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Empirical validation of closed population abundance estimates and spatially explicit density estimates using a censused population of North American red squirrels.

by

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Abstract

Capture-mark-recapture (CMR) data is widely used to estimate a range of population parameters including abundance and density. Closed population estimators have gained wide acceptance and have become increasingly sophisticated. More recently, spatially explicit capture-recapture (SECR) models implemented have gained popularity. Although model accuracy has been tested via simulation studies there have been few empirical tests of either method. I took advantage of a fully enumerated population of red squirrels (*Tamiasciurus hudsonicus*) to test the accuracy of closed population abundance estimator and the maximum likelihood SECR density estimator. I found abundance estimates were positively biased by 45%, largely due to trapping grid edge effects. Adjusting for edge effects via the boundary strip method decreased bias to -22%. With the addition of inter-trap movements, SECR models produced density estimates that were negatively biased by only 4.6%. These empirical validations support the use of SECR models for density estimates or derived population abundance.

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CHAPTER I: General Introduction

One of the most fundamental measures required in ecology, especially population ecology, is a species' population size (Otis et al. 1978, Parmenter et al. 2003, Amstrup et al. 2005). This measure is preferably taken within a defined area for a value of density that may be compared across time and space or between species (Parmenter et al. 2003, Efford 2004). However, counting all individuals within a given area is rarely possible except for stationary or sessile organisms. Mobile organisms must be sampled by direct observation, capture-mark-recapture, or removal methods (Williams et al. 2002, Parmenter et al. 2003). Statistical estimators have been developed to derive estimates of population size or density for species that cannot be enumerated in nature.

Statistical estimators have long been used to estimate the size of a population. In 1786, Laplace was one of the first people to use a simple estimator to predict the human population living in France (Williams et al. 2002). Since then, there has been a proliferation of estimators used to quantify the abundance of wildlife populations. Peterson developed a simple two sample method for estimating population abundance for tagged fish in 1894 (LeCren 1965). Lincoln used the same method to estimate duck populations in North America, hence the method is called the Lincoln-Peterson estimator (Williams et al. 2002). In 1938, Schnabel developed an estimator using more than two sampling occasions when tagging fish in a closed lake system (Schnabel 1938). In 1952 and 1958, Chapman and Darroch further developed the Schnabel method respectively, by recognizing that assumptions of random sampling and constant population are approximations and may be violated (Seber 1986). To account for these violations authors like Otis, Burnham, White and Anderson have developed a further suite of models to accommodate capture probability as it varies across sampling occasions, between individuals, or within individuals when initial capture alters the behaviour of the animals (Otis et al. 1978). These additional models were first released in the program CAPTURE, which also ranks the models by maximum likelihood to identify the optimal model. Later, Chao implemented the full hierarchy of eight models that is now broadly available (Seber 1986). Though limited in model complexity, this program has long been acknowledged as being straightforward and requiring little training to operate (Pacheco et al. 2013).

Closed population estimators use data collected over a short duration of sampling, typically 5 to 10 days is viewed as acceptable (Otis et al. 1978, Lettink and Armstrong 2003, Rees et al. 2011). These estimators have become increasingly sophisticated, but all are used to estimate local population abundance (Cooch and White 2011). The assumptions of the closed estimators are that the population size is constant (i.e. not increasing or decreasing), and therefore no recruitment, death, immigration, or emigration is allowed during the sampling period (Williams et al. 2002, Amstrup et al. 2005).

Open population models, first developed as Jolly-Seber and Cormack-Jolly-Seber models, require more data over a longer time period to measure survival estimates and rates of population growth or decline (Cormack 1964, Jolly 1965, Seber 1965). These models are more complex due to the need to model the recruitment, mortality and movement of the population. The open estimator does not require the population to be geographically or demographically closed over the period of data collection. The model is not, however, robust to heterogeneity of capture (i.e. trap happy or shy individuals), consequently there is an added assumption of equal capture probability between all individuals.

The more recent development of the robust design model type combines the abilities of the closed and open population estimators and allows for the estimation of abundance as well as survival of the population (Kendall and Nichols 1995, Kendall et al. 1997). This model type is suited to long-term population monitoring programs where data collection occurs annually and over multiple years. However, the abundance estimates produced with this model require more sampling periods and are less accurate and precise when compared to closed population models (Lettink and Armstrong 2003).

Choosing to use a closed versus open population estimator has a strong influence on study design as the data required are typically mutually exclusive due to the extra data needed by open population models (Otis et al. 1978). Due to the infrequent ability to meet these assumptions, Otis et al. (1978) suggests closed population abundance estimates rarely perform well. If abundance estimates are required and the population is closed to recruitment, death, immigration and emigration, the closed population estimators should be used. Conversely, if demographic estimates of survival or recruitment rate are needed and individuals exhibit equal trappability, then open population estimators should be used.

Program CAPTURE has since been superseded by program MARK (White and Burnham 1999), due to the implementation of advances that model heterogeneity found in natural systems. There is increased flexibility of input requirements to allow for varying experimental design, which increases the number of field designs capable of calculating estimates (Lettink and Armstrong 2003). The ability to use Akaike's Information Criterion (AIC) model selection or the Bayesian statistical framework as well as estimate survival rate and simulate data to test models under different trapping regimes has made the program a major contribution to the field of abundance estimation (White 2008).

Another major development in population enumeration estimators is the introduction of spatially explicit models implemented by Murray Efford in the program DENSITY (Efford et al. 2004). These models require the spatial layout of the detectors (i.e. traps) in addition to the capture history with detector location for each capture event. Using a hierarchical model, the program uses the inter-trap movement distances and the probability of detecting an animal at each trap to derive the density of animals irrespective of trapping grid (Efford 2004). The spatially explicit capture-recapture (SECR) models are now available by simulated inverse-prediction, maximum-likelihood, and Bayesian frameworks within the user-friendly GUI program DENSITY or the R package secr (Efford et al. 2004, Efford et al. 2009, Royle et al. 2009a). Inverse-prediction estimates have been compared against enumerated wild populations and were found to have a small negative bias (-17.2%; Efford et al. 2005). Maximum-likelihood estimators were found to produce adequate estimates when compared to inverse-prediction models using empirical data and Bayesian models have been found to produce estimates similar to maximum-likelihood estimates (Borchers and Efford 2008, Gopalaswamy et al. 2012). Thus, all estimators have been validated via computer simulation, but only inverse prediction has been directly compared in a wild enumerated population.

With many new estimators available for population enumeration there are promising signs for increased flexibility in study design and a high level of accuracy and precision. Though many of these estimators involve complex algorithms, user-friendly GUIs have been developed to limit the amount of statistical and technical training users require before implementing these methods. However, the gap in research currently resides in the lack of empirical validation of these models. The objective of this thesis is to validate two commonly used models. The first test will be on the closed population estimator in program MARK and the second test will focus on the maximum likelihood spatially explicit capture-recapture (ML SECR) estimator in program DENSITY. Each test will compare the estimate to the values derived from an enumerated wild population of red squirrels (*Tamiasciurus hudsonicus*) to determine the bias and precision of the estimators.

Study Species

The North American red squirrel (*Tamiasciurus hudsonicus*) is a small diurnal and arboreal rodent that is active year round. The range distribution of the red squirrel covers most of the mixed and coniferous forests of Canada, continuing down the Rocky Mountains and the Northeastern United States (Steele 1998).

Both males and females defend exclusive food-based territories typically centered on a food cache, called a midden (Smith 1968). Cones are cached after they ripen in the fall and cone production within the territory is negatively related to its size (LaMontagne and Boutin 2007). A midden is traditional in nature and there is often rapid replacement after a midden owner dies, typically the new owner defends an area similar to the previous territory delineation (Price et al. 1986). Conspecific intruders are expelled in order to defend the territory against pilfering, which is important due to the relationship between the amount of cones in the midden and over-winter survival of the individual (Larivée et al. 2010, Donald and Boutin 2011). Red squirrels efficiently defend their territory using vocalizations called rattles, and physical confrontations are rare (Smith 1978). It has been found that 35% of individuals will rattle within 3 minutes of observation, thus behavioural observation is an efficient method for territory mapping (Gorrell et al. 2010, Shonfield et al. 2012).

The mating system in red squirrels is male scramble competition, whereby multiple males compete for females when they come into estrus once a year (Lane et al. 2010). There is no paternal care in this species and females nurse the young until weaning at 70 days of age (McAdam and Boutin 2004). Juvenile survival is low due to the need for juveniles to disperse off their natal-territory and acquire a territory to survive the winter (Smith 1968). Females have been found to bequeath their territory, which increases juvenile over-winter survival and is thus a form of parental investment (Berteaux and Boutin 2000).

Red squirrels are ideal for population level studies because of their reliance on stored food, their aggressive vocal territorial defense, and their high trappability. This makes it feasible to enumerate all individual squirrels within a study site. In areas of high cone production, squirrels live in relatively high density, which allows for appropriate sample size in population studies.

Study Area

The Kluane Red Squirrel Project (KRSP) has observed several subpopulations of red squirrels in southwestern Yukon, since 1987 (McAdam et al. 2007). Regular and systematic trapping of all territories within the study sites allows for the tagging and enumeration of all individuals with a territory within the site boundaries. Squirrels are fitted with ear tags and unique combinations of coloured wires for identification of individuals from a distance. This allows for behavioural observations of the animals and provides a secondary source of information on territory ownership. The locations from these trapping and behaviour records are used to complete a census of all individuals defending a territory within the study sites.

The reproductive status of each female is monitored with regular trapping to determine the parturition date and locate the nest using radio telemetry for further data collection on the pups. After the pups are weaned they begin making exploratory forays in order to disperse to a territory of their own (Larsen and Boutin 1994). In years of food abundance, females will more often exhibit territory bequeathal and this change in the population in addition to recruitment is quantified by second annual census of the population. The main features of this red squirrel system that are important to my project are the large sample size of individuals and the location of all active middens and their owners, making it possible to determine the abundance and density of the squirrels on the study grid.

Thesis Goals and Overview

In chapter II “An empirical validation of closed population abundance estimates using a censused wild population”, I tested closed population estimates of abundance against censused values of abundance. To quantify the performance of the closed population estimators I calculated accuracy and precision of the abundance estimates. In chapter III “An empirical validation of spatially explicit capture-recapture (SECR) estimates using a censused wild population”, I tested spatially explicit methods of estimating density of a local population and again derived the accuracy and precision of the estimates. Chapter IV is a summary of the major findings of the data chapters and suggests future directions for research given the current status of the field.

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CHAPTER II: An Empirical Validation of Closed Population Abundance Estimates using a Censused Wild Population

Introduction

Estimation of population size is fundamental to population ecology and applied aspects of biology such as evaluating wildlife management strategies for conservation and harvesting. Due to the cost and effort required to fully enumerate a wild population, capture-mark-recapture (CMR) trapping methods were developed and the models produced to evaluate the trapping data have increased in sophistication. However, all of the models are built on a set of assumptions that must be met for the model to perform well. When using empirical data, the degree to which assumptions are upheld in the wild population will determine the models' accuracy. Estimators must be robust against both false negatives, when individuals are rarely encountered due to camouflage, elusive behaviour or trap shyness, as well as false positives, when individuals are encountered too often due to trap happiness, high mobility, or a baiting effect. Computer simulation has been used for validation of these models, nevertheless empirical validation remains essential for ground-truthing the validity of these assumptions. Without empirical validation there is a risk of using abundance estimates with either positive or negative bias. Both situations are problematic, for example, a positive bias when trapping a species at risk could jeopardize conservation efforts by overestimating the number of individuals (Sunarto et al. 2013). Conversely, a negative bias could foster poor resource allocation by requiring more effort than is needed to protect a population to a set abundance target (Zhan et al. 2009).

