

Density estimates for Canada lynx vary among estimation methods

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Abstract. Unbiased population density estimates are critical for ecological research and wildlife management but are often difficult to obtain. Researchers use a variety of sampling and statistical methods to generate estimates of density, but few studies have compared estimates across methods. During 2016–2017, we surveyed Canada lynx (*Lynx canadensis*) in southwestern Yukon Territory, Canada, using track transect counts, hair snares, camera traps, live traps, and Global Positioning System (GPS) collars. From these data, we estimated lynx density with two linearly scaled count methods, one spatial mark–recapture method, three spatial mark–resight methods, and one cumulative-time method. We found up to fivefold variation in point density estimates despite adhering to method requirements and assumptions in a manner consistent with other studies. Our results highlight the dependency of density estimates on sampling process and model assumptions and demonstrate the value of careful and unbiased sampling design. Further research is needed to fully assess the accuracy and limitations of the many wildlife density estimation methods that are currently in use so that techniques can be appropriately applied to typical study systems and species.

Key words: camera trap; density estimation; DNA; *Lynx canadensis*; mark–recapture; mark–resight; REM; REST; SCR; SECR; SMR; Yukon.

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INTRODUCTION

Reliably estimating population density is a common but challenging objective for ecologists and other wildlife researchers. This is particularly true for species that occur at low densities, are difficult to observe, or are unmarked (Balme et al. 2009, Foster and Harmsen 2012, Moeller et al. 2018). Many recent sampling and statistical methods have been developed leading researchers to

use a variety of methods for density estimation (Long et al. 2008, Balme et al. 2009, Riley et al. 2017, Lamb et al. 2019). Because each method claims to produce unbiased estimates when applied appropriately, a reasonable assumption is that these different approaches will produce population estimates that are directly comparable. However, this assumption has rarely been tested across multiple, dissimilar methods (but see Anile et al. 2014, Burgar et al. 2018).

Recent technological advances provide opportunities to improve sampling, especially for low-density and elusive wildlife species. Remote, motion-triggered camera traps collect detections of wildlife without direct observation or interaction (Hamel et al. 2013, Surnato et al. 2013, Burton et al. 2015). Camera traps have typically been used to survey large-bodied mammals (e.g., tigers (*Panthera tigris*; Carbone et al. 2001, Karanth et al. 2006), bobcats (*Lynx rufus*; Silvy et al. 2006), and zebras (*Equus grevyi*; Zero et al. 2013)), but can be used for a broad spectrum of species (Hobbs and Brehme 2017). Advances in genotyping provide another option for data collection of elusive species. Genetic data can be collected non-invasively (e.g., hair samples, fecal samples) and used to identify individuals in a population (Humm et al. 2017, Lamb et al. 2019). This approach has been applied to a range of mammals including grizzly bears (*Ursus arctos*; Lamb et al. 2018), wolverines (*Gulo gulo*; Awan and Boulanger 2016), bobcats (Stricker et al. 2012), and Eurasian lynx (*Lynx lynx*; Davoli et al. 2013).

Statistical advances have provided opportunities to improve density estimation and capitalize on modern data collection techniques. Capture–recapture statistical methods are a common approach for estimating density when individuals are identifiable (Krebs 2014). Likelihood-based spatially explicit capture–recapture (SECR) (Efford 2004, 2011, Borchers and Efford 2008, Efford and Fewster 2013) and Bayesian-inference spatial capture–recapture (SCR) (Royle and Young 2008, Chandler and Clark 2014) model individual heterogeneity in detection probability as a function of the spatial distribution of individual activity centers, home range size, and detectors (Efford 2004, Obbard et al. 2010). Such models avoid ad hoc definitions of effective trapping area, reduce error from edge effects, and account for spatial differences in individual detection probability (Efford 2004, Efford and Fewster 2013). Modifications of SCR methods include spatial capture mark–resight (SCMR) (Efford and Hunter 2017) and spatial mark–resight (SMR) models (Chandler and Royle 2013, Alonso et al. 2015, Whittington et al. 2018) for partially marked populations, in which counts of unmarked animals are included alongside individual capture histories. Density of unmarked populations can be estimated with linearly scaled

count methods, which use a detection rate, area surveyed, and a 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). Similarly, the random encounter and staying time (REST) model uses the cumulative time of camera trap detections and the area surveyed (Nakashima et al. 2018). Most of these statistical approaches have been introduced, tested, and implemented within the last 15 yr.

There have been few studies that examine how density estimates using dissimilar approaches compare. Comparisons of density estimation methods in the literature have compared recently developed methods to more conventional methods of density estimation like distance sampling (Zero et al. 2013), Global Positioning System (GPS)-telemetry enumeration (Soisalo and Cavalcanti 2005), and non-spatial capture–recapture (Obbard et al. 2010). Studies that compare across current methods have done so by altering only the inference method (Noss et al. 2012, Efford and Hunter 2017) or augmenting the dataset with auxiliary data (Sollmann et al. 2013a, Rich et al. 2014, Alonso et al. 2015) while keeping the base method the same. Comparisons of individually well-tested but dissimilar methods in typical field conditions are needed to assess the reliability and limitations of the many methods that are currently in use.

We applied multiple data collection and statistical techniques to estimate Canada lynx (*Lynx canadensis*) density as part of an ongoing study of snowshoe hare and lynx population cycles in the southwestern Yukon. Many studies have sought to estimate lynx density (Bailey et al. 1986, Koehler 1990, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 1997, Vashon et al. 2008, 2012, Crowley and Hodder 2017), but lynx can be difficult to survey because they live in dense habitat (Mowat et al. 2000), are averse to direct observation, are periodically found at low density (O'Donoghue et al. 1997), and lack features for distinguishing between individuals. Use of camera traps to survey lynx populations has been limited (Nielsen and McCollough 2009, Crowley et al. 2013) and has never been used to estimate lynx density. 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 estimate lynx density (Crowley and Hodder 2017).

