Methodological Comparison of Canada Lynx Density Estimation

by

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Abstract

Reliable population density estimates are critical for ecological research and species management but can be difficult to obtain. Sampling methods like noninvasive genetic sampling and remote camera traps, combined with appropriate statistical models, provide opportunities to estimate density from a variety of approaches. However, it is unknown if these methods result in similar density estimates and precision of estimates. I applied and compared methods for estimating Canada lynx (*Lynx canadensis*) density for a cyclic population in southwestern Yukon Territory. Canada lynx are a species of ecological, economic, and conservation interest, but few studies have estimated density of lynx and even fewer have used contemporary methods. I collected lynx data using hair snares, camera traps, track transect counts, and GPS collars, then applied and compared density estimation methods across data types. Estimation methods included linearly-scaled count methods, spatial mark-recapture, spatial mark-resight, and a cumulative time method. I calculated six estimates and found five-fold variation in point estimates and two-fold variation in precision, despite closely following the methods described in current literature and making every effort to meet model assumptions. My results indicate that a single approach to wildlife density estimation is likely insufficient, and that density estimation requires careful consideration of methodological assumptions and sources of error.

Preface

This thesis is an original work by Darcy Doran-Myers. No part of this thesis has been previously published. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “Canada lynx density estimation using non-invasive hair sampling,” No. AUP00001988, 6 December 2016.

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Introduction

Population density estimation is a common objective in ecology and is of particular importance for population ecologists, wildlife managers, and species conservationists. Estimating wildlife density, however, remains a central challenge. Many methods have been proposed but no single best method exists for density estimation of populations with different characteristics. Mobile species that are rare or elusive limit the implementation of census methods relying on direct observation. To measure such populations often necessitates the use of indirect observation and sampling methods to estimate density. When rare or elusive populations are additionally unmarked, density estimation requires either invasive marking methods or statistics adapted for unmarked populations. Wildlife managers and ecologists are now using variety of recent statistical and technological advances in wildlife population sampling and density estimation. It is as yet unknown how these emerging methods compare in point density estimation and in precision of density estimates.

The Canada lynx (*Lynx canadensis*) is a species of ecological interest due to its role in predator-prey cycling with the snowshoe hare (*Lepus americanus*) (Poole 2003), conservation concern in the peripheral parts of its range (U.S. Fish and Wildlife Service 2017), and is an important fur-bearing species in some North American economies (Kluane National Park and Reserve 2015). Knowledge of lynx population size is fundamental to lynx research in both ecology and management. Lynx can be difficult to survey because they live in dense boreal habitat (Mowat et al. 2001), are averse to direct observation, are periodically rare (O'Donoghue et al. 1997), and are generally unmarked. As a result, studies of lynx including estimates of population size have been infrequent.

Early investigations of lynx ecology and the lynx-snowshoe hare cycle used relative abundances of lynx across years. Extensive fur trapping records were summarized to describe the predator-prey cycling exemplified by lynx and hares (Elton and Nicholson 1942). Although these records revealed the general timing of fluctuating lynx population size, the data may have been biased by spatial and temporal variation in trapping effort and reporting rates (Brand and Keith 1979). Ward and Krebs (1985) noted that lynx susceptibility to trapping is likely to vary when movement rates change in response to prey density, further confounding relative abundance indices from trapping data across time. Relative density of lynx has also been estimated from lynx tracks (O'Donoghue et al. 1997; Krebs 2011). Krebs (2011) reported counts of lynx tracks observed per length of transect across 23 years as an index of lynx abundance over time. Like historical fur trapping data, snow tracking can show the timing of population density fluctuations. Tracking indices are subject to error resulting from differences in movement rates across years when prey density is not constant (Keeping and Pelletier 2014). Changes in movement rate are likely to change the probability of detecting lynx tracks. Despite these limitations, both fur trapping records and snow track transect counts are cited as indices of lynx abundance (Clark 2000; Krebs 2011).

Some research questions require estimates of absolute abundance or density. Studies aiming to establish harvest quotas of a managed population, for example, may involve estimates of population density to calculate percent of the population harvested. Investigations of kill rate on a prey population, or of energy or nutrient flow through ecological communities, also require density to quantify relationships in ecological communities. The first published attempt to estimate absolute lynx density was conducted using a snow track transect survey. Brand et al. (1976) estimated density of lynx by conducting track counts on road transects. Researchers traversed track transects daily and, by assuming that all lynx were detected and that individual lynx could be identified by tracks, directly counted individuals in a predetermined study area (Brand et al. 1976). Track misidentification could be a source of error in this method (Evans et al. 2007). The resulting density estimate from this study included no measurement of precision.

The most common method for lynx density estimation uses a combination of snow tracking and radio telemetry (Bailey et al. 1986; Koehler 1990; Poole 1994; Slough and

Mowat 1996; O’Donoghue et al. 1997; Vashon et al. 2008; Vashon et al. 2012). With this method, researchers directly count individuals in a predetermined area using tracks and additional spatial data from telemetered lynx. Snow tracks within the observed home ranges of lynx are assumed to belong to the telemetered individuals whereas tracks outside the home ranges are assumed to belong to unknown individuals and are added to the total number of lynx (Koehler 1990; O’Donoghue et al. 1997). Parker et al. (1983) used telemetry alone, assuming that all lynx resident to the study area were captured and collared. In general, these methods likely underestimate the number of transient individuals (Koehler 1990) and individuals with overlapping territories (Mowat et al. 2001; Vashon et al. 2008). Thus, densities estimated from this method are reported as conservative values (Ward and Krebs 1985; Poole 1994) or are sometimes converted to more biologically plausible numbers (Parker et al. 1983). This approach necessitates the use of multiple sampling methods and provides no estimate of precision.

Recent technological advances in wildlife research provide opportunities to improve surveys and density estimation for rare and elusive wildlife populations. Remote, motion-triggered camera traps can provide data on these populations while remaining less invasive than conventional survey methods like live-trapping (Hamel et al. 2013; Surnato et al. 2013). Camera traps are ideally suited to lynx research because lynx, like other felids, are readily detected using remote camera technology (Surnato et al. 2013). Cameras reliably detect large, homeothermic animals (Kelly 2008) and are more successful in detecting rare and nocturnal wildlife than direct observation or live traps (Foster and Harmsen 2012). Density has been estimated using camera traps for species like tigers (*Panthera tigris*) (Karanth 1995; Carbone et al. 2001; Karanth et al. 2006), bobcats (*Lynx rufus*) (Silvy et al. 2006), coyotes (*Canis latrans*) (Séquin et al. 2006), spectacled bears (*Tremarctos ornatus*) (Ríos-Uzeda et al. 2007), and tapirs (*Tapirus terrestris*) (Trolle et al. 2008). A variety of statistical analyses have been applied to camera trap data to estimate density, including both capture-recapture methods for marked animals and detection rate-based methods for unmarked animals.

Advances in genotyping and improved, less invasive sampling methods provide another option to estimate population size for some species. Genetic material can be extracted from hair follicles collected from rub-posts, hair snares, kill sites, or beds and used to identify individuals in the population. Capture-recapture methods can be applied to the resulting individual capture histories for species such as grizzly (*Ursus arctos*) (Dumond et al. 2015; Lamb et al. 2016) and black bears (*Ursus americanus*) (McCall et al. 2013), pumas (*Puma concolor*) (Russell et al. 2012), bobcats (Stricker et al. 2012), and Eurasian lynx (*Lynx lynx*) (Davoli et al. 2013). Canada lynx can be detected by hair snares (McKelvey et al. 1999; McDaniel et al. 2000), but only one study has used this method to attempt to estimate their density (Crowley and Hodder 2017) due to challenges related to the quantity of genetic material retrieved from felid hair follicles (Long et al. 2008) and mixed samples from multi-catch hair snares.

Statistical advances provide opportunities to improve density estimation from existing sampling methods. Whereas most density estimates of lynx have been attempts at direct enumeration, capture-recapture (CR) methods are a common and reliable way to estimate wildlife population sizes when some sample of the population can be marked (Krebs 2014). Likelihood-based spatially explicit capture-recapture (SECR) and Bayesian spatial capture-recapture (SCR) models are an improvement upon conventional CR because they combine CR with distance sampling concepts and model the probability of detection by distance from an estimated home range center (Efford 2004; Obbard et al. 2010). SECR models (Efford 2004; Borchers and Efford 2008; Efford et al. 2009b; Efford 2011; Efford and Fewster 2013) and SCR models (Royle and Young 2008; Chandler and Clark 2014) avoid *ad-hoc* definitions of effective trapping area, remove error from edge effects, and account for spatial differences in individual detection probability (Efford 2004; Efford and Fewster 2013). Modifications of SECR and SCR include spatially explicit mark-resight models (maximum-pseudolikelihood SCMR (Efford and Hunter 2017) and Bayesian SMR (Chandler and Royle 2013; Alonso et al. 2015)) for partially marked populations. Analyses for estimating density of unmarked populations are typically based on detection rates combined with an estimate of probability of detection. These models include the Random Encounter Model (REM) (Rowcliffe et al. 2008; Cusack et al. 2015) and the Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006). Among more recent additions to the list of statistical methods for density estimation is a random encounter and staying time (REST) model (Nakashima et al. 2017). Applying any of these contemporary estimation methods to lynx survey data could improve upon existing methods of lynx density estimation by removing some common sources of error of enumeration for elusive species and by providing a measure of precision to estimates. It is as yet unknown how density estimates from these emerging methods compare.

Relevance to Ecology and Management

Ecological investigations of population cycling and predator-prey relationships could benefit from applying contemporary methods of density estimation. Canada lynx populations have been studied as examples of specialist predators that are dependent on prey densities (O’Donoghue et al. 1997). Lynx are associated with North American boreal forests (Mowat et al. 2001) and rely on snowshoe hares as their main prey (Ward and Krebs 1985; O’Donoghue et al. 1997; Poole 2003; Krebs 2011). Lynx dependency on snowshoe hares is evident in the numerical responses of lynx populations to 10-year cycles in hare density, particularly in northern parts of their range (Ward and Krebs 1985; Poole 1997). Lynx densities estimated from direct enumeration can vary by an order of magnitude depending on fluctuating snowshoe hare densities. In peak years, lynx densities have been reported from 10 to 45 individuals (Brand et al. 1976; Parker et al. 1983; Poole 1994; O’Donoghue et al. 1997; Mowat et al. 2001) per 100 km^2; in a low, lynx density can drop to 2 to 3 individuals (Poole 1994; O’Donoghue et al. 1997; Mowat et al. 2001) per 100 km^2. Lynx population declines are a result of increased mortality (Breitenmoser et al. 1993; Poole 1994; Mowat et al. 2001), reduced recruitment (Parker et al. 1983; Mowat et al. 1996; Poole 2003), and high dispersal rates (Poole 1994; Poole 1997; Mowat et al. 2001) in response to limited food supply. Refined estimates from an improved method of lynx density estimation could allow for further insights into the lynx-hare cycle and predator-prey systems in general. Absolute density estimates may allow researchers to answer questions regarding predation pressure on prey species, population recruitment, or energy and nutrient flow through communities (Krebs 2014). Explorations of error and assumption violations using contemporary methods could also inform interpretations of earlier estimations of lynx density.

Wildlife management for the conservation and harvest of lynx will also benefit from this research. Climate change (Carroll 2007), encroaching human development and recreation (Aubry et al. 2000), and habitat loss (Murray et al. 2008) may threaten peripheral populations of lynx at the southern extent of their range. Estimates of population size are fundamental indicators of population status and viability, but there have been few recent attempts to assess lynx population size in these areas (Koehler 1990; Vashon et al. 2008). In the 2017 "Species Status Assessment for the Canada Lynx" for the contiguous United States, managers in all lynx management units described their historical and current density estimates as either imprecise and uncertain or lacking entirely (U.S. Fish and Wildlife Service 2017). Despite this fundamental gap in knowledge, The U.S. Fish & Wildlife Service recommended in 2017 that protections currently offered to lynx by the Endangered Species Act be removed (U.S. Fish and Wildlife Service 2018). In northern regions of Canada lynx range where lynx are more abundant, lynx are often managed as a game species and harvested for fur (Poole 2003; Carroll 2007; Kluane National Park and Reserve 2015). Knowledge of lynx density may be informative for species management in these areas, providing data upon which harvest quotas can be based and increasing the probability of persistence of both lynx populations and the northern economies to which they contribute. Attempts to estimate Canada lynx density anywhere in their management range have been minimal. Knowledge of the comparative performance of contemporary density estimation methods for lynx could help managers develop appropriate and informed methods for lynx density estimation.

Objectives

I used temporally and spatially overlapping sample data from four sources—camera traps, hair snares, snow track transects, and location data from radio-collared individuals—as a basis for lynx population density estimation. I used this information to estimate density from six contemporary statistical analyses: the Formozov–Malyshev–Pereleshin (FMP) formula (Dzięciolowski 1976; Stephens et al. 2006; Keeping and Pelletier 2014), spatially explicit capture-recapture (SECR) (Borchers and Efford 2008; Efford et al. 2009b), the Random Encounter Model (REM) (Rowcliffe et al. 2008; Rowcliffe et al. 2013), spatial capture mark-resight (SCMR) with a likelihood-based inference method (Efford and Hunter 2017; Efford 2018a), spatial mark-resight (SMR) with a Bayesian inference method (Sollmann et al. 2013a; Whittington et al. 2018), and the Random Encounter and Staying Time (REST) method (Nakashima et al. 2017). I compared the point estimates and the associated precision of the estimates resulting from each method. I then explored potential violations of underlying assumptions and other possible sources of negative or positive bias as explanations for observed differences in point estimates and estimate precision.