Program MARK has made a major contribution to abundance estimation by combining many popular estimators within one software program and allows for the ability to choose Akaike's Information Criterion (AIC) model selection or the Bayesian statistical framework as well as simulate data to test models under different trapping regimes (White 2008). Newly implemented algorithms included in the program are routinely validated with computer simulation and numerous studies have focused on bias in statistical or methodological techniques (Wiewel et al. 2009, Ivan et al. 2013a). However, with over 65 types of models, model development has out-paced empirical validation and few field studies have the requirements to evaluate the accuracy of even the most basic and commonly used models (Rodda and Campbell 2002, White 2008, Krebs et al. 2011). Available empirical studies are limited in their conclusions by the use of enclosed or laboratory-reared populations (Edwards and Eberhard 1967, Davis et al. 2003, Parmenter et al. 2003, Conn et al. 2006), small sample sizes (Manning et al. 1995, Katano 2010), or the use of non-censused populations (Rosenberg et al. 1995, Tioli et al. 2009, Krebs et al. 2011, Pacheco et al. 2013).

When using closed population estimators the population is assumed to be closed to recruitment, death, immigration, and emigration for the short period during data collection. The estimator does not allow for local or within territory movement of animals and it is common for empirical studies to add a boundary strip around the outer capture points to derive an estimate of the effective area trapped (Royle and Young 2008, Ivan et al. 2013a). The boundary strip incorporates the average distance moved by the animals during each session in an attempt to correct for the effective trapping area beyond the edges of the grid (Otis et al. 1978). Typically, the distance moved between traps during each session is used to calculate the trap revealed mean maximum distance moved (MMDM) or the trap revealed asymptotic range length (ARL). Then full or half measures (i.e. MMDM/2) are used to set boundary strip width, with current literature suggesting the use of the full measures (Parmenter et al. 2003, Efford et al. 2009, Krebs et al. 2011). Due to resource constraints, investigations into the most effective boundary strip width assessments have been limited to simulation studies or empirical studies using enclosures, or only partially enumerated populations (Parmenter et al. 2003, Tioli et al. 2009, Krebs et al. 2011).

To increase accuracy of CMR estimates it is generally suggested that efforts be made to increase capture probability, which requires knowledge of life-history traits in the population to be sampled (Chao 1967, Krebs and Boonstra 1984, Lettink and Armstrong 2003). For example, the breeding season is an effective period to sample songbird populations because territories tend to be distinct and males defending their territory are easier to detect and capture (Bibby et al. 2000). Alternatively, the breeding season is to be avoided when trapping small mammals due to increased off-territory movements that will significantly change the distance moved and capture probability between the sexes (Bisi et al. 2011). Increasing capture probability may involve starting a sampling occasion during the most active period of the day or may require the sessions to be done when animals are least likely to show heterogeneous or trap avoidance behaviours (Lettink and Armstrong 2003).

In addition to the accuracy of abundance estimates, it is important to consider the precision of the estimates (i.e. the standard error) to produce exact values. To reduce the standard error of an estimate, more trapping occasions are added with the assumption that after enough sampling, the estimate will plateau due to inclusion of all animals from the area at which point the standard error should be negligible (Rees et al. 2011). Therefore precision increases in response to trapping occasions, but this response has typically been tested in simulation studies and has resulted in suggestions for minimum trapping occasions ranging from 5 to 12 occasions (Rosenberg et al. 1995, Wiewel et al. 2009, Rees et al. 2011).

In this chapter, I compared abundance estimates from closed population estimators in MARK to a fully enumerated population of individuals occupying a trapping grid from a long-term project in the Yukon Territory. The Kluane Red Squirrel Project (KRSP) has maintained intensive trapping and observation of several subpopulations of North American red squirrels (*Tamiasciurus hudsonicus*) in the Yukon Territory, Canada for over 25 years. Red squirrel life history lends itself to a complete census of the local population, primarily through high trappability, diurnal behavior, and high sight fidelity. Using KRSP census values I evaluate the accuracy and precision of abundance estimates as produced by program MARK. I asked 3 principle questions: Are the abundance estimates closely related to the censused abundance over a range of densities? Is there any bias and if so, what is the cause? How does precision of the estimates increase with trap effort?

Methods

Site Description and Study Species

The KRSP has monitored a wild population of North American red squirrels in the Shakwak Trench system of southwestern Yukon (61°N, 138°W) since 1987 (for more details, see Berteaux and Boutin 2000). Each of the 6 study sites are located in open-canopied boreal forest dominated by white spruce (*Picea glauca*) with a sparse understory of willow (*Salix* spp.), forbs, and mosses. Study sites are ~36 ha grids marked with grid stakes at 30 m intervals. Three of the study sites have experimentally increased densities due to regular systematic food addition in winter to each midden (for details see Dantzer et al. 2013).

Red squirrels in the boreal forest are active year-round and defend individual-based territories centered on a primary food cache, called a midden. Without an exclusive territory squirrels are unable to survive the winter due to their reliance on hoarded cones (Larsen and Boutin 1994). Squirrel territories have distinct boundaries that are defended by territorial calls to expel intruders. Individuals do make occasional forays off-territory to search for mates (males) or to occasionally forage, though off-territory forays are rare (83% of behaviour observations are within territory, unpublished data; also see 1984, Krebs et al. 2001, Boon et al. 2008, Lane et al. 2010). High midden fidelity causes few dispersal events outside of when juveniles disperse from their natal territory

(Boutin et al. 1993). Average territory diameter in this population is 65.8 m with 95% confidence intervals from 61.8 m to 68.6 m (LaMontagne et al. 2013).

Squirrels are live-trapped from March through August. All squirrels are marked with metal ear tags (National Tag and Band Co.) and given unique colour combinations of wires or disks for visual identification. Most are tagged as juveniles in the nest at 25 days of age. High trappability is observed within this system as 77% of attempts to trap the midden owners are successful in the first day of targeting the midden, 9% of attempts are successful on the second day and 14% require 3 or more days of trapping before the owner is caught (S. Boutin, A. McAdam & M. Humphries, unpublished data). The midden fidelity, high trappability, and vocal nature of squirrels allows target trapping and behavioural observations to be a successful means of documenting all individuals defending a midden in the study site (McAdam and Boutin 2003).

Female squirrels are trapped at regular intervals as often as every 3-5 days to biweekly depending on their reproductive status; males are trapped at least once per month. As an indication of the effort involved in core data collection, an average of 5 person hours per day, from March to August, on each grid was spent in 2012 giving a total of 6375 trapping records and 4139 behavioural observations on 611 total squirrels (S. Boutin, A. McAdam & M. Humphries, unpublished data). I am confident that all squirrels on the study areas are enumerated as only 471 of 10833 (4%) behavioural observations (including consecutive records, likely on the same squirrel) and 383 of 12863 (3%) trapping records are of individuals not previously tagged. When an untagged squirrel is observed, additional effort in trapping and behavioural observation is spent to determine if the squirrel will claim an existing midden on the study site. However, in most cases the squirrel is never seen again indicating he/she is not part of the territorial population.

Census

Beginning in March, all middens are visited and trapped to confirm the presence of a squirrel and its identity. Midden ownership is established by recording the identity of squirrels giving territorial calls on the midden, regular trapping of the individual on the midden and behavioural observation of individuals feeding on the midden. On the rare occasion a new midden is established, its location is recorded and it is monitored as long as it is active. During continuous monitoring between March and August, changes in midden ownership are noted as they occur but a full census occurs in mid-May and mid-August to record all squirrels defending a midden on the study sites.

Capture-Mark-Recapture Trapping

All CMR trapping sessions, hereafter referred to as sessions, were completed on a 300 m × 300 m array of 50 traps within one of the six 600 m × 600 m study sites (see Appendix A for a schematic diagram). Tomahawk live traps were placed at alternating grid stakes at least 24 hours before trapping rounds and were pre-baited with peanut butter. Each session was conducted over two days and included six trap checks with 1.5 hours of trap exposure between each check; a trapping occasion is the interval when the animals are exposed to capture (Borchers and Efford 2008). The short duration of trapping occasions was necessary to prevent squirrel mortality from exposure. Tag numbers, grid coordinates, sex, and trap-check round were recorded at every capture. One exception to the above trapping protocol was in March 2012 where trap placement was permitted to deviate from the grid stake by a maximum of 10 m in order to target runways that are easily visible in the snow. This deviation from the protocol allowed for increased trappability in winter conditions, which were lower due to cold temperatures.

Trapping sessions began on one study site in 2006 and occurred biannually in spring (range of start dates: May 20 to June 6) and late summer (range of start dates: July 27 to August 7) through 2008, with one additional session in spring 2011. Additional sessions were conducted in early and late summer of 2011 on all 6 study sites. Finally, in March 2012 four of the study sites were trapped entirely by subdividing the study grid into 4 trapping grids, though two sessions were discarded due to poor weather. A total of 34 sessions took place between 2006 and 2012.

Closed Population Estimation

I used the Huggins full heterogeneity closed population estimator within the R (R Core Team 2013) package RMark (Laake et al. 2012) to build models within program MARK, version 7.1 (White and Burnham 1999). Specifically, I produced estimates of abundance, capture probability and recapture probability (White and Burnham 1999). The Huggins estimator allows for a behavioural response to capture by estimating an initial capture probability in addition to the recapture probability (White 2008). It is also capable of modeling a Pledger mixture effect that allows different levels of capture probability to account for potentially trap happy and trap shy groups of individuals (Pledger 2000). The advantage of this closed population estimator is the ability to produce all eight models originally described by Otis et al. (1978). Therefore the full model set included: null model (M_0, restricting all capture heterogeneity), time varying capture probability model (M_t), behavioural trap response model (M_b), Pledger individual heterogeneity model (M_h), and all combinations of these factors including the full heterogeneity model (M_{tbh}, accounting for time, behavioural and individual heterogeneity; see Appendix B for full model set). I used the full *a priori* model set and model averaged the estimates based on their AIC weight (Boulanger and Krebs 1996, Pledger 2005, Conn et al. 2006). No covariates were included so the study design remains widely applicable to other systems with limited information.

I evaluated each model of the model set for fit to the data by assessing the abundance, capture probability, and recapture probability estimates based on values that would be biologically probable (White G. personal communication, 2012). Models were rejected if abundance estimates were larger than 1000 individuals ($\hat{N} > 1000$) or estimates were smaller or equal to the number of animals marked ($\hat{N} \leq M_{t+1}$). If capture probability and recapture probability estimates approached 1 or if they were a thousandth of a decimal, the model was excluded. Any derived estimate with a standard error larger than the estimate itself ($\hat{N}$ (SE) $> \hat{N}$) was also removed from the model set. Rejected models were deleted from the model set and only the remaining models were included in the model-averaged estimate.

The model set applied to each session was unique based on the data for each session. The model averaged abundance estimate, standard error, and the upper and lower 95% confidence intervals were derived for each session. Any session with a confidence interval range of more than 70 was removed (n = 4) due to low precision of these estimates; this had little effect on the relationship between the estimated and censused abundance. Consequently a total of 30 sessions were analysed.