We compared lynx density estimates obtained from 5 temporally and spatially overlapping datasets: track transects, hair snares, camera traps, live captures, and GPS collar data. All data were collected in typical field conditions with common logistical constraints. We then applied seven statistical methods to the resulting datasets: the FMP formula (Dzięciolowski 1976, Lindén et al. 1996, Stephens et al. 2006, Keeping and Pelletier 2014), SECR (Borchers and Efford 2008, Efford et al. 2009b), the REM (Rowcliffe et al. 2008, 2013), SCMR (Efford and Hunter 2017), generalized SMR (gSMR) (Sollmann et al. 2013b, Whittington et al. 2018), a novel combination of SECR and gSMR, and REST (Nakashima et al. 2018). Our main objective was to test the assumption that these various sampling and density estimation techniques would produce similar point density estimates. We then compared the plausibility of the estimates, the assumptions and possible sources of bias, and the precision of the estimates resulting from each method. We considered more reliable methods to be less subject to restrictive assumptions and potential sources of bias. We considered that acceptable methods would have high precision as measured by relative standard error (RSE). Near or less than 20% RSE is considered reasonable precision in published literature (Efford et al. 2009b, 2016, Newey et al. 2015, Stenevik et al. 2015). Although our study system, like most other natural systems, did not allow for knowledge of true density, we compared the plausibility of each density estimate based on all sources of information and discuss possible reasons for differences observed between estimates.

STUDY AREA

We conducted the study in the Kluane Lake region of southwestern Yukon Territory, Canada, from November 2016 through June 2017. Ecological research has been conducted in this area for 40 yr (described in Krebs et al. 2001, 2014). The approximately 300 km² unbounded study area (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-m 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). Snow was present throughout the study period with average temperatures ranging from -17°C in January 2017 to +11°C in June 2017. White spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), willow (*Salix glauca*), and American dwarf birch (*Betula glandulosa*) are the dominant vegetation (Ward and Krebs 1985). Sympatric carnivores inhabiting the Kluane area with Canada lynx included coyotes (*Canis latrans*), wolverines, grizzly and black bears (*Ursus americanus*), and gray wolves (*Canis lupus*). Potential prey of lynx in the area included snowshoe hares (*Lepus americanus*), red squirrels (*Tamiasciurus hudsonicus*), grouse (*Bonasa umbellus*, *Lagopus lagopus*, *Dendragapus canadensis*), and small mammals (e.g., *Peromyscus maniculatus*, *Myodes rutilus*) (Murray et al. 1994, O'Donoghue et al. 1998, Krebs et al. 2014). Trap lines set for furbearers including lynx were located adjacent to the study area.

METHODS

This research was approved by the University of Alberta Animal Care and Use Committee, No. AUP00001988 and by McGill University Animal Use Protocol No. 4728.

Live trapping

We captured lynx for marking and collaring using lured and baited box traps. Between November 2016 and April 2017, up to 25 wire mesh box traps (dimensions 1 m × 2 m × 1.5 m) at a time were deployed within the study area (Fig. 1). These traps were placed along trails and other high capture probability areas and were baited with meat and beaver (*Castor canadensis*) castoreum. In and near the traps, we placed visual lures including feathers and mirrors. Adult lynx (those weighing over 5 kg) caught in the traps were chemically immobilized and fitted with a GPS collar (Telemetry Solutions UHF remote download, 375 g; or Followit Tellus Iridium, 400 g) set to record lynx locations at 30-min intervals. Captured individuals were marked with colored ear tags (Nasco[®] Standard Nylon Rototags) incorporating infrared-reflective heat