Methods

Study Area

The study was conducted in the Kluane Lake region of southwestern Yukon Territory, Canada. This area has been well-studied for 40 years and the research is thoroughly described in Krebs et al. (2001) and Krebs et al. (2014). The approximately 300 km^2 unbounded study area (center coordinates: 61°N, 138°W, Fig. 1) is part of the northern boreal forest ecosystem (Douglas 1974). It is located in a glacial valley bordered by the St. Elias Mountains, the Kluane Hills, and Kluane Lake, sits between 800 and 1600 meters elevation, and is bisected by the Alaska Highway. The area is in the climatic rain shadow of the St. Elias Mountains (Krebs et al. 2001). Average precipitation ranges from 9 mm to 55 mm per month and snow is present from late October through May (Government of Canada 2015). Average temperature ranges from -16°C in January to +13°C in July (Government of Canada 2015). White spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), willow (*Salix glauca*), and American dwarf birch (*Betula glandulosa*) are among dominant vegetation (Ward and Krebs 1985). Sympatric carnivores inhabiting the Kluane area with Canada lynx include coyotes (*Canis latrans*), wolverines (*Gulo gulo*), and gray wolves (*Canis lupus*). Potential prey of lynx in the area include snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), grouse (*Bonasa umbellus, Lagopus lagopus, Dendragapus canadensis*) and small mammals (e.g., *Peromyscus maniculatus, Myodes rutilus*) (Murray et al. 1994; Donoghue et al. 1998; Krebs et al. 2014). Community trap lines occur adjacent to the study area; as a result, human harvesting by trapping is the greatest cause of mortality for lynx in the Kluane area (Ward and Krebs 1985).

Data Collection

Three survey methods were employed to sample lynx in the study area: remote motion-activated camera traps, hair snares, and snow track transects. In addition, lynx were live-captured, marked, and fitted with Global Positioning System (GPS) and very high frequency (VHF) radio collars. These four data sources were used to provide datasets from which density could be estimated.

Live Capture Methods

Lynx were captured for marking and collaring using lured and baited box traps. Between November 2016 and April 2017, up to 25 box traps (dimensions 1 m x 2 m x 1.5 m) were deployed and active within the study area (Fig. 1). Traps were placed along trails and other suspected high lynx traffic areas and baited with meat and a beaver (*Castor canadensis*) castoreum scent lure. Trap sites also used visual lures in and near the trap, including feathers, hanging blank CDs, and mirrors. Adult lynx (weighing over 5 kg) that were captured were immobilized, collared, visually marked, and genetically sampled. Collars consisted of a remote-download GPS unit and a VHF radio locator. Each collar provided 1 to 4 months of location data at 30-minute intervals per individual. Location data were used to verify individual identity from detections on cameras and hair snares, to determine home range size and location, and to estimate average movement rate. Captured individuals were marked with colored ear tags (Nasco© Standard Nylon Rototags) with heat shrink (Gardner Bender© heat shrink tubing) patterns for day and nighttime identification on camera traps. A biopsy tissue punch was taken from each ear before inserting ear tags, both to improve ear tag retention and ear healing and to collect high-quality genetic samples from captured lynx. Tissue samples were stored in microcentrifuge tubes in 70% ethanol. Genetic samples from these known individuals, in combination with the hair snare dataset, were genotyped and used to empirically define the level of allelic mismatch required to genetically differentiate individuals.

Snow Track Transect Methods

Snow track transects were completed from November 2016 through March 2017 while snow conditions allowed, following methods in O'Donoghue et al. (1997) and Krebs (2011). Lynx track crossings were counted along a 25-km transect (Fig. 2) that ran the length of the study area by one local expert tracker. The transect was split into eight roughly similar transect lengths. The transect was traveled by snowmobile after a minimum of 18 hours since the last snowfall event or high wind that erased previous tracks, and then for 1 to 2 days afterward as long as fresh tracks could be distinguished (O'Donoghue et al. 1997). A track crossing was counted when tracks were observed entering and exiting the transect. Tracks that were observed to be from the same individual re-entering the transect were not double-counted. Days since last snowfall, nights since last count, temperature, and weather conditions were recorded before each tracking day. Date, location, habitat type, species, apparent group size, and apparent group age composition were recorded for each observed set of lynx tracks. Days were spread evenly across the winter months with the aim of completing at least 15 tracking occasions per winter season, with days spread evenly across winter months but necessarily dependent upon conditions. Total 'track days' were defined as the product of the number of track segments traveled by the number of days that tracks could have accumulated.

Hair Snares and Genotyping Methods

I used hair snares and scent lures to passively collect hair samples from lynx following the methods described in McKelvey et al. (1999), McDaniel et al. (2000), Weaver et al. (2005), Ruell and Crooks (2007), Davoli et al. (2013), and Crowley and Hodder (2017). The scent lure was a mixture of beaver castoreum, glycerin, catnip (*Nepeta spp*.) oil (Davoli et al. 2013), and aniseed (*Pimpinella anisum*) oil. The liquid mixture was spread onto a 10 cm x 10 cm carpet pad. A loop of barbed wire was stapled to the hair snare to snag hair. The carpet pad with lure and attached barbed wire was nailed to the base of a tree approximately 30 cm above the ground or snow surface to allow lynx to rub. Hair snare stations also included a hanging CD as a visual lure (Kendall and McKelvey 2008). Hair snares were checked at the end of 14-day sampling occasions. Successful snares with hair samples were collected as whole pads, placed into paper envelopes with five-gram desiccant packets, and stored dry until genetic analysis.

Sixteen hair snare stations were placed along a 35-km stretch of the Alaska Highway, 14 stations along 25 km of the Old Alaska Highway, and six off-trail (Fig. 3). In total, 36 hair snares were deployed within the study area at an average spacing of 1.5 km. Hair snare locations were biased toward placement on trails to exploit lynx trail use and maximize detection rate. Hair snares were spaced relative to lynx home range size so that individual lynx had an opportunity to encounter more than one hair snare (Efford 2017a).

Hair snaring pilot seasons were completed in 2015/16 to refine the data collection and genotyping methods, then the final methods were employed from January through April 2017. Multi-locus genotyping of hair samples was achieved by typing eight microsatellite loci (Fca090, Fca126, Fca176, Fca043, Fca045, Fca096, Fca008, and Lc120) and a zinc-finger sex marker from genetic material in the follicle of the hair. Loci Lc110, Lc118, and Lc111 were tested on preliminary hair snare samples and on high-quality tissue samples from Alberta lynx, but were discarded because of low genotyping success. The zinc-finger sex marker, which uses primer sequences for the zinc-finger region of the X and Y chromosomes, has been shown to be an accurate sex identification test in Canada lynx (Pilgrim et al. 2005) and was accurate in preliminary tests on Alberta lynx samples in our study. Compared to hair from bears and mustelids, on which the majority of passive hair sampling research has been conducted, hair from felids is finer with smaller follicles (Long et al. 2008). Felid hair follicles frequently do not contain sufficient amounts of genetic material to genotype hair samples to individual (Long et al. 2008), meaning that successful genotyping procedures to identify individuals from passive hair sampling had not yet been established at the start of this project.

Refinement of the genotyping protocol used hair and tissue genetic samples from Kluane lynx collected in 2016. Allele calling was done blind with respect to pad, hair snare station, and date collected. Although genotyping success typically increases and error decreases with the number of hairs included in testing (Goossens et al. 1998; Lamb et al. 2016), I first tested single hairs to avoid mixed samples. Single hairs were unsuccessful in producing genotypes, where success was defined as more than 65% of samples resulting in a multi-locus genotype (Lamb et al. 2016). Samples of a single hair achieved 20% success from 20 samples. I then attempted the same procedure with five hairs per sample from a localized part of each pad at the risk of mixing samples from multiple individuals. Results improved to approximately 40% success from 21 samples. By extracting tufts of plucked hair from barbs, most with 15 or more hairs with intact follicles per tuft, genotyping reached nearly 100% success for 40 samples from 17 pads. Among these 40 samples was one mixed sample where there was evidence of more than one allele at a locus, indicating that the genetic material of more than one lynx was present in the sample. Extracting several (2 to 4) samples from each pad provided replication of samples and safeguarded against data loss when mixed samples were present on a pad.

Tissue samples were collected from live-trapped lynx from November 2016 through April 2017 during ear tagging efforts. Fifty tissue samples collected from 25 lynx were used to assess the genetic variability of the lynx population and to empirically define the level of allelic mismatch required to genetically differentiate individuals. Spatial locations of hair snare-captured individuals were cross-checked with known individuals' home ranges from telemetry data and camera data (Davoli et al. 2013). Telemetry data from animals that were both captured in live traps and detected on hair snares were used to estimate sigma as a parameter of interest related to home range size in hair snare-based density analysis.

The identification of individuals from unknown genetic samples requires knowledge of the level of genetic mismatch that differentiates one individual from another. Using known samples from captured lynx and the hair snare dataset from January through April 2017, I conducted a pairwise comparison across samples. From the results, I produced allelic mismatch curves for both the captured lynx and the hair snared lynx genotype datasets. Both curves showed a clear break in allelic mismatch at four of 16 possible dissimilar alleles (Fig. 5 and 6). The captured lynx mismatch curve was compared to known identities of samples. I determined that no two individuals in the captured sample differed at fewer than four alleles. I therefore defined unique individuals from pairs of samples in the hair snare dataset as having allelic mismatch greater than or equal to four alleles, assuming no allelic dropout or genotyping errors. Mismatched pairs of samples that differed at 1, 2, or 3 alleles were individually examined for instances of potential allelic dropout or genotyping errors, then were assigned to individuality manually.

Camera Trap Methods

I deployed passive camera traps (Reconyx^{TM} PC900 Hyperfire, Reconyx, Inc., Holmen, Wisconsin, USA) at 76 locations within the study area (Fig. 4) from January through June 2017. Cameras were programmed to run continuously and to take one rapid-fire photo upon motion and heat trigger, without delay. Date, time, and temperature were automatically stamped onto each image. I set cameras on trees 30 to 50 cm above the ground or snow surface. Vegetation was cleared directly in front of cameras but was otherwise left undisturbed. Cameras were not visited by researchers anytime between the start and end of the session.

Cameras were deployed semi-systematically across the study area with flexible microhabitat placement in order to evenly cover the study area and to maximize the probability of detection where lynx were present. Stations were placed within a maximum 100 meters of a predetermined target location, with care taken to choose, where possible, microhabitats and landscape features that maximized area in front of the camera, showed signs of lynx presence (tracks, scat), and/or exploited apparent lynx preferences for paths, ridges, and forest edge (Brand et al. 1976; Surnato et al. 2013). Camera stations were at least 1 km and not more than 2 km from their nearest neighbor; on average, cameras were 1.3 km from their nearest neighbor. Cameras were spaced relative to lynx home range size (Nellis et al. 1972; Poole 1995; Mowat et al. 2001) so that individual lynx had an opportunity to encounter more than one camera (Efford 2017a). Final camera locations were random with respect to human-created trails and roads. There was no difference in distance from human-introduced trails to 76 camera stations (mean = 753 m, SD = 633) and to 76 randomly generated points (mean = 752 m, SD = 616 across three iterations) on the landscape.

For three density estimation methods it was necessary to define a photographic "detection" such that detections are temporally independent. Using a sample of count data (n = 40 camera stations over 10 months), I compared total detection counts with different minimum time intervals between photo captures to define a detection. I compared 10, 20, 30, 40, 50, and 60-minute intervals between photos to define detections, and found that 20, 30, and 40-minute intervals resulted in minimal change in total count. A ten-minute change in either direction from the 30-minute interval resulted in less than 1% change in total count (+/- 5 detections of 753 detections). Overall, changes to the definition of detection by time interval affected the total count minimally. I also observed marked individuals on cameras from January through June 2017 and found that there was only one instance in which a marked individual was detected with a different individual (other than distinguishable juveniles) within a 30-minute window. I therefore defined a photographic "detection" of unmarked animals as a series of lynx photos separated from the next series of photos by at least 30 minutes. Lynx photos taken within 30 minutes were defined as the same detection.

For two analyses it was necessary to estimate the average area sampled in front of the camera, or the area of the detection zone in which lynx could be detected. I measured the area of the detection zone in the field from 40 cameras in January 2017 and from the same 40 cameras in June 2017. I used the WalkTest mode on Reconyx^{TM} cameras by moving in front of the camera on all fours, observing the red light on the camera that indicates a detection of heat and motion, and marking the edges of the detection zone with wooden stakes that remained throughout the sampling session. I placed three wooden stakes at each measured camera station: one at the furthest detectable straight-line distance from the camera, and one each at the right-most and left-most extent of the zone. Using the distance of each stake from the camera and the width between the right-most and left-most stakes, I was able to approximate the detection zone as a circular sector. I excluded area beyond trees or vegetation or other obstacle limiting perfect detection. I averaged the measured interior angles and radii from June and January for use in analysis. The area of the detection zone in January 2017 was 6.9 m^2 (mean radius = 5.0 m, mean angle = 32 degrees). The area of the detection zone in June 2017 was 5.5 m^2 (mean radius = 4.7 m, mean angle = 28 degrees). The average area of the camera detection zone for the period between January and June 2017 was 6.2 m^2.

Density Estimation Methods

Six statistical methods were used to estimate the density of lynx. Each method is described conceptually below, including the data requirements for application of the method (Table 1) and key assumptions of the method (Table 2).