Evaluation of Estimates

Statistical analysis was completed in the R statistical environment, version 3.0 (R Core Team 2013). To compare the number of censused individuals defending a midden within the trapping grid to the abundance estimates produced in MARK, I tallied all individuals recorded in the census as defending a midden within the boundaries of the trapping grid; I hereafter refer to these individuals as residents. All juveniles without a defended midden were removed from the CMR trapping data. Thus, each abundance estimate ($\hat{N}$) was compared to the number of residents (N) recorded in the closest available biannual census.

Typically the trapping occasions occurred within a month of the closest census, with the maximum time being 2 months in the case of the March trapping sessions. I justified comparing the March estimates against the May census because 91% of the residents in May were also midden owners from the previous August 2011 census (S. Boutin, A. McAdam & M. Humphries, unpublished data). This consistency coupled with the tendency for strong midden fidelity means it is likely the individuals were present through the winter. The majority of new residents in the May census were young-of-the-year, which must have claimed a midden the previous fall, after the August census, for them to have survived the winter.

The number of residents defending a midden within the bounds of the trapping grid were considered to be the censused resident population that were compared to CMR abundance estimates to determine the relative bias (RB) and whether or not the census value fell within the 95% confidence interval for the CMR estimate (confidence interval coverage; referred to as coverage for short) The relative bias was calculated as a percentage given by

$$\mathrm{RB} = \frac{[\hat{\mathrm{N}} - \mathrm{N}]}{\mathrm{N}} \times 100$$

where $\hat{\mathrm{N}}$ is the population abundance estimate and N is the censused number of residents with middens in the trapping grid. Precision of the estimates was calculated by the percent coefficient of variation (CV), computed as

$$\mathrm{CV} = \frac{\hat{\mathrm{N}}\ (\mathrm{SE})}{\hat{\mathrm{N}}} \times 100$$

where $\hat{\mathrm{N}}$ (SE) is the standard error of the population abundance estimate. To determine how estimates compared to census values, I regressed the estimated abundance against the censused abundance and assessed the intercept, slope, and R^2 of the regression line. If the estimates perfectly predict the censused abundance I expect the intercept to be 0, the slope to be 1, and the R^2 to be 1. For the estimates to be highly accurate and precise, I expect all confidence intervals to achieve coverage of the census value and CV to approach 0%.

I added a boundary strip to account for the potential positive bias created by individuals with only a portion of their territory in the trapping grid (Otis et al. 1978). Literature suggests the use of the full mean maximum distance moved as the boundary strip width, which attempts to quantify the average range of animal movement (Parmenter et al. 2003). Red squirrels of KRSP regularly patrol the edge of their territory, thus the average range of movement within a trapping session may best be approximated by using the known territory width of the KRSP population; this was the measure used for the boundary strip. The squirrels defending a midden within a territory width (65.8 m; LaMontagne et al. 2013) of the trapping grid will henceforth be called boundary individuals. The number of boundary individuals was added to the number of trapping grid residents to find the boundary-adjusted census abundance. This adjusted census value was compared to the estimated abundance to find the RB, confidence interval coverage, CV and the linear regression analysis in the same manner as above. Any further discrepancy between the estimate and census abundance was investigated by performing an analysis of variance (ANOVA) on the residuals of the estimates to the regression line and variables that may explain the observed variation. Explanatory variables were chosen by literature recommendations for covariates that explain heterogeneity in capture probability and accessibility of the measurement. The explanatory variables included: probability of capture (Krebs and Boonstra 1984), mean maximum distance moved (MMDM; Stickel 1954), and sex ratio of individuals captured in each session (Davis et al. 2003, Pledger

2005). In each case, I expect slope of 0 and a low R^2 if the explanatory variable had no influence on the residual of the estimate.

Additionally, I tested the effect of boundary strip width on the RB by finding the RB that results from different fractions of the territory used as the boundary strip. To do this I found the number of squirrels defending a midden in boundary strips that increased by eighths of a territory (8.2 m) up to a full territory width beyond the edge of the trapping grid. The number of censused individuals defending a midden in each incrementally larger boundary strip was added to the residents within the trapping grid to find the total number of individuals defending a midden within effective trapping areas. I regressed the percent territory included in the boundary strip against the average RB from using the number of individuals in each effective trapping area and derived the percentage of territory required to reduce RB to 0%.

Finally, I examined how the precision of CMR estimates varied with the number of trapping occasions required to increase precision. To do this I combine the capture histories from the July and August sessions collected from the same locations on 6 grids and sequentially eliminated the last trapping occasion from the capture histories to rerun the same model set in RMark (Laake et al. 2012). A total of 6 sessions with 12 trapping occasions resulted. I had to make the assumption that the sampled part of the population remained the same during each of the trapping sessions. However, it is biologically reasonable to assume that between July and August 2011, little death, recruitment, or territory changes occurred within the trapping grids. The individuals caught in both sessions had their capture histories concatenated while individuals caught only during July or August had the last or first 6 trap checks filled with zeros. Thus, six sessions with 12 capture histories were run in RMark according to the above protocol. This procedure was repeated after stripping the last capture history to produce a series of datasets varying length from 3 to 12 capture occasions; thus, each grid (n = 6) was evaluated at each length of capture history (n = 10) giving a total of 60 estimates. Assessment of model fit differed from the previous protocol because this analysis evaluates the effect of number of trapping occasions on the precision of the estimates. Therefore, I only removed models from the model set if the $\hat{N}$ was larger than 1000 or the standard error of $\hat{N}$ was larger than the estimate itself. This allowed more models to stay in the model set and react to the decreasing amount of information on which to base the estimate. To show the relationship between the precision and number of trapping occasions I regressed the coefficient of variation against the number of trapping occasions used to derive the estimates.

Results

Performance of Closed Population Estimators

No individual model within the model set was consistently weighted as the top AIC ranked model and the top model did not reliably have the smallest standard error or bias (Table B.1; Appendix B). CMR estimates were successfully derived from 30 sessions that included a total of 1766 captures of 770 unique individuals (Table 2-1). For these sessions, census abundances ranged from 4 to 38 individuals and on average 70% of the trapping grid residents were caught at least once (range 19% - 100%). Overall, estimated abundances compared poorly to the census values (Spearman's $\rho = 0.60$; Table 2-1) and there was an average relative bias of 45% (Figure 2-1). All but 5 estimates showed positive bias and only 1 estimate came within 5% of the censused value. The 95% confidence intervals included the censused abundance value in 16 of the 30 estimates (53% achieved confidence interval coverage), while the precision as shown by the percent coefficient of variation was 22%. The average probability of capture, from model averaged estimates within program MARK, was 0.4 with a range from 0.07 to 0.69. Using a linear regression analysis, I confirmed the positive bias from the regression of the estimated abundances as the intercept was larger than 0 (intercept = 8.6) and the correlation was poor ($R^2 = 0.37$). I found bias was stable across the range of censused abundance as shown by a slope of 0.98, which was not significantly different from 1 based on a significance level of $p = 0.05$ ($F_{1,28} = 0.01$, $p = 0.9$). Thus it was not significantly different from the slope of the line indicating equality between estimated and censused abundance.

When the effective trapping area was adjusted by adding the boundary strip individuals, the mean relative bias of the CMR estimates dropped from +45% to -22%, but the confidence interval coverage also dropped from 53% to 43%. Using a linear regression analysis, I found the intercept decreased to 2.37, slope decreased to 0.71, and R^2 of the regression line increased to 0.4 (Figure 2-2). The slope of the regression was almost statistically different from 1 ($F_{1,28} = 3.6$, $p = 0.068$), indicating the negative bias decreased over the range of censused abundance. Using ANOVA, I found there was no significant effect of capture probability ($F_{1,28} = 0.16$, $p = 0.7$), MMDM ($F_{1,28} = 0.01$, $p = 0.9$), or sex ratio ($F_{1,28} = 0.24$, $p = 0.6$) on the residuals from the estimates to the regression of estimated and censused abundance.

Using a sensitivity analysis of boundary strip width I found that 61% of a territory width (40.1 m) adjusts the boundary strip for there to be negligible bias on average (Figure 2-3 and Table B2 in Appendix B). Though the range between the upper and lower quartiles shows there is a large variation between estimators at a given boundary strip width.

The linear regression of the number of trapping occasions against the coefficient of variation showed a significant negative relationship ($y = 30.4 – 1.7x$, $p = 0.004$, $R^2 = 0.63$) indicating that increased trapping occasions improves precision of the abundance estimate. Coefficient of variation (CV) drops below 20% after 5 trapping occasions and it drops below ~10% after 11 trapping occasions (Figure 2-4).

Discussion

Estimator Accuracy

Using a wild population I assessed if closed population abundance estimates are accurate compared to census values. My protocol is typical of many small mammal trapping regimes. I had relatively high capture probability ($\hat{p} = 0.4$) and caught an average of 70% of the residents within the trapping grid; with these values one would expect closed population estimators to perform well. However, I conclude the closed population abundance estimator performed poorly: the estimates had a 45% positive bias on average, though this level of bias was constant across almost tenfold range of censused abundance. This bias is partially due to failing to account for the effective trapping area because nonresidents located adjacent to the trapping grid were often caught and thus influenced the estimates (see below). Previous studies using enclosures have reported a negative bias for estimates, but the fence prevents animal movements from outside the trapping grid, a situation that the estimator should account for (Stickel 1954, Edwards and Eberhard 1967, Carothers 1973, Davis et al. 2003, Parmenter et al. 2003, Conn et al. 2006). Although enclosure studies do give informative conclusions, they do not provide effective techniques to account for animal movements when trapping a wild population and there is potential for large bias. The present study is more comparable to previous simulation studies, which found positive bias ranging from +10% to +100% (Rosenberg et al. 1995, Boulanger and Krebs 1996, Rees et al. 2011).

Current literature suggests using the mean distance moved within a trapping session (i.e. mean maximum distance moved, MMDM, or asymptotic range length, ARL) as a boundary strip to adjust the area of animals exposed to traps (Tioli et al. 2009, Krebs et al. 2011). After making a boundary strip adjustment the correlation between estimated and censused abundance increased, however the resulting negative bias of the abundance estimates indicates this boundary strip width was too large. There was also a gradual trend for increasing negative bias with larger censused abundance values. This may be explained by the density dependence of the average movements of the animal. Parmenter et al. (2003) noted an analogous trend as animals in low density areas tend to travel farther, thus requiring larger boundary strips, than animals in high density area, which require small boundary strips. This behavioural change in animal movement leads to overestimates of abundance at low density and underestimates of abundance at high density. Many previous studies have documented bias when applying a static boundary strip to trapping occasions taking place in different places or times, however the alternatives include the use of MMDM as a boundary strip or concurrently conducting home-range mapping via radio telemetry (Stickel 1954, Gurnell and Gipps 1989, Parmenter et al. 2003, Tioli et al. 2009, Ivan et al. 2013a). Neither alternative is highly attractive due to additional assumptions, as well the estimation of MMDM assumes an adequate sample of inter-trap distance measures and radio telemetry necessitates increased sampling effort.