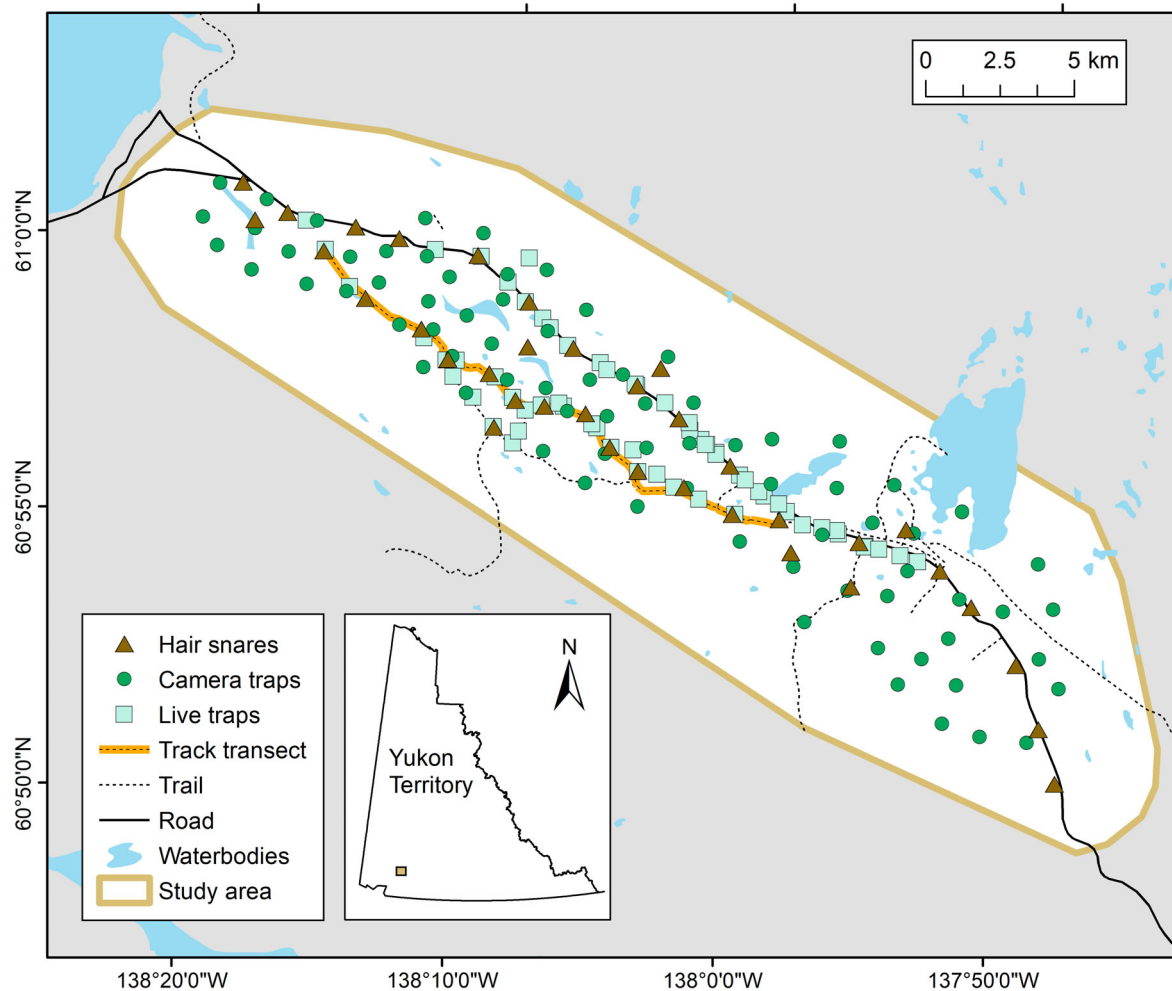


Fig. 1. Map of approximate study area (gold polygon), snow track transect (orange line), camera traps (green circles), hair snares (brown triangles), and live traps (teal squares) in southwestern Yukon, Canada. Roads are represented as solid black lines and trails as dashed black lines. Geospatial data for waterbodies, transportation features, and Yukon boundary from Geomatics Yukon (2017). Created in ArcMap 10.7.

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 to improve ear tag retention and to collect high-quality genetic samples from captured lynx. Tissue samples were stored in microcentrifuge tubes in 70% ethanol and subsequently used to genotype known individuals.

We estimated movement rates of GPS-collared lynx between November 2016 and April 2017. First, we excluded fixes that occurred during and immediately following the collaring process or

recorded no location. We found the mean hourly and daily (24-h) distance moved for each lynx in R (RStudio version 1.1.386) by converting 30-min fix coordinates from degrees to radians and then converting the difference between consecutive fixes to meters using the haversine formula (Robusto 1957). To remove probable location errors, we excluded step lengths that were greater than 2 km/30 min. We calculated the mean step length for each individual and multiplied this by 2 (for hourly movement) or 48 (for daily movement). Lastly, we calculated the median movement rate across all individuals.

Snow track transects

We completed snow track transects from November 2016 to March 2017, following methods in O'Donoghue et al. (1997). An experienced wildlife tracker counted lynx track crossings along a 25-km transect (Fig. 1) that was split into 8 similar-length segments. The tracker traveled the transect by snowmobile after a minimum 18 h since the last snowfall event or high wind had erased previous tracks and then for 1–2 d afterward while fresh tracks could be distinguished (O'Donoghue et al. 1997). We counted a track crossing when tracks were observed entering and exiting the approximately 2-m wide transect. Tracks from evidently the same individual re-entering the transect were not re-counted. We recorded days since last snowfall, nights since last count, temperature, and weather conditions before each tracking day. In addition, for each set of lynx tracks, we recorded date, location, habitat type, species, apparent group size, and apparent group age composition. Tracks from all age classes were included in final counts. We aimed to complete at least 15 tracking occasions per winter season, with days spread evenly across winter months, but necessarily dependent upon conditions. Sampling effort in “track days” was defined as the product of the number of track segments traveled and the number of days that tracks could have accumulated.

Hair snares

We used 36 scent-lured rub pads, at an average spacing of 1.5 km, to collect hair samples from lynx (McKelvey et al. 1999, McDaniel et al. 2000, Weaver et al. 2005, Ruell and Crooks 2007, Davoli et al. 2013, Crowley and Hodder 2017) between January and April 2017. Of these, 16 hair snare stations were placed in the forest near a paved road, 14 stations along a dirt road, and 6 in forest off-trail (Fig. 1). The rub pads consisted of carpet squares (10 cm × 10 cm) nailed to trees 30 cm above snow level with a hanging, blank CD as a visual lure (Kendall and McKelvey 2008). A liquid scent lure containing beaver castoreum, glycerin, imitation catnip (*Nepeta cataria*) oil, and aniseed (*Pimpinella anisum*) oil was applied to each carpet pad. We included a loop of barbed wire (double-stranded, 4 points per barb) stapled to the carpet pad to snag hair. Snares were checked and re-lured every 14 d.

Successful snares with hair samples were collected as whole pads (Ruell and Crooks 2007), placed into paper envelopes with 5-g desiccant packets, and stored dry at room temperature for 1–5 months. For genetic analysis, we took between 1 and 4 samples from each successful hair snare by pulling clumps of hair from individual barbs. Each sample contained 10–20 guard hairs (Appendix S1).

Camera traps

We placed camera traps (Reconyx PC900 Hyperfire, Reconyx, Holmen, Wisconsin, USA) at 75 locations within the study area (Fig. 1) from January through June 2017 and programmed them to run continuously, taking 1 time-stamped photograph upon motion and heat trigger, without delay. We set cameras on trees 30–50 cm above the snow surface and cleared vegetation directly in front of cameras. We did not visit cameras between the start and end of the camera trapping session.

We placed camera stations within 100 m of a predetermined systematic target location and chose, where possible, landscape features that maximized area in front of the camera (forest edge, ridges). Rarely, we placed cameras at locations that showed signs of lynx presence (tracks, scat) or on animal paths (Brand et al. 1976, Surnato et al. 2013). Camera stations were between 1 and 2 km from their nearest neighbor (average distance 1.3 km). We ensured detections were temporally independent and measured the area of the detection zone of each camera (see Appendix S1 for details). Detected lynx of all age classes and group sizes were included in the final camera dataset.

Genotyping

Multi-locus genotypes were obtained from hair and tissue samples by typing eight polymorphic microsatellite loci (Fca090, Fca126, Fca176, Fca043, Fca045, Fca096, Fca008, and Lc120) and a Zn-finger sex marker (Pilgrim et al. 2005). We calculated Hardy-Weinberg probability of identity ($p_{(ID)}$; probability that two individuals will have the same multi-locus genotype) and $p_{(ID)sib}$ (probability that two siblings will have the same multi-locus genotype) as measures of confidence for individual identification (Waits et al. 2001).

Density estimation

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 daily travel distance of an individual in the population, and the total transect length (Stephens et al. 2006) (Figs. 2, 3; Appendix S2).

We 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) and RSE (Stephens et al. 2006).