1. Formozov-Malyshev-Perelishin (FMP) Formula

The FMP formula was applied to snow track transect data to estimate lynx density. The formula uses the total number of track crossings counted, the mean daily travel distance of the lynx population, and the total transect length, as in Equation (5) of Stephens et al. (2006):

$$D = \frac{\pi}{2}\frac{x}{S\widehat{M}}$$

where *D* density equals the product of $\frac{\pi}{2}$ and *x* track crossings divided by the total transect length S and an estimate of daily travel distance *M* (Dzięciolowski 1976; Stephens et al. 2006; Keeping and Pelletier 2014). The formula models the probability of the intersection of lines of specified lengths (Keeping and Pelletier 2014). A current estimate of daily travel distance can account for changing detection probability and is used here to linearly scale track counts to density (Stephens et al. 2006). Only tracks made in the 24 hours before track counting occurs are counted to correspond with the daily movement rate.

I used daily winter travel distance from 13 lynx (8 female, 5 male) collared from November 2016 through April 2017 to estimate the average daily travel distance (movement rate) for the population. VHF and GPS collars provided location data for each animal in 30-minute fixes. I calculated the step lengths between any two consecutive fixes as a distance traveled in km (n = 27,514 step lengths; in Rstudio Version 1.1.386). I excluded fixes that occurred during and immediately following the collaring process, were zeroes, or were implausibly far distances to have travelled in 30 minutes (greater than two km) to remove probable location errors. I calculated the average step length for each collared animal over the duration of the collar life. I weighted the sample mean by the number of fixes for each collar. The mean daily movement rate was 7.06 km (SD = 2.17), or hourly movement 294 meters (SD = 93).

The FMP formula assumes no sampling bias from transect placement, behavioral responses like attraction or repulsion from the transect, or missed track crossings (Keeping and Pelletier 2014). It assumes geographic and demographic closure, but simply returns the average density over the sampling period for open populations (Rowcliffe et al. 2008). It requires an accurate estimate of movement rate (Stephens et al. 2006), which may vary over time and by location. The method avoids subjective definitions of study area and edge effects by directly estimating density (Stephens et al. 2006; Keeping and Pelletier 2014). I used nonparametric bootstrapping (R package ‘boot’ Version 1.3-20, RStudio Version 1.1.386) with replacement of transect segment to estimate the 95% confidence interval (CI), as suggested in Stephens et al. (2006), and the relative standard error (RSE) as a measure of precision.

2. Spatially Explicit Capture-Recapture (SECR)

Hair snare data were analyzed with likelihood-based SECR models (Efford 2004; Efford et al. 2009b) to estimate lynx population density. SECR density estimation methods model the probability of specified capture histories by the estimated point locations of animal activity centers and distance of the detectors from these centers (Efford et al. 2009a). Detection probability of an individual at any passive detector is a function of the distance of the individual’s estimated activity center from the detector (Efford et al. 2009a).

The method estimates the density of activity centers in the area of integration as an approximation of the density of individuals (Efford et al. 2009b). Precision of the estimate is dependent on sample size, defined as the sum of the number of individuals detected and the number of recaptures (Efford 2017b). In this study, density was estimated for a four-month hair snaring session divided into eight two-week occasions.

SECR models rely on some key assumptions. Each animal in the population is assumed to have a stable activity center and the population is assumed to be demographically and geographically closed (Efford et al. 2009b; Efford and Fewster 2013). Because density is estimated directly, however, SECR avoids *ad-hoc* definitions of study area and edge effects (Efford and Fewster 2013). Detection probability of any one individual at a detector is assumed to decay as the detector distance increases from the activity center (Efford et al. 2009a). Detector locations are assumed to be random with respect to activity center locations (Efford and Fewster 2013), but not necessarily random with respect to landscape features. Activity centers are randomly distributed according to a Poisson process (Borchers and Efford 2008). Each individual detection is independent of any other detections (Efford et al. 2009a), meaning this method may be less appropriate for grouped animals. All animals included in the sample are marked, they do not lose their marks, and they are always identifiable to individual throughout the sampling session (Borchers and Efford 2008).

Density was estimated from hair snare data using the R package 'secr' version 3.1.0 (Efford 2017, in RStudio 1.1.386). Data input included capture histories of known individuals and spatial data from trap locations. A habitat mask denoting non-habitat (large water bodies over 30 hectares and elevation above 1600 meters) was used to limit the area of integration to only lynx habitat and buffer the sampling area by 6 km (Efford 2018b) (created in ArcGIS Version 10.5). Candidate models for density included home range size predicted by sex, probability of detection predicted by sex, sigma fixed across all individuals, and probability of detection predicted by sampling occasion. I calculated average sigma to be 1.3 km in the R package ‘secr’ version 3.1.0 (in RStudio 1.1.38) using telemetry data from 11 telemetered individuals that were also detected on hair snares. I calculated 95% CI and RSE as a measure of precision (Efford 2017a).

3. Random Encounter Model (REM)

The REM was applied to the camera trap dataset to estimate lynx density as an unmarked population (Rowcliffe et al. 2008). The method uses the detection rate of independent captures, an estimate of movement rate, average group size, and the area sampled by the remote camera (Rowcliffe et al. 2008; Rowcliffe et al. 2013). The model is analogous to the FMP formula, described above, because it uses movement rate to linearly scale detection rate with density. The equation, from Rowcliffe et al. (2008):

$$D = \frac{y}{t}\frac{\pi}{vr(2+\theta)}$$

gives density *D* as a function of detection rate $\frac{y}{t}$ (detections per unit time), animal movement speed *v*, the radius *r* of the camera detection zone, and the interior angle of the detection zone θ.

This method assumes demographic and geographic closure, though non-closure simply leads to estimates that are averages over the sampling period (Rowcliffe et al. 2008). The REM assumes random placement of cameras relative to landscape features and activity centers and no behavioral response (attraction or aversion) to detectors (Rowcliffe et al. 2008). Possible sources of error include inaccurate detection zone area measurements and movement rate measurements (Rowcliffe et al. 2013; Cusack et al. 2015). The REM does not require marked animals or identification of individuals and can use detector layouts spaced without regard to population home range size (Rowcliffe et al. 2008). Direct estimation of density avoids *ad-hoc* definitions of study area (Rowcliffe et al. 2008).

Density estimation was completed using the equation above for camera units active from January through June 2017 and by using measured interior angles and radii of circular sector camera detection zones. I used the mean hourly movement rate (as calculated for the FMP formula). I used nonparametric bootstrapping (R package ‘boot’ Version 1.3-20, RStudio Version 1.1.386) with replacement of camera station to estimate 95% CI, as suggested in Rowcliffe et al. (2008), and RSE as a measure of precision.

4. Spatial Capture-Mark-Resight (SCMR)

SCMR models allow for density estimation from partially marked populations by combining individual capture histories of marked animals with counts of unmarked detections (Efford 2018a). Study sessions are split into ‘marking’ and ‘resighting’ occasions, where resighting occasions involve detecting marked animals but not marking new animals (Efford and Hunter 2017; Efford 2018a). SCMR capture histories and detector locations are modeled as in conventional SECR with the addition of spatially correlated count data of unmarked and unknown animals (Efford and Hunter 2017). These data are taken together to estimate the number of home range centers in the area of integration by maximizing the pseudolikelihood (Efford and Hunter 2017; Efford 2018a). In conventional SECR, unmarked detections are discarded which in some studies can represent a meaningful loss of data (Rich et al. 2014).

There are several key assumptions associated with implementation of a SCMR model. The population is assumed to be demographically and geographically closed during the sampling period (Efford 2018a). Marks are not lost during the sampling period for maximum precision, but SCMR does allow for the inclusion of detections from marked but unknown individuals (Efford 2018a). Animals are assumed ungrouped so that detections on cameras are independent (Efford and Hunter 2017). Unless otherwise modeled, there is an underlying assumption that marked animals are an unbiased sample of the population and are evenly distributed across the trapping area (Efford and Hunter 2017). The number of marked animals present in the trapping area should be known before resighting occasions (Efford 2018a). Counts of unmarked animals are modeled with a Poisson distribution (Efford 2018a). Individual covariates (e.g., sex) and telemetry data are not compatible with or useful for SCMR models (Efford 2018a). As in SECR, all animals are assumed to have stable activity centers within home ranges where detection probability is greatest (Efford et al. 2009b). Detection probability decays as the detector distance increases from an activity center (Efford et al. 2009a). Detector locations are assumed to be random with respect to activity centers (Efford and Fewster 2013).

Density estimation in SCMR was completed using capture data from the marking process, individual capture histories from camera traps, counts of unmarked and unknown lynx detections, and spatial information from the marking and sighting processes in R package 'secr' version 3.1.0 (in RStudio 1.1.386). I used camera data from January through June 2017 divided into 12 two-week sighting occasions and two two-week marking occasions. A habitat mask denoting non-habitat (large water bodies over 30 hectares and elevation above 1600 meters) was used to limit the area of integration to only habitat and buffer the sampling area by 6 km (Efford 2018b) (created in ArcGIS Version 10.5). I modeled the marking process so that animals were 'marked' at the nearest camera to the box trap location of first capture. I approximated the timing of marking by interposing two marking occasions between sighting occasions, once before the sighting process began and once mid-session. This approach was intended to approximate continuous marking during the sampling session. Candidate models included models that fixed home range size across all individuals, modeled detection probability by occasion type (marking or sighting), fixed the probability of identity at the proportion of 'marked' photos with identifiable lynx, and adjusted for overdispersion of count data (Efford 2018a). I calculated 95% CI and RSE as a measure of precision (Efford 2017a).

5. Spatial Mark-Resight (SMR)

SMR is similar to SCMR except that it utilizes a Bayesian inference method as opposed to a likelihood-based method (Efford and Hunter 2017). SMR is intended for density estimation for partially marked populations by combining individual capture histories of marked animals with counts of unmarked detections over several occasions (Sollmann et al. 2013b; Rich et al. 2014; Whittington et al. 2018). SMR models allow for increased complexity of models and inclusion of auxiliary data, like telemetry data from marked animals, to inform model parameters (Sollmann et al. 2013b; Sollmann et al. 2013a; Whittington et al. 2018). 'Marking' and 'sighting' occasions are modeled separately as sub-models, where different trap types (live traps, camera traps) can be differentiated within the same session (Whittington et al. 2018). SMR can accommodate studies where animals are marked over the same time period as they are sighted (Whittington et al. 2018), removing the need to approximate the marking process. SMR models allow for the inclusion of individual covariates, like known sex or age of marked and unmarked animals (Whittington et al. 2018). When included, these data have potential to improve upon conventional mark-resight models. SMR models have been shown to provide more precise estimates of density than SCMR models (Efford and Hunter 2017).

SMR models assume demographic and geographic closure of the population during the sampling period and that animals have stable activity centers (Rich et al. 2014). Individual marks are not lost for maximum precision, but SMR does allow for inclusion of marked but unidentified resighting detections (Sollmann et al. 2013b; Whittington et al. 2018). The number of marked animals present in the study area is known before resighting occasions (Sollmann et al. 2013b; Rich et al. 2014). Detections are assumed to be independent and animals are ungrouped (Sollmann et al. 2013a). Counts of unmarked animals are modeled with a Poisson distribution (Rich et al. 2014). Detection probability decays as the detector distance increases from an activity center (Sollmann et al. 2013b; Rich et al. 2014). Detectors are assumed to be randomly placed with respect to activity centers (Sollmann et al. 2013b). Marked animals are a random sample of the population with home ranges located inside the state space (Sollmann et al. 2013a; Rich et al. 2014).

Density estimation was completed using capture data from the marking process, individual photographic capture histories, photographic counts of unmarked lynx detections, spatial information from both marking and sighting processes, and reduced telemetry data from 15 collared animals (7 female, 8 male). We used camera data from January through June 2017 with 12 two-week occasions. We designed our SMR modeling method using R script and concepts from Whittington et al. (2017) to build upon a hierarchical model for camera trap SMR data. We developed sub-models for the marking and sighting processes, excluded non-habitat (large water bodies over 30 hectares and elevation above 1600 meters), and buffered the study area by 6 km (in ArcGIS Version 10.5). A prior for population sex ratio was estimated using separate SECR hair snare density models for female and male lynx (43% female, 57% male) (in R package ‘secr’ version 3.1.0). Candidate models modeled home range size by sex and modeled detection probability by sex. We analyzed these data using Markov chain Monte Carlo (MCMC) sampling. We ran 3 chains for 20,000 iterations and discarded the first 5,000 iterations as a burn-in.

6. Random Encounter and Staying Time (REST)

The REST model is a recent modification of the REM (Nakashima et al. 2017) that uses cumulative time in the camera detection zone to estimate population density from camera trap datasets. Modified from Nakashima et al. (2017),

$$D = \frac{\sum \overline{n}t}{\bar{a}T}$$

density *D* is given by the sum of the average number of animals per time series *n* and the time animals were present in the detection zone *t* across cameras, divided by the product of the average area of the detection zone *a* across all cameras and the total operating time *T* of all cameras. A time series is any consecutive series of photos where the animal is continuously within the camera detection zone. If an animal leaves the detection zone and then returns, a new time series begins. Area of the detection zone can be approximated as a circular sector by measuring the radius and interior angle of the sector. The REST method avoids the use of movement rate required in the REM and the FMP formula. It also avoids definitions of a photographic detection. Populations can be unmarked and there is no need for prior knowledge of population parameters like home range size (Efford 2017a). The REST model directly estimates density (Nakashima et al. 2017) and so avoids *ad-hoc* definitions of study area and edge effects.

The REST model assumes that the population is closed, though open populations will produce a density estimate that is simply the average density over the time period (Rowcliffe et al. 2008). Within the detection zone, the probability of detection is assumed to be perfect ($p = 1$) unless otherwise modeled (Nakashima et al. 2017). The method assumes random placement of cameras and that camera locations are representative of the available habitat (Nakashima et al. 2017). REST assumes that animal movement and behavior are not affected by the detector (Nakashima et al. 2017). Attraction or aversion to camera traps is exhibited in some species (Meek et al. 2016), and could affect the time within the detection zone and subsequently affect estimates of density. Application of the REST model requires accurate measurements of the area of the camera detection zone, which has been a challenge in previous studies (Rowcliffe et al. 2011; Anile and Devillard 2014; Cusack et al. 2015; Hofmeester et al. 2016; Nakashima et al. 2017).