To further investigate the low correlation between estimated and censused abundance I used an ANOVA with several explanatory variables previously cited as potential causes for poor estimator performance. It is common knowledge that estimators perform better when the probability of capture is high and Parmenter et al. (2003) gave an empirical example of decreased bias with increased capture probability. Interestingly, I found the capture probability did not significantly explain the residuals taken from the adjusted boundary strip regression. There was also no significant relationship between the residuals over the range of MMDM measures of distance from each session. Finally, the sex ratio of each session also did not hold a statistically significant relationship with the residuals. These explanatory variables are generally thought to be the key metrics for heterogeneity of capture that cause estimators to poorly model the number of animals in the sampled population. I am not concluding that these factors may not be important in other populations, nevertheless after adjustment for effective trapping area as given from previous literature, the residual variation in the estimates did not have a significant relationship with any of these factors.

To find an appropriate boundary strip width, I followed up with a sensitivity analysis that incrementally increased the percentage of territory width included as a boundary strip until I obtained a measure that extended the effective trapping area to account for individuals beyond the trapping grid that were still exposed to traps. The best measure was found to be 61% of the territory width, which more closely follows the use of a boundary strip equaling half the territory width, as suggested by Dice (1938). Therefore, this *post hoc* assessment to find ideal boundary strip width still had a quartile range from 15 to -20% RB, which highlights the problem of using a static boundary strip adjusting for movements that are temporally and spatially variable.

Estimator Precision

I found the confidence intervals of the abundance estimates achieve poor coverage as only 53% of the confidence intervals overlapped the censused abundance value and this decreased to 43% with the boundary strip adjustment. In many cases the overlap was due to estimates with high coefficient of variation, with few precise estimates successfully overlapping the censused abundance. This is substantially different from Parmenter et al. (2003) who found that all models achieved ≥ 90% coverage when using the full MMDM adjustment in an enclosure study. Simulating an 'ideal' population conforming to all assumptions of CMR, Rees et al. (2011) found the precision increased such that after 20 trapping occasions the 95% confidence interval still did not overlap the true abundance. Rosenberg et al. (1995) previously concluded closed population estimators are not adequate in precision or accuracy until at least 12 or more trapping occasions.

Due to the thorough data collection at KRSP, I was able to determine that all residents of the CMR trapping grids present in July 2011 were still present in August, therefore the CMR trapping sessions in July were sampling the same population of individuals as the August sessions. This allowed me to combine trapping occasions from July and August in order to assess the precision of the estimates as trapping occasions increase from 3 to 12 occasions. Though Rees et al. (2011) used the simplistic Schnabel estimator in their simulations, my findings agree that there is a sharp increase of precision from 3 to 5 trapping occasions and after 10 to 11 occasions the increase in precision levels off. Abadi et al. (2010) simulated small datasets not capable of producing survival estimates separately and reported increased precision when data were analysed simultaneously, even if data independence was violated. Similarly, Conn et al. (2006) simultaneously analysed simulated low abundance populations for a satisfactory result when individually the models failed to produce adequate results. This empirical evaluation helps to confirm the trends predicted by the simulation studies.

Conclusion

Requiring prior knowledge of territory size or many recaptures for estimating MMDM could be a point of weakness for sampling novel populations (Tioli et al. 2009). When this situation arises determining the width of the boundary strip may depend on whether more harm will be done by under or overestimating the number of individuals. If it is riskier to overestimate the population, for example, when setting tag limits for game species, it would advisable to use the full territory width as a boundary strip for a conservatively small density estimate. Conversely, if underestimating the number of individuals could have hazardous impacts, for example, when monitoring an invasive species, using half the territory width would give a conservative overestimate of the population (Tioli et al. 2009). In the KRSP, if the effective trapping area is adjusted with half the territory width boundary strip, on average the estimates had little bias. This finding is dependent on the heterogeneity of capture and movements of the squirrels during the trapping sessions and may not be accurate when applied to other populations or species (Tioli et al. 2009, Krebs et al. 2011, Pacheco et al. 2013). Even if the abundance estimates are accurate, I question the utility of an estimator that requires extensive knowledge of population movements for accurate adjustment of the abundance estimate. Future research will investigate spatially explicit mark-recapture techniques that use capture location data to estimate animal movements and the individual detection; this estimator is theoretically more rigorous, has proven robust in simulation studies thus far and is gaining in popularity (Efford et al. 2004, Efford 2011, Borchers 2012, Efford and Fewster 2013)

My main conclusion is that CMR estimates are often positively biased when sampling wild populations, thus the boundary strip adjustment of the effective trapping area is essential to account for animal movements in natural systems. The poor accuracy of the estimator was found to have no significant relationship across a range of capture probability, MMDM, or sex ratio. The optimal size of the boundary strip was found to be just over half the territory width; however, this will likely vary between populations with different movement patterns. It is then necessary to have prior knowledge of the territory width or have sufficient number of recaptures to estimate the mean maximum distance moved between capture locations to make an appropriate boundary strip adjustment. I found the closed population estimator had poor precision since fewer than half the 95% confidence intervals included the censused value of abundance. I was able to confirm the influence of number of trapping occasions on the precision of the estimate. I conclude that at least 5 trapping occasions, but preferably 11 occasions be sampled for dependable levels of precision. There are few empirical studies in the validation of CMR estimation techniques and although enclosure and simulation studies greatly benefit model development, further work is needed to evaluate the effectiveness of these models in wild enumerated populations.

Table 2-1. Comparison of censused abundance (N) with model-averaged abundance estimates ($\hat{N}$) and corresponding 95% confidence intervals (95% CI) from Huggins full heterogeneity closed population estimator within program MARK. Summary statistics include relative bias (RB) and coefficient of variation (CV) as described in the methods. All estimates derived from CMR live trapping on 6 grids in the KRSP, 2006-12.

Session number	N	$\hat{N}$	95% CI	RB (%)	CV (%)
1	27	39.7	36.6 - 42.9	47.2	4.1
2	25	38.8	31.1 - 46.6	55.4	10.2
3	27	47.3	38.9 - 55.7	75.1	9.0
4	14	15.5	13.5 - 17.4	10.4	6.4
5	16	28.4	24.5 - 32.3	77.6	7.0
6	20	17.9	14.3 - 21.4	-10.6	10.1
7	25	13.2	11.4 - 14.9	-47.3	6.8
8	16	39.0	26.1 - 51.8	143.5	16.8
9	21	30.1	22.1 - 38.2	43.5	13.6
10	19	22.4	18.8 - 26.1	18.1	8.4
11	20	28.8	12.0 - 45.7	44.1	29.8
12	20	26.3	24.5 - 28.1	31.6	3.4
13	38	56.4	45.8 - 67.0	48.3	9.6
14	26	39.5	22.7 - 56.4	52.1	21.7
15	38	46.2	40.9 - 51.5	21.5	5.9
16	24	20.1	-7.3 - 47.5	-16.3	69.6
17	27	12.5	1.6 - 23.4	-53.6	44.4
18	26	45.1	32.4 - 57.7	73.3	14.3
19	26	30.0	25.9 - 34.0	15.2	6.8
20	24	38.8	20.5 - 57.2	61.9	24.1
21	16	30.8	8.7 - 52.8	92.2	36.6
22	27	44.4	24.7 - 64.2	64.5	22.7
23	15	27.1	-2.4 - 56.6	80.8	55.5
24	33	38.2	32.5 - 43.9	15.7	7.6
25	33	30.8	17.9 - 43.7	-6.6	21.3
26	21	32.1	24.9 - 39.3	52.8	11.5
27	21	27.8	24.6 - 30.9	32.2	5.8
28	17	24.6	8.3 - 41.0	44.9	33.9
29	13	13.6	-8.7 - 35.9	4.7	83.7
30	4	14.8	-1.2 - 30.7	268.9	55.0
Mean	**22**	**30**		**45%**	**22%**

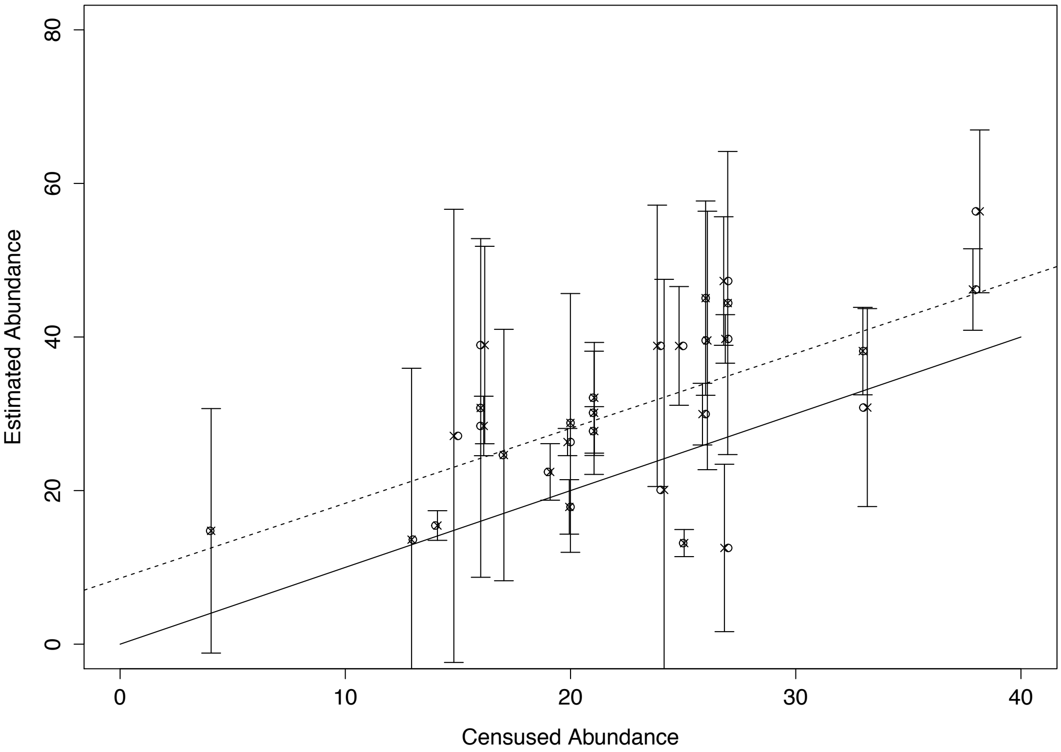

Figure 2-1. Relationship between census abundance and estimated abundance from closed population abundance estimators with 95% confidence intervals as calculated in program MARK (dashed line; $R^2 = 0.37$). The solid line represents equality between estimated and censused abundance.