Spatially explicit capture-recapture (SECR).—We estimated lynx density from hair snare data with a likelihood-based SECR model (Efford 2004, Efford et al. 2009b). The SECR method models the probability of spatially explicit capture histories by the estimated locations of animal activity centers and the distance between detectors and these centers (Efford et al. 2009a) (Figs. 2, 3).

We applied SECR models to the hair snare dataset divided into 8, 2-week occasions using the R package “secr” version 3.1.0 (in RStudio

1.1.386). The sampling area was buffered by 6 km and a habitat mask denoting non-habitat (large water bodies over 30 ha and elevation above 1600 m; created in ArcGIS version 10.5) was applied within the area of integration. Candidate models for density included σ (home range size parameter) predicted by sex, g_0 (probability of detection at home range center) predicted by sex, σ fixed across all individuals, and g_0 predicted by the sampling occasion. We report the 95% CI and RSE of the density estimate.

Random encounter model (REM).—The REM uses the detection rate of independent, unmarked detections, an estimate of movement rate, average group size, and the area sampled by camera traps to estimate density (Rowcliffe et al. 2008, 2013) (Figs. 2, 3; Appendix S2).

Density was estimated using detections from camera traps and by using the measured area of the camera detection zones. We used the mean hourly movement rate calculated from GPS-collared lynx. We used nonparametric bootstrapping (R package “boot” version 1.3-20, RStudio version 1.1.386) with replacement of camera

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	GPS/ Telemetry	
FMP										
REM										
REST										
SECR										
SCMR										
gSMR										
SECR + gSMR										

Fig. 2. Summary of key data requirements of seven statistical methods used to estimate density: the Formozov-Malyshev-Perelishin (FMP) formula (Stephens et al. 2006), the random encounter model (REM) (Rowcliffe et al. 2008), random encounter and staying time (REST) (Nakashima et al. 2018), spatially explicit capture-recapture (SECR) (Efford et al. 2009b), spatial capture mark-resight (SCMR) (Efford and Hunter 2017), gSMR (Whittington et al. 2018), and combined SECR and generalized spatial mark-resight (gSMR). Grey cells indicate that the method required the corresponding data type.

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	Grey	Grey	Grey	Grey					Grey
REM	Grey	Grey	Grey	Grey					Grey
REST	Grey	Grey	Grey	Grey					Grey
SECR	Grey	Grey		Grey	Grey	Grey			
SCMR	Grey	Grey		Grey	Grey	Grey	Grey		
gSMR	Grey	Grey		Grey	Grey	Grey	Grey		
SECR + gSMR	Grey	Grey		Grey	Grey	Grey	Grey		

Fig. 3. Summary of key model assumptions of seven statistical methods used to estimate density: the Formozov-Malyshv-Pereleshin (FMP) formula (Stephens et al. 2006), the random encounter model (REM) (Rowcliffe et al. 2008), random encounter and staying time (REST) (Nakashima et al. 2018), spatially explicit capture–recapture (SECR) (Efford et al. 2009b), spatial capture mark–resight (SCMR) (Efford and Hunter 2017), gSMR (Whittington et al. 2018), and combined SECR and generalized spatial mark–resight (gSMR). Grey cells indicate that the method relied on the corresponding assumption.

station to estimate 95% CI and RSE (Rowcliffe et al. 2008).

Spatial capture–mark–resight (SCMR).—Spatial capture mark–resight models allow for density estimation of partially marked populations by combining individual capture histories of marked animals with counts of detected unmarked animals over several sampling occasions (Efford and Hunter 2017) (Figs. 2, 3).

We estimated lynx density with the R package “secr” version 3.1.0 (in RStudio 1.1.386) using capture data from the marking process, individual capture histories from camera traps, counts of unmarked and unknown lynx detections, and spatial data from the marking and sighting processes. Camera trap data were divided into 12, 2-week sighting occasions and 2, 2-week marking occasions. A habitat mask was applied as described above for SECR. The marking process was modeled such that animals were “marked” at the nearest camera to the live trap location of

first capture. We approximated the timing of continuous marking by interposing two marking occasions between sighting occasions. Counts of unmarked animals were modeled as a Poisson process (Efford and Hunter 2017). Candidate models fixed σ across all individuals, modeled g_0 by occasion type (marking or sighting), fixed the probability of identity to the proportion of “marked” photographs with identifiable lynx, and adjusted for overdispersion of count data (Efford and Hunter 2017). We calculated 95% CI and RSE (Efford and Hunter 2017).

Generalized spatial mark–resight (gSMR).—gSMR is similar to SCMR but differs in that it uses Markov chain Monte Carlo (MCMC) methods to estimate density (Whittington et al. 2018). Markov chain Monte Carlo methods provide flexibility for interspersed mark and resight data and for combining GPS, mark, and resight data to inform parameters. gSMR models estimate density for

partially marked populations by combining individual capture histories of marked animals with counts of unmarked detections over several occasions (Sollmann et al. 2013a, Rich et al. 2014, Whittington et al. 2018) (Figs. 2, 3).

Our gSMR model used capture–recapture data from the live trapping/markings process, camera trap resight histories, camera trap counts of unmarked lynx, locations of live traps and cameras, and weekly GPS locations from collared lynx. We divided camera trap data into 12, 2-week occasions. We developed sub-models for the marking and sighting processes. We applied a buffer of 7.5 km beyond the sampling area (to include a longer distance movement by 1 collared lynx) and a habitat mask as described for SECR. We modeled the capture process with a binomial distribution and the resighting process with a Poisson distribution (Rich et al. 2014). We ran each of 10 MCMC chains for 100,000 iterations, discarded the first 5000 iterations as a burn-in, and thinned the data to every 10th iteration. We report the 95% highest posterior density interval (Bayesian credible interval; BCI) and RSE.

Spatially explicit capture–recapture + generalized spatial mark–resight (SECR + gSMR).—We used MCMC methods to combine three spatially explicit survey methods with telemetry data to estimate density. Building on the gSMR models of Whittington et al. (2018), we combined GPS collar data, DNA-based hair snare captures, trapping-based live captures, and camera trap resights of marked lynx and unmarked lynx detections into a single model. We linked individual identities across all data sets. We used Normal (0, 10) priors for $\ln(\sigma)$, $\text{logit}(\lambda_0^{\text{DNA}})$, $\text{logit}(\lambda_0^{\text{Capture}})$ and $\text{log}(\lambda_0^{\text{Camera}})$. We ran each of 10 MCMC chains for 50,000 iterations, discarded the first 5000 iterations as a burn-in, and thinned the data to every 10th iteration. We report the 95% BCI and RSE of the estimate.