Density was estimated using the equation above for camera units active from January through June 2017. Area of the detection zone was estimated using the average of the field measurements for January and June. I excluded all detections of lynx beyond the measured detection zone. I removed lynx residence time spent investigating the camera or other sampling equipment and time beyond the measured detection zone. Photos showing ‘investigating’ behavior were classified based on observation of behaviors directed at equipment like smelling, rubbing, and staring. I began the sampling session five days after camera deployment in January to avoid possible attraction from snowshoe trails. I used nonparametric bootstrapping (R package ‘boot’ Version 1.3-20, RStudio Version 1.1.386) with replacement of camera station to estimate 95% CI and RSE as a measure of precision.

Results

Live Captures

Twenty-five unique lynx (12 male, 13 female) were captured in live box traps. Of these, 21 were fitted with VHF and GPS collars (11 male, 10 female) and 19 provided useable location data by the end of the study. Collared animals provided between 325-5077 point locations each (mean = 2322). All of the 25 captured lynx provided complete multi-locus genotypes from tissue samples and 22 were given unique ear tags for identification on cameras.

Snow Track Transects

Total length of the transect traveled over the sampling session was 238 km after 14 snowfall events. Over 69 track days, 171 track crossings were observed. The detection rate was 2.5 detections per track day.

I used the average movement rate estimated from GPS and VHF location data (7.06 km/day, SD = 2.17) and the FMP formula applied to the snow track transect data to obtain a density estimate of 16 lynx/100km^2 (95% CI 13-19; RSE 10.3% of the estimate).

Hair Snares

Hair snares were active for a total of 4032 trap nights over the sampling session. Hair snares averaged 40-50% success in each occasion except in late April, when hair snare success dropped to 20%. I collected 239 samples from 102 instances of successful snares (average 2.3 samples per successful snare). The detection rate was 5.9 hair samples per 100 trap nights. Of the 239 samples, none failed to amplify due to low quality or quantity samples. Thirty-five samples (15%) showed evidence of more than one allele at a single locus, indicating that the sample was mixed. These samples did not produce a unique genotype and were discarded, leaving 204 useable samples. In three instances, two unique lynx genotypes were detected on the same hair snare from the same occasion and were retained.

For hair snare genotypes, probability of identity (probability that two unique genotypes will be scored as one individual) was 7.3 x 10^{-8}, and probability of sibling identity (probability that two unique siblings will be scored as one individual) was 1.2 x 10^{-3}. Hair snares detected 41 unique lynx (15 female, 26 male) 96 times across eight occasions (Fig. 7). Twenty of 41 lynx were detected only once. The most extensive capture history for one individual (male) was 9 detections over 6 hair snare locations. Of the 25 live-trapped lynx that provided tissue samples, 15 were detected on hair snares. Live-trapped individuals comprised 37% of hair snare detections. A maximum of two females were detected at a single location (two instances), whereas a maximum of four males were detected at a single location (three instances).

The most precise SECR model applied to the hair snare dataset fixed sigma based on the average sigma from telemetry data at 1.3 km. Lynx density estimated by this model was 20 lynx/100 km^2 (95% CI 14-28; RSE 16.9% of the estimate). The model estimate of probability of detection at an activity center was $g_0 = 0.13$. The null model incorporating no telemetry data estimated sigma at 1.6 km and resulted in a density estimate of 17 lynx/100 km^2 (95% CI 12-24; RSE 18.9% of the estimate).

Camera Traps

The camera trapping study session resulted in 7,651 trap nights from 73 camera traps. Within this time period, I documented 29 species and genera, including 303 lynx detections. The detection rate was 3.9 detections per 100 trap nights. Marked animals were present in 13% (41) of lynx detections. I was able to identify marked lynx to individual in 78% of marked lynx detections (84% in daytime detections; 73% in nighttime detections). Fifteen of the 22 marked lynx were detected at least once on camera. The most extensive capture history was for a marked individual (male) that was detected 6 times at 6 different locations.

For the REM analysis I used the average area of the measured detection zone (6.2 m^2) and the average hourly movement rate estimated from location data (294 m/hour). Lynx density estimated using the REM and applied to the camera trapping dataset was 11 lynx/100 km^2 (95% CI 8-14; RSE 13.5% of the estimate).

The most precise likelihood-based SCMR model for the camera trapping dataset approximated two marking occasions and modeled the probability of detection g_0 differently for marking and sighting occasions. Lynx density estimated by this model was 55 lynx/100 km^2 (95% CI 37-81; RSE 19.9% of the estimate). An alternative model with two marking occasions but no differential modeling of g_0 resulted in a density estimate of 64 lynx/100 km^2 (95% CI 44-94; RSE 19.9% of the estimate).

The Bayesian inference SMR model applied to the camera trapping dataset and augmented with live trapping and telemetry data modeled home range size by sex. Lynx density was estimated to be 46 lynx/100 km^2 (95% Bayesian credible intervals 35-61; RSE 14.1%).

For the REST method, I excluded time when lynx investigated survey equipment, when they followed snowshoe trails to cameras, and when they were detected beyond the measured detection zone. I used the average area of the measured detection zone. Lynx density was estimated to be 52 lynx/100 km^2 (95% CI 32-75; RSE 21.2% of the estimate).

Comparison of Methods

Point density estimates from the six estimation methods varied five-fold and fell into two groups, each with overlapping confidence or credible intervals (Fig. 8). The FMP formula for track transects, SECR for hair snares, and the REM for camera traps returned density estimates between 11 and 20 lynx/100 km^2. SCMR, SMR, and REST for camera traps returned density estimates between 46 and 55 lynx/100 km^2. Confidence or credible intervals did not bridge the gap between the two groups (Fig. 8).

Precision of estimates varied two-fold, ranging between RSE 10.3% (FMP formula) to RSE 21.2% (REST model) of the density estimate (Fig. 9). All RSE values were reasonably precise (Efford et al. 2009b; Newey et al. 2015; Stenevik et al. 2015; Efford et al. 2016).

Discussion

I compared methods of density estimation for Canada lynx using overlapping survey data of a lynx population and contemporary statistical methods. I obtained adequate sample size to apply six methods of lynx density estimation and achieve reasonably high precision of estimates. I provided the first density estimates of lynx using the FMP formula, REM, SCMR, SCR, and REST models. I also developed a successful noninvasive hair snaring method and genotyping procedure to estimate lynx density from SECR and hair snares, building on the progress of similar methodological studies (Crowley and Hodder 2017). Despite making every effort to follow existing methods in the literature and meet model assumptions (Stephens et al. 2006; Rowcliffe et al. 2008; Efford et al. 2009b; Efford and Hunter 2017; Nakashima et al. 2017; Whittington et al. 2018), I show that density estimates varied among contemporary estimation methods.

Comparison to Literature

The three lowest density estimates (range 11-20 lynx/100 km^2) resulting from this work are similar to previous estimates of lynx density from years preceding a population peak. These studies used snow tracking and/or radio telemetry data to directly enumerate lynx in defined study areas (Brand et al. 1976; Bailey et al. 1986; Koehler 1990; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997; Vashon et al. 2008; Vashon et al. 2012). Densities in cyclic lynx populations the year before a peak were reported at 7 lynx/100 km^2 in Alberta (Brand et al. 1976), 15 lynx/100 km^2 in both Kluane, Yukon

(O’Donoghue et al. 1997) and the Northwest Territories (Poole 1994), and 24 lynx/100 km^2 near Teslin, Yukon (Slough and Mowat 1996). Estimates resulting from these methods were typically reported as conservative estimates (Ward and Krebs 1985; Poole 1994) and may have missed individuals with overlapping home ranges. Applying similar methods to estimating density with my dataset, the result is a density of 14 lynx/100 km^2, which is similar to the density reported by O’Donoghue et al. (1997) from the same study area just before a population peak (15 lynx/100 km^2). When compared to camera and hair snare datasets from this study, however, it becomes clear that this approach underestimates overlap of lynx home ranges near a population peak and therefore underestimates density.

The three highest density estimates (range 46-55 lynx/100 km^2) resulting from this work are higher than any previously published density estimates from the year before a cyclic peak. However, Slough and Mowat (1996) reported density estimates of 45 lynx/100 km^2 in a peak year in Teslin, Yukon. They calculated this density based on radio-collar location data and snow tracking, but differed from other, similar studies in that they included a conversion factor to include potentially missed kittens (Slough and Mowat 1996).

Before this study, there was little existing research to suggest that contemporary and emerging density estimation methods varied widely in their results. Methodological comparisons of density estimators in the literature have typically compared new methods to conventional methods of density estimation, particularly distance sampling (Zero et al. 2013), GPS-telemetry enumeration (Soisalo and Cavalcanti 2005), and non-spatial capture-recapture (Obbard et al. 2010). Those studies that do compare across contemporary methods typically compare them by using the same dataset but either changing the inference method (Noss et al. 2012; Efford and Hunter 2017) or augmenting the method with more data types (Sollmann et al. 2013b; Rich et al. 2014; Alonso et al. 2015). Anile et al. (2014) compared estimates derived from the REM for unidentifiable camera trap photos, SECR from identifiable camera trap photos, and SECR from identifiable scat, but found no significant difference in point estimation. This work provides the first evidence that density estimation methods currently in use return a variety of estimates, even when rigorously following the methods described in existing literature and making every effort to meet model assumptions (Stephens et al. 2006; Rowcliffe et al. 2008; Efford et al. 2009b; Efford and Hunter 2017; Nakashima et al. 2017; Whittington et al. 2018).

Plausibility of Estimates

The accuracy of the results remains uncertain in the absence of a known density of lynx. It is worthwhile, however, to explore the plausibility of each density estimate using all data sources available. Using the number of unique individuals genotyped from both live-trapping and hair snaring, there were at minimum 49 lynx present in the unbounded study area. If the study area is defined at approximately 300 km^2, this leads to a minimum density of 16 lynx/100 km^2. The REM and the FMP formula, then, likely underestimated density at 11 lynx and 16 lynx/100 km^2 respectively given that not all lynx were marked in the study area. The study area would have to be defined at 445 km^2 (over four times the area within the perimeter of the hair snaring and live trapping detectors) to decrease the estimate from this approach as low as the estimate that resulted from the REM, and would still represent only a minimum density from identified individuals.

An alternative approach to estimate density is to use GPS-telemetry data and camera data. I defined a 100 km^2 area within the core of the study area covered by both live traps and cameras. Of 16 telemetered animals observed within this area, 13 had home range centers within the area. These 13 marked and telemetered animals comprised 25.4% of camera detections within the area in April and May, after collaring and marking processes were completed. Assuming that marked lynx had the same probability of detection on cameras as unmarked lynx, I converted the minimum density known from telemetry to 51 lynx/100 km^2. However, this method may have produced high densities due to edge effects. Observations of marked animals with home range centers outside the 100 km^2 core area within the time period comprised 16% (3) of all marked detections. Assuming this proportion remains constant for unmarked animals, the number of unmarked detections can be equivalently reduced to remove edge effects so that the 13 telemetered individuals comprise 30% of all marked and unmarked detections. This modification reduces the density from this approach to 43 lynx/100 km^2. This approach provides evidence that the three lowest estimates, including SECR with hair snares, were underestimates of density.

A third approach, however, indicated that the higher density estimates were overestimates. SECR density estimates for snowshoe hares were conducted in fall 2016 and in spring 2017 using individual hare capture histories from 86 live traps on three grids spanning the length of the valley (Krebs, 2017). Over this approximately 182-day period, hare density was observed to decline 33% from 182/km^2 (95% CI 150-221) to 122/km^2 (95% CI 93-160) (Krebs, 2017). Preliminary estimates of average kill rate from lynx on hares from classified accelerometer data are approximately 1.4 hares/day per lynx for this same time period (Studd, 2017). Additionally, kill sites of collared hares suggest that lynx were the cause of death in 71% of known-cause hare mortalities in winter 2017/18 (Peers, 2018). First, I assumed that all lynx individuals in the population killed the same number of hares and that the hare population was closed. I then predicted the decline of hares by lynx density, kill rate, and cause of mortality (Fig. 10). The three lower lynx density estimates predicted a hare decline between 20% and 36% over this period. The three higher estimates predicted a hare decline between 83% and 99%. This exercise suggests that the three lower estimates are biologically plausible, whereas the three highest estimates are not. Indeed, the highest estimate (SCMR; 55 lynx/100 km^2) predicted near extirpation of the hare population. The predicted lynx density estimate from this approach is 19 lynx/100 km^2. However, the proximity of this predicted density to the minimum density known from genotyped individuals (16 lynx/100 km^2) suggests that nearly all individuals were detected by a combination of hair snares and box traps. The kill rate estimate would need to be adjusted to 0.5 hares killed/day per lynx for the lowest of the high estimates (SMR; 46 lynx/100 km^2) to be plausible given the observed hare decline. A lower kill rate may be possible if kill rates differ between adults and juvenile lynx or if the existing sample was biased. However, it is unlikely that the kill rate has been overestimated by nearly three times the true kill rate. Overall, this approach provides evidence that the three highest lynx density estimates are likely overestimates.