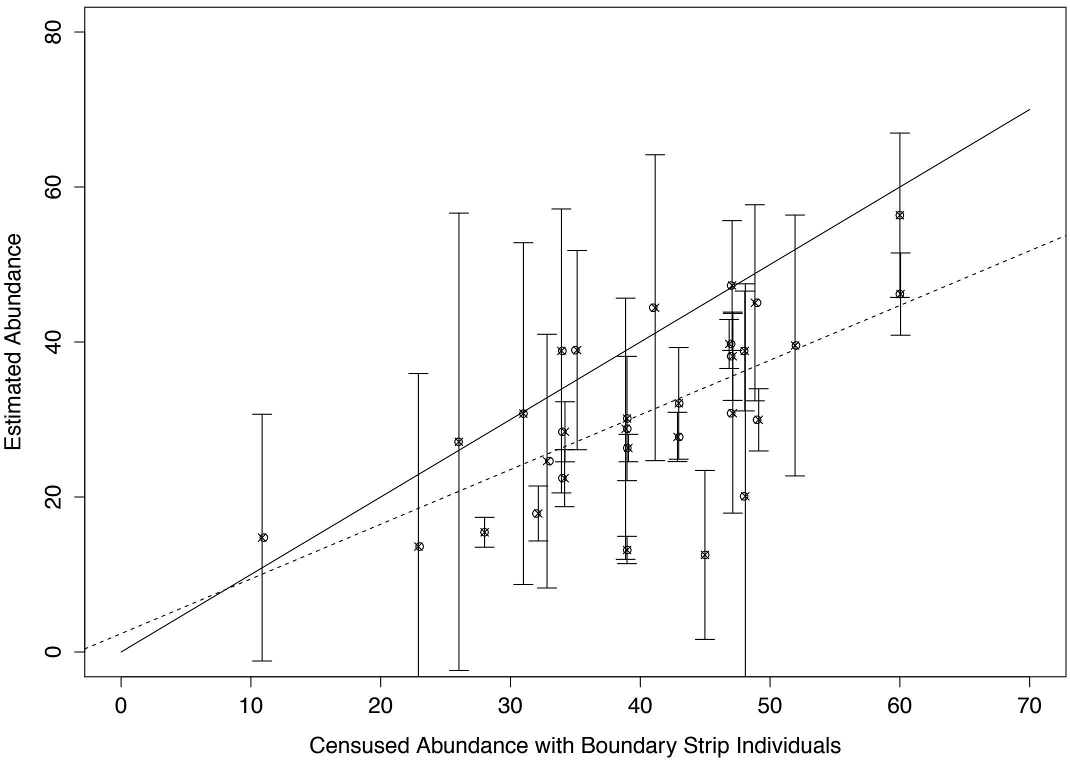

Figure 2-2. Relationship between census abundance from the effective trapping area adjusted by a boundary strip equivalent to average territory diameter (65.8m) and estimated abundance with 95% confidence intervals (dashed line; $p = 0.00001$, $R^2 = 0.41$). The solid line represents equality between estimated and censused abundance.

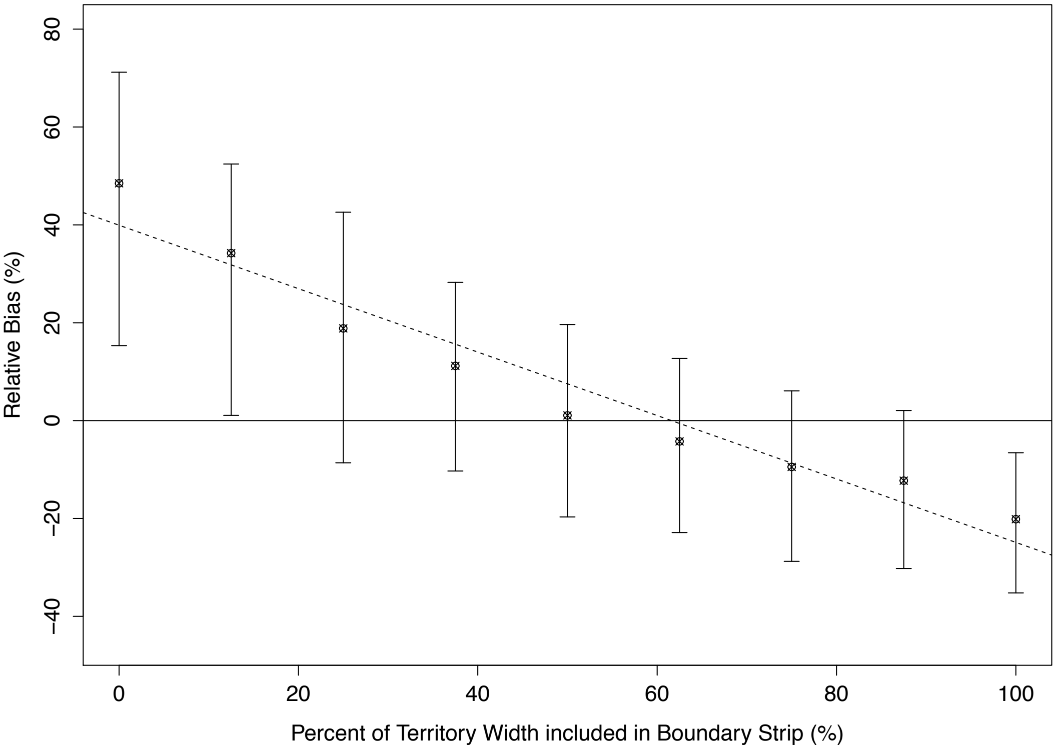

Figure 2-3. The mean relative bias (showing the upper 75th and lower 25th quartiles for n = 30 estimates) resulting from varying levels of territory width included in the boundary strip. A fitted linear regression (dotted line) interpolates the relative bias to be null (indicated by the solid line) when 61% of the territory width is included in the boundary strip.

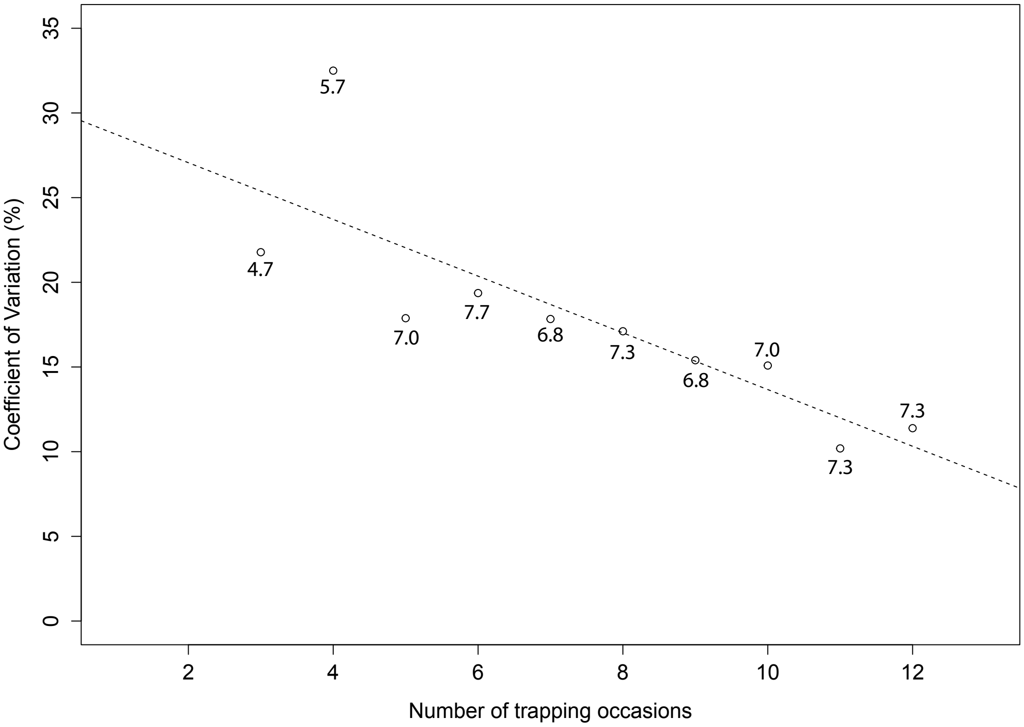

Figure 2-4. Coefficient of variation as the number of trapping occasions increases from 3 trapping rounds to 12 trapping rounds, showing a significant increase in precision ($y = 30.4 - 1.7x$, $p = 0.004$, $R^2 = 0.63$). The mean number of models (n) included in the model set are given at each point.

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CHAPTER III: An Empirical Validation Of Spatially Explicit Capture-Recapture Estimates (SECR) Using A Censused Wild Population

Introduction

Density of animals within a landscape is an essential component of understanding the ecology of a population and the larger natural system. There are a variety ways to derive an estimate of density and many studies have been devoted to finding an estimator that is both precise, unbiased and requires a minimum amount of information to successfully compute estimates. The numerous approaches developed to adjust closed capture abundance estimates to calculate density by estimating effective trapping area have generally been found to perform poorly due to the requirement of large amounts of animal movement information (Parmenter et al. 2003, Ivan et al. 2013b). Non-spatial estimators were found to have a higher bias than estimators with a spatial component in even if geographic closure was satisfied by trapping an entire island (Efford and Fewster 2013). Trapping webs based on the principles of distance sampling were found to be positively biased for small mammal density estimates due to the increased trappability of highly mobile animals in the center of the grid (Efford et al. 2005). The recently developed TELEM method within program MARK (Ivan et al. 2013a;b) uses a traditional closed mark-recapture abundance estimate with additional telemetry information to derive the proportion of time animals spend within the trapping grid to compensate for animals living outside of the trapping grid. As well the Bayesian SECR analysis implemented through R (Royle et al. 2009a) or in the program SPACECAP (Gopalaswamy et al. 2012) have shown promising results via simulations or when compared to other density estimators, yet these models have not been assessed in a wild population where it possible to derive an estimate of true density.

A significant advance in density estimation has been the spatially explicit capture-recapture (SECR) density estimator implemented through the program DENSITY GUI or the R package secr (Efford 2004, Efford et al. 2004, Royle and Young 2008). These density estimators require the spatial information for each capture event of an animal in order to build a probability model of the capture histories given the location of each encounter. This probability model has two submodels: the distribution model of the home range centres across the landscape and the detection submodel of capture probability for an individual in a trap, given the distance to animal's home-range center (Efford 2004, Ivan et al. 2013a). The density of animals, irrespective of grid area, can be estimated assuming there is a decreasing probability of capture as distance between the home-range centre and the trap increases (Efford et al. 2004, Borchers and Efford 2008, Royle et al. 2009a, Royle et al. 2009b). Therefore the SECR density estimators are theoretically more rigorous than the common approach of taking estimated abundance ($\widehat{N}$) over estimated area ($\widehat{A}$) because they do not rely on *ad-hoc* estimation of effective area trapped.

SECR density estimators have several additional requirements beyond the assumptions of CMR trapping. The distribution model assumes animals occupy a static home range for the duration of sampling and home-range centers can be modeled as a realization of a homogeneous random spatial point process (Efford

2004, Efford et al. 2004). This model also assumes home ranges are symmetrical and the trapping process does not affect the probability or location of recapture (Efford et al. 2005). One further requirement for the estimator is a minimum number of recaptures for proper parameterization of the distribution model (Efford 2004). These requirements are reasonable for many moderately abundant territorial species. Due to site fidelity, it is common for individuals to keep the same home range for at least the duration of a sampling period (Price et al. 1986). Similarly, the movement patterns of territorial species are often symmetrical around the territory center, barring large landscape features. However, rare or elusive species may not meet the necessary number of recaptures for the models to perform well.

Theoretical and empirical tests have shown the inverse prediction SECR method produces accurate density estimates with high precision and both the maximum likelihood and Bayesian SECR models have been comparable when natural populations were sampled (Efford 2004, Efford et al. 2005, Efford et al. 2009, Efford and Fewster 2013). However, if the trapping process disrupts natural movement patterns the models may not perform as predicted.

Despite recent advances in the development of methods for estimating density, few studies have empirically validated these models. In this study, I compare density estimates from SECR models with density measured in a completely enumerated wild population. Over the last over 25 years, the Kluane Red Squirrel Project (KRSP) has maintained an intensive trapping and observational study of several subpopulations of North American red squirrels

(*Tamiasciurus hudsonicus*) in the Yukon Territory, Canada. Red squirrels are highly trappable, and display diurnal behavior and high sight fidelity, allowing complete enumeration of the population. The distinguishing feature of this empirical validation is the use of behavioural observations to derive an activity range for all animals censused as defending a territory within or around the trapping grid. I first investigate if density estimates are accurate and precise and then examined the relationship of precision increase with the number of recapture events.