See Appendix S3 for full details of this method. We also provide in Supplementary Materials a simple, self-contained R-code to simulate data and estimate SECR + gSMR model parameters: “Data S1: RScript simulate and run JAGS SECR gSMR model.R.”

Random encounter and staying time (REST).—The REST model uses cumulative time in the camera trap detection zone and the area of the camera detection zone to estimate population

density from camera trap datasets (Nakashima et al. 2018) (Figs. 2, 3, Appendix S2).

We excluded lynx from this analysis when they moved beyond the measured camera detection zone. We also excluded lynx time spent investigating (sniffing, rubbing) the camera or other sampling equipment. The sampling session began 5 d after camera deployment in January to avoid possible attraction from researcher snowshoe trails. We 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.

RESULTS

Live trapping

We captured 25 adult lynx (12 males, 13 females) in live traps (Table 1). Of these, 21 were fitted with GPS collars (11 males, 10 females); at the end of the study, GPS data were retrieved from 19 lynx. We deployed ear tags on 23 lynx. Collared individuals provided between 325 and 5077 point locations each (mean = 2322) over 1–4 months. All 25 captured lynx provided complete multi-locus genotypes from tissue samples. Across all tissue samples, $p_{(\text{ID})}$ was 7.9×10^{-8} and $p_{(\text{ID})\text{sib}}$ was 1.3×10^{-3} . We calculated the median movement rate from 15 (7 female, 8

Table 1. Summary of overlapping datasets by month in Kluane, Yukon, from November 2016–June 2017, where “detections” are a count of observations and “live trap marking” is the number of new individuals captured.

Month	No. live trap marking	No. track transect detections	No. hair snare detections	No. camera trap detections
2016/2017				
November	3	11	–	–
December	6	51	–	–
January	5	48	29 (22)	20 (3, 0)
February	8	46	29 (7)	63 (6, 1)
March	3	15	31 (8)	30 (0, 0)
April	–	–	9 (4)	33 (2, 2)
May	–	–	–	62 (6, 2)
June	–	–	–	95 (10, 4)
Total	25	171	98 (41)	303 (27, 9)

Notes: No. hair snare detections values in parentheses are new lynx detected. Camera trap detections values in parentheses are numbers of marked and identified, followed by numbers of marked and not identified. Blank cells indicate no collected data.

male) GPS-collared lynx to be 6.92 km/d ($n = 34,235$ step lengths, interquartile range [IQR] = 2.09 km) or 288 m/h (IQR = 87 m/h). We calculated an average σ of 1.3 km using GPS data from 11 collared lynx that were also detected on hair snares for use in the SECR model.

Snow track transects

We surveyed a total of 238 km along the snow track transect after 14 snowfall events occurring November 2016 through March 2017. Over 69 track days, we observed 171 lynx track crossings (2.5 detections per track day; Table 1).

Hair snares

Hair snares were active for a total of 4032 trap nights and yielded a detection rate of 5.9 hair samples per 100 trap nights. We collected 239 samples for genetic analysis from 102 successful snares by taking an average of 2.3 individual hair samples (range 1–4) per successful snare. Of these, none failed to amplify due to low quality or quantity. Thirty-five samples (15%) were mixed with hair from more than one lynx and were discarded, leaving 204 samples for analysis (Table 1). In three instances, we retained two unique lynx genotypes that were detected on the same hair snare from the same occasion.

For the 204 successful genotypes, $p_{(ID)}$ was 6.9×10^{-8} and $p_{(ID)sib}$ was 1.3×10^{-3} . Hair snares detected 41 unique lynx (15 females, 26 males) 98 times across 8 sampling occasions (Table 1). Twenty of the 41 lynx were detected a single time, whereas one individual (male) was detected nine times at seven hair snare locations. A maximum of four individuals were detected at a single location through the sampling period. Of the 25 live-trapped lynx that provided tissue samples, 15 were detected on hair snares 43 times (44% of hair snare detections).

Camera traps

Camera traps documented 303 lynx detections over 7651 trap nights (3.9 detections per 100 trap nights; Table 1). Marked (ear-tagged) lynx were present in 36 detections (12% of all lynx detections). We identified individual lynx in 78% of the marked lynx detections. We detected 15 of 23 marked lynx (65%) at least once on camera. The most extensive capture history from a marked

individual (male) was six detections at six different camera locations.

The average area of the camera detection zone was 6.2 m² with a larger detection zone in January 2017 (6.9 m², mean radius = 5.0 m, mean interior angle = 32 degrees) than in June 2017 (5.5 m², mean radius = 4.7 m, mean interior angle = 28 degrees).

Density estimates

The FMP formula produced a density estimate of 16 lynx/100 km² (95% CI 13–19; RSE 10.3% of the estimate).

The most precise SECR model applied to the hair snare dataset fixed σ at 1.3 km. We estimated density from this model at 20 lynx/100 km² (95% CI 14–27; RSE 16.7% of the estimate). The model estimate of g_0 was 0.13. The alternative, null model incorporating no GPS data estimated σ at 1.6 km, g_0 at 0.14, and found density to be 17 lynx/100 km² (95% CI 12–24; RSE 18.9% of the estimate).

The REM returned a density estimate of 11 lynx/100 km² (95% CI 8–14; RSE 13.5% of the estimate).

The most precise SCMR model for the camera trapping dataset approximated 2 marking occasions and modeled detection probability (g_0 and λ_0) by occasion type. We estimated density with this model to be 55 lynx/100 km² (95% CI 37–81; RSE 19.9% of the estimate). This model estimated σ at 2.5 km and g_0 at 0.01.

We estimated density with the gSMR model to be 45 lynx/100 km² (95% BCI 33–57; RSE 13.8%). The model estimated σ at 1.6 km, g_0 of live capture 0.002, and λ_0 of camera sighting 0.05.