Possible Sources of Positive Bias

Closure Assumption

All methods assumed population demographic and geographic closure. There were no recorded deaths of collared lynx during the sampling period, nor were there births. Kittens in southwestern Yukon are typically born in mid-June (Mowat et al. 1996). The earliest camera trap detections of same-year kittens outside of the natal den in Kluane were in early July and detections remained rare until September (from 2016 camera trap data). However, May and June months, included only in the camera dataset, may be periods of increased lynx dispersal (Poole 1997). None of the 19 lynx for which collar data were retrieved were observed dispersing from the study area during the study period, though one (female) dispersed after the conclusion of the study session and two (male) were observed dispersing during this period the year before. For REM and REST methods, non-closure of a study population simply returns an estimate of the mean density over the study period (Rowcliffe et al. 2008). For SCMR and SMR, however, non-closure of a study population violates the assumption that activity centers are stable throughout the study period, underestimates detection probability, and may overestimate density (Ivan 2018). Removing May and June from the capture history datasets, however, also removed 38% of an already low sample size for marked animal recaptures. A SCMR model excluding May and June leads to high estimates at 102 lynx/100 km^2 (95% CI 64-163) and reduced precision to RSE 24% of the estimate. I retained May and June months for camera trap-based estimates at the risk of an open population but for the benefit of greater sample size and improved precision of estimates (Efford 2017a).

Attraction to Detectors

The REST and the REM methods assumed that cameras were randomly located with respect to landscape features (Rowcliffe et al. 2008; Nakashima et al. 2017), where areas that are attractive (like trails, (Kolowski and Forrester 2017)) or repellant to lynx are only sampled in the proportion that they exist in the landscape. The high density estimate from REST may suggest that attractive landscape features were sampled in a higher proportion than they exist in the landscape. The relatively low density estimate from REM, however, suggests the opposite. Of the 73 active cameras, 19 (26%) were placed on landscape features classified as "trails." Here, the definition of a trail includes maintained human trails, unmaintained human trails, animal trails, dry creek beds, and ridges. Cameras were placed randomly with respect to approximately 115 km of human-created trails within the study area, but it is unknown if the remaining landscape features classified as "trail" were sampled more often than random. Because of the five-fold difference between the REM and REST estimates, it is unlikely that increased or decreased detection probability from biased camera placement was a leading source of error in either estimation. Regardless, both methods are sensitive to camera placement. When "trail" camera locations are removed from the camera dataset, REST estimates fall to 25 lynx/100 km^2 and density from the REM estimation falls to 6 lynx/100 km^2. Camera placement for these methods requires careful consideration during study design.

The FMP formula assumes that animals are not attracted to the track transect. In this study the transect was a snowmobile trail and a possible attractant for lynx seeking energy-efficient travel (Shepard et al. 2013; Kolowski and Forrester 2017). Cameras on the transect and similar landscape features ("trails" as described above) (n=19) detected lynx for greater lengths of time on average than cameras off-trail (n=54). Lynx spent 85 seconds on average in the detection zone of an on-trail camera over the course of the sampling session compared to 15 seconds on average in the detection zone of an off-trail camera. Interestingly, density estimates from the FMP formula using the track counts from the transect are among the low estimates. If lynx were attracted to the track transect, the high track count would be expected to result in an overestimate of density from the FMP formula (Keeping and Pelletier 2014). That the FMP formula estimate was an underestimate is either evidence that track counts were not higher than they would be at an unattractive landscape feature, or that another component of the analysis is drawing the estimate lower.

I modified the camera dataset to better meet the assumptions of the REST model and avoid positive bias. The density estimate from REST was sensitive to behavioral responses to sampling equipment (Nakashima et al. 2017); for lynx, the primary concern was attraction to equipment and investigating behaviors that would increase the cumulative time in the detection zone. Cameras, area stakes, and, temporarily, snowshoe trails leading to cameras were suspected attractants. Without modifying the dataset for these attractants, the density estimate was high at 87 lynx/100 km^2. Only modifying for snowshoe trails, the density estimate remained high at 76 lynx/100 km^2. Modifying for snowshoe trails and investigating behavior brought the estimate down to the more biologically plausible (though perhaps still high) estimate of 52 lynx/100 km^2. For a population that displays a behavioral response to sampling equipment or sampling activities these modifications may be necessary to obtain plausible density estimates.

Possible Sources of Negative Bias

Non-Detectability

Some individuals within the lynx population may not be attracted to or respond to a catnip lure, which could lead to non-detectability for some individuals and a bias in sampling using hair snares. In domestic cats (*Felis catus*), approximately 70% of all individuals had some positive response to a catnip lure (Todd 1962; Bol et al. 2017). In ocelots (*Leopardus pardalis*), 84% of individuals positively responded to a lure including catnip (Weaver et al. 2005). A systemic bias against detection of a subset of the population would be expected to proportionally reduce the density estimate. If only 77% (average of literature cited above) of lynx behaviorally respond to the lure, the SECR density estimate should be increased by

23% to 25 lynx/100 km^2. More research should be done on lynx attraction to beaver castor, catnip, and anise seed oil lures before implementing this conversion.

The hair snare dataset may have been biased away from juvenile detections. It is unknown if lynx are attracted to the catnip and beaver castor lure before maturation. There is some evidence that domestic cats do not develop responses to catnip before three months of age (Todd 1962), but there were most likely no lynx younger than three months by the beginning of the survey in January (Mowat et al. 1996). A similar hair snaring project in British Columbia, Canada observed juvenile lynx rubbing on hair snares but only sporadically (Shannon Crowley, *pers. comm.,* 3 April 2018). If hair snares did detect juveniles, their detections may be disproportionately represented in discarded, mixed samples (15% of samples) because of an increased likelihood that they were traveling in, and rubbing in, groups. If hair snares were systemically missing juveniles, whether from lack of attraction or from discarded samples, the effect of the bias is potentially fixable given an independent estimate of juvenile density. Of eight live-trapped female lynx with known reproductive status in winter 2016/17, six had kittens with an average litter size of 3.0 kittens. A conversion of the SECR density estimate to include juveniles, using the estimated population sex ratio (43% female), adds 19 potentially missed kittens and nearly doubles density from this method to 39 lynx/100 km^2. Further research on the efficacy of hair snares to detect juveniles and the reproductive success of lynx in the population should be done before implementing this conversion.

Missed Detections

The FMP formula assumes that track crossings on the transect are not missed (Stephens et al. 2006). Lynx were observed walking in existing tracks from conspecifics on camera traps, which, if repeated on track transects, could result in overlaid tracks that may not be distinguishable during tracking counts. Although this was not expected to be a principal concern for this study due to the short period in which tracks could accumulate (18 hours), the low density estimate from the FMP formula suggests that tracks could have been missed. Animals traveling in groups were the most likely to display this behavior in the short period between the snowfall event and track counting. I compared apparent group sizes from snow tracking records and camera traps to determine if lynx in groups were being missed by tracking more than they would be from visual observations. Groups greater than one animal were detected in 4% of camera detections but in 15% of track crossings. Average group size for detections greater than one animal was 2.42 lynx from cameras and 2.83 lynx from tracks. Track counts are at least as successful, if not more successful, at detecting groups and group size compared to cameras. Missed lynx detections from overlaid tracks were therefore not a likely negative bias in density estimation from the FMP formula.

It is possible that by avoiding "double-counting" lynx track crossings from the same animal during the tracking survey the assumption that tracks were not missed was violated and the density estimate was reduced from the FMP formula. It is a common practice in tracking protocols to eliminate obvious re-crossings of the same individual (O'Donoghue et al. 1997; Stephens et al. 2006). Keeping and Pelletier (2014), however, found through simulation that this approach produces error in FMP formula density estimation for species with non-linear and tortuous movement paths. Individuals with more tortuous movement paths displace shorter distances per day but, when the movement path does intersect the transect, are detected (and should be counted) more often (Keeping and Pelletier 2014). In this study, records were not kept to indicate the frequency with which re-crossings were ignored. Further research could be done to determine if this approach was a significant factor that lowered density estimates for this method.

Parameter Estimation

Movement rate was an input common to both the FMP formula and the REM, both of which were among low estimates. A sensitivity analysis using study data showed that both the FMP formula and the REM are proportionally affected by changes in movement rate, where a 1% change in movement rate corresponded to a 1% change in density. If the mean movement rate from a collared sample of the population was faster than the true population mean, it could result in underestimates of density from these methods. Individuals that move faster have a higher probability of detection (Ward and Krebs 1985; Broadley 2017; Neilson et al. 2018), so it is possible that the live-trapped animals are a biased sample of faster-moving animals in the population. Without an independent movement rate with which to compare the marked population and the unmarked population it is difficult to assess the existence or extent of this bias. Another possibility for movement rate error is that movement estimates are erroneously high due to inaccuracies in the step length analysis. I removed zeroes in the location data and step lengths over two km (per 30 minutes) as likely errors, but the deletions left gaps in the dataset greater than the 30-minute fix. These gaps could have increased movement rates when included in the step length analysis. On inspection, these gaps represented only 2.2% of total step lengths and were on average 1.2 hours. I do not expect that these errors considerably reduced the density estimates from the FMP formula and the REM. To increase estimates from these methods to 46 lynx/100 km^2 (the lowest of the high estimates, from SCMR), movement rate for the FMP formula method needed to be reduced by 65% (to 2.5 km/day) and movement rate for the REM needed to be reduced by 73% (to 74 m/hr). This reduction in movement rate is not easily explained by biased samples or analytical errors. In addition, winter lynx movement rates estimated in previous studies agree with the movement rate estimated from my methods (approximately 7.6 km/day in Parker et al. (1983)). Although movement rate may have been a factor in low density estimation from these methods, it is likely not the sole factor.

The REST and the REM methods relied on accurate measurement of the area of the detection zone with perfect probability of detection (p = 1) (Rowcliffe et al. 2008; Nakashima et al. 2017). This task has been a challenge for other studies and the literature does not yet provide a flawless method (Rowcliffe et al. 2011; Anile and Devillard 2014; Cusack et al. 2015; Hofmeester et al. 2016; Nakashima et al. 2017), especially for animals that are rarely detected. In this study, area was estimated using the WalkTest camera mode on a sample of 40 Reconyx^{TM} cameras and measurements from two seasons, winter and spring. Possible sources of error in area estimation include body size differences between researchers performing the WalkTest and lynx (Rowcliffe et al. 2011), WalkTest inaccuracies relative to the true camera detection zone area, and inherent inaccuracies in the approximation of detection zone as a simple circular sector (Rowcliffe et al. 2011; Reconyx 2017). The average radius measured across 40 stations and two seasons was 4.9 m; the average interior angle was 30 degrees. Reconyx^{TM} cameras advertise a 30-m radius and a 42-degree interior angle (Reconyx 2017), but the closed habitat of the study area limited detection area at most camera stations. I performed a sensitivity analysis using my dataset for the REM. Density estimates changed 1% from a 1% change in radius length and 0.9% from a 1% change in interior detection angle. The same analysis for the REST model found that the density estimate changed 2.3% from a 1% change in radius length and 1.3% from a 1% change in detection angle. Errors in area measurement, then, can affect the density estimate from both methods but more so for the REST method. If the detection area is measured without error, there remains the possibility that detection probability inside the detection zone is not perfect ($p < 1$). Perfect detection probability within the detection zone is convenient for these analyses and unlikely to be far from truth for large-bodied animals like lynx, but there is some evidence that even at close distances animals are not perfectly detected by camera traps (Rowcliffe et al. 2011; Nakashima et al. 2017). Imperfect detection within the measured zone would reduce the number of detections and the observed staying time, proportionally reducing density estimates from each of these methods. However, the REST and REM estimates were at opposite extremes of the range of density estimates in this study. If errors in area estimation or a violation of the detectability assumption are affecting density estimation, the inaccuracy is not large enough to result in a consistent effect on both of these estimates.

Factors Affecting Precision

All density estimation methods returned estimates with reasonable precision, but there was two-fold variation across estimates. The FMP formula produced the most precise of six estimates (RSE 10.3% of estimate), explained in part by little variability in detection rate by sampling units (range 0.54-0.98 detections/km). The REST method produced the least precise estimate (RSE 21.2% of the estimate) due to higher variability by sampling unit in cumulative residence time (0.0-2.6 seconds residence time/100,000 seconds sampling time).

SECR, SCMR, and SMR assume that animals in the study population have permanent identifying markers. Multi-locus genotypes from hair snares reliably distinguished between individuals and upheld this assumption (probability of identity = 7.3×10^{-8}), except in cases where detections were discarded due to mixed samples. Discarding mixed samples would not affect density estimates unless the mixed samples were biased, but would reduce the number of recaptures (sample size) and therefore reduce precision of the estimate (Efford 2017a). SCMR and SMR both allow for imperfect probability of identity with the implicit trade-off that a greater number of unknown detections reduces precision of the density estimate (Efford 2018a; Whittington et al. 2018). In this study, 78% of marked animal photographic detections were identified. The remaining marked lynx detections were included in data input as marked but unknown animals. Unknown detections were less informative than known marked animal detections but more informative than unmarked animal detections. Improvements to the probability of identity from photographic detections would increase precision of estimates from SCMR and SMR (Efford 2018a).

The SECR estimate from hair snares returned similar density estimates from reduced hair snare effort. The hair snare detector layout included 36 detectors extending beyond the core study area common to snow tracking and live trapping to the southeast (Fig. 3). Reducing the detector layout to 27 detectors in the area common to other methods, while maintaining detector spacing, returns a density estimate of 19 lynx/100 km^2 (95% CI 13-

28) and reduces precision to RSE 20% of the estimate. Reducing the layout further to 16 detectors returns a density of 18 lynx/100 km^2 (95% CI 11-29) and reduces precision to RSE 25% of the estimate. Overall, reducing hair snare effort affected precision but not the point density estimate from SECR.

