DI BITETTI, L. MAFFEI, R. ARISPE, A. PAVIOLO, ET AL. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* 89:408–418.
- KREBS, C. AND K. COWCILL. 2010. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? *Journal of Mammalogy* 91:500–509.
- KREBS, C. J., R. BOONSTRA, S. GILBERT, D. REID, A. J. KENNEY AND E. J. HOFER. 2011. Density estimation for small mammals from livetrapping grids: rodents in northern Canada. *Journal of Mammalogy* 92:974–981.
- KREBS, C. J., S. BOUTIN AND R. BOONSTRA (eds.). 2001. Ecosystem Dynamics of the Boreal Forest: The Kluane Project. P. 511 in. Oxford University Press, New York.

- KREBS, C., K. KIELLAND, J. BRYANT AND M. O'DONOGHUE. 2013. Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. *Canadian Journal of Zoology* 91:562–572.
- MAFFEI, L., E. CULLAR AND A. NOSS. 2004. One thousand jaguars (*Panthera onca*) in Bolivias Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology* 262:295–304.
- MANZO, E., P. BARTOLOMMEI, J. M. ROWCLIFFE AND R. COZZOLINO. 2011. Estimation of population density of European pine marten in central Italy using camera trapping. *Acta Theriologica* 57:165–172.
- MARCSTRÖM, V., L. KEITH, E. ENGREN AND J. CARY. 1989. Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology* 67:658–668.
- MARCSTROM, V., R. KENWARD AND E. ENGREN. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. *The Journal of Animal Ecology* 57:859–872.
- MCCALLUM, J. 2013. Changing use of camera traps in mammalian field research: habitats, taxa and study types. *Mammal Review* 43:196–206.
- MCCARTHY, K. P., T. K. FULLER, M. MING, T. M. MCCARTHY, L. WAITS AND K. JUMABAEV. 2008. Assessing Estimators of Snow Leopard Abundance. *Journal of Wildlife Management* 72:1826–1833.
- MERGEY, M., R. HELDER AND J.-J. ROEDER. 2011. Effect of forest fragmentation on space-use patterns in the European pine marten (*Martes martes*). *Journal of Mammalogy* 92:328–335.
- O'BRIEN, T. G., M. F. KINNAIRD AND H. T. WIBISONO. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* 6:131–139.
- O'CONNELL, A. F., J. D. NICHOLS AND K. U. KARANTH (eds.). 2011. *Camera Traps in Animal Ecology*. Springer Japan, Tokyo.
- PEARSON, O. 1959. A traffic survey of *Microtus-Reithrodontomys* runways. *Journal of Mammalogy* 40:169–180.
- PEARSON, O. 1960. Habits of *Microtus californicus* revealed by automatic photographic recorders. *Ecological Monographs* 30:231–250.
- R DEVELOPMENT CORE TEAM. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- ROVERO, F. AND A. R. MARSHALL. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46:1011–1017.
- ROWCLIFFE, J., J. FIELD, S. T. TURVEY AND C. CARBONE. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228–1236.
- SHERIFF, M. J., C. J. KREBS AND R. BOONSTRA. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *The Journal of animal ecology* 78:1249–58.
- SHIRAS, G. 1913. Wild animals that took their own pictures by day and by night. *The National Geographic Magazine* 24:762–834.
- SILVER, S. C., L. E. T. OSTRO, L. K. MARSH, L. MAFFEI, A. J. NOSS, M. J. KELLY, ET AL. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture / recapture analysis 38:1–7.
- TROLLE, M. 2003. Mammal survey in the southeastern Pantanal, Brazil. *Biodiversity & Conservation* 12:823–836.
- TROLLE, M. AND M. KÉRY. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of mammalogy* 84:607–614.
- TURKINGTON, R., E. JOHN, S. WATSON AND P. SECCOMBE-HETT. 2002. The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology* 90:325–337.
- VENABLES, W. N. AND B. D. RIPLEY. 2002. *Modern Applied Statistics with S*. 4th edition. Springer, New York, New York.
- VINE, S. J., M. S. CROWTHER, S. J. LAPIDGE, C. R. DICKMAN, N. MOONEY, M. P. PIGGOTT, ET AL. 2009. Comparison of methods to detect rare and cryptic species: a case study using the red fox (*Vulpes vulpes*). *Wildlife Research* 36:436.
- WALLACE, R. B., H. GOMEZ, G. AYALA AND F. ESPINOZA. 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Journal of Neotropical Mammalogy* 10:133–139.
- WANG, S. AND D. MACDONALD. 2009. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation* 142:606–613.