The SECR + gSMR model returned a density estimate of 32 lynx/100 km² (95% BCI 25–38; RSE 10.8%). The model estimated σ at 1.6 km, g_0 of live capture 0.002, g_0 of hair snare detection 0.08, and λ_0 of camera sighting 0.08.

The REST method estimated density to be 52 lynx/100 km² (95% CI 32–75; RSE 21.2% of the estimate).

Point density estimates from the seven estimation methods varied up to fivefold (Fig. 4). The REM returned the lowest density estimate at 11 lynx/100 km² and overlapped 95% CI with estimates from the FMP formula and SECR. Spatial capture mark–resight estimated the highest density at 55 lynx/100 km² and overlapped 95% CI

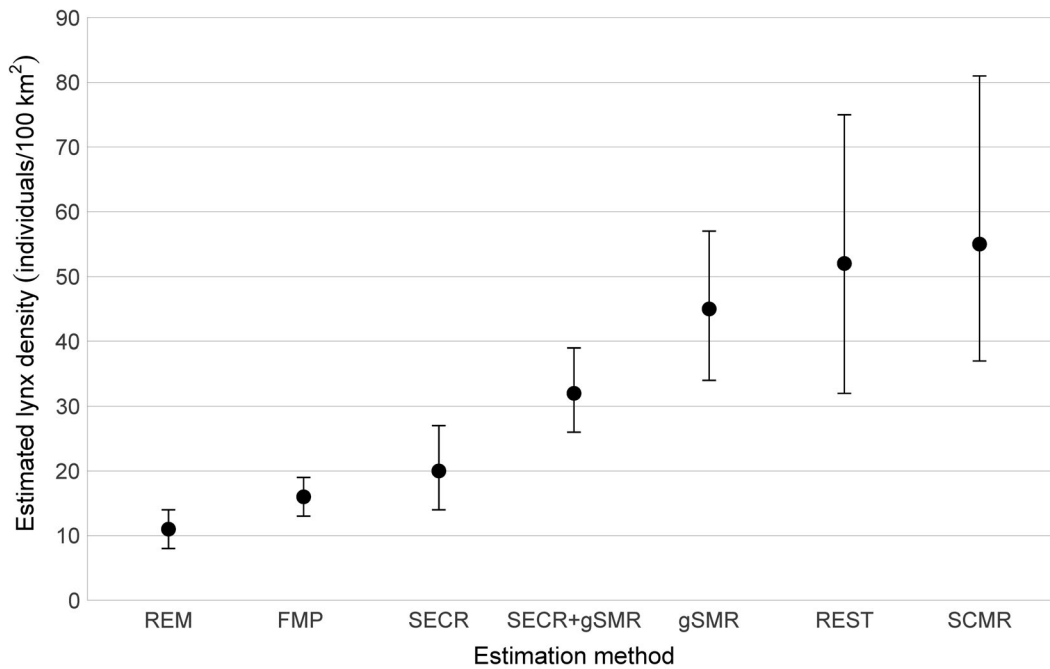


Fig. 4. Lynx density estimates (individuals/100 km²) and 95% confidence or Bayesian credible intervals resulting from seven density estimation methods: the random encounter model (REM) (Rowcliffe et al. 2008), the Formozov-Malyshev-Pereleshin (FMP) formula (Stephens et al. 2006), spatially explicit capture-recapture (SECR) (Efford et al. 2009b), combined SECR and generalized spatial mark-resight (gSMR), gSMR (Whittington et al. 2018), random encounter and staying time (REST) (Nakashima et al. 2018), and spatial capture mark-resight (SCMR) (Efford and Hunter 2017).

or BCI with estimates from REST, gSMR, and SECR + gSMR.

Precision of estimates varied twofold, ranging between RSE 10.3% (FMP formula) and RSE 21.2% (REST model) of the density estimate (Fig. 5).

DISCUSSION

We compared methods of density estimation using spatially and temporally overlapping survey data and current statistical methods. Results from seven methods show that point density estimates varied fivefold and precision of estimates varied twofold. Confidence and credible intervals overlapped between adjacent estimates but did not overlap across all estimates (Fig. 4). Despite following existing methods in the literature (Stephens et al. 2006, Rowcliffe et al. 2008, Efford et al. 2009b, Efford and Hunter 2017, Nakashima et al. 2018, Whittington et al. 2018),

we show that density estimates varied among estimation methods. This study also provides the first density estimates of Canada lynx using the FMP formula, REM, SCMR, gSMR, SECR + gSMR, and REST models, and the second using SECR with hair snares (Crowley and Hodder 2017).

Comparison to literature

The three lowest density estimates (range 11–20 lynx/100 km²) resulting from this work are similar to previous estimates of lynx density from the same cyclic phase of a lynx population (i.e., in years preceding a cyclic population peak). Previous studies have used snow tracking and/or radio telemetry data to directly count 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, 2012). Densities were reported at 7 lynx/100 km² in Alberta (Brand et al. 1976), 15 lynx/