SCMR density estimates from camera data were affected by reduced effort. The camera detector layout included 73 operational detectors extending beyond the core study area common to snow tracking and live trapping (Fig. 4). Reducing the detector layout to 60 detectors in the area common to other methods, while maintaining detector spacing, returns a density estimate of 50 lynx/100 km^2 (95% CI 34-75) and only slightly reduces precision to RSE 20.6% of the estimate. Reducing the detector layout further to 40 detectors returns a density estimate of 55 lynx/100 km^2 (95% CI 33-93) and reduces precision to RSE 27% of the estimate. A detector layout with 20 cameras returns a density estimate of 34 lynx/100 km^2 (95% CI 18-64) and further reduces precision to RSE 40% of the estimate. Overall, reduced camera trapping effort within the core of the study area affected both point estimation and precision of estimates, but only after almost halving the number of detectors.

Relevance to Ecology and Management

Lynx are a species of particular interest in ecological research of predator-prey relationships and population cycling. Using contemporary methods to estimate density would allow ecologists to answer advanced questions related to underlying components driving cyclic population growth and decline in lynx and their prey. In this study, lynx were nearing a population density peak because densities of snowshoe hare, their primary prey, were high (Krebs, 2017). As an example, I explore kill rate by lynx on snowshoe hare using varying density estimates of lynx and current density estimates of hare from spring 2017 (Krebs, 2017) and the average number of hare kills per day per lynx for winter 2017 (Studd, 2017).

Different density estimates cause differences in kill rate, measured as a fraction of the hare population removed by lynx over time. Using the lowest point density estimate (from REM for camera data; 11 lynx/100 km^2), I calculated that lynx remove approximately 15 hares per day per 100 km^2. Using the highest point density estimate (from SCMR for camera data; 55 lynx/100 km^2), I calculated that lynx remove approximately 77 hares per day per 100 km^2. This difference in kill rate equates to approximately 1 in every 1000 hares killed by the lynx population per day for the low lynx density, or 6 in every 1000 hares killed per day by lynx for the high lynx density. The true predation pressure of lynx on hares is of fundamental interest to understand the initiation and continuation of hare population declines, but methodological differences in density estimation may complicate answers to this question.

Lynx are also a species of management interest and conservation concern. In peripheral parts of lynx range in the United States, lynx are listed as a threatened species (U.S. Fish and Wildlife Service 2017). Estimates of population size are frequently used to assess population status and viability of endangered species, but few recent attempts have been made to estimate densities of lynx in these regions (U.S. Fish and Wildlife Service 2017). Despite this fundamental gap in knowledge, the U.S. Fish & Wildlife Service recommended in 2017 that protections currently offered by the Endangered Species Act to lynx be removed (U.S. Fish and Wildlife Service 2018). Conservation decisions regarding lynx in their peripheral range may be improved by adopting appropriate and precise density estimation methods after methodological exploration.

In northern regions of lynx range where lynx are naturally more abundant, lynx are regularly managed as a game species and harvested for fur (Poole 2003; Carroll 2007; Kluane National Park and Reserve 2015). Knowledge of lynx density can be important for species management in these areas, providing data upon which harvest quotas can be based and increasing the probability of persistence of both lynx populations and the northern economies and cultures to which they contribute. Lynx were trapped directly adjacent to parts of the study area during the study period. Assuming that densities do not vary significantly from the study area to the closest adjacent trap lines, I used harvest data, area of trapping concessions, and lynx density estimates to demonstrate fundamental calculations of percent of the lynx population harvested per year. In winter 2016/17, exactly 100 lynx were harvested from the 12 trapping concessions nearest the study area (Yukon Territorial Government, 2018). These trapping concessions covered approximately 5,430 km^2. Using the lowest point density estimate (from REM for camera data; 11 lynx/100 km^2), I calculated that 588 lynx inhabit the area covered by these 12 trapping concessions. If 100 lynx were harvested from this density over a trapping season then this is a removal of 17% of resident lynx. Using the highest point density estimate (from SCMR for camera data, 55 lynx/100 km^2), I calculated that 2,987 lynx inhabit the area covered by the 12 trapping concessions. If 100 lynx were harvested from this density over a trapping season then this a removal of 3% of lynx. These differing percent harvest estimates may have different implications for species management in areas with harvest quotas. Managers developing harvest quotas or other wildlife management guides that use density should carefully consider the density estimation method before reaching conclusions and implementing wildlife management actions.

Conclusion

Contemporary density estimation methods for wildlife population research are an improvement on some conventional methods because they produce estimates with measures of precision and remove sources of error typical to direct enumeration. However, density estimates vary among common and emerging estimation methods. The range of density estimates resulting from this study show that point estimates can vary five-fold and precision two-fold. Three methods apparently underestimated lynx density in this study whereas three other methods may have overestimated density, despite closely following methods described in the literature. This outcome has clear implications for research and management relying on density estimates of wildlife populations. It casts doubt on the equivalence of a density estimate from any appropriate method and suggests that multiple approaches to density estimation can be informative or necessary. Researchers and managers estimating density should carefully consider model assumptions and possible sources of error before implementing methods and accepting density estimates. This study is directly applicable to ecological research and species management of lynx, but is also relevant to density estimation of any behaviorally and functionally similar wildlife population from which an estimate of density is required.

Density Estimation Method	Data Requirement							
	Sampling effort	Count or time data	Partially marked sample	Fully marked sample	Locations of detectors	Movement rate	Home range size	Area sampled by detector
FMP		■				■		■
SECR				■	■		■	
REM	■	■				■		■
SCMR		■	■		■		■	
SMR		■	■		■		■	
REST	■	■						■

Table 1. Summary of key data requirements of each statistical method used to estimate lynx density. Grey cells indicate that the method required the corresponding data type. The Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006) was applied track transect data. Spatially explicit capture-recapture (SECR) (Efford et al. 2009b) was applied to hair snare data. The random encounter model (REM) (Rowcliffe et al. 2008), likelihood-based spatial capture mark-resight (SCMR) (Efford and Hunter 2017), Bayesian spatial mark-resight (SMR) (Whittington et al. 2018), and the random encounter and staying time (REST) (Nakashima et al. 2017) models were applied to camera trap data.

Density Estimation Method	**Assumption**								
	Demographic and geographic closure	Random detector placement (home ranges)	Random detector placement (landscape)	No behavioral response to detector	Independent detections	Stable activity centers	Marks not lost	Marks not biased	Perfect detection within detection zone
FMP	■	■	■	■					■
SECR	■	■			■	■	■		
REM	■	■	■	■					■
SCMR	■	■			■	■	■	■	
SMR	■	■			■	■	■	■	
REST	■	■	■	■					■

Table 2. Summary of key assumptions of each statistical method used to estimate lynx density. Grey cells indicate that the method relied on the corresponding assumption. The Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006) was applied track transect data. Spatially explicit capture-recapture (SECR) (Efford et al. 2009b) was applied to hair snare data. The random encounter model (REM) (Rowcliffe et al. 2008), likelihood-based spatial capture mark-resight (SCMR) (Efford and Hunter 2017), Bayesian spatial mark-resight (SMR) (Whittington et al. 2018), and the random encounter and staying time (REST) (Nakashima et al. 2017) models were applied to camera trap data.

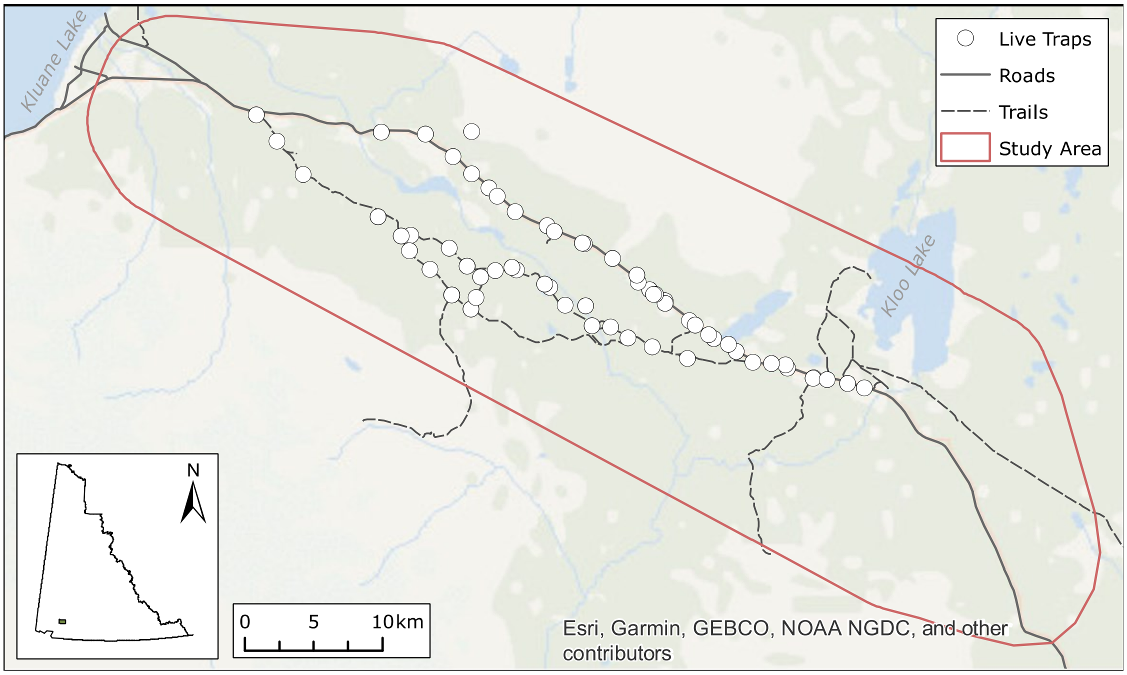

Figure 1. Map of approximate study area (red) and live trap locations (white circles) in southwestern Yukon, Canada. Roads are represented as solid grey lines and trails as dashed grey lines. Created in ArcGIS Version 10.5. Geospatial data for elevation, waterbodies, transportation features, and Yukon Territory boundary from Geomatics Yukon (2017).

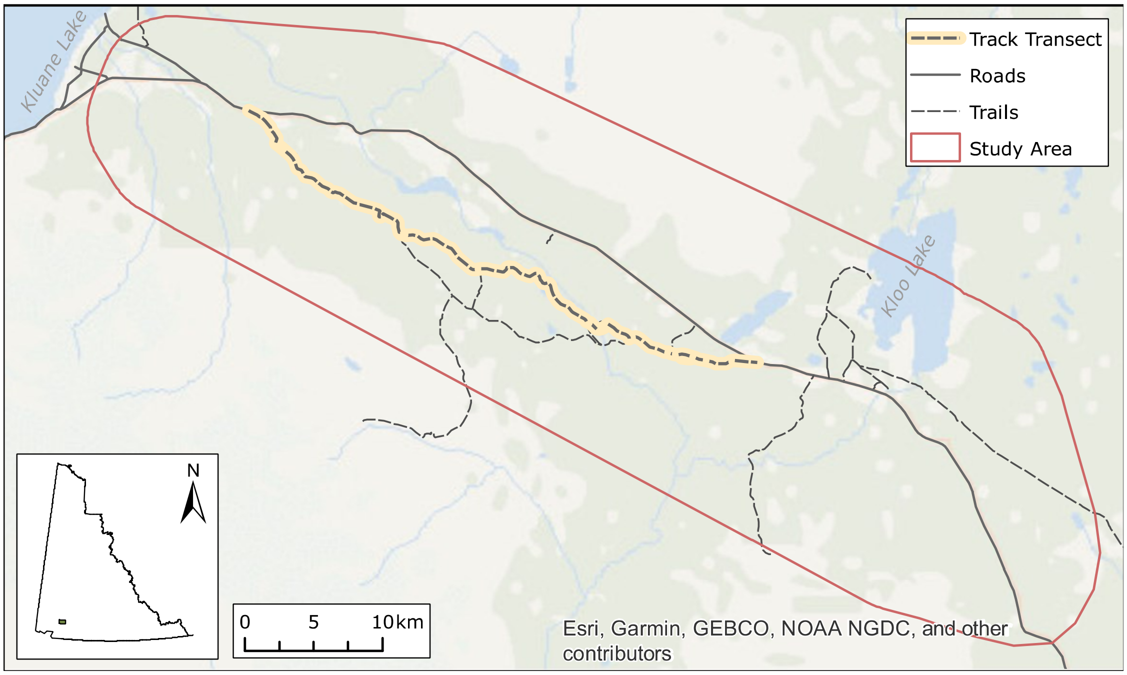

Figure 2. Map of approximate study area (red) and snow track transect (yellow) in southwestern Yukon, Canada. Roads are represented as solid grey lines and trails as dashed grey lines. The track transect bisects the study area along an existing trail system. Created in ArcGIS Version 10.5. Geospatial data for elevation, waterbodies, transportation features, and Yukon Territory boundary from Geomatics Yukon (2017).