Methods

Site and Species Description

See Chapter II for description.

Census

See Chapter II for description.

Calculation of Estimated True Density Using Animal Equivalents

To determine the estimated true density I first refer to the biannual census, which lists all squirrels defending a midden as well as the midden location within the study grid. I do not typically determine territory boundaries due to the number of behavioral observation locations needed to delineate a territory. Therefore, I use an estimate of true density similar to methods described by Boutin (1984) and Ivan et al. (2013a). The method involves determining the individuals living within the trapping grid and following them to establish the proportion of time they spend within the grid. This proportion is known as the ‘animal equivalent’ because it is equal to the amount an individual contributes to the density of the grid; for example, if the animal spends half its' time on grid it is equivalent to 0.5 of an animal. To find the total density of the grid, the animal equivalent value for each resident of the grid is tallied and divided by the area of the grid. I used the locations obtained from extensive behavioural observations of the marked population to calculate the proportion of time each animal spent within the trapping grid. Finally, density was calculated by dividing the sum of animal proportions by the minimum convex polygon area of the trapping grid; this will be referred to as the animal equivalent density (Boutin 1984, Ivan et al. 2013b;a) and be used as the estimated true density (D).

Capture-Mark-Recapture Trapping

See Chapter II for description.

Spatially Explicit Density Estimation

Due to the minimum number of recaptures needed for proper model function (Efford et al. 2004), sessions with less than 10 recaptures were discarded; therefore from the available 34 sessions only 20 sessions were used. CMR trapping data were analysed using maximum likelihood spatially explicit density (ML SECR) estimators as contained in the R (Team 2013) package secr, version 2.6.1 (Efford 2004, Borchers and Efford 2008, Efford et al. 2009). All default settings were maintained for wide applicability to other study systems, thus I assumed a 2D Poisson distribution of home range centres, a half-normal detection function for detection probability and no starting values were specified. The default 100 m buffer was maintained to model the region of integration, which encloses the trappable population. The buffer is required to be at least 3 times the spatial scale (σ) and I found the σ to be an average of 30 m based on the distance moved from the home-range center to the trap, therefore the buffer satisfies the requirements (Efford 2011). I specified 3 candidate models to be applied to the data and the resulting density estimates were model averaged based on the AIC weight of the model. The 3 candidate models included: the null model (M_0), a model accounting for a behavioural effect of trapping (M_b) and an individual heterogeneity model (M_h). Thus I produced 20 model averaged density estimates with their standard errors and 95% confidence intervals.

Evaluation of Estimates

All statistical analysis was completed in the statistical environment R, version 3.0 (Team 2013). I compared the density estimate ($\widehat{\mathrm{D}}$) for each session with the estimated true density (D) via animal equivalents by finding the relative bias (RB) using the equation

$$\mathrm{RB} = \frac{[\widehat{\mathrm{D}} - \mathrm{D}]}{\mathrm{D}} \times 100.$$

The coefficient of variation (CV) was derived as a percentage by

$$\mathrm{CV} = \frac{\widehat{\mathrm{D}}(\mathrm{SE})}{\widehat{\mathrm{D}}} \times 100$$

where $\widehat{\mathrm{D}}(\mathrm{SE})$ is the standard error of the density estimate. I defined achieved confidence interval coverage when the true density estimate fell within the bounds of the estimates 95% confidence interval.

To ascertain if the degree of bias changed across a range of density values, I used a linear regression analysis to establish if the regression of the SECR density estimates against the estimated true density were significantly different from 1 based on a significance level of $p = 0.05$. I also conducted a pairwise *t*-test of the true density and the SECR estimates to determine if the magnitude of the bias significantly different from zero.

Finally, I regressed the number of recaptures from each session against the coefficient of variation for that session to determine the minimum number of recaptures needed for a certain level of precision.

Results

Estimated True Density

A total of 6490 behavioural observations were used to derive animal equivalent proportions for 783 squirrels defending a midden within and immediately surrounding the trapping grid. Therefore an average of 8.3 observations were used for each individual, which is similar to the 10.4 telemetry locations that Ivan et al. (2013a) obtained for use in the TELEM method. The estimated true density of the trapping grid was 3.0 animals ha^{-1} on average (range 1.5 to 4.8 animals ha^{-1}; Table 1).

Performance of SECR Density Estimator

A total of 620 animals were captured in 20 CMR trapping sessions, which included 15 to 92 recapture events (Figure 3-1). When density estimates were compared to the density via animal equivalents I found an average 4.6% negative bias, ranging from -35.7% to 26.7% (Table 3-1). The 95% confidence intervals achieved coverage of the animal equivalent density in all 20 sessions (100% confidence interval coverage). Finally, I determined the intercept was 0.38 and the R^2 was 0.76 (Figure 3-2).

The linear regression analysis of the estimated density against the density via animal equivalents was found to have a slope of 0.95, which is not statistically different from 1 ($F_{1,18} = 0.2$, $p = 0.7$). Using a pairwise *t*-test I found the SECR estimates were not significantly different from the estimated true density values ($t_{19} = 1.15$, $p = 0.27$).

When regressing CV against the number of recaptures, I found the breakpoint between 51 and 59 recaptures resulted in the highest R^2 for the linear regression and held a significant negative slope ($y = 34.7 - 0.4x$, $F_{1,14} = 28.9$, $p = 0.0001$, $R^2 = 0.65$; Figure 3-3). The linear regression beyond the breakpoint did not have a significant slope ($y = 20.3 - 0.04x$, $R^2 = -0.24$; $F_{1,2} = 0.4$, $p = 0.6$).

Discussion

I successfully produced density estimates from 20 CMR trapping sessions over a range of true density values (1.5 to 4.8 animals ha^{-1}). This empirical study represents the first test of ML SECR estimators in a censused wild population for which estimation of true density is possible. I acknowledge that true density derived by territory mapping would have been a more thorough approach than the present method of finding the proportion of time spent on grid with an average of 8.7 observed locations. However the effort required by field personnel to fully delineate the boundaries of approximately 39 individuals living in and around the trapping grid for all 20 sessions analysed is beyond the capabilities of this, and most other field projects. Therefore this is the most thorough study capable of relating ML SECR density estimates to true density derived by thorough observation of the animals in a natural system.

Overall I found the ML SECR density estimates had a small negative bias of -4.6%, this is not significantly different from the true density values for each session. Therefore, there is no statistical difference between the SECR estimates and the true value. The small amount of negative bias may be due to unmodeled heterogeneity as suggested by Efford et al. (2005). It is encouraging that 100% of the trapping sessions achieved confidence interval coverage of the true value. Using a rudimentary breakpoint analysis I established that after ~51 recaptures there is not a significant increase in precision with additional recaptures. The slope of the regression up to the breakpoint was found to be significant, which indicates precision will increase significantly with additional recaptures. Although I used a minimum cutoff of 10 recaptures, all the remaining CMR datasets produced SECR density estimates with reasonable precision of ≤35% CV. However, adjusting the experimental design to increase the number of recaptures could efficiently increase the precision of the resulting estimates. These findings suggest fewer recaptures are needed than previously thought by Efford et al. (2004) and Efford et al. (2009).

The TELEM method employed by Ivan et al. (2013a) has an inherent potential for positive bias by capturing animals with more of their home range on the grid, thus the estimated proportion of time these animals spend on the grid is more likely to be high. This positive bias is potentially cancelled by the reduced capture probability of animals with less home-range overlapping the grid. A positive bias may still result if the cancelling effect is negated by a high capture probability of these individuals. This problem does not affect the animal equivalent metric I employ because I use the census to determine the animals defending a midden in and around the trapping grid. As well, the locations of behavioural observation are taken opportunistically across the study grid, which is four times the size of the CMR trapping grid. Therefore I take behavioural observation locations from all individuals and this is reflected in the fact that I have an overall negative bias.

I have shown the ML SECR estimators produce density estimates with acceptable levels of bias and precision from mark-recapture data of a wild population. This supports previous validations of the method using simulation and by comparing the maximum likelihood density estimate with the inverse prediction density estimate (Borchers and Efford 2008). The main drawback of using the SECR estimator is the necessity for at least 10, but preferably 50 recaptures to produce estimates with high precision. However, if trapping effort can obtain the minimum required recaptures, the estimates will likely be accurate and precise without the necessity for additional telemetry information or the need to estimate effective area trapped.

Table 3-1. Estimated true density via the animal equivalent method and the SECR density estimated by maximum likelihood with associated 95% confidence intervals (both density values measured in animal ha^{-1}). Summary statistics included relative bias (RB) and coefficient of variation (CV) of the SECR estimate.

Session	Density via Animal Equivalents	SECR Estimated Density	SECR 95% Confidence Interval	RB	CV
1	3.6	3.2	2.3 - 4.5	-10.7	17.2
2	3.4	3.4	2.4 - 4.8	1.9	17.6
3	3.6	4.4	3.2 - 6.2	22.7	17.3
4	1.6	1.0	0.6 - 1.8	-35.7	29.2
5	2.1	2.2	1.4 - 3.3	4.6	21.4
6	1.5	1.0	0.6 - 1.8	-31.8	28.6
7	2.2	2.8	1.9 - 4.0	26.7	19.1
8	2.8	2.2	1.5 - 3.2	-23.6	19.6
9	2.4	1.8	1.1 - 2.9	-24.4	24.3
10	2.3	2.2	1.3 - 3.7	-6.0	28.0
11	2.4	3.0	1.5 - 5.8	22.9	35.3
12	4.8	4.4	3.3 - 6.1	-6.6	15.9
13	3.3	3.2	2.2 - 4.8	-2.6	20.1
14	4.8	4.6	3.4 - 6.3	-3.1	16.1
15	3.3	3.5	2.5 - 4.9	7.3	16.8
16	3.3	2.5	1.7 - 3.7	-23.3	19.8
17	4.1	3.8	2.8 - 5.3	-5.7	17.0
18	4.1	3.1	2.2 - 4.5	-23.1	18.5
19	2.5	3.0	1.9 - 4.9	20.1	24.1
20	2.5	2.5	1.6 - 3.7	-2.1	21.4
Mean	**3.0**	**2.9**		**-4.6%**	**21.4%**