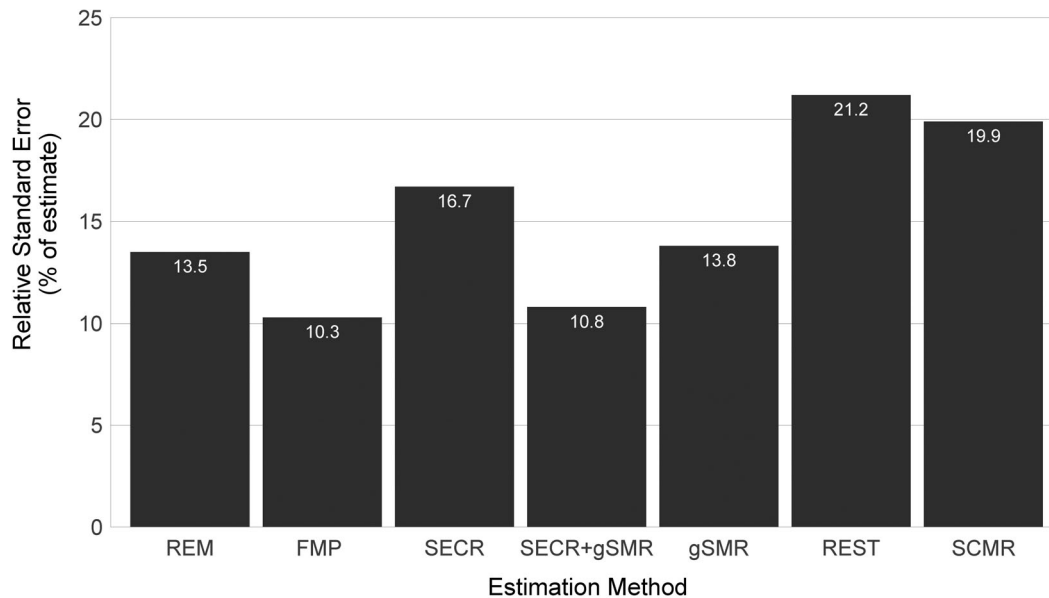


Fig. 5. Relative standard error as percent of the density estimate resulting from seven density estimation methods: the random encounter model (REM) (Rowcliffe et al. 2008), the Formozov-Malyshev-Pereleshin (FMP) formula (Stephens et al. 2006), spatially explicit capture–recapture (SECR) (Efford et al. 2009b), combined SECR and generalized spatial mark–resight (gSMR), gSMR (Whittington et al. 2018), random encounter and staying time (REST) (Nakashima et al. 2018), and spatial capture mark–resight (SCMR) (Efford and Hunter 2017).

100 km² in Kluane, Yukon (O’Donoghue et al. 1997), and the Northwest Territories (Poole 1994), and 24 lynx/100 km² near Teslin, Yukon (Slough and Mowat 1996). These count methods may have missed individuals with overlapping home ranges (Ward and Krebs 1985) and were accordingly reported as conservative estimates (Poole 1994). By applying similar methods to our dataset from snow tracking and GPS data, we estimated a density of 13 lynx/100 km²—in line with the density reported by O’Donoghue et al. (1997) from Kluane, Yukon, just before a population peak (15 lynx/100 km²).

The four highest density estimates (range 32–55 lynx/100 km²) resulting from this work are higher than any previously published lynx density estimates from years preceding a cyclic peak. Slough and Mowat (1996), however, reported high-density estimates of 45 lynx/100 km² in a population peak year, and although they calculated density based on radio telemetry data and snow tracking, they differed from other studies in that they included a correction factor to include missed kittens. When we applied a similar correction factor to our data, our density

estimate increased to 33 lynx/100 km². This is in line with our central estimate resulting from SECR + gSMR of 32 lynx/100 km² and may indicate that sampling bias contributes to reported differences in lynx density estimates.

Plausibility of estimates

The accuracy of our results remains uncertain in the absence of a known density of lynx in our study area. It is worthwhile, however, to explore the plausibility of each density estimate. We added the number of unique individuals genotyped from live trapping to the number of unique individuals genotyped from hair snaring to determine that there were at least 51 genetically unique lynx in the unbounded study area. If the study area is bounded at approximately 300 km² (by applying a buffer of 3 km beyond trap locations, double the estimated home range radius), this leads to a minimum density of 17 lynx/100 km². The REM and the FMP formula, then, likely underestimated density at 11 lynx and 16 lynx/100 km², respectively.

We also explored the plausibility of estimates by combining GPS and camera trap data. We

drew a 100 km² area within the core of the study area covered by camera traps. Thirteen GPS-collared animals had home range centers within the area. These marked and GPS-tracked animals comprised 25.4% of camera detections within the 100 km² area during a 61-d period after marking was complete. Assuming that marked lynx had the same probability of detection on cameras as unmarked lynx, we used the known number of marked animals and the number of unmarked detections to estimate an initial density. We then corrected for edge effects by using the percent of detections of marked animals with home range centers outside the area (16% of marked detections within area), resulting in an estimated density of 43 lynx/100 km². Although not rigorous enough to include as an independent density estimate, this simple test further indicates that our lowest estimates of density may have been underestimates.

Possible sources of estimation bias

Closure assumption.—There were no known deaths of collared lynx during the sampling period. May and June, however, may have been periods of increased lynx dispersal (Poole 1997) and were included in the camera dataset only. None of the 19 lynx for which collar data were retrieved were observed dispersing from the study area during the study period, although 1 female dispersed after the conclusion of the study and 2 males were observed dispersing during this period the previous year. For SCMR, gSMR, and SECR + gSMR non-closure of a study population violates the assumption that activity centers are stable throughout the study period (Fig. 3), resulting in an underestimate of detection probability (g_0) and an overestimate of density (Ivan 2018). An exploratory analysis that removed the May–June period from the camera capture history datasets reduced the sample of photographs by 38%, leading to an implausibly high SCMR estimate of 102 lynx/100 km² (95% CI 64–163) and reducing precision to RSE 24% of the estimate. We therefore retained May and June months for camera trap-based estimates to achieve adequate sample size but it is possible that a small number of individuals may have dispersed during sampling creating some potentially unstable activity centers that may have led to higher density estimates

from SCMR, gSMR, and SECR + gSMR methods.

Non-detectability.—Some individuals within the lynx population may not have been responsive to the catnip lure, which we expect would lead to non-detectability for some individuals and a negative bias in estimates derived from hair snare data. In domestic cats (*Felis catus*), ~70% of individuals respond positively to catnip (Todd 1962, Bol et al. 2017); in ocelots (*Leopardus pardalis*), 84% of individuals respond positively (Weaver et al. 2005). We expected any systemic bias against detection of a subset of the population to proportionally reduce the density estimate. Non-detectability of some individuals on hair snares could have lowered density estimates from the SECR and SECR + gSMR methods (Fig. 3).

Missed detections.—It is common in animal tracking protocols to eliminate clear re-crossings of the same individual (O'Donoghue et al. 1997, Stephens et al. 2006). Keeping and Pelletier (2014), however, found that avoiding “double counting” of tracks produces negative bias in FMP formula densities for species with tortuous movement paths by reducing the estimate of detection probability. In our study, we avoided “double counts” for consistency with past tracking protocols. This may have led to an underestimate of density using the FMP formula.