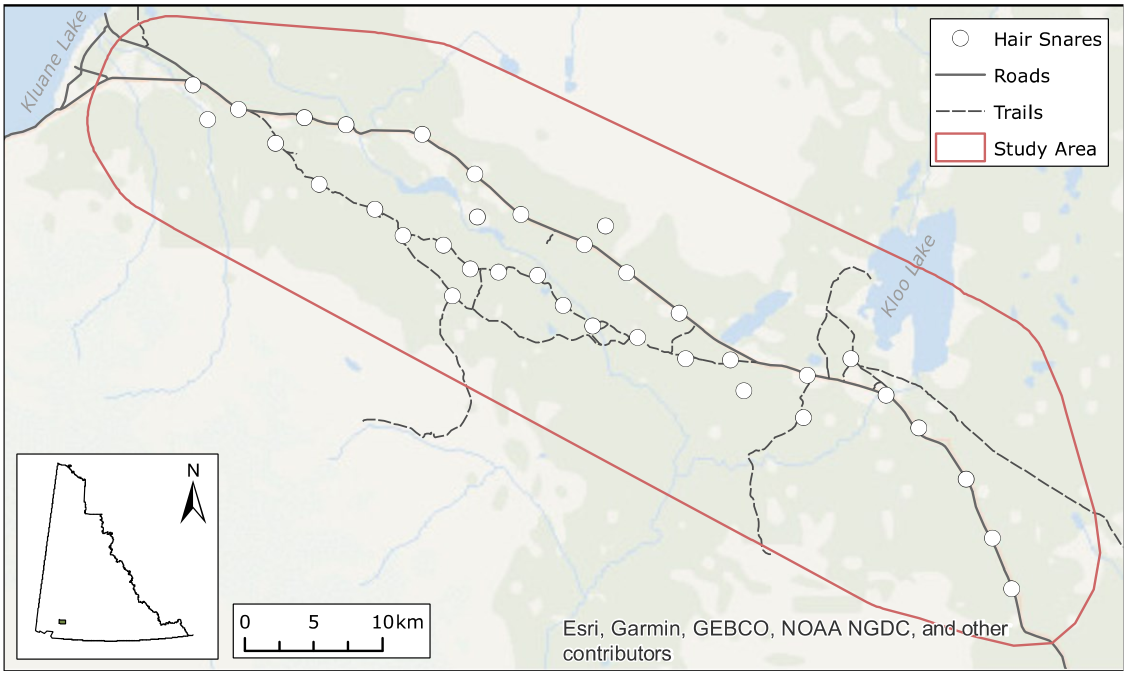

Figure 3. Map of approximate study area (red) and hair snare locations (white circles) in southwestern Yukon, Canada. Roads are represented as solid grey lines and trails as dashed grey lines. Created in ArcGIS Version 10.5. Geospatial data for elevation, waterbodies, transportation features, and Yukon Territory boundary from Geomatics Yukon (2017).

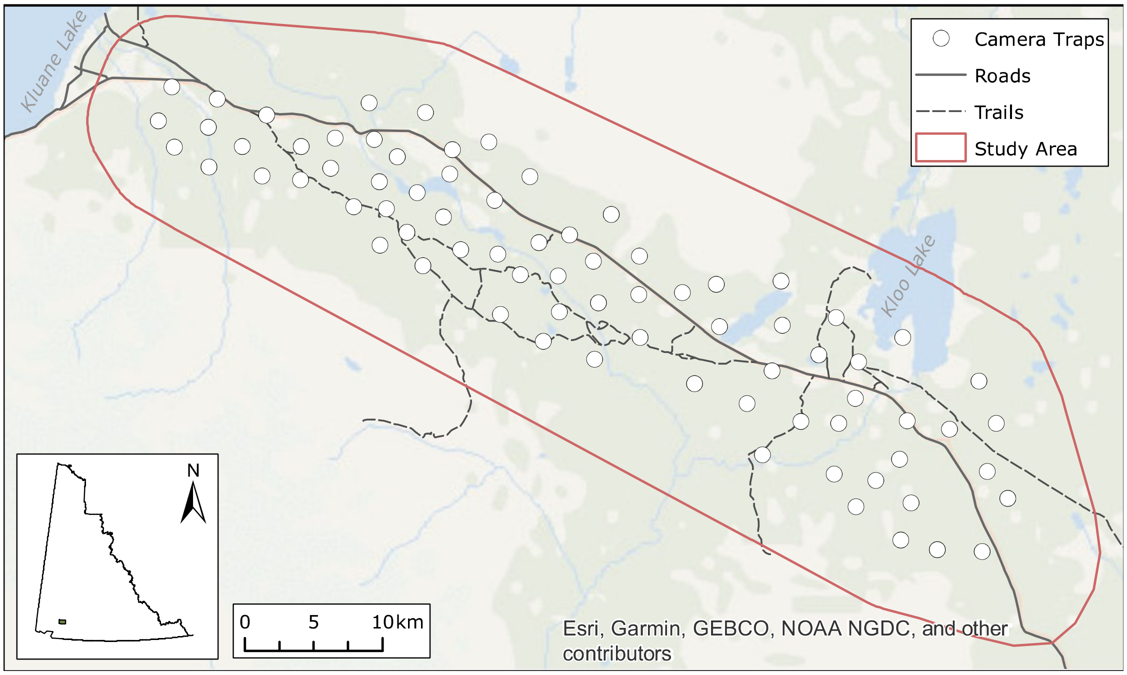

Figure 4. Map of approximate study area (red) and camera trap locations (white circles) in southwestern Yukon, Canada. Roads are represented as solid grey lines and trails as dashed grey lines. Created in ArcGIS Version 10.5. Geospatial data for elevation, waterbodies, transportation features, and Yukon Territory boundary from Geomatics Yukon (2017).

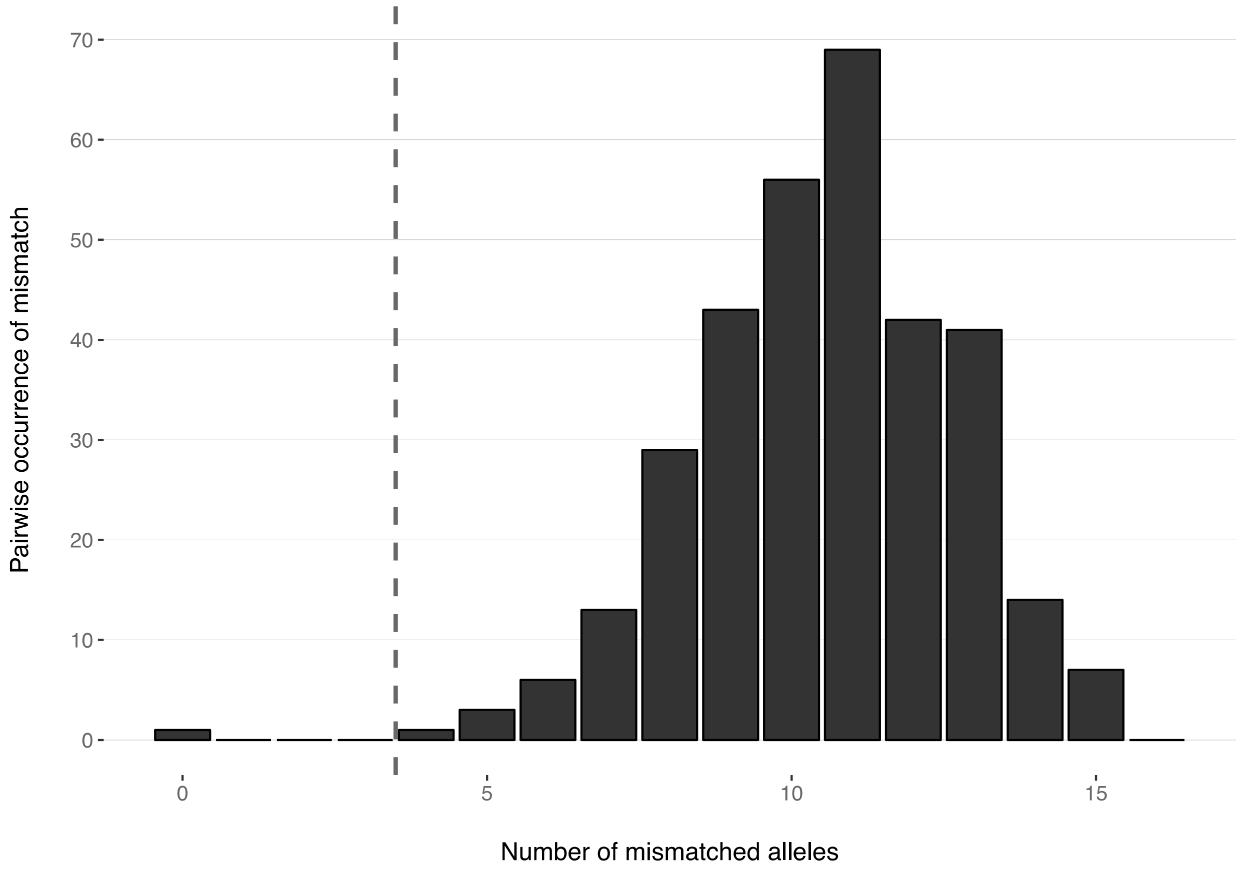

Figure 5. Allelic mismatch curve generated from 26 tissue samples from 25 live-trapped lynx. Samples were collected from November-April 2017 in Kluane, Yukon. All genotype scoring was done blind to lynx identity, capture location, and capture time. Each tissue sample provided a unique eight-locus genotype (excluding sex). Frequency of the number of allelic differences between pairs of tissue samples are shown as bars. Pairs of samples from different individuals were mismatched at four or more alleles from all other samples. One pair of samples was taken of the same individual and was scored at zero allelic mismatch. The dashed line shows the allelic cutoff for individuality, where mismatch pairs to the right of the line were defined and later validated as unique individuals.

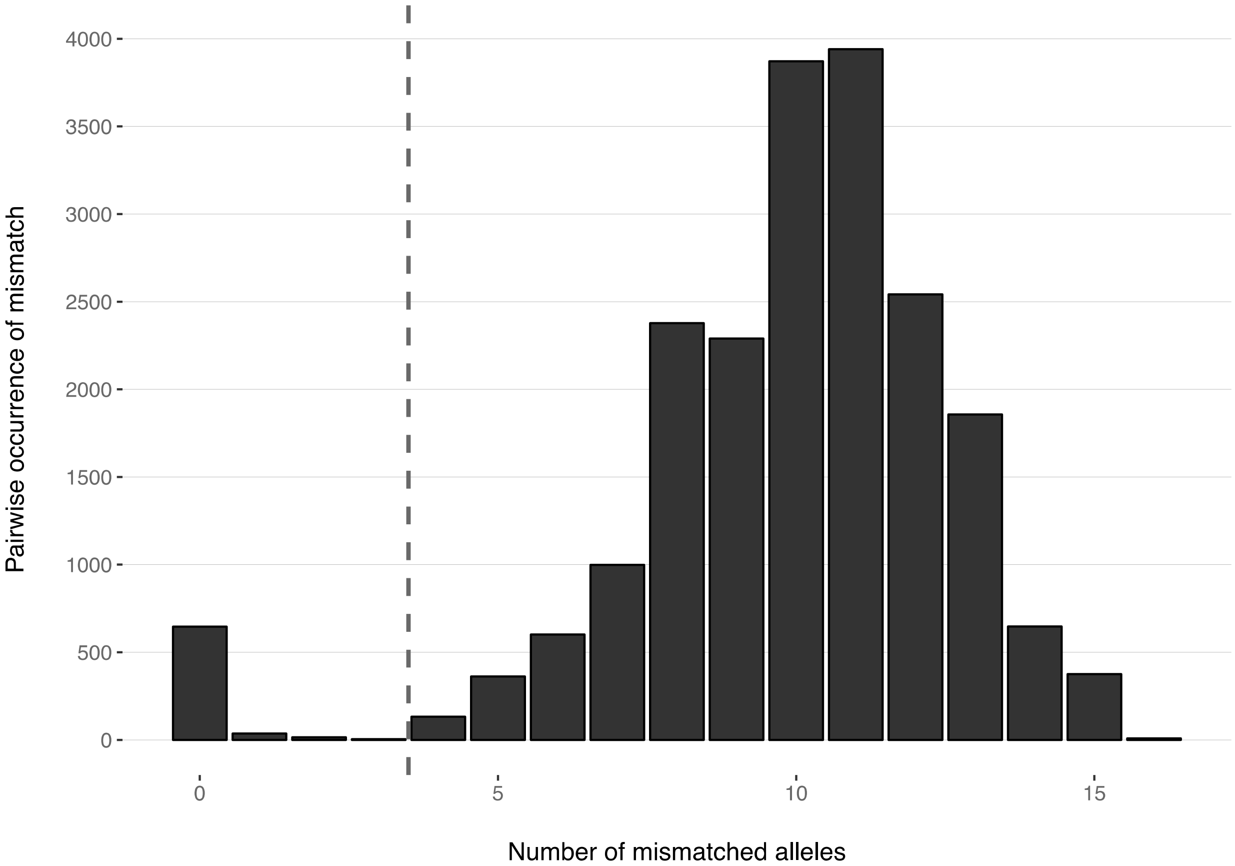

Figure 6. Allelic mismatch curve generated from 204 lynx hair samples collected on hair snares from January-April 2017 in Kluane, Yukon. All genotype scoring was done blind to hair snare location and collection time. Each tissue sample provided a unique eight-locus genotype (excluding sex). Frequency of the number of allelic differences between pairs of tissue samples are shown as bars. Following from an empirical investigation of allelic mismatch in known individuals (Fig. 4), pairs of samples mismatched at four or more alleles were defined as unique individuals. The dashed line shows the allelic cutoff for individuality, where mismatch pairs to the right of the line were defined as unique individuals. Mismatch pairs between one and three mismatched alleles were examined for evidence of allelic dropout and then assigned to individuality manually.