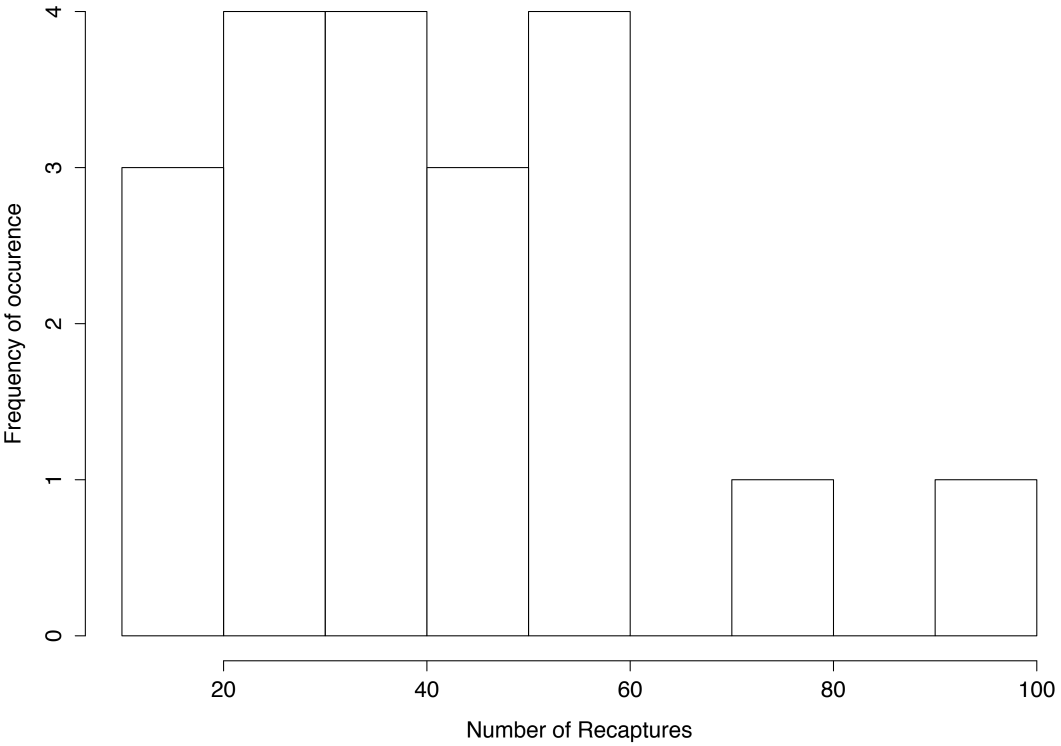

Figure 3-1. Frequency distribution of sessions with given number of recaptures from the 20 CMR trapping sessions from 6 grids at KRSP, 2006-2011.

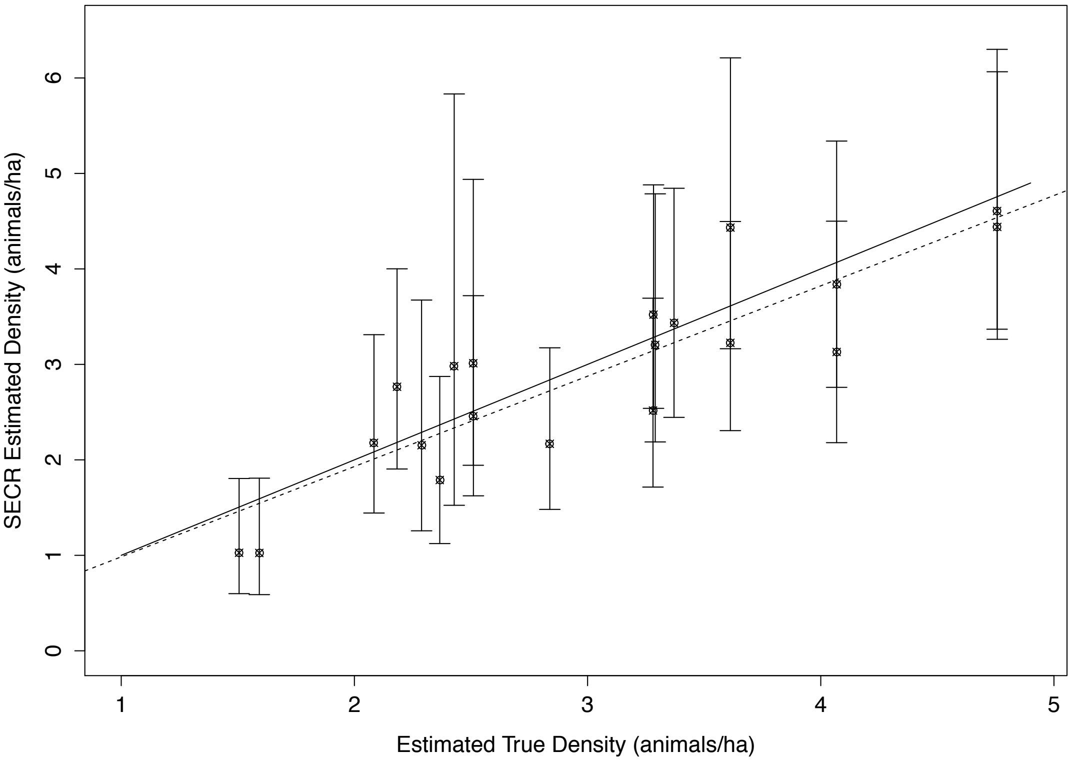

Figure 3-2. Relationship between density estimated by spatially explicit capture-recapture (SECR) with 95% confidence intervals (dashed line; $R^2 = 0.76$) and estimated true density (both densities are measured as individuals per hectare). The solid line represents the equality between SECR estimates and estimates true densities.

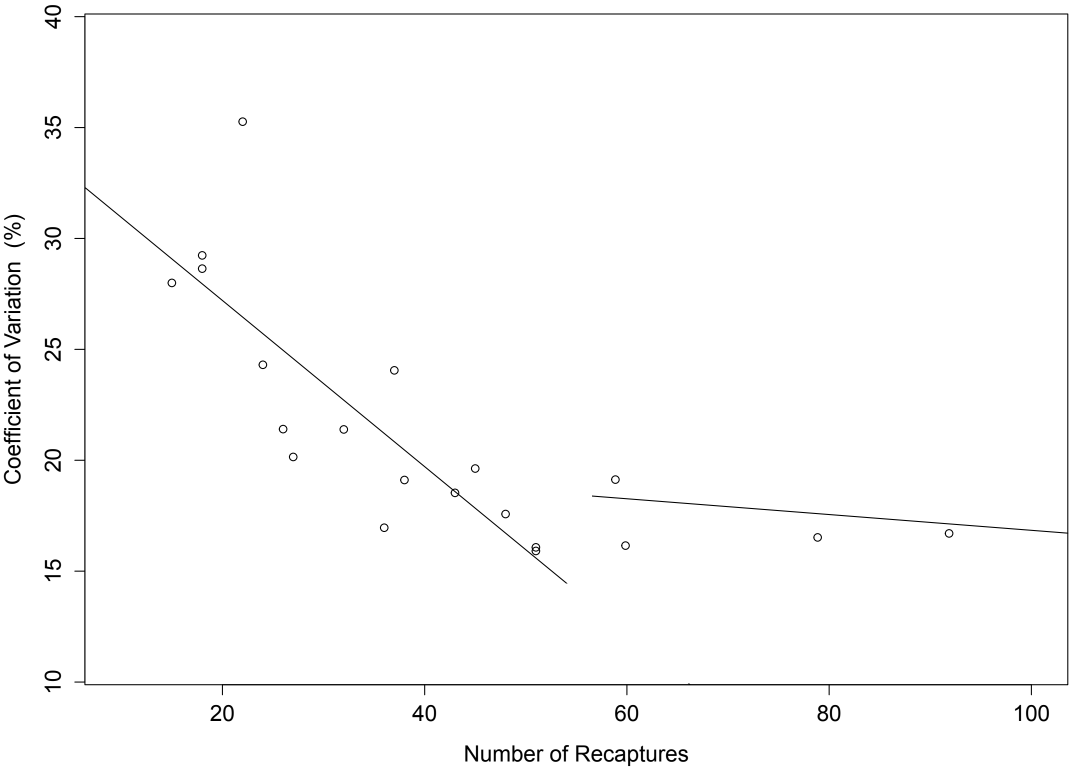

Figure 3-3. Precision of SECR density estimates measured by the coefficient of variation (CV($\widehat{D}$)%), as a function of the number of recaptures from 20 CMR trapping sessions in the KRSP, 2006-2012. The linear regression up to the breakpoint at 51 recaptures, had a significant negative slope ($y = 34.7 - 0.4x$, $R^2 = 0.65$; $F_{1,14} = 28.9$, $p = 0.0001$) and beyond the breakpoint was not significant ($y = 20.3 - 0.04x$, $R^2 = -0.24$; $F_{1,2} = 0.4$, $p = 0.6$).

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CHAPTER IV: General Conclusion

The focus of my thesis was to validate two population enumeration models commonly used today: Huggins closed population abundance model and maximum likelihood spatially explicit capture-recapture (ML SECR) density model. Simulation studies have provided valuable validations of model robustness, however, empirical tests are needed to evaluate if the model assumptions apply in wild populations. To do this I used the KRSP as a model system to complete a typical capture-mark-recapture (CMR) survey for small mammals and produced abundance and density estimates of the population. With the extensive knowledge of individuals within the system I was able to determine the accuracy and precision of the model estimates by comparing them to the true census values. The empirical validation provided by this thesis is a significant contribution to current validation studies of closed population estimators and SECR estimators due to the absence of assessments using a natural, wild, and censused population (Krebs et al. 2011).

Summary of Findings

In the validation of closed population abundance estimators (Chapter II) I found the estimates to have a large positive bias. This is due to the well-known issue of geographic closure, which is ubiquitous for most populations, except in whole island surveys or populations with physically delineated edges. The most common approach to remedy this problem is to add a boundary strip around the trapping grid that adjusts the area effectively trapped, accounting for the individuals adjacent to the grid that are exposed to trap. When I added a full territory width boundary strip (Parmenter et al. 2003) the average bias became negative indicating too many individuals were included in the effective trapping area. I then used a sensitivity analysis to find the optimal a boundary strip width. Average bias was reduced to zero when 61% of an average territory width was used as a boundary strip, though the suitability of this measure for other populations is unknown.

Even with an appropriate boundary strip there was still a range of biased estimates from +15 to -20%. Further, I found no significant relationship between the variance of the estimates and the distance mean maximum distance moved (MMDM). This may be an artifact of the number of recaptures used to calculate the MMDM if the value of MMDM is a poor representation of the true average movement rate. I observed a similar lack of relationship between variance of estimator accuracy and capture probability as well as sex ratio. This is surprising given that previous literature cites these variables as potential sources of error in estimates of abundance (Chao 1967, Boulanger and Krebs 1996, Parmenter et al. 2003, Pledger 2005, Bisi et al. 2011).

This variation in bias between estimates of the same population illustrates the difficulty to determine an appropriate boundary strip adjustment. Based on my results I agree with Gurnell and Gipps (1989) that a session specific boundary strip may be necessary. A constant boundary strip width may overestimate the population when abundance is low and underestimate it when abundance is high because of the tendency for animals to move longer distances with lower population size, especially if the trend is food driven (Parmenter et al. 2003). In general, this calls into question the utility of an estimator that requires large amounts of data to determine the proper adjustment for the estimate produced from each sampling session.

In the final analysis of Chapter II I found the precision of the closed population estimates performed poorly with less than half of the 95% confidence intervals achieving coverage of the true abundance. Moreover, many of the confidence intervals were larger than 30% of the estimated abundance. It becomes hard to trust the method when the confidence intervals are found to be this large. However, I did confirm that with increased sampling the precision increased and after 11 trapping occasions the coefficient of variation was below 10%, which would promote confidence in the method.

In the validation of spatially explicit capture-recapture density estimators (Chapter III) I found the estimator to be remarkably accurate and did not observe a significant difference between the SECR estimates and the estimated true density. The precision of the SECR estimator also performed well as the 95% confidence intervals achieved coverage of true density for all of the sessions. My findings support previous simulation studies of the SECR method, and tests of the ML estimator when compared to the previously validated inverse prediction estimator (Efford et al. 2005, Borchers and Efford 2008).