The low ratio of marked to unmarked individuals detected on camera traps (Table 1) caused us to consider that we missed marked individuals or that animals may have lost their ear tags during the sampling session. We concluded that this was unlikely after a review of all lynx photographs returned no new marked-animal captures, after subsequent live trapping showed no loss of ear tags on recaptured animals, and because heat shrink markers were highly visible at night (Majchrzak et al., *unpublished manuscript*) and bright tag colors and collars were visible during day. We resolved that any error in marked animal identification was equal to or lesser than that found in similar camera trapping studies and therefore do not consider missed marked detections on camera traps to be a possible source of estimation error.

Detector placement.—The REST model and the REM assume that cameras are randomly located with respect to landscape features (Fig. 3; Rowcliffe et al. 2008, Nakashima et al. 2018). The

high estimate from REST may suggest that attractive landscape features were sampled in a higher proportion than they exist in the landscape. The low estimate from REM, however, suggests the opposite. When “trail” camera locations (26% of total) were removed from the camera dataset, the REST estimate fell to 25 lynx/100 km² and the REM estimate fell to 6 lynx/100 km². Removing lynx detections on attractive landscape features did not improve agreement of the estimates.

The FMP formula assumes that animals are not attracted to the track transect (Fig. 3). Cameras located on the transect and similar landscape features (“trails” as described above) detected lynx for greater lengths of time than cameras off-trail. The comparatively low estimate from the FMP formula is either evidence that track counts were not oversampled on the transect due to attraction or that another component of the analysis drew the estimate low.

The overlap of our detector arrays was not perfect (Fig. 1) but we are confident that this had little influence on our findings. The camera trap array covered the largest area, the perimeter of which contained all other detector arrays (hair snares, live traps, and track transect) except one hair snare. When we measured the area within the outermost traps of each array type, hair snares surveyed 61% and live traps surveyed 37% of the area of the camera array. The track transects (as a line) surveyed 58% of length of the camera array. In addition, wherever we could identify individuals, we found the same individuals across methods: 15 of 25 tissue-sampled lynx were detected at hair snares; 15 of 23 ear-tagged lynx were detected on cameras; 12 of 19 GPS-tracked lynx crossed the track transect at least once. Thus, we sampled the same population and often the same individuals suggesting that local densities differing among detector arrays cannot explain the differences we observed between density estimates.

Parameter estimation.—Movement rate was an input common to both the FMP formula and the REM (Fig. 3), both of which were among low estimates. A sensitivity analysis showed that these estimates proportionally increased when movement rate decreased. Review of the data and step-length analysis did not reveal significant errors or biases. Winter lynx movement rate

estimated in a previous study (7.6 km/d in Parker et al. 1983) is similar to our movement rate (6.9 km/d).

The REM and REST methods relied on accurate estimation of the detection zone area and detection probability within the zone (Fig. 3). This task has been a challenge for other camera trap studies (Rowcliffe et al. 2011, Anile and Devillard 2014, Cusack et al. 2015, Hofmeester et al. 2016, Nakashima et al. 2018). We found that estimates from both methods were sensitive to changes in zone area and that the REST method was more sensitive (Appendix S1). We assumed perfect detection within the measured detection zone (Fig. 3), but there is evidence that even at close distances animals are not perfectly detected by camera traps (Rowcliffe et al. 2011, Nakashima et al. 2018). The REST density was high and the REM density was low, indicating that there was not a consistent effect of detection zone area or detection probability on density from these models.

Factors affecting precision

We predicted that acceptable methods would show reasonable precision. All density estimation methods were considered acceptable based on precision, but there was variation across estimates. The FMP formula produced the most precise of the 7 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). SECR + gSMR had similarly high precision at 10.8% of the estimate because of increased sample size pulled from several data sources. The REST method produced the least precise estimate (RSE 21.2% of the estimate) because of high variability by sampling unit in cumulative residence time (0.0–2.6 s residence time/100,000 s sampling time). Variation in precision did not exclude any density estimation methods but indicated that some (FMP formula, SECR + gSMR) were more precise methods given the available data.

Model reliability

All methods and models tested in our study are conceptually sound, have been independently tested, and are accurate and reliable in ideal systems. We tested these models using datasets that included natural factors and

potential biases affecting density estimates as well as realistic sample sizes that could reasonably be obtained in many wildlife population estimation studies.

Although we do not know true density for this natural population, we consider some models to be more reliable than others. The models with the fewest possible sources of estimation bias in our study, as discussed above, were SCMR, gSMR, and SECR. The models with the most possible sources of estimation bias were the REM and the FMP formula. The number and types of sources of bias will vary by study system and design, so we consider other factors as well when comparing model reliability.

We consider the combined SECR + gSMR model to be a more reliable estimator of density than others in this study because individuals were detected and missed across multiple methods. This model used all available data except track counts and therefore mitigated the biases associated with singular data sources. The combination of these data informed estimates of detection probability and animal activity centers and increased sample size for the overall model, improving precision of parameters that informed density.

The SECR + gSMR model was data-intensive and statistically advanced and may be an unrealistic option for many wildlife population estimation studies. The REST method, by comparison, was the most accessible approach but was highly sensitive to assumption violations. Instead of recommending one method over the others, we recommend that researchers select estimators after fully considering study design, study constraints, model assumptions, and sample size. More research on and discussion of inherent assumptions and biases of available methods will help with interpretation of model outcomes.

CONCLUSIONS

The methods explored in this study are currently used for various applications in ecological research and wildlife management. For example, Finland bases much of its game management on a modified FMP formula for estimating animal density (“wildlife triangles”; Helle et al. 2016). Density estimates derived from genetic SECR are increasingly used to guide wildlife management

(e.g., the Florida black bear; Humm et al. 2017). Camera traps, with the REM or capture–recapture methods, are used to monitor rare and vulnerable species like African lions (*Panthera leo*) (Cusack et al. 2015) and zebras (Zero et al. 2013). Our work provides evidence that density estimation methods currently in use return a range of estimates when appropriately applied to typical study systems and datasets.

Our results suggest that assumption violations and sources of bias, even those generally accepted in scientific literature, can have strong influence on model outcome. Combining datasets may help to minimize bias and improve precision. We recommend that researchers fully consider study design constraints and model assumptions before selecting a density estimation method.

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DATA AVAILABILITY

Data are available from the Knowledge Network for Biocomplexity (KNB): <https://doi.org/10.5063/7P8WT2>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3774/full>