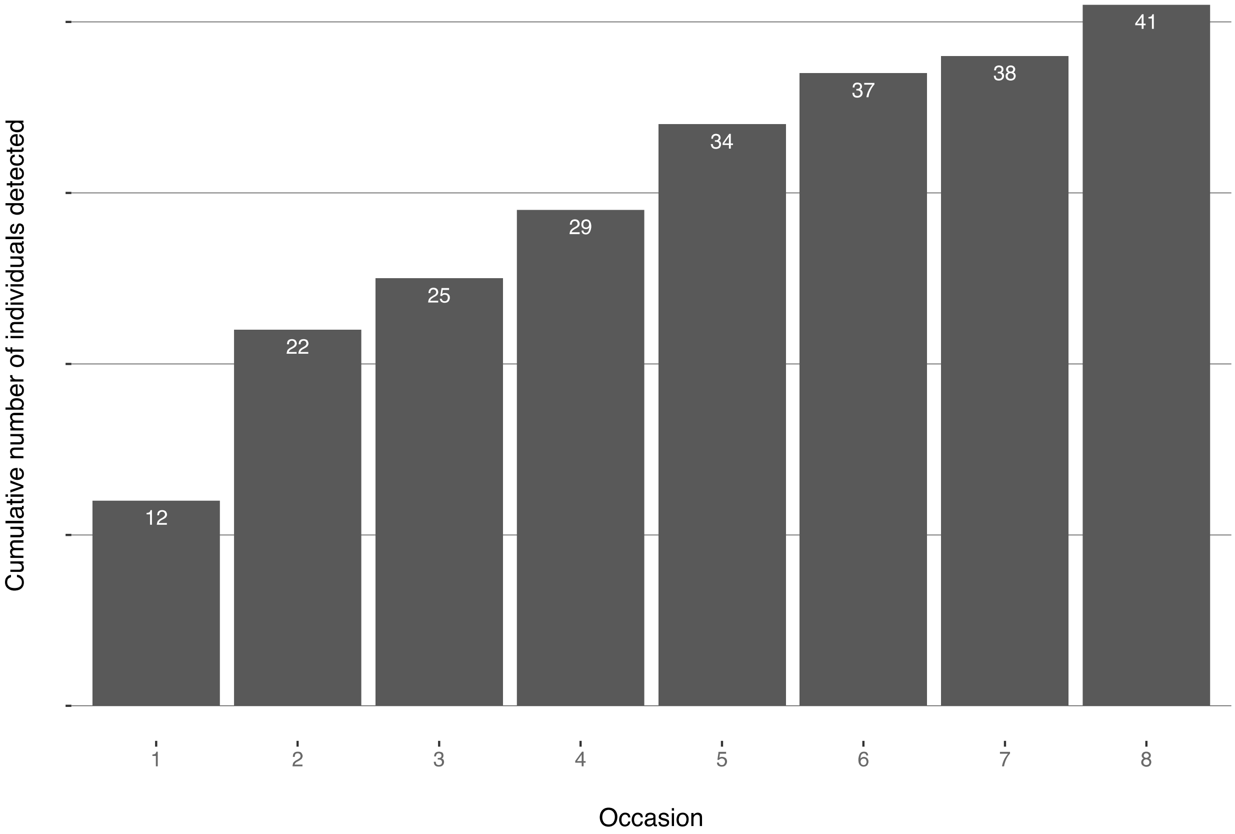

Figure 7. Accumulation of unique lynx individuals across 14-day hair snare sampling occasions. Forty-one lynx individuals were detected over eight occasions in Kluane, Yukon from January-April 2017.

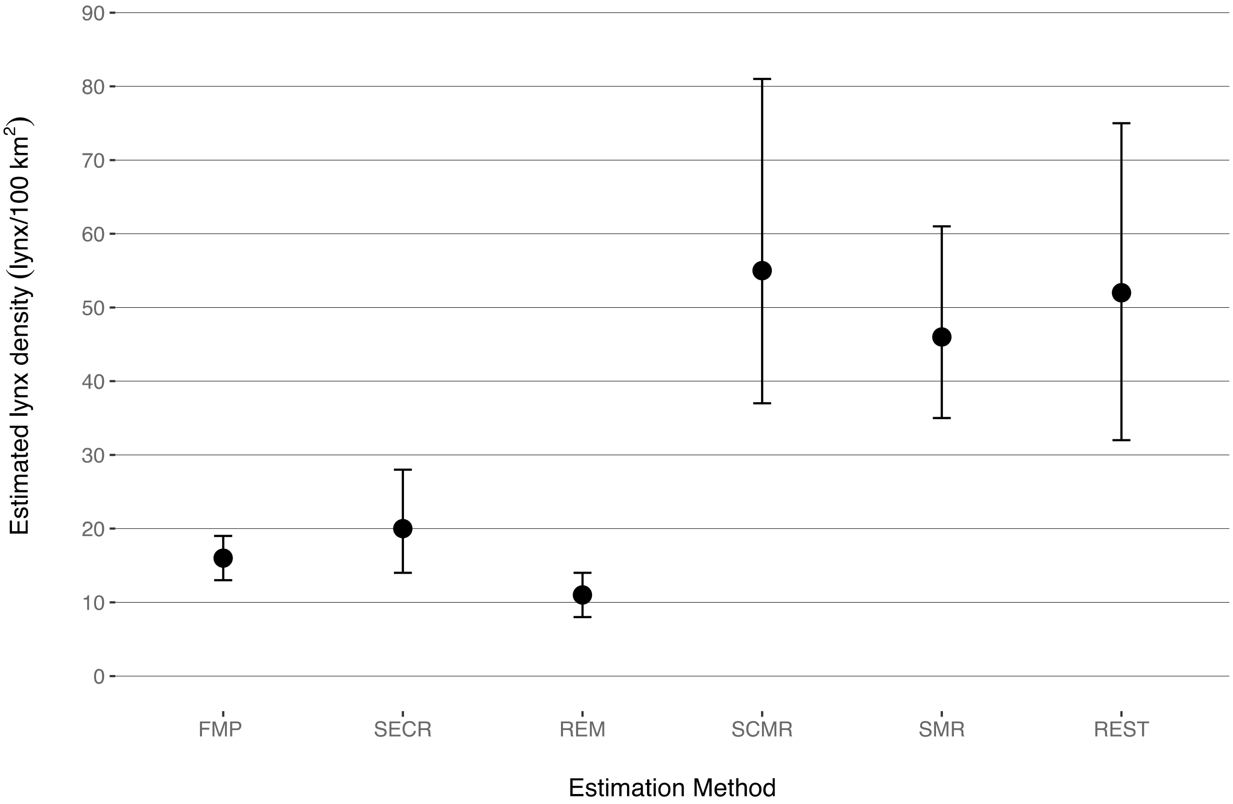

Figure 8. Lynx density estimates (lynx/100 km^2) and 95% confidence or credible intervals resulting from six estimation methods. The Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006) was applied track transect data. Spatially explicit capture-recapture (SECR) (Efford et al. 2009b) was applied to hair snare data. The random encounter model (REM) (Rowcliffe et al. 2008), likelihood-based spatial capture mark-resight (SCMR) (Efford and Hunter 2017), Bayesian spatial mark-resight (SMR)(Whittington et al. 2018), and random encounter and staying time (REST) (Nakashima et al. 2017) models were applied to camera trap data.

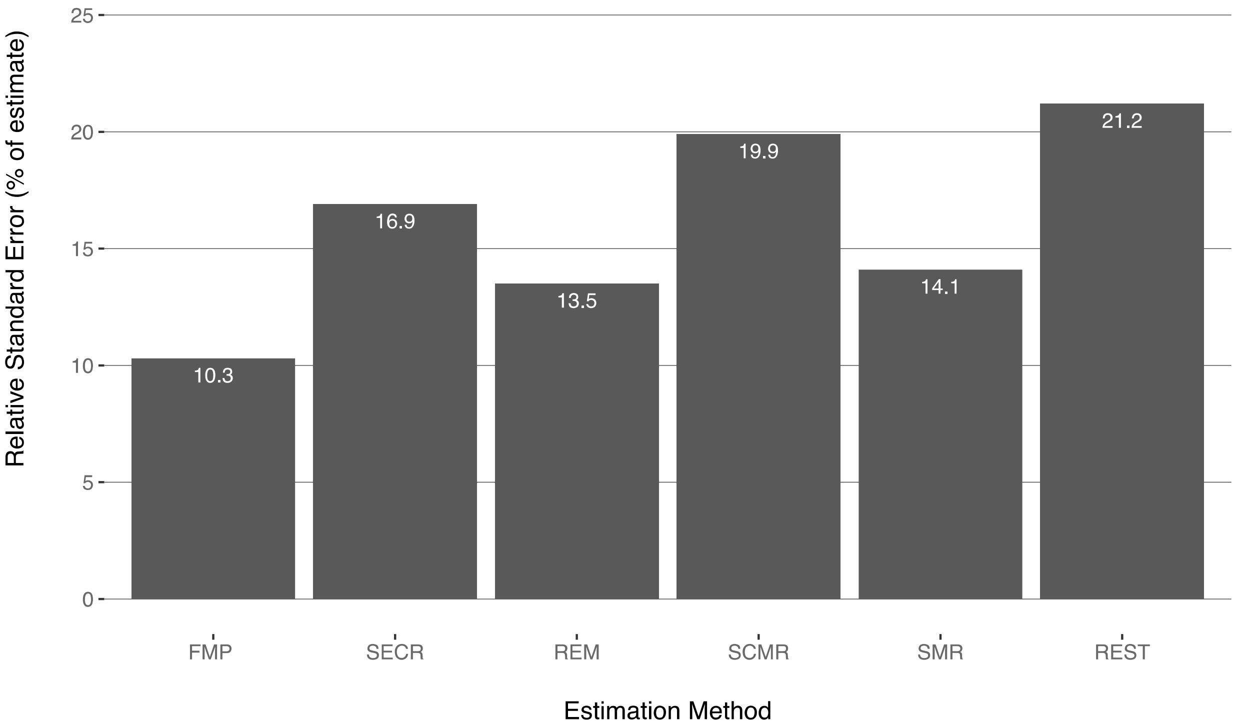

Figure 9. Relative standard error as percent of the density estimate from six estimation methods. The Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006) was applied track transect data. Spatially explicit capture-recapture (SECR) (Efford et al. 2009b) was applied to hair snare data. The random encounter model (REM) (Rowcliffe et al. 2008), likelihood-based spatial capture mark-resight (SCMR) (Efford and Hunter 2017), Bayesian spatial mark-resight (SMR) (Whittington et al. 2018), and random encounter and staying time (REST) (Nakashima et al. 2017) models were applied to camera trap data.

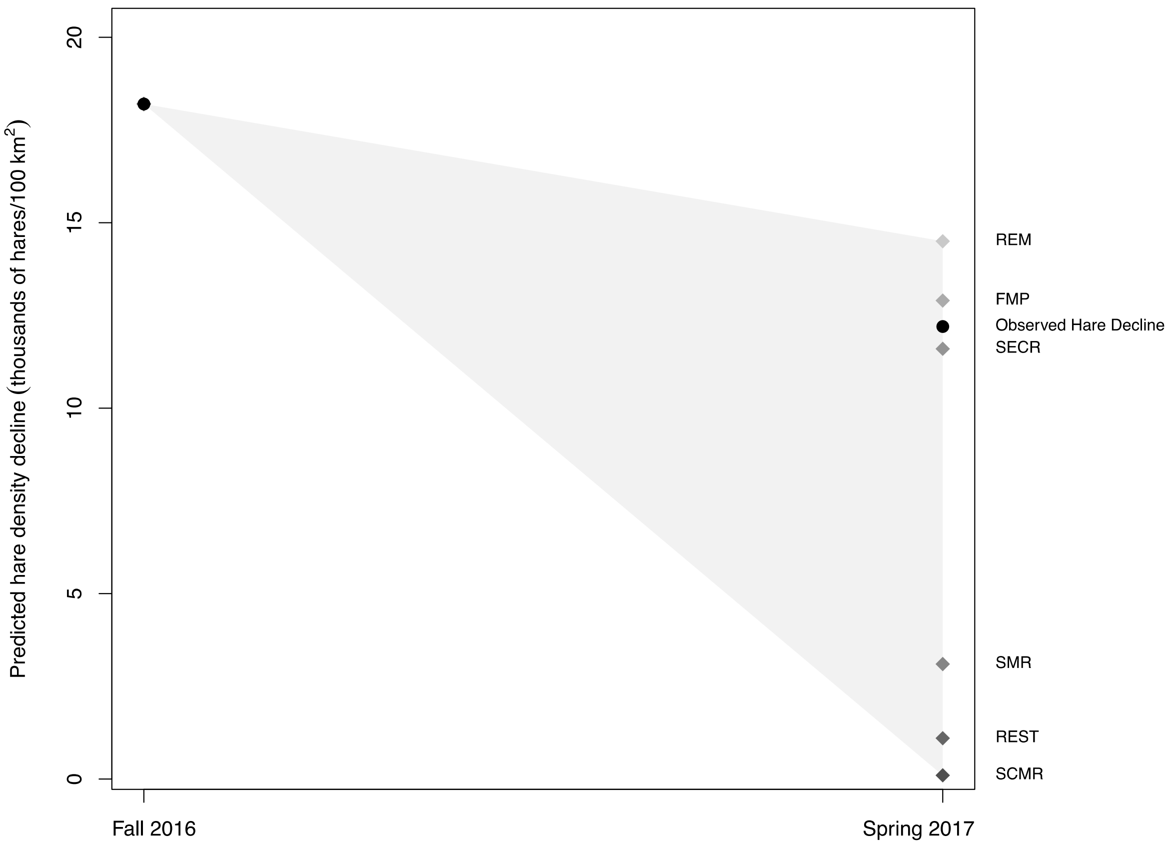

Figure 10. Observed and predicted snowshoe hare density decline from fall 2016 to spring 2017. Observed hare densities were estimated from live-capture SECR methods (Krebs, 2017). The number of hares killed per lynx per day was estimated from classified accelerometer data from collared lynx (Studd, 2017). The percent hare mortalities attributed to lynx was estimated from kill site investigations of collared hares (Peers, 2018). The predicted hare decline was calculated from six lynx density estimates. Lynx density estimation methods included the Formozov–Malyshev–Pereleshin (FMP) formula (Stephens et al. 2006), spatially explicit capture-recapture (SECR) (Efford et al. 2009b), the random encounter model (REM) (Rowcliffe et al. 2008), likelihood-based spatial capture mark-resight (SCMR) (Efford and Hunter 2017), Bayesian spatial mark-resight (SMR) (Whittington et al. 2018), and the random encounter and staying time (REST) model (Nakashima et al. 2017).

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