For proper parameterization of the SECR models, a minimum of 10 to 20 recaptures are required. Thus, due to the lower recapture rate in the winter trapping sessions, I was not able to produce estimates for 15 of the 35 trapping sessions. With careful planning this situation could be avoided in many systems, but when sampling rare or elusive animals with naturally low recapture rates, this could be a barrier in the utility of this estimator. If researchers can obtain the minimum required recaptures, I have shown the SECR estimator to have the capacity to produce accurate and precise estimates without the need for additional telemetry information or estimation of effective area trapped.

Conclusions and Implications

The dataset of CMR trapping records I used to derive the estimates of abundance and density are of high quality as shown by a high capture probability (average $\hat{p} = 0.4$, compared to $\hat{p} = 0.35$ deemed acceptable by Otis et al. (1978)), high percentage of residents caught (70% of residents were caught in MARK subset of sessions, 80% of residents were caught in the SECR subset of sessions), and a realistic number of animals marked in each session (an average of 24 were marked and an average of 22 animals lived within the trapping grid, in the SECR sessions). Thus, one would expect the resulting estimates to be precise and accurate.

Instead, I found the closed capture abundance estimates were biased, even when using a boundary strip adjustment, and estimator precision performed poorly as well. Alternatively, with added information of the spatial locations of the capture events the SECR estimates produced unbiased and precise estimates on average. Therefore, I suggest using the SECR estimator if the spatial information is available and there are at lest 10 or more recaptures.

In summary, this highlights that the estimator works irrespective of the trapping grid area when animal movements are modeled and will produce values that more accurately follow the population fluctuations (Efford 2004). This model is theoretically more rigorous, has proven robust in simulation studies thus far and is gaining in popularity (Efford et al. 2004, Efford 2011, Borchers 2012, Efford and Fewster 2013). However, the added requirement of inter-trap movement measurements may be limiting, but there is a significant increase in the accuracy and precision of the estimator.

When using any model to approximate a biological system, the quality of the results will be heavily dependent on the data on which the model is based. This weakness of any estimator becomes a problem when logistical constraints, or the population itself, limits the number of individuals captured or number of recaptures. Both the closed population estimator and the SECR estimator require a reasonable number of recaptures to measure the magnitude of animal movement. Therefore effort is best spent in increasing the recaptures so that SECR methods may be applied to the data.

Due to the complexity of higher-level models, there are some studies still using program CAPTURE and even minimum number alive (MNA) enumerations of the population to avoid the steep learning curve of more advanced models (Pacheco et al. 2013). Parmenter et al. (2003) highlighted the analytical problems introduced by model complexity and number of decisions required by performing a double-blind test with a panel of experts analysing data from an enclosed rodent population. The expert analysts produced estimates with an average +53% bias (range -2% to 134%) and 50% confidence interval coverage (range 0% to 91%). Therefore, future research should aim to provide robust estimators formatted in user-friendly GUIs so that biologists can become comfortable using these more theoretically robust estimators. For example, the program SPACECAP implements Bayesian SECR estimators in user-friendly format (Gopalaswamy et al. 2012). In addition, more empirical evaluations of newly developed methods are required to demonstrate these estimators are worth the effort. This will be needed for TELEM, the novel density estimator incorporated in program MARK (Ivan et al. 2013a;b).

Population size and density are fundamental measurements in population ecology and often required before any further study of a population may take place (Williams et al. 2002, Amstrup et al. 2005). Methods for the accurate assessment of population size and especially density have been unresolved for decades (Otis et al. 1978). A plethora of statistical estimators have been developed to fill this need, however both simulation and empirical validations are required to test the accuracy and precision of these estimators (Parmenter et al. 2003, Krebs et al. 2011). Only when sufficient validations have occurred and the results are consistent across time, space, and study systems will the development of estimators not be required for continued study of biological populations.

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Appendix A

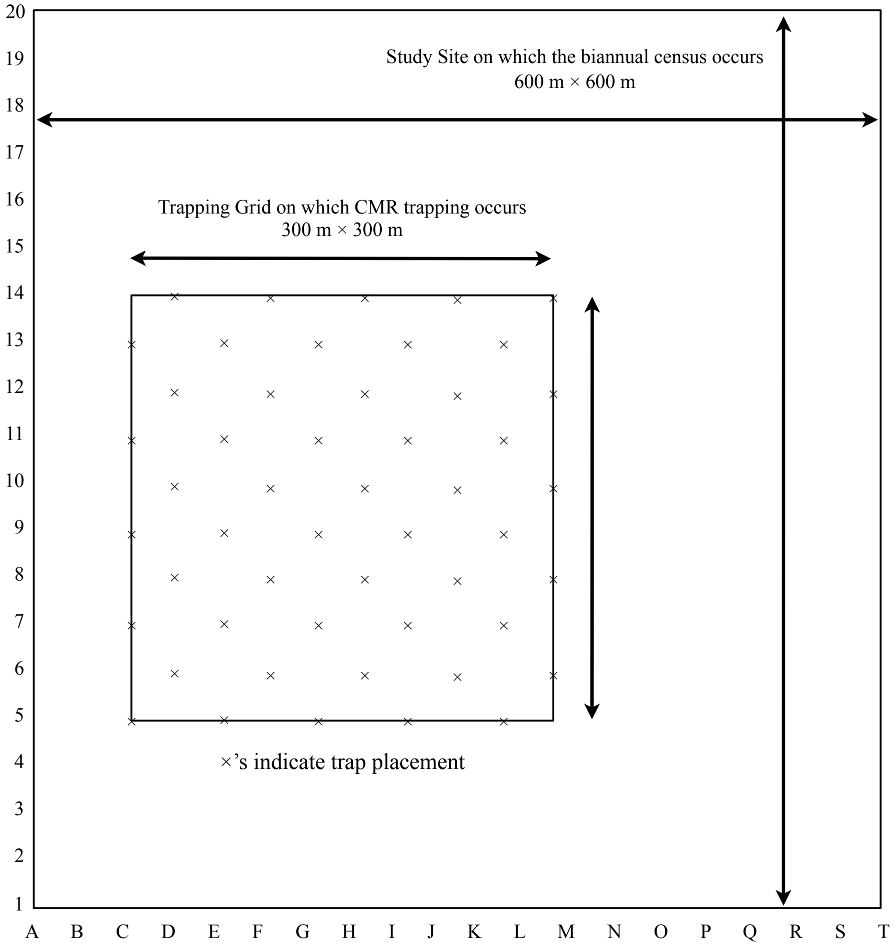

Figure A.1 Spatial layout of a typical 36 ha study site and a CMR trapping grid with 50 traps indicated with x's at every second and alternating grid stake. The entire study grid is delimitated in 30 m intervals with an alpha x-axis and a numeric y-axis. Location data is taken to the tenth of a grid stake distance (i.e. 30 m) therefore locations are recorded to the nearest meter.

Appendix B

Table B.1 Total AIC weights for each model of the complete model-set built in RMark and applied to 30 sessions of CMR data.

Otis et al. convention	Model description	Number of times model included in model set	Total model weight
M_0	Null model	30	5.56
M_b	Behaviour model	26	5.20
M_h	Heterogeneity model	17	2.27
M_t	Time model	24	5.50
M_{bh}	Behaviour and heterogeneity model	15	3.45
M_{tb}	Time and behaviour model	22	1.80
M_{th}	Time and heterogeneity model	15	2.78
M_{tbh}	Full model	15	3.45

Table B.2 Relative bias observed for each session with buffer strips increasing by an eighth of a territory width (8.2 m). Mean (x̄) and total (∑) summary statistics indicated in bottom rows.

	RB 0% Buffer	RB 12.5% Buffer	RB 25% Buffer	RB 37.5% Buffer	RB 50% Buffer	RB 62.5% Buffer	RB 75% Buffer	RB 87.5% Buffer	RB 100% Buffer
1	47.2	42.0	20.4	10.4	4.6	1.9	-9.7	-9.7	-15.4
2	55.4	43.9	25.3	14.2	5.0	-5.3	-11.7	-17.4	-19.1
3	75.1	68.9	43.3	31.4	24.4	21.3	7.5	7.5	0.6
4	10.4	-14.2	-22.7	-26.4	-32.8	-40.6	-40.6	-40.6	-44.8
5	77.6	42.1	13.7	9.3	5.2	-8.3	-11.2	-11.2	-16.4
6	-10.6	-10.6	-10.6	-10.6	-36.2	-36.2	-38.4	-38.4	-44.1
7	-47.3	-47.3	-47.3	-47.3	-62.4	-62.4	-63.4	-63.4	-66.2
8	143.5	85.5	55.8	49.8	34.3	18.0	18.0	14.6	11.3
9	43.5	20.5	0.4	-2.8	-5.8	-16.3	-16.3	-20.7	-22.7
10	18.1	-6.5	-13.7	-16.9	-19.9	-29.9	-29.9	-29.9	-34.0
11	44.1	37.2	31.0	15.2	-12.7	-15.3	-24.2	-24.2	-26.1
12	31.6	25.3	19.6	5.3	-20.2	-22.6	-30.7	-30.7	-32.5
13	48.3	34.2	34.2	22.5	12.7	12.7	6.3	0.6	-6.1
14	52.1	41.2	16.3	6.9	-1.1	-12.1	-17.6	-19.3	-23.9
15	21.5	10.0	10.0	0.4	-7.6	-7.6	-12.9	-17.5	-23.0
16	-16.3	-22.7	-33.0	-39.1	-42.6	-49.8	-53.3	-55.4	-58.1
17	-53.6	-56.8	-62.0	-64.2	-65.2	-67.9	-67.9	-70.9	-72.1
18	73.3	50.2	28.7	28.7	21.8	12.6	4.8	4.8	-8.0
19	15.2	-0.1	-14.4	-14.4	-19.0	-25.1	-30.3	-30.3	-38.9
20	61.9	61.9	49.4	49.4	43.9	43.9	25.3	25.3	14.3
21	92.2	80.9	61.9	53.8	23.0	18.3	13.9	2.5	-0.8
22	64.5	53.2	43.3	30.7	23.4	23.4	20.1	13.9	8.3
23	80.8	80.8	50.7	42.8	23.3	17.9	17.9	17.9	4.3
24	15.7	15.7	6.0	0.4	-4.6	-4.6	-11.2	-11.2	-18.8
25	-6.6	-6.6	-14.4	-18.9	-23.0	-23.0	-28.3	-28.3	-34.4
26	52.8	33.7	18.8	7.0	-2.8	-8.3	-13.3	-15.6	-25.4
27	32.2	15.6	2.8	-7.5	-15.9	-20.7	-25.0	-27.0	-35.5
28	44.9	23.1	7.1	2.6	-8.8	-15.1	-20.6	-23.0	-25.4
29	4.7	4.7	-2.8	-9.3	-9.3	-14.9	-24.4	-35.2	-40.8
30	268.9	195.1	110.8	110.8	110.8	110.8	110.8	110.8	34.1
x̄	**48.5**	**34.2**	**18.8**	**11.2**	**1.1**	**-4.2**	**-9.5**	**-12.3**	**-20.1**
∑	**1648.9**	**1163.6**	**640.8**	**380.1**	**36.2**	**-144.4**	**-321.9**	**-417.2**	**-684